

Limnology and Aquatic Birds

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Limnology and Aquatic Birds

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Working Group on Aquatic Birds of Societas
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TABLE OF CONTENTS

Preface	ix–x
<i>In Memoriam: Stuart Frederick Mitchell BSc (Hons), PhD</i>	1–2
PART I. AQUATIC BIRDS – FORAGING, COMMUNITY ECOLOGY AND LIMNOLOGY	
A comparison between aquatic birds of lakes and coastal rivers in Florida M.V. Hoyer, S.K. Notestein, T.K. Frazer, D.E. Canfield Jr.	5–18
Foraging guilds of aquatic birds on productive boreal lakes: environmental relations and concordance patterns C.A. Paszkowski, W.M. Tonn	19–30
Water bird guilds and their feeding connections in the Bodrogzug, Hungary S. Andrikovics, L. Forró, G. Gere, G. Lakatos, L. Sasvári	31–42
Effects of small-bodied fish on invertebrate prey and foraging patterns of waterbirds in Aspen Parkland wetlands C.E. McParland, C.A. Paszkowski	43–55
A comparison of three methods to investigate the diet of breeding double-crested cormorants (<i>Phalacrocorax auritus</i>) in the Beaver Archipelago, northern Lake Michigan N.E. Seefelt, J.C. Gillingham	57–67
Pattern of natural ¹⁵N abundance in lakeside forest ecosystem affected by cormorant-derived nitrogen K. Kameda, K. Koba, S. Hobara, T. Osono, M. Terai	69–86
PART II. WATERFOWL – HABITAT USE, FORAGING BEHAVIOUR AND LIMNOLOGY	
Temporal processes and duck populations: examples from Mývatn A. Gardarsson	89–100
Effects of water quality on habitat use by lesser scaup (<i>Aythya affinis</i>) broods in the boreal Northwest Territories, Canada K.A. Walsh, D.R. Halliwell, J.E. Hines, M.A. Fournier, A. Czarnecki, M.F. Dahl	101–111
Diurnal time-activity budgets of redheads (<i>Aythya americana</i>) wintering in seagrass beds and coastal ponds in Louisiana and Texas T.C. Michot, M.C. Woodin, S.E. Adair, E.B. Moser	113–128
Foraging behavior of redheads (<i>Aythya americana</i>) wintering in Texas and Louisiana M.C. Woodin, T.C. Michot	129–141

Macroinvertebrate abundance, water chemistry, and wetland characteristics affect use of wetlands by avian species in Maine	
J.R. Longcore, D.G. McAuley, G.W. Pendelton, C.R. Bennatti, T.M. Mingo, K.L. Stromborg	143–167
Breeding waterbird wetland habitat availability and response to water-level management in Saint John River floodplain wetlands, New Brunswick	
K.J. Connor, S. Gabor	169–181
Populations of ducks and trout of the River Laxá, Iceland, in relation to variation in food resources	
Á. Einarsson, A. Gardarsson, G.M. Gíslason, G. Gudbergsson	183–194
Influence of migrant tundra swans (<i>Cygnus columbianus</i>) and Canada geese (<i>Branta canadensis</i>) on aquatic vegetation at Long Point, Lake Erie, Ontario	
S.S. Badzinski, C.D. Ankney, S.A. Petrie	195–211
PART III. LOONS – POPULATION TRENDS, BEHAVIOUR, HABITAT USE AND ECOTOXICOLOGY	
Factors influencing productivity of common loons (<i>Gavia immer</i>) breeding on circumneutral lakes in Nova Scotia, Canada	
S.S. Badzinski, S.T.A. Timmermans	215–226
A landscape-scale model of yellow-billed loon (<i>Gavia adamsii</i>) habitat preferences in northern Alaska	
S.L. Earnst, R. Platte, L. Bond	227–236
Testing hypotheses of social gatherings of common loons (<i>Gavia immer</i>)	
J.D. Paruk	237–245
Feeding behavior and modeled energetic intake of common loon (<i>Gavia immer</i>) adults and chicks on small lakes with and without fish	
B.A. Gingras, C.A. Paszkowski	247–261
Assessment of mercury exposure and potential effects on common loons (<i>Gavia immer</i>) in Québec	
L. Champoux, D.C. Masse, D. Evers, O.P. Lane, M. Plante, S.T.A. Timmermans	263–274
Bioaccumulation of mercury in yellow perch (<i>Perca flavescens</i>) and common loons (<i>Gavia immer</i>) in relation to lake chemistry in Atlantic Canada	
N.M. Burgess, K.A. Hobson	275–282
PART IV. SHOREBIRDS – HABITAT USE, LIMNOLOGY AND TROPHIC DYNAMICS	
Shorebirds, snails, and the amphipod (<i>Corophium volutator</i>) in the upper Bay of Fundy: top-down vs. bottom-up factors, and the influence of compensatory interactions on mudflat ecology	
D.J. Hamilton, A.W. Diamond, P.G. Wells	285–306
Trophic structure and avian communities across a salinity gradient in evaporation ponds of the San Francisco Bay estuary	
J.Y. Takekawa, A.K. Miles, D.H. Schoellhamer, N.D. Athearn, M.K. Saiki, W.D. Duffy, S. Kleinschmidt, G.G. Shellenbarger, C.A. Jannusch	307–327

Spatial and temporal fluctuations in presence and use of chironomid prey by shorebirds in the Odiel salt pans, south-west Spain

M.I. Sánchez, A.J. Green, E.M. Castellanos

329–340

Anostracans and microcrustaceans as potential food sources of waterbirds on sodic pans of the Hungarian plain

E. Boros, S. Bánfi, L. Forró

341–349

Preface

During the International Limnological Congress in Munich, Germany in 1989, it became apparent to a small group of participants that the time had come for waterbirds to be treated in a limnological context. This led to an *ad hoc* Symposium, “Aquatic Birds in the Trophic Web of Lakes”, held in Sackville, New Brunswick, Canada, in August 1991. The proceedings of this symposium were published in *Hydrobiologia* (1994) (Kerekes & Pollard, 1994) and *Developments in Hydrobiology* (1994) (Kerekes & Pollard, 1994). The outstanding success of this symposium led to the formation of the Working Group on Aquatic Birds of Societas Internationalis Limnologiae (SIL) during the XXV SIL Congress in Barcelona, Spain, in 1992. The first conference of the SIL Working Group on Aquatic Birds was held in Sopron, Hungary in November 1994. These proceedings were published by Wetlands International (Faragó & Kerekes, 1997). The second conference was convened in Mérida, Yucatan, Mexico in November 1997 (Comín et al., 2000) and the third conference took place in Trebon, Czech Republic in May 2000 (Musil & Albrecht, 2000). These conferences are held at least once every 3 years between SIL Congresses. These Proceedings are the record of the fourth such conference “Limnology and Water Birds 2003” held in Sackville, New Brunswick, Canada, August 3–7, 2003.

The Working Group on Aquatic Birds also held workshops and paper sessions during the SIL congresses in São Paulo, Brazil (1995), Dublin, Ireland (1998), Melbourne, Australia (2001) and Lahti, Finland (2004).

The main objective of the Working Group on Aquatic Birds is to integrate waterbirds into hydrobiology and treat waterbird studies in a limnological context. Long-term population monitoring of waterbirds is an important tool in our quest to understand the role waterbirds play in their environment. To achieve this goal, the Working Group organizes conferences to facilitate communications among limnologists interested in aquatic birds and ornithologists interested in the aquatic habitat. The efforts of the SIL Working

Group on aquatic birds has resulted in a new emphasis on the links between aquatic birds and their environment, as evidenced by limnology textbooks in the last few years which include sections on waterbirds, and use references from the SIL Aquatic Birds Working Group Conferences.

Papers presented in this volume further our understanding of the important role that limnology has in determining habitat suitability for waterbirds. The potential for waterbirds to impact water quality or fish stocks has received much study in the past. Continued population declines of many species of aquatic birds indicate the need for additional understanding of how human activities negatively impact water quality and bird populations and what mitigative actions can be taken.

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Alan Hanson and Joseph Kerekes

Co-Chairs of the 4th Conference Working Group on Aquatic Birds SIL

Co-Guest Editors of *Developments in Hydrobiologia* 'Limnology and Aquatic Birds 2003'

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In Memoriam: Stuart Frederick Mitchell BSc (Hons), PhD

25 September 1940 – 10 August 2001

Joseph Kerekes

Stuart Frederick Mitchell died on 10 August 2001 after a long illness; he was 60 years old.

Stuart grew up in Canterbury, New Zealand, where he attended High School and subsequently the University of Canterbury. It was there, in 1962, during his fourth year (Honours year) at Canterbury that he was introduced to limnology. Stuart embarked on a study of phytoplankton productivity in three bodies of water for his PhD degree at the University of Otago. His PhD thesis established a valuable basis for numerous studies, conducted on these lakes over the next 30 years, by Stuart, his students and his colleagues. Stuart was employed briefly (1966–1967) by the New Zealand Marine Department before his appointment, in 1967, as a Lecturer in Zoology at the University of Otago. He remained a member of staff of this department until May 2001 when deteriorating health forced him to retire. As a member of staff, Stuart contributed to the teaching of several environmental courses, especially limnology and ecology. During his 34 years on staff, Stuart supervised, or co-supervised, the research projects of 7 doctoral students, 7 MSc students and 17 BSc (Hons) and Postgraduate Diploma students.

His interest in controlling the effects of eutrophication turned his attention to physical, chemical and biological interactions in shallow lakes, and modeling these interactions. Eventually Stuart developed an interest in the role of waterfowl in shallow lakes that arose from his observations over several years. He noticed that the numbers of swans in Tomahawk Lagoon were positively related to macrophyte biomass and negatively related to phytoplankton productivity in the preceding summer. His study was one of the first reports of 'switching' in shallow lakes between the alternative stable states of dominance by macrophytes and dominance by phytoplankton. In subsequent

research with his students, he studied various aspects of the effects of grazing by black swans on macrophytes. Stuart's contributions to limnological research over more than 30 years have been published in 42 scientific papers and 2 book chapters.

In 1974–1975 Stuart spent a year's sabbatical leave first at the Institute of Terrestrial Ecology, Edinburgh, and later at Michigan State University where he carried out a bioassay study with R. G. (Bob) Wetzel of the effects of iron, NTA and zooplankton grazing on phytoplankton productivity in a marl lake. Subsequent leaves were spent at McGill University, Canada, 1981–1982, with Frank Rigler, and at the University of Connecticut, 1989–1990, with F. R. Trainor. He spent 5 months research leave doing research on the ecology of shallow lakes in Silkeborg, Denmark in 1997.

Stuart was a foundation member of the New Zealand Limnological Society, and edited the Society's Newsletter from 1970 to 1973. He was a member of SIL, ASLO (American Association for Limnology and Oceanography), and a life member of the Freshwater Biological Association (UK).

I first met Stuart at the airport when he arrived to attend the symposium *Aquatic Birds in the Trophic Web of Lakes in Sackville*, New Brunswick, Canada in 1991. Encouraged by the enthusiasm of the participants of the symposium, with Stuart's active participation, we formed a committee that led to the formation of the Aquatic Birds Working Group of International Limnological Society (SIL) in 1993. Stuart remained a bedrock supporter of the Working Group. He was an active participant in the first formal conference of the Aquatic Birds Working Group, *Limnology and Waterfowl*, Sopron, Hungary in 1994. There he chaired and later reported on the workshop *Bird Populations and Their Habitats*. Sudden illness prevented him to join us at our second conference in Mérida, Yucatán, México, 1997. To our delight he joined us

again in Trebon, Czech Republic where he presented a paper in May 2000. To our sorrow, by the time of this Sackville Symposium he was no longer with us.

We, in the Aquatic Birds Working Group, benefited greatly from his knowledge, experience and advice. We shall miss a valued colleague and a dear friend.

Acknowledgement

I am grateful to Professor Carolyn W. Burns, University of Otago, Dunedin, New Zealand for providing me biographical material on Stuart Mitchell.

Publications of Stuart Mitchell associated with the Aquatic Birds Working Group of Societas Internationalis Limnologiae

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Part I
Aquatic Birds – Foraging, Community Ecology and Limnology

A comparison between aquatic birds of lakes and coastal rivers in Florida

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Key words: aquatic birds, biodiversity, habitat use, coastal rivers, Florida

Abstract

Aquatic birds were counted on five Gulf coast Florida rivers to determine if these river systems supported densities, biomass and species richness similar to those found on Florida lakes. Forty-two species were identified and for the species that were found on both Florida streams and lakes similar densities and biomass were encountered. As with Florida lakes, stream bird abundance and species richness were higher in winter months than in summer months, a consequence of migratory bird populations. Total bird abundance, biomass per unit of phosphorus, and species richness per unit of area were similar to data collected on Florida lakes. Thus, Florida rivers are capable of supplying sufficient resources to maintain bird densities, biomass and species richness values similar to lakes of equal size and nutrient concentrations and are therefore important habitats for aquatic bird populations. An examination of individual habitat characteristics indicates that water depth was inversely correlated and submersed aquatic vegetation was positively correlated with bird density, biomass and species richness within the river systems. While both habitat characteristics are important they are also inversely related making it difficult to separate the individual significance of each characteristic.

Introduction

Florida supports a rich and diverse population of aquatic birds, which increases dramatically in the winter as migratory populations move through (Hoyer & Canfield, 1990; Hoyer et al., 2001). However, nesting populations of many species have reportedly declined over the past few decades (Kushlan et al., 1984; Ogden, 1994). This decline has been attributed, in part, to the loss of wetland habitat. From 1950 to the mid-1970s, there was a tremendous loss of palustrine emergent wetlands (freshwater marshes and wet prairies including the Everglades) in Florida, accounting for 74% of the total wetland loss in the state (Hefner, 1986). With this reduction in wetland habitats, the importance of Florida's lake and river systems to aquatic bird

populations may be increasing and warrants more study (Edelson & Collopy, 1990).

Most studies of aquatic birds have been conducted in marsh systems, with some studies examining aquatic bird populations using lake systems (Jenni, 1969; Johnson & Montalbano, 1984; Hoyer & Canfield, 1994). One research group from Hungary has monitored waterbirds and water quality on the Danube River, concluding that the river must be considered as aquatic habitat of international importance to waterbirds (Farago, 1997; Horvath & Bartalis, 1997). To our knowledge, there is no information on either bird abundance or species richness for Florida river systems. Approximately 1700 streams exist in Florida with an aggregate total length of approximately 17,000 km (Bass & Cox, 1988). The primary

objectives of this study were to document the aquatic bird abundance, biomass and species richness along five coastal rivers and to compare these values to the abundance, biomass and species richness reported for Florida lakes (Hoyer & Canfield, 1994). In addition we examined relations among bird density, biomass, species richness and physical habitat characteristics of the five rivers.

Methods and materials

Study area

Five rivers were included in this study. The Chassahowitzka, Crystal, Homosassa, and Weeki Wachee are head waters of first magnitude springs while the Withlacoochee is a drainage river just below a dam at Inglis (Citrus County, Florida). All five occur within a region commonly referred to as the Springs Coast, an area of western peninsular Florida that extends from the Pithlachascotee River basin located north of Tampa Bay to the Waccasassa River area which is south of the Suwannee River Basin (Wolfe et al., 1990; Fig. 1). The Springs Coast watershed covers approximately 892 square miles (SWFWMD, 2001) and as the regional name suggests, spring-fed systems are a prevalent feature. All of these five rivers discharge directly into the Gulf of Mexico.

Over 4 million cubic meters of ground water are discharged annually into the Springs Coast region from a variety of point and diffuse seepage sources (Sinclair, 1978). This water is derived primarily from the Upper Floridan aquifer, which is at or near the surface in the Springs Coast region. The quantity and chemical composition of water discharged by many of the springs in this area are strongly influenced by tidal cycles (Yobbi & Knochenmus, 1989; Yobbi, 1992). The climate is subtropical, with mean annual precipitation ranging from 132 cm to 142 cm (United States Fish and Wildlife Service 1988).

Methods

Physical, chemical and biological data were generated using sampling methods similar to those employed by Canfield & Hoyer (1988) in their study of 17 inland Florida streams and described

in detail by Frazer et al. (2001). In brief, water chemistry data and physical samples were collected during 10 quarterly sampling events between August 1998 and January 2001. In each of the five study systems, sampling was carried out at 10 transects (perpendicular to stream flow) regularly spaced along the length of the river, from just below the main spring to just above the marsh complex where the river opens and no longer has defined banks. For the Withlacoochee River, sampling was conducted from just below the dam at Inglis (Citrus County, Florida) to just above the marsh complex. Along each transect, physical and chemical parameters were sampled at three stations, one at the midpoint between the waters edge from bank to bank and one to either side of the midpoint approximately one-third the distance to the shore. Along each transect, submersed aquatic vegetation (SAV) was sampled at five stations, one located in the center of the river and two equidistant on either side of the center station. Submersed aquatic vegetation was sampled only three times during this study, during the summers of 1998, 1999 and 2000.

Physical parameters

All sampling locations were determined and relocated with a differentially corrected GPS receiver. Coordinates were recorded at the endpoints (shoreline) of each in-river transect and the stream width at each transect was calculated using ArcView GIS software (Environmental Systems Research Institute, Inc., 1998). The following physical parameters were recorded during daylight hours coincident with the water chemistry-sampling regime (described below): stream velocity (m s^{-1}), bottom depth (m), light attenuation ($K_d \text{ m}^{-1}$) and percent of incident light reaching the substrate. Depth was measured with a collapsible fiberglass survey rod while stream velocities were measured with a Marsh–McBirney model 201D portable flow meter. Light attenuation at each station was determined with the following equation;

$$K_d = [\ln(I_0/I_z)]/z \quad (1)$$

where I_0 is incident irradiance at the water surface and I_z is light intensity at depth z (m) (Kirk, 1994). Li-Cor Instruments, Inc. quantum light sensors



Figure 1. Location of five Florida Gulf coast rivers.

were employed to simultaneously measure surface and downwelling light intensity with a data logger. Light readings were taken at the deepest possible depth at each station (generally 0.25 m above the bottom substrate). Corrections to light attenuation calculations were not made for cloud cover or sun angle. K_d was used with water depth measurements to calculate the percent of incident radiation reaching the substrate. During vegetative sampling terrestrial canopy cover was visually estimated.

Chemical parameters

Surface water samples were collected in 250 ml acid-cleaned bottles and transported on ice to the laboratory where they were analyzed within 24 h of collection for total nitrogen (TN), and total phosphorus (TP). Total nitrogen concentrations ($\mu\text{g l}^{-1}$) were determined from whole water samples by oxidizing water samples with persulfate and determining nitrate-nitrogen concentrations

with an Bran-Luebbe autoanalyzer with a cadmium column reduction method (American Public Health Association, 1992). Following persulfate digestion (Menzel & Corwin, 1965), total phosphorus concentrations ($\mu\text{g l}^{-1}$) were determined using the procedures of Murphy & Riley (1962).

Aquatic vegetation

Sampling of submersed aquatic vegetation (SAV) was conducted during the period August through September for each year of the project, 1998, 1999, and 2000. SAV samples were collected at each transect coincident with the water samples. SAV refers to the total of both submersed macrophytes and macroalgae but for some analyses submersed macrophytes (aquatic macrophytes) and macroalgae (primarily filamentous algae) were analyzed separately. Along each transect, five stations were sampled for SAV, with one in the middle and two to either side approximately one-third and two-thirds the distance to the shoreline. At each of the resulting 50 stations for each river, a 0.25 m² quadrat was placed on the bottom and the above-ground biomass contained within the quadrat was removed by divers and transported to the surface. All submersed aquatic macrophytes and macroalgae were separated and spun in a nylon mesh bag to remove excess water. Samples were then weighed with calibrated hand-held scales and no attempt was made to remove attached periphyton. Weights were recorded to the nearest 10 g for samples less than 1 kg and to the nearest 100 g for samples greater than 1 kg.

Bird counts

Birds that were observed on or feeding from aquatic habitats were censused. Counts were conducted every time water chemistry data were collected with the exception of rainy days with extreme wind. This yielded eight census counts for Homosassa and Weeki Wachee rivers, seven counts for Chassahowitzka and Crystal rivers and six counts for Withlacoochee River. Birds were counted by two observers each watching a single shoreline as a boat was motored down the middle of the river from transect to transect during water

sampling events. Counts were typically conducted between 9:00 a.m. and 2:00 p.m. Birds were identified to species except for gulls, terns and crows, and care was taken not to count birds twice that flushed ahead of the boat.

Total species richness was defined as the total number of species observed throughout the study on a given river. Section species richness was defined as the total number of species observed on a given section of river throughout the project. Total Bird abundance (birds km⁻²) was the average of all counts for a given river divided by the surface area of the river. Literature values (Terres, 1980; Dunning, 1993) for the average biomass of each species, were multiplied by counts to yield bird biomass values. Total bird biomass (kg km⁻²) was the average of all counts multiplied by biomass values for a given river divided by the surface area of the river. Section number 1 in the Weeki Wachee River is immediately below an amusement park and during the study feed was placed on large platforms to attract birds for park visitors to watch. For this reason data from Section 1 of the Weeki Wachee River was removed for analyses of bird abundance and biomass values. Section bird abundance (birds km⁻²) and section bird biomass (kg km⁻²) were defined as the average number and biomass estimated on a section of river throughout the study divided by the area of water in that section.

Data summaries and statistical analyses

Mean values for individual transects were based on all sampling events and used to summarize all physical, chemical and vegetative measures. For analyses of variance and regression analyses all variables were log₁₀-transformed to accommodate heteroscedasticity in the data (Sokal & Rohlf, 1981). SAV biomass were sometimes equal to 0.0 kg wet wt m⁻², therefore 0.1 kg wet wt m⁻² were added to biomass values prior to logarithmic transformation and subsequent statistical analyses. Additional analyses, when employed, are described in the Results and Discussion sections below. All statistical computations were performed with the JMP statistical software package (SAS Institute, Inc 2000). Statements of statistical significance imply $p < 0.05$.

Results and discussion

The average sectional area of each river where birds were counted ranged in size from 0.006 km^{-2} to 0.066 km^{-2} , while the whole surface area of the five rivers where birds were counted ranged from 0.105 km^{-2} to 1.293 km^{-2} (Table 1). The width, depth and flow of the five rivers ranged from 14.6 m to 185.1 m, 0.88 m to 3.96 m, and 0.04 m s^{-1} to 0.29 m s^{-1} , respectively. SAV was generally abundant in these rivers with the exception of the Withlacoochee River, which supported only an average of $0.01 \text{ kg wet wt m}^{-2}$. The average biomass of submersed macrophytes and macroalgae for the five rivers ranged $0.0 \text{ kg wet wt m}^{-2}$ to $0.96 \text{ kg wet wt m}^{-2}$ and $0.0 \text{ kg wet wt m}^{-2}$ to $0.98 \text{ kg wet wt m}^{-2}$, respectively. Water clarity was generally sufficient in these rivers to allow an average of 23% of incident light to reach the bottom of the rivers. All of the rivers had very little canopy cover with the exception of the Weeki Wachee River, which averaged 20% canopy cover. The river waters contained moderate levels of

nutrients with average total phosphorus and total nitrogen concentrations ranging from 10 to $32 \mu\text{g l}^{-1}$ and 291 to $516 \mu\text{g l}^{-1}$, respectively.

The number of bird species identified in the five rivers ranged from 15 in the Withlacoochee River to 33 in the Homosassa River (Table 1). Species richness curves were constructed showing an increase in the number of bird species with each sampling event (Fig. 2). An evaluation of the cumulative species richness curves indicates that by the fifth or sixth sampling period the curves began to reach an asymptote. While this suggests that the river species richness values were representative of each system's potential maximum, it should be remembered that in a Florida lake it took approximately 32 consecutive monthly counts to reach a maximum species richness (Hoyer et al., 2001). These river species richness values are similar to the range of 1 to 30 species reported by Hoyer & Canfield (1994) for 46 Florida lakes. River densities averaged $278 \text{ birds km}^{-2}$ and ranged from 58 birds km^{-2} to $647 \text{ birds km}^{-2}$ (Table 1). These density values also fell within the

Table 1. Summary statistics for habitat characteristics, water chemistry and bird population parameters for 9 river sections from each of five Florida Gulf coast rivers

Parameters	Chassahowitzka	Crystal	Homosassa	Weeki Wachee	Withlacoochee
<i>Habitat Characteristics</i>					
Section Area (km^2)	0.022	0.066	0.042	0.006	0.012
Width (m)	93.8	185.1	127.9	14.6	28.2
Depth (m)	0.88	3.42	1.98	1.25	3.96
Flow (m s^{-1})	0.09	0.10	0.04	0.29	0.19
Light Attenuation (m^{-1})	1.44	0.96	1.10	1.01	1.00
% Light to Bottom	37.99	9.05	18.16	40.89	7.10
Macroalgae Biomass (kg wet wt m^{-2})	0.48	0.03	0.69	0.98	0.00
Macrophyte Biomass (kg wet wt m^{-2})	0.96	0.46	0.28	3.05	0.00
<i>Water Chemistry</i>					
Total Phosphorus ($\mu\text{g l}^{-1}$)	22	30	24	10	32
Total Nitrogen ($\mu\text{g l}^{-1}$)	418	291	416	516	475
<i>Bird population</i>					
Section species richness	13	11	15	8	5
<i>Whole river</i>					
River Area (km^{-2})	0.358	1.293	0.71	0.105	0.222
River Bird Abundance (Birds km^{-2})	268	141	276	647	58
River Bird Biomass (kg km^{-2})	291	181	331	682	69
River Bird Species Richness	28	23	33	22	15

Data for each section is the average of 10 quarterly samples collected between August 1998 and May 2000.

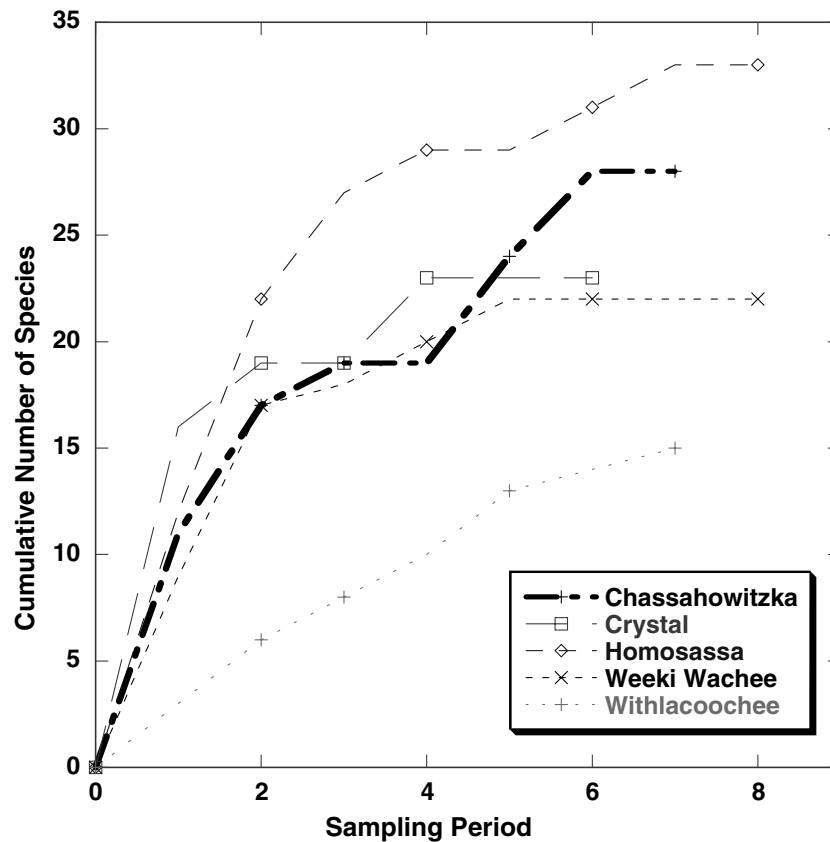


Figure 2. Cumulative aquatic bird species richness plotted by consecutive quarterly bird counts for five Florida Gulf coast rivers.

range of 7 birds km^{-2} to 803 birds km^{-2} reported by Hoyer & Canfield (1994) for Florida lakes. River biomass averaged 310 kg km^{-2} and ranged from 69 kg km^{-2} to 682 kg km^{-2} . All rivers except the Weeki Wachee River fell within the range of 1 kg km^{-2} to 465 kg km^{-2} reported by Hoyer & Canfield (1994) for Florida lakes. As mentioned above, the high values in the Weeki Wachee may be due to the large amount of artificial feeding that takes place near the headwaters of the river.

Combining data from all rivers, 42 species (39 species and 3 genera) of aquatic bird were identified (Table 2). There were several species (e.g., common loon, *Gavia immer* and greater scaup, *Aythya marila*) counted on the rivers that were not recorded by Hoyer & Canfield (1994) for 46 Florida lakes. This is most likely due to the fact that most of the lakes were located inland from the Gulf of Mexico or the Atlantic Ocean and not subject to visitations from birds primarily using Florida's coastal areas (Peterson, 1980). Where the species

from the rivers did overlap with the lake data set, the bird density values were similar (Table 2). However, some of the migratory waterfowl species (e.g., Mallard, *Anas platyrhynchos*) were much more abundant in the lake systems.

Florida lakes show a large increase in bird abundance and species richness during winter months (Hoyer & Canfield, 1990; Hoyer et al., 2001). This also appears to be the case for bird populations on Florida rivers. Splitting the river bird counts into summer (May and August) and winter (February and November) periods and using an analysis of variance shows that both bird density (F-Ratio = 4.64; $p \leq 0.05$) and species richness (F-Ratio = 6.22; $p \leq 0.05$) have significant seasonal effects. Bird abundance averaged 193 birds km^{-2} in the summer and 377 birds km^{-2} in the winter and species richness averaged 9.7 in the summer and 13.1 in the winter.

The abundance of aquatic organisms in Florida lakes as well as other lakes around the world has

Table 2. List of aquatic bird species identified and counted on five Florida Gulf Coast rivers between August 1998 and May 2000

Common name	Genus	Species	Lakes	Chassahowitzka	Crystal	Homosassa	Weeki Wachee	Withlacoochee
American Coot	<i>Fulica</i>	<i>Americana</i>	32.8	0.4	38.7	0.2	0	0
American White Pelican	<i>Pelecanus</i>	<i>erythrorhynchos</i>	0.9	0	0	2.1	0	0
Anhinga	<i>Anhinga</i>	<i>Anhinga</i>	10.8	14.8	2.6	10	9.5	4.5
Bald Eagle	<i>Haliaeetus</i>	<i>Leucocephalus</i>	1.7	0.8	0	0	0	0
Barn Swallow	<i>Hirundo</i>	<i>Rustica</i>		0	0	0.2	0	3.2
Belted Kingfisher	<i>Ceryle</i>	<i>Alcyon</i>	3.1	8	0.6	1.2	10.9	7.7
Black Vulture	<i>Coragyps</i>	<i>Atratus</i>	5.6	0.4	7.9	2.6	24.4	0
Black-crowned Night Heron	<i>Nycticorax</i>	<i>Nycticorax</i>	3.7	0	0	0	0	0.6
Boat-tailed Grackle	<i>Quiscalus</i>	<i>Major</i>	43.1	10.8	3.4	44.4	1.4	0
Brown Pelican	<i>Pelecanus</i>	<i>Occidentalis</i>		4.4	8.9	26.4	124.8	0.7
Bufflehead	<i>Bucephala</i>	<i>Albeola</i>		0	0	0.2	0	0
Cattle Egret	<i>Bubulcus</i>	<i>Ibis</i>	14.4	0	0	0	1.4	0
Common Loon	<i>Gavia</i>	<i>Immer</i>		2.4	0	0	0	0
Common Moorhen	<i>Gallinula</i>	<i>Chloropus</i>	26.2	1.2	0	0	0	0
Crows	Corvidae	sp.	15.6	0	0	23.9	0	0.6
Double-crested Cormorant	<i>Phalacrocorax</i>	<i>Auritus</i>	9.5	13.6	12.8	29	16.3	11.6
Great Blue Heron	<i>Ardea</i>	<i>Herodias</i>	5.6	8	3.1	13.6	51.6	5.1
Great Egret	<i>Casmerodius</i>	<i>Albus</i>	5.9	10	3.7	9	59.7	0.6
Greater Scaup	<i>Aythya</i>	<i>Marila</i>		0	19.5	8.5	0	0
Green-backed Heron	<i>Butorides</i>	<i>Striatus</i>	4.3	2	0.1	0.7	14.9	3.2
Gulls	<i>Laridae</i>	<i>Larinae</i>	20.4	19.2	7.3	54.1	4.1	0
Hooded Merganser	<i>Lophodytes</i>	<i>cucullatus</i>		0	0	0.5	0	0
Killdeer	<i>Charadrius</i>	<i>vociferus</i>	3.7	0	0	1.1	0	0
Little Blue Heron	<i>Egretta</i>	<i>Caerulea</i>	2.4	12	0.4	2.5	17.6	0.6
Mallard	<i>Anas</i>	<i>platyrhynchos</i>	42.4	0	0	1.6	0	0
Mixed Vultures	<i>Coragyps</i>	sp.		53.9	23.5	7.9	0	0
Mottled Duck	<i>Anas</i>	<i>fulvigula</i>	2.1	0.8	0	0	63.8	0
Northern Harrier	<i>Circus</i>	<i>Cyaneus</i>	0.4	0	0	0.4	0	0
Osprey	<i>Pandion</i>	<i>haliaetus</i>	2.1	2.4	2.1	3.5	13.6	2.6
Pied-billed Grebe	<i>Podilymbus</i>	<i>podiceps</i>	1.1	7.6	1.7	3.7	0	1.3
Red-breasted Merganser	<i>Mergus</i>	<i>Serrator</i>		0	1.3	1.8	0	0
Red-shouldered Hawk	<i>Buteo</i>	<i>Lineatus</i>	1	1.6	0	0	2.7	0
Red-winged Blackbird	<i>Agelaius</i>	<i>phoeniceus</i>	19.4	39.9	0	0	0	0
Ring-necked Duck	<i>Aythya</i>	<i>Collaris</i>	31.6	0.4	0.3	1.2	0	0
Roseate Spoonbill	<i>Ajaia</i>	<i>Ajaia</i>		0	0	0	1.4	0
Snowy Egret	<i>Egretta</i>	<i>Thula</i>	3	5.2	1.7	3.3	6.8	0
Terns	Laridae	Sterninae	5	0	0.1	0.2	0	0
Tricolored Heron	<i>Egretta</i>	<i>Tricolor</i>	2.1	6	0.1	0.2	1.4	0
Turkey Vulture	<i>Cathartes</i>	<i>Aura</i>	7.6	31.9	0	2.8	8.1	14.8
White Ibis	<i>Eudocimus</i>	<i>Albus</i>	8.7	0	0.3	1.2	9.5	0
Wood Duck	<i>Aix</i>	<i>Sponsa</i>	7.5	9.2	0	17.4	36.6	0
Wood Stork	<i>Mycteria</i>	<i>americana</i>	1.8	1.2	0	0.5	166.9	0
Yellow-crowned Night Heron	<i>Nyctanassa</i>	<i>Violacea</i>		2	0.9	0	0	0.6

Mean of all counts (birds km⁻²) for each river is listed with mean counts from 46 Florida lakes (Hoyer & Canfield, 1994).

been shown to be positively related to lake trophic state indicators. Chlorophyll concentrations (Canfield, 1983; Brown et al., 2000), zooplankton abundance (Canfield & Watkins, 1984), fish biomass (Jones & Hoyer, 1982; Bachmann et al., 1996), bird abundance (Nilsson & Nilsson, 1978; Suter, 1994) and even the abundance of top predators like the alligator (Evert, 1999) have all been shown to be positively related to the trophic status of the lake systems. In river systems direct relations between nutrients concentrations (primarily phosphorus) and periphyton biomass (Van Nieuwenhuysse & Jones, 1996; Lohman & Jones, 1999), aquatic plants (Sosiak, 2002) and fish biomass (Herrman, 1981; Hoyer & Canfield, 1991) have also been shown, suggesting that similar to lakes, the productivity of a river systems determines the overall abundance of aquatic organisms. Comparing the river bird data to lake bird data collected by Hoyer & Canfield (1994) shows that the river bird density, total phosphorus concentrations, and bird biomass all fall within the range of data collected on Florida lakes (Fig. 3).

Species richness of many types of flora and fauna are related to area sampled (Flessa & Sepkoshi, 1978; Connor & McCoy, 1979), including aquatic birds (Elmberg et al., 1994; Suter, 1994; Paszkowski & Tonn, 2000). A comparison of the river data to lake data collected by Hoyer & Canfield (1994) shows that the whole river aquatic bird species richness and river area data fall within the range of data collected on lakes (Fig. 4).

The flow of energy, habitat availability and basic ecology of streams and lakes are considerably different (Hynes, 1970; Benfield, 1981). However, the above two comparisons suggest that rivers are capable of supplying sufficient resources to maintain bird densities and species richness values similar to lakes of equal size and nutrient concentrations. These comparisons, however, do not necessarily suggest that the relations between phosphorus and bird density or stream area and species richness among streams are functionally the same as lakes. The range in phosphorus concentrations and stream areas of these five Florida streams are insufficient to make this determination. The similarities between the stream and lake data, however, indicate that streams are important habitats for Florida's aquatic bird populations.

While a large portion of the variance in bird density and species richness among lakes systems can be accounted for by lake trophic status and lake area respectively, additional habitat characteristics can also account for considerable within lake variance. For example, aquatic macrophyte abundance has been shown to be a major variable in the distribution and abundance of aquatic birds in lake and wetland systems (Weller & Fredrickson, 1974; Johnson & Montalbano, 1984; Lillie & Evrard, 1994). Water depth has also been shown to be an important factor influencing distribution and abundance of aquatic birds in lakes and wetland systems (DuBow, 1996; Davis & Smith, 1998; Colwell & Taft, 2000). Unfortunately, it is difficult to separate the effects of water depth from that of aquatic macrophytes on the distribution and abundance of aquatic birds as both factors are related in lake, coastal and river systems (Canfield et al., 1985; Duarte, 1991; Hoyer et al., 2004). Indeed, both factors are most likely working simultaneously with other factors to determine the distribution and abundance of aquatic birds (Bancroft et al., 2002).

Because we observed a significant positive relation between section species richness and section area (Table 3) we used the ratio of section species richness to section area to further examine species richness relations with other section habitat characteristics. Significant correlations between both section bird abundance and bird biomass, and macroalgae biomass, macrophyte biomass, water depth and percent light reaching the bottom of the river of the section were found (Table 3). However, when performing a stepwise multiple linear regression analyses using all of the habitat variables and a probability of 0.05 that must be attributed to a dependent variable for it to be considered a forward step, only macroalgae biomass accounted for significant variance in bird abundance (Table 4). Both macroalgae and width accounted for significant variance in bird biomass. Section species richness per unit area was significantly correlated with section area, macroalgae biomass, macrophyte biomass, water depth, percent light reaching the bottom of the river and river width (Table 3). Again, performing a stepwise multiple linear regression analyses using all of the habitat variables, only section area, macroalgae biomass and depth were significant (Table 4).

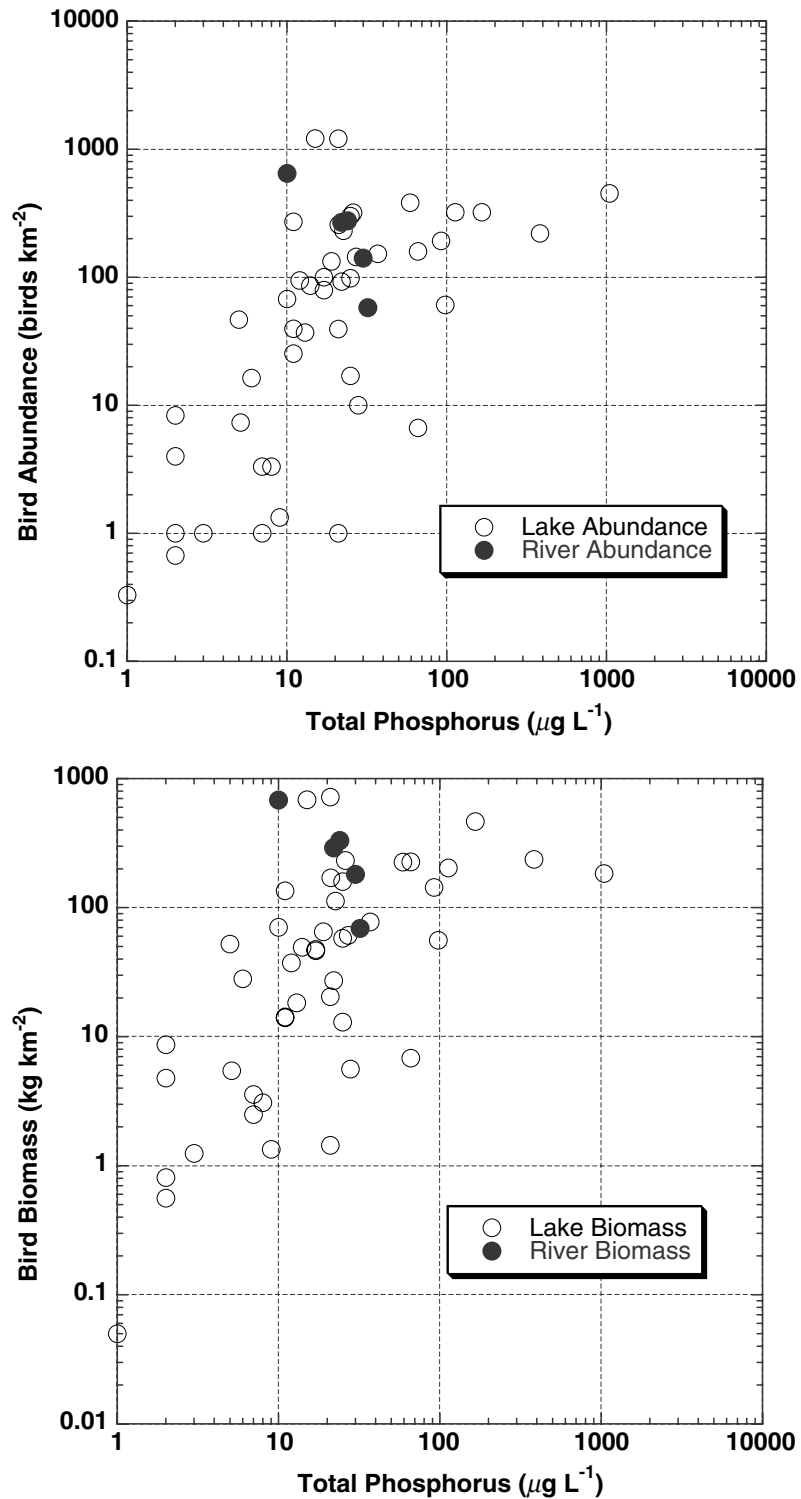


Figure 3. Relations between total phosphorus concentration and bird abundance (correlation coefficient for all data pooled = 0.63) and total phosphorus and bird biomass (correlation coefficient for all data pooled = 0.64) for five Florida Gulf coast rivers plotted with similar data from Florida lakes (Hoyer & Canfield, 1994).

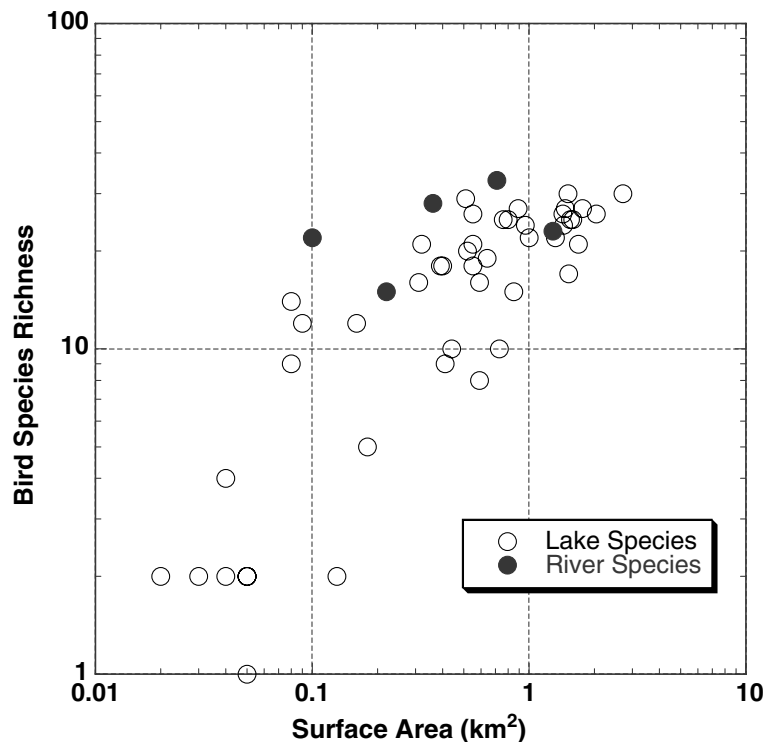


Figure 4. Relations between surface area and bird species richness (correlation coefficient for all data pooled=0.83) for five Florida Gulf coast rivers plotted with similar data from Florida lakes (Hoyer & Canfield, 1994).

These data suggest that, as with lake systems, SAV and water depth are important habitat characteristics that can help determine the distribution and abundance of aquatic birds in river systems.

Both macroalgae and aquatic macrophytes were positively correlated with bird abundance, bird biomass and species richness per unit area, suggesting an important role of SAV in the distribution, abundance and biomass of aquatic birds in the five study rivers. This is not surprising considering that SAV can be a direct food for some species of aquatic birds and also provides habitat for macroinvertebrates and fish that are food for other aquatic birds (Kiorboe, 1980; Gawlik, 2002). However, individual bird species may require different types and quantities of SAV (Weller & Spatcher, 1965; Weller & Fredrickson, 1974). In Florida lakes, whole lake bird densities and species richness were not significantly correlated with whole lake aquatic macrophyte abundance (Hoyer & Canfield, 1994), although species composition changed dramatically with aquatic macrophyte abundance.

Similar to many studies on lake and wetland systems (Boshoff et al., 1990; Colwell & Taft, 2000; Bancroft et al., 2002), stream water depth was negatively correlated with bird abundance, bird biomass and species richness per unit area. Unfortunately, the sampling design employed here was not rigorous enough to statistically measure the changes in bird abundance as tidal fluctuations changed the water depth in the rivers. However, our observations during this study suggest that foraging activity and bird abundance was greatest along the shoreline, where most of the SAV occurs, during low tides. Examining the impact of lake water level on six species of wintering herons and egrets, DuBowoy (1996) found that larger (longer-legged) species tended to be found in deeper water, although these species were frequently found with other smaller birds in shallow water. Similarly, great blue herons and great egrets were observed in river sections that had average depths of 2.00 m and 1.97 m, respectively, while river sections with little blue and tricolored herons averaged 1.4 m and 1.33 m, respectively (Table 5).

Table 3. Pearson product-moment pairwise correlations between section bird abundance (birds km⁻²), ratio of section species richness to area (species ha⁻¹) and habitat characteristics and water chemistry variables

Dependent variable	Independent variable	Correlation	Probability
Log ₁₀ Bird abundance	Log ₁₀ Section Area (ha)	-0.2509	0.0961
Log ₁₀ Bird abundance	Log ₁₀ Width (m)	-0.0369	0.8097
Log ₁₀ Bird abundance	Log ₁₀ Depth (m)	-0.5467	0.0001
Log ₁₀ Bird abundance	Log ₁₀ Flow (m s ⁻¹)	-0.0894	0.5638
Log ₁₀ Bird abundance	Log ₁₀ Light Attenuation (m ⁻¹)	-0.0947	0.5359
Log ₁₀ Bird abundance	Log ₁₀ % Light to Bottom	0.6450	0.0000
Log ₁₀ Bird abundance	Log ₁₀ Macroalgae	0.7160	0.0000
Log ₁₀ Bird abundance	Log ₁₀ Macrophytes	0.5586	0.0001
Log ₁₀ Bird biomass	Log ₁₀ Section Area (ha)	-0.0738	0.6338
Log ₁₀ Bird biomass	Log ₁₀ Width (m)	0.1499	0.3313
Log ₁₀ Bird biomass	Log ₁₀ Depth (m)	-0.4230	0.0042
Log ₁₀ Bird biomass	Log ₁₀ Flow (m s ⁻¹)	-0.1683	0.2808
Log ₁₀ Bird biomass	Log ₁₀ Light Attenuation (m ⁻¹)	0.0102	0.9475
Log ₁₀ Bird biomass	Log ₁₀ % Light to Bottom	0.4663	0.0014
Log ₁₀ Bird biomass	Log ₁₀ Macroalgae	0.5273	0.0002
Log ₁₀ Bird biomass	Log ₁₀ Macrophytes	0.3854	0.0098
Log ₁₀ Section species richness	Log ₁₀ Section Area (ha)	0.4886	0.0000
Log ₁₀ Section species ha ⁻¹	Log ₁₀ Width (m)	-0.5646	0.0001
Log ₁₀ Section species ha ⁻¹	Log ₁₀ Depth (m)	-0.5170	0.0003
Log ₁₀ Section species ha ⁻¹	Log ₁₀ Flow (m s ⁻¹)	0.3647	0.0149
Log ₁₀ Section species ha ⁻¹	Log ₁₀ Light Attenuation (m ⁻¹)	-0.0859	0.5748
Log ₁₀ Section species ha ⁻¹	Log ₁₀ % Light to Bottom	0.6089	0.0000
Log ₁₀ Section species ha ⁻¹	Log ₁₀ Macroalgae	0.6236	0.0000
Log ₁₀ Section species ha ⁻¹	Log ₁₀ Macrophytes	0.4877	0.0007

Data were collected from nine sections in each of five Florida Gulf Coast rivers ($n = 45$) between August 1998 and May 2000.

Table 4. Multivariate linear regression models with significant variables after running stepwise multiple regression between section bird abundance section bird biomass, section species richness per unit area and width, depth, flow, light attenuation, percent light to the bottom, macroalgae biomass and macrophyte biomass

Dependent variable	Independent variables	F	$p > F$	r^2
Log ₁₀ section bird abundance	0.77*Log ₁₀ macroalgae	45.2	< 0.05	
Whole model	Intercept = 2.93	45.2	< 0.05	0.52
Log ₁₀ section bird biomass	3.55*Log ₁₀ macroalgae	19.9	< 0.05	
	0.29*Log ₁₀ Width	4.0	< 0.05	
Whole model	Intercept = 2.38	10.7	< 0.05	0.34
Log ₁₀ Section species richness per unit area	-0.39*Log ₁₀ Width	21.4	< 0.05	
	-0.39*Log ₁₀ Depth	5.5	< 0.05	
	0.30*Log ₁₀ Macroalgae	9.4	< 0.05	
Whole model	Intercept = 1.65	22.8	< 0.05	0.63

Table 5. Mean depth of river sections in which each of six heron and egret species were observed

Species	Body mass (g)	Number counted	Mean water depth (m)	Standard error
Tricolored Heron	300	16	1.33	0.21
Little Blue Heron	400	50	1.42	0.12
Snowy Egret	350	39	1.82	0.17
Great Egret	1000	92	1.97	0.12
Great Blue Heron	3500	100	2.00	0.11
Green-backed Heron	225	23	2.12	0.30

These data suggest that water depth is indeed an important factor determining the distribution of some aquatic birds in these five rivers.

Conclusions

Forty-two species were identified on the five Florida Gulf Coast rivers and for the species that were found in both Florida rivers and lakes similar densities and biomass were encountered. Similar to Florida lakes both bird abundance and species richness was higher in winter months than summer months when migratory populations are utilizing the river systems. Total bird abundance and biomass values per unit of phosphorus and individual river species richness per unit of area were also similar to data collected on Florida lakes. Water depth and presence of SAV were two major factors determining the distribution and abundance of aquatic birds in the river systems. Both factors appear to be important but they are inversely correlated making it difficult to separate the magnitude each factor has on stream bird populations. The similarities between river and lake bird populations suggest that these systems in Florida are supplying similar resources for aquatic bird populations, and both should be considered to be valuable resources for avian fauna.

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Foraging guilds of aquatic birds on productive boreal lakes: environmental relations and concordance patterns

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Abstract

We surveyed aquatic birds on 41 eutrophic lakes at the southern edge of the boreal forest in Alberta, Canada to determine if patterns of species composition of five foraging guilds paralleled patterns of lake characteristics (morphometry, water chemistry, fish assemblage, and landscape features) and if composition patterns were concordant among guilds. We encountered 49 species of nonpasserine birds that could be classified into five foraging guilds: Diving Carnivores, Diving Omnivores, Herbivores, Surface-foraging Carnivores, and Shoreline Omnivores. Individual lakes supported three to five guilds and guild composition was most strongly and frequently related to lake area, maximum depth, water color, pH, a fish assemblage index, and catchment slope. Randomization tests of matrix concordance based on Principal Components Analyses indicated similar patterns between lake characteristics and species composition for four of five guilds (Diving Carnivores excepted). Randomization tests also showed that patterns of species composition among lakes were similar between foraging guilds for eight out of 10 pairwise comparisons (both exceptions involved Surface-foraging Carnivores). Because of the largely concordant patterns among different guilds, monitoring the status of one guild should provide a useful bioindicator of the status of the aquatic bird assemblages as a whole.

Introduction

The guild concept has a long and fruitful history in ecology (Grinnell, 1917; Root, 1967). This concept has contributed substantially to the description and understanding of bird communities with the primary focus being on foraging guilds (see Wiens, 1989). Although the traditional, taxonomically anchored foraging guild can limit biologists' appreciation of the scope and complexity of ecological interactions (Yodzis, 1994) and ecosystem function (Blondel, 2003), grouping species based on shared ecological or life history traits remains a useful framework for assessing community composition and organization (O'Connell et al., 2000) or for providing suites of bioindicators

linked to environmental conditions of interest (McNicol et al., 1990; Croonquist & Brooks, 1991; Miller & Cale, 2000).

Studies of freshwater birds have a tradition of incorporating the guild concept, both explicitly and implicitly. An example is the long-standing distinction between the guilds of "dabbling ducks" and "diving ducks" (Kortright, 1942; Savard et al., 1994). Fish-eating birds are also often treated as an ecological unit (Nilsson & Nilsson, 1976), with further categorizations made on the basis of foraging behavior (Eriksson, 1985). Because aquatic birds have strong links to the abiotic environments and food webs of lakes (Kauppinen, 1993; Paszkowski & Tonn, 2000a), an increasing number of researchers seek to integrate these birds into studies

of their ecosystems (see Kerekes & Pollard, 1994). The foraging guild concept thus provides a promising framework for identifying relationships between bird communities and lake environments. If consistent relationships exist between guilds and diverse components of lake environments, e.g., morphometry, chemistry, and landscape position (e.g., Riera et al., 2000), the structure or composition of one guild of birds on a lake could be used as a bioindicator for other guilds (Gaston, 1996; Howard et al., 1998), or help identify key localities, i.e., “biodiversity hotspots”, for conservation initiatives (Kareiva & Marvier, 2003).

Community–environment relations need to be tested statistically to be considered robust and legitimate, and methods based on community concordance are especially appropriate (Jackson, 1995; Peres-Neto & Jackson, 2001). Such analyses determine if two different sets of variables that characterize a collection of objects vary in concert, e.g., environmental variables and species composition for a set of lakes or species composition of two co-occurring assemblages (Jackson & Harvey, 1993; Paszkowski & Tonn, 2000a). By integrating concordance with the guild concept, such analyses can be applied at a finer scale to examine relations between the environment and the composition of individual guilds, and to compare patterns in the structure of guilds co-existing at a set of sites.

In the present study, we examine the structure of five foraging guilds of aquatic birds on small, naturally eutrophic lakes in the boreal forest of north-central Alberta, Canada. Our goal is to explore linkages between birds and lakes by addressing the following questions:

- (1) Does the species composition of guilds display concordance with the environmental features of lakes? If so, what are the important features related to guild composition?
- (2) Are patterns of species composition across lakes concordant among guilds? For example, do lakes sharing a particular suite of shorebirds also share a characteristic suite of diving ducks?

Study area

The study investigated assemblages of aquatic birds on lakes located in the aspen-dominated

mixedwood forest of the Boreal Plains of Alberta (Strong & Leggat, 1992). Lakes in this region are typically circumneutral to basic, naturally eutrophic, and relatively shallow (Table 1) with broad littoral zones and abundant macrophytes and macroinvertebrates (Mitchell & Prepas, 1990; Clifford, 1991). They provide excellent habitat for aquatic birds, with over 50 nonpasserine species breeding in the region (Semenchuk, 1992). In contrast, local assemblages of fishes in the region are depauperate, with lakes typically supporting only a few species (Tonn et al., 2003). These local assemblages can be categorized as those dominated by large-bodied species, e.g., northern pike (*Esox lucius* (L.)) and yellow perch (*Perca flavescens* (Mitchell)), vs. assemblages that are dominated by small-bodied fishes, e.g., fathead minnow (*Pimephales promelas* (Rafinesque)) and brook stickleback (*Culaea inconstans* (Kirtland); Robinson & Tonn, 1989). As well, fishless lakes are fairly common (Paszkowski & Tonn, 2000b).

The 41 study lakes were centered around Meanook Biological Research Station, Athabasca County, Alberta (54° 13′–54° 59′ N, 112° 27′–113° 47′ W; Table 1), where the mixedwood boreal forest interfaces with the aspen parkland. These lakes were in a heterogeneous landscape of forest and agriculture land, with about 75% of the land cleared, primarily for pasture (see also Paszkowski & Tonn, 2000a). However, all lakes sampled had most of their shorelines in forest or wetlands.

Table 1. Environmental characteristics of 41 lakes in north-central Alberta used in ordinations

Characteristic	Mean ± SE (range)
Lake area (ha)	82 ± 13 (3–305)
Maximum depth (m)	6.2 ± 1.2 (0.6–38.0)
Catchment slope (%)	2.7 ± 0.2 (0.6–6.6)
Total phosphorus (µg/l)	74 ± 14 (11–500)
Color (mg/l Pt)	40 ± 6 (3–160)
pH	8.4 ± 0.1 (6.4–9.9)
Conductivity	260 ± 15 (80–535)
Shoreline development	1.66 ± 0.09 (1.02–3.65)
Lake order	–0.2 ± 0.3 (–3 to 3)
Fish index	338.1 ± 70.2 (0.0–1021.1)
Bird species richness	13.8 ± 1.0 (3–28)

See text for descriptions of shoreline development, lake order, and fish index.

Methods

Data collection

Our study was designed to document broad patterns of avian composition across a variety of lakes during the breeding season, rather than to record in detail the reproductive success or foraging behavior of individual species (e.g., Gingras & Paszkowski, 1999). Lakes were surveyed between 4 May and 9 July 1993. Typically, a boat was slowly propelled around a lake's perimeter, 3–8 m from shore, and a running record was kept of all birds encountered. A few small lakes were surveyed from shore with a 45× spotting scope. On-water censuses required 30 min–3 h to complete, whereas shore-based censuses took 20–30 min. Twenty-eight of the 41 lakes were revisited later in July and August, 1993; agreement in species observed during repeat visits was consistently good (C. Paszkowski, unpublished data).

To characterize lake environments, measurements of water quality (total phosphorus concentration, color, pH, conductivity) and maximum depth were made at the time of the bird surveys or were obtained from earlier studies (Prepas et al., 1988; Robinson & Tonn, 1989; Table 1). Information on 30 fish assemblages came from surveys conducted in conjunction with the bird surveys (Paszkowski & Tonn, 2000a) while data for the remaining eleven came from earlier studies (Robinson & Tonn, 1989).

Data analysis

For analyses, we used only nonpasserine birds known to breed in the study area (Semenchuk, 1992). In a few cases, multiple species that were identified inconsistently were combined into a single category for analysis, e.g., “large white gull” (Table 2). We recognized five foraging guilds, based on *a priori* classification (*sensu* Wiens, 1989), integrating personal observations, published information, and previous classifications (e.g., Eriksson, 1985; Elmerberg et al., 1993). The foraging guilds were as follows (see Table 2 for a full listing):

- (1) Diving Carnivores: species that eat fish and large invertebrates, foraging underwater *via*

Table 2. Species composition of five foraging guilds of aquatic birds encountered on 41 study lakes in north-central Alberta

<i>Diving Carnivores</i>	
Common loon (COLO) (<i>Gavia immer</i> (Brünnich))	
Double-crested cormorant (DCCO)	
(<i>Phalacrocorax auritus</i> (Lesson)) ^a	
Eared grebe (EAGR) (<i>Podiceps nigricollis</i> (Brehm))	
Hooded merganser (HOME) (<i>Lophodytes cucullatus</i> (L.)) ^a	
Horned grebe (HOGR) (<i>Podiceps auritus</i> (L.))	
Pied-billed grebe (PBGR) (<i>Podilymbus podiceps</i> (L.))	
Red-necked grebe (RNGR) (<i>Podiceps grisegena</i> (Boddaert))	
Western grebe (WEGR) (<i>Aechmophorus occidentalis</i> (Lawrence)) ^a	
<i>Diving Omnivores</i>	
Bufflehead (BUFF) (<i>Bucephala albeola</i> (L.))	
Canvasback (CANV) (<i>Aythya valisineria</i> (Wilson))	
Common goldeneye (COGO) (<i>Bucephala clangula</i> (L.))	
Lesser scaup (LESC) (<i>Aythya affinis</i> (Eyton))	
Redhead (REDH) (<i>Aythya americana</i> (Eyton))	
Ring-necked duck (RNDU) (<i>Aythya collaris</i> (Donovan))	
Ruddy duck (RUDU) (<i>Oxyura jamaicensis</i> (Gmelin))	
Surf scoter (SUSC) (<i>Melanitta perspicillata</i> (L.)) ^a	
White-winged scoter (WWSC) (<i>Melanitta fusca</i> (L.))	
<i>Herbivores</i>	
American coot (AMCO) (<i>Fulica americana</i> (Gmelin))	
American wigeon (AMWI) (<i>Anas americana</i> (Gmelin))	
Blue-winged teal (BWTE) (<i>Anas discors</i> (L.))	
Canada goose (CAGO) (<i>Branta canadensis</i> (L.))	
Gadwall (GADW) (<i>Anas strepera</i> (L.))	
Green-winged teal (AGWT) (<i>Anas crecca</i> (L.))	
Mallard (MALL) (<i>Anas platyrhynchos</i> (L.))	
Northern pintail (NOPI) (<i>Anas acuta</i> (L.))	
Northern shoveler (NSHO) (<i>Anas clypeata</i> (L.))	
<i>Surface-foraging Carnivores</i>	
American bittern (AMBI) (<i>Botaurus lentiginosus</i> (Rackett)) ^a	
Bald eagle (BAEA) (<i>Haliaeetus leucocephalus</i> (L.))	
Belted kingfisher (BEKI) (<i>Ceryle alcyon</i> (L.))	
Black tern (BLTE) (<i>Chlidonias niger</i> (L.))	
“Black-headed gull” (BHGu):	
Bonaparte's gull (<i>Larus philadelphia</i> (Ord))	
& Franklin's gull (<i>Larus pipixcan</i> (Wagler))	
Great blue heron (GBHE) (<i>Ardea herodias</i> (L.))	
“Large white gull” (LWGu):	
California gull (<i>Larus californicus</i> (Lawrence)),	
Herring gull (<i>Larus argentatus</i> (Pontoppidan)),	
& Ring-billed gull (<i>Larus delawarensis</i> (Ord))	
Osprey (OSPR) (<i>Pandion haliaetus</i> (L.))	

Continued on p. 22

Table 2. (Continued)

“White tern” (WhTe):
 Common tern (*Sterna hirundo* (L.))
 & Forester’s tern (*Sterna forsteri* (Nuttall))

Shoreline Omnivores
 Common snipe (COSN) (*Gallinago gallinago* (L.))
 Killdeer (KILL) (*Charadrius vociferous* (L.))

“Yellowlegs” (YeLe):
 Greater yellowlegs (*Tringa melanoleuca* (Gmelin))
 & Lesser yellowlegs (*Tringa flavipes* (Gmelin))
 Marbled godwit (MAGO) (*Limosa fedoa* (L.))
 Sandhill crane (SACR) (*Grus canadensis* (L.))^a
 Solitary sandpiper (SOSA) (*Tringa solitaria* (Wilson))
 Sora (SORA) (*Porzana carolina* (L.))
 Spotted sandpiper (SPSA) (*Actitis macularia* (L.))
 Wilson’s phalarope (WIPH) (*Phalaropus tricolor* (Vieillot))

Four groups of two or three species could not be reliably distinguished (names in quotes) and were treated as one taxonomic unit in all analyses. Abbreviations of names used in ordination graphs are given in parentheses following the common names.^aSpecies was observed on only one lake and not included in Principal Components Analyses.

- foot-propelled diving (loon, grebes, cormorant, merganser),
- (2) Diving Omnivores: omnivorous waterfowl that forage for invertebrates, and to a lesser extent plant material, while submerged underwater using foot-propelled diving (*Aythya* and *Bucephala* spp., scoters, ruddy duck),
 - (3) Herbivores: species that consume more plant material and less invertebrate food than Diving Omnivores, and are shallow, surface foragers and grazers (dabbling ducks, goose), or foot-propelled divers (coot),
 - 4) Surface-foraging Carnivores: species that eat fish and large invertebrates, searching from above or on the water’s surface while perched (kingfisher), standing near shore (herons), in flight (raptors, gulls, terns), or swimming (pelican),
 - 5) Shoreline Omnivores: omnivorous and invertebrate-feeding species that forage while walking along the water’s edge and in adjacent wetland vegetation (sandpipers, plover, rail, crane).

To summarize richness and size-structure of each lake’s fish assemblage, we calculated a “fish

index”. The nine fish species present in the study lakes (see Paszkowski & Tonn, 2000a for species lists) were each assigned a score ranging from 1.6 (Iowa darter, *Etheostoma exile* (Girard)) to 832.1 (northern pike) based on the mean mass (g) of individual fish captured with gill-nets in boreal Alberta lakes (W. Tonn, unpublished data). For three species, found only in single lakes, an average mass was obtained from the literature (Scott & Crossman, 1973). The fish index was then calculated for each lake by summing the score of each fish species present, e.g., a lake containing Iowa darter and northern pike would be assigned an index of $1.6 + 832.1 = 833.7$. Fishless lakes received a score of 0.

Information on lake area and three other morphometric/geographic parameters were obtained from national topographic maps scaled at 1:50 000. The shoreline development index (D), a measure of lake shape, was calculated as $D = \frac{L}{2\sqrt{\pi A}}$, where L = lake perimeter and A = lake area (Horne & Goldman, 1994). Slope of the catchment of each lake was calculated by dividing the watershed into six to 16 equal units, depending on lake and catchment size and catchment topography, measuring the change in elevation from the catchment boundary to the shoreline of the lake for each unit, then calculating the average slope for the whole catchment (Prepas et al., 2001). Lake order is a “lakescape” metric that describes the position and connectivity of a lake within the larger drainage network (Riera et al., 2000). It consists of an integer value between -3 (most isolated) and 3 (best connected) assigned as follows: lakes with permanent inlets and outlets received a positive score based on the order of the streams that drained them, headwater lakes with outlets only were assigned a score of 0, lakes connected only to intermittent streams received a score of -1 , lakes connected only to wetlands received a score of -2 , and isolated lakes with no detectable connections to the regional drainage systems received a score of -3 (Conlon, 2002).

Patterns of avian species composition were summarized for each foraging guild with Principal Components Analysis (PCA) on presence-absence data with cross product matrices based on correlation (PCORD Version 3.20; McCune & Mefford, 1997). PCA was chosen for multivariate

analysis because preliminary Detrended Correspondence Analysis ordinations (Gauch, 1982) showed that primary gradient lengths were all <4 SD units, indicating that ordination based on a linear response model was appropriate (ter Braak, 1987). Species that occurred on only one lake were not included in ordinations (Gauch, 1982).

To examine the relationship between the ordination scores and environmental variables, we produced joint plots in which environmental vectors radiate from the center of the ordination scores. The angle and length of each vector is proportional to the correlation of the environmental variable with the ordination axes (McCune & Mefford, 1997). Only variables having a significant correlation ($p \leq 0.05$) with PCA axis 1 or 2 were included in joint plots. Environmental characteristics of each set of study lakes were also summarized with PCA, using the 10 variables (Table 1). Values for environmental data (except pH and lake order) were transformed [$\log_{10}(x+1)$ or arcsin-square root] as appropriate for analysis.

PROTEST, a randomization test of matrix concordance based on Procrustean matrix rotation (Jackson, 1995; Peres-Neto & Jackson, 2001), was used to assess concordance between pairs of matrices generated by PCA. The method examines how well the positions of lakes in one multivariate space (e.g., the PC scores of the Diving Carnivore foraging guild) match the positions of the same lakes in a second multivariate space (e.g., the PC scores of the lake environments), thereby assessing the degree to which both data sets display similar interlake patterns (Jackson & Harvey, 1993). Comparisons of “broken-stick eigenvalues” (Jackson, 1993) vs. calculated eigenvalues indicated that two to three PC axes were significant; to standardize PROTEST analysis, we used the first three axes scores throughout. Tests for concordance were made between the environmental matrix and each of the five foraging guild matrices. Tests of concordance were also performed on PCA matrices for pairs of guilds (e.g., Diving Carnivores vs. Diving Omnivores). Because evaluation of patterns of concordance across the five guilds required multiple PROTESTs, we applied a Bonferroni correction when assessing significance.

Results

We encountered a total of 49 bird species in our surveys; 38 species/species-groups occurred on at least two lakes and were included in Principal Components Analyses (Table 2). Richness on a single lake, including rare species, ranged from 3 to 28 species (Table 1). The five foraging guilds as used in multivariate analyses contained 5–9 species or species-groups overall (Table 2). Richness of single guilds on individual lakes ranged from 0 to 8 species, and averaged 1.8–3.8 species. The frequency of occurrence of the five guilds were as follows: Diving Carnivores = 97.6% of lakes, Diving Omnivores = 97.6%, Herbivores = 95.1%, Surface-foraging Carnivores = 85.4%, and Shoreline Omnivores = 80.5%. All lakes contained at least three guilds and 27 lakes (65.8%) supported all five.

The PCA ordinations revealed a number of similarities among foraging guilds in their relationship to environmental features (Fig. 1). For each guild, scores on the first axis (accounting for 25–35% of the variance in species composition), and often the second axis as well (14–23% of variance), were significantly correlated ($p \leq 0.05$) with total numbers of aquatic bird species. Thus, lakes with more species in any one guild tended to support more species of aquatic birds across all guilds. In general, each guild was built around a core of widespread species that occurred on at least half of the lakes; in some cases, core species might be the only species present. These core species were: common loon and red-necked grebe (Diving Carnivores); bufflehead, ring-necked duck, lesser scaup, and common goldeneye (Diving Omnivores); mallard, American wigeon, blue-winged teal, and green-winged teal (Herbivores); black tern and great blue heron (Surface-foraging Carnivores); spotted sandpiper (Shoreline Omnivores).

For all five foraging guilds, scores on axis 1 or 2 of species ordinations were significantly correlated with lake area (Fig. 1). Other environmental variables that were significantly correlated ($r > 0.3$) with ordination scores on axis 1 or 2 for at least three guilds encompassed morphometric (maximum depth), water quality (color, pH), biotic (the fish index), and landscape (catchment slope) features of lakes. Lake order was the only environmental variable that was not significantly

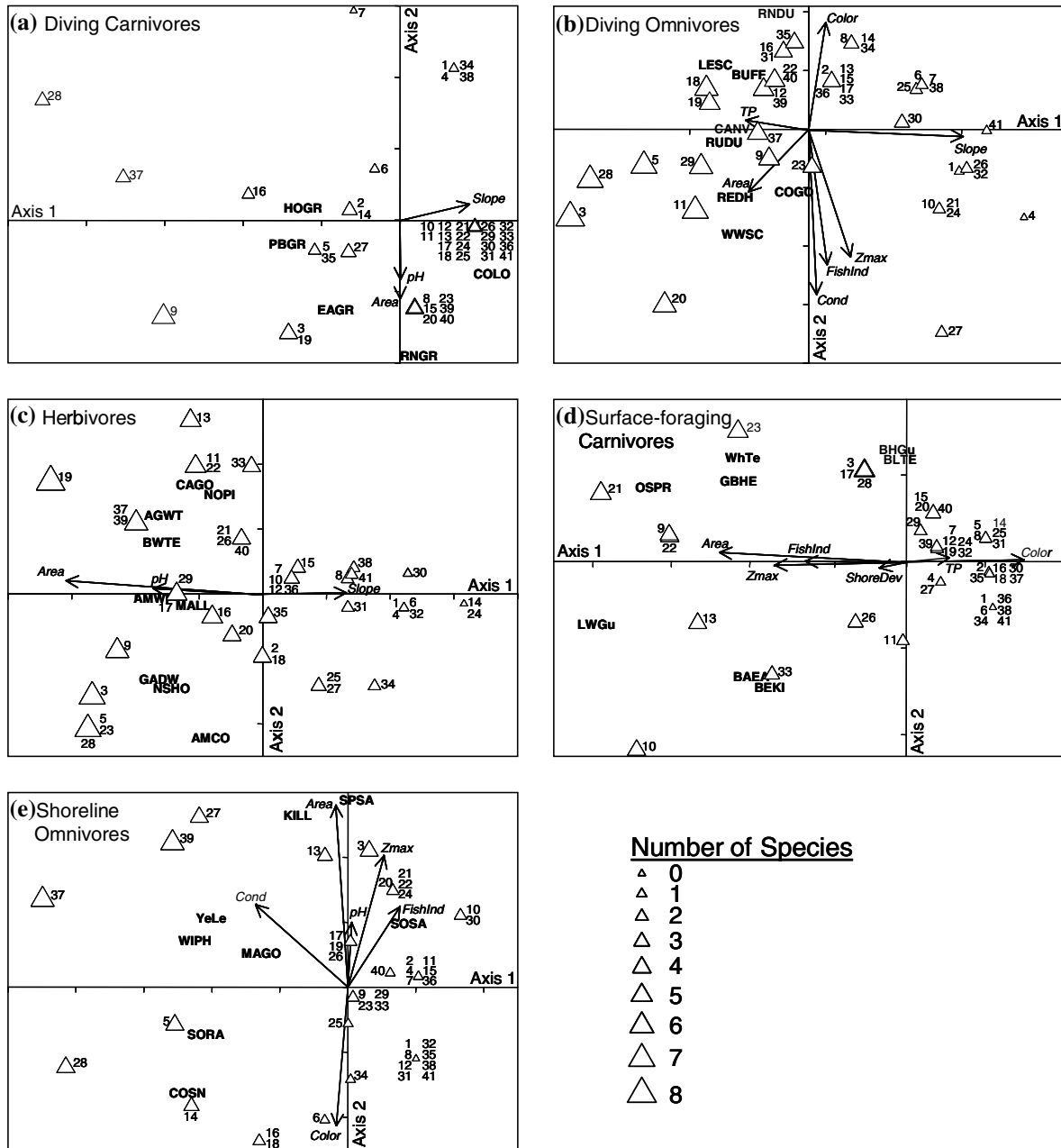


Figure 1. Ordination plots of Principal Components Analyses for 41 lakes in north-central Alberta based on the presence-absence of aquatic bird species belonging to five foraging guilds ((a) Diving Carnivores, (b) Diving Omnivores, (c) Herbivores, (d) Surface-foraging Carnivores, and (e) Shoreline Omnivores)). Joint plot environmental vectors indicate correlations between an environmental factor and scores on either principal component axis 1 or axis 2 with $r > 0.3$. For visual clarity, only the endpoints of the species vectors have been plotted (see Table 2 for species codes), and both environmental and species vectors have been scaled to match site scores. Individual lakes are designated with same number (1–41) on all five ordinations. The size of the triangles is proportional to the richness of the guild on each lake. Cond=conductivity, FishInd=Fish index, ShoreDev=shoreline development, TP=total phosphorous concentration, ZMax = maximum depth.

correlated with PC scores on axis 1 or 2 for any of the five guilds. The third PCA axes (not shown but used in PROTEST analyses below) explained an additional 12–17% of variance in guild composition.

The first three axes of the environmental PCA explained 40, 14 and 12%, respectively, of the variance in characteristics for the study lakes. The resultant ordination plot separated on axis 1 relatively deep, large lakes with low water color and large-bodied fish assemblages from shallow, small, fish-poor lakes with high water color (Fig. 2). The second axis differentiated lakes with low catchment slopes and relatively high values for pH and total phosphorus concentrations (high scores) from lakes with the opposite suite of features. With the exception of Diving Carnivores, all foraging guilds displayed significant concordance with these lake environmental patterns (Table 3).

Also consistent with the shared relationships described above, concordance was widespread between pairs of foraging guilds. Eight of 10

inter-guild comparisons with PROTEST were significant (Table 3). The two exceptions both involved Surface-foraging Carnivores; composition of this guild was not concordant with either the Diving Carnivore or the Shoreline Omnivore guild.

Discussion

Bird assemblages on the study lakes were rich and complex, comprising species that exploit diverse food sources using a variety of behavioral tactics and morphological adaptations. All lakes supported at least three foraging guilds, with two-thirds supporting five. Similar to the full assemblages (Paszkowski & Tonn, 2000a), each guild displayed an additive pattern of membership. For each guild, a core of widespread species, apparently habitat generalists, occurred reliably wherever the guild was present. Less common, specialist species joined these core species on

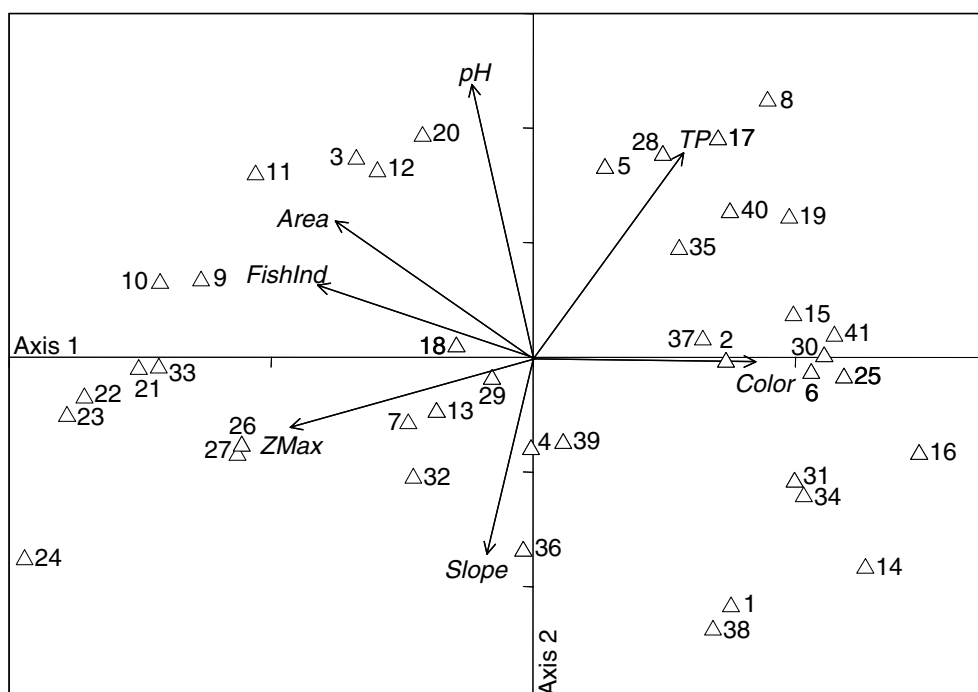


Figure 2. Ordination biplots of Principal Components Analyses of lake environments for 41 study lakes (1–41) in north-central Alberta based on 10 environmental factors (Table 1). For visual clarity, vectors have been scaled to match site scores, and only components with eigenvectors >0.35 are shown. FishInd = Fish index, TP = total phosphorous concentration, ZMax = maximum depth.

Table 3. Results (p -values) of pairwise tests for concordance in the composition of foraging guilds of aquatic birds and between patterns of guild composition and the environment for 41 study lakes in north-central Alberta

	Diving Omnivores	Herbivores	Surface-foraging Carnivores	Shoreline Omnivores	Environment
Diving Carnivores	0.001	0.001	0.181	0.000	0.025
Diving Omnivores		0.000	0.002	0.000	0.000
Herbivores			0.000	0.001	0.004
Surface-foraging Carnivores				0.269	0.000
Shoreline Omnivores					0.006

Concordance was assessed by PROTEST (Jackson, 1995) using 9999 permutations, and was based on comparisons of matrices consisting of scores from the first three axes of Principal Component ordinations of species composition (presence-absence) for each guild or lake environments. Significant concordance (Bonferroni adjusted p -value, 0.005 for guild-guild tests, 0.01 for guild-environment tests) indicated in bold.

certain subsets of lakes. Thus, the richness of each guild paralleled richness of the whole avian assemblage among lakes, suggesting that common environmental factors shaped species richness across all five foraging guilds.

Foraging guild–lake environment relationships

Patterns of species composition and richness of foraging guilds were related to aspects of lake morphometry, water chemistry, and the larger landscape. Lake area, in particular, had a strong and pervasive effect on species composition and richness among all guilds. A positive relationship between area and species richness is widespread and has been previously documented for aquatic bird assemblages (e.g., Nilsson & Nilsson, 1978; Brown & Dinsmore, 1986; Gibbs et al., 1991; Hoyer & Canfield, 1994). However, its extension to individual guilds is of note (see also Nudds, 1992) since it is perhaps more typical for total species richness in larger habitat patches to increase by the addition of guilds that require resources that occur at low densities, e.g., top predators (Kareiva & Marvier, 2003), or that specialize in resources confined to large patches (Miller & Cale, 2000). Maximum depth was another morphometric feature that showed strong correlations with guild composition and richness for a diverse group of guilds, but this pattern may have in part been an outcome of the correlation of depth with area and the fish index rather than direct effects of lake depth on foraging conditions and guild composition.

Water-quality variables were also related to the composition of all five foraging guilds, although no single variable was linked to patterns for all guilds. pH was strongly correlated with ordination scores for three guilds (Diving Carnivores, Herbivores, and Shoreline Omnivores), but unlike lake districts in eastern North America and northern Europe affected by acid precipitation (Eriksson, 1985; McNicol & Wayland, 1992), pH did not act as a master variable affecting bird assemblages by dramatically altering water clarity, fish populations or invertebrate food resources. Similarly, total phosphorus concentration, reflective of the productivity and trophic status of a lake, can be a master variable shaping food resources and bird assemblages in some lake districts, especially in the context of cultural eutrophication (Nilsson & Nilsson, 1978; Hoyer & Canfield, 1994; Suter, 1994). For our study lakes, however, total phosphorus concentration was strongly correlated with PCA scores for only two foraging guilds, and then in opposite directions. Richness of Diving Omnivores increased with phosphorous levels, whereas richness of Surface-foraging Carnivores decreased. The lakes did not span a large productivity gradient, as most were naturally eutrophic, and this may have contributed to the lack of strong and consistent patterns.

At the landscape level, foraging guilds were richer on lakes with shallower catchment slopes. Such lakes are typically surrounded by shallow wetlands and peatlands that can provide habitat for nesting and foraging for many aquatic birds. Indeed, these complex ecotones provide important habitat for both aquatic and terrestrial birds, and

the structure of riparian vegetation significantly affects avian community composition around lakes in the boreal mixedwood forest (Pierre, 2001; Hannon et al., 2002) and aspen parkland (Puchniak, 2002) in Alberta.

Surprisingly, lake order was the only environmental feature that was not correlated with the first two principal components for any guild. As a measure of surface connectivity of a lake with the larger drainage basin, lake order has been shown to be related to the distribution of more fully aquatic animals, including snails and fishes (Lewis & Magnuson, 2000; Riera et al., 2000; Conlon, 2002). Likewise, characteristics of aquatic bird communities, such as species richness, have frequently been related to wetland isolation (Brown & Dinsmore, 1986; Gibbs et al., 1991) and landscape patterns (Naugle et al., 2001). It may be that lake order is not an effective measure of connectivity for highly mobile, migratory organisms such as birds or does not reflect regional habitat availability for lake-dwelling birds.

The fish index represented our attempt to relate foraging guilds directly to a biotic variable and to a group of organisms that is known to have a significant effect on aquatic birds (Eriksson, 1979; Giles, 1990; McNicol & Wayland, 1992; Wagner, 1997). Not surprisingly, richness and the occurrence of taxa such as osprey and “large white gull”, species that depend on fish as prey, were positively correlated with the fish index for the Surface-foraging Carnivore guild. However, the index was not related to compositional patterns for the Diving Carnivore guild, in part because the common loon and red-necked grebe were nearly ubiquitous, occurring even on fishless lakes where leeches and large aquatic arthropods provide prey (Wagner, 1997; Gingras & Paszkowski, 1999). The fact that loons and large grebes feed extensively on invertebrates in the study area was one reason that these “piscivorous” species were placed in the same guild as smaller grebe species that typically concentrate their feeding on macroinvertebrates rather than fish. In contrast to Diving Carnivores, compositional patterns for Diving Omnivores and Shoreline Omnivores were correlated with the fish index. For example, white-winged scoter and spotted sandpiper were present on lakes where the fish index was high whereas ring-necked duck and common snipe frequented lakes where the index was low.

Environmental and inter-guild concordance

Our results thus suggest that guilds responded to a collection of characteristics presented by the 41 study lakes, with key environmental features tending to vary in concert, e.g., lake size, depth, water color, and fish populations. Indeed, four of the five foraging guilds displayed significant concordance with integrative measures of lake environmental patterns, complementing our previous study that demonstrated concordance between the entire aquatic bird assemblage and the lake environment, as well as concordance between the species composition of local bird and fish assemblages (Paszkowski & Tonn, 2000a).

The result of inter-guild comparisons with PROTEST showed patterns of species composition to be concordant for 8 of 10 pairwise comparisons. Such widespread concordance was consistent with strong parallel linkages between individual guilds and lake environments and the recurrent additive-pattern of guild assembly. Because of this, we do not feel that concordance resulted from direct interactions between guilds, although competition within guilds is possible (see Nudds, 1992). Rather, we propose that species-environment relations generally ran in parallel for the five guilds.

The study lakes are located in a transitional zone between the aspen parkland and the boreal mixedwood forest (Strong & Leggat, 1992). These lakes thus spanned a substantial range of morphometric and landscape conditions and included a number of open, “prairie-like” lakes that were large, shallow, and hypereutrophic (Paszkowski & Tonn, 2000a). As a result, species characteristic of prairie wetlands (e.g., American coot, killdeer, northern shoveler, eared and pied-billed grebes, teal species) occurred together on a subset of lakes, contributing to parallel, concordant patterns among foraging guilds.

Concordant patterns were the rule, but there were exceptions. Diving Carnivores did not display significant concordance with the overall lake environment, although the guild’s composition was related to individual factors (lake area, catchment slope, and pH). The lack of strong concordance was somewhat unexpected since loons and other freshwater carnivores have often been considered as sensitive indicators of “ecosystem health” and human disturbance for lakes in

central North America (Alvo et al., 1988; McNicol et al., 1990; McNicol & Wayland, 1992) and Europe (Eriksson, 1985; Kauppinen, 1993). That seems not to be the case in Alberta's Boreal Plains. Although it was the smallest foraging guild (five species used in the ordination), Diving Carnivores were very widespread (occurring on all but one lake). The two core species, common loon and red-necked grebe, were dominant guild members and each occurred on over 80% of the lakes. In contrast to better-studied boreal regions, the naturally high productivity of lakes in western Canada allows even common loons to inhabit and to breed successfully on small and fishless lakes because of the abundance of macroinvertebrate prey (Gingras & Paszkowski, 1999). Given this widespread distribution, there was little foundation for discrimination among lakes by Diving Carnivores based on environmental characteristics.

This lack of strong concordance with the environment may have also contributed to Diving Carnivores being one of three foraging guilds that failed to display perfect concordance with other guilds. In contrast, compositional patterns for Surface-foraging Carnivores were strongly correlated with the environment, but this guild too failed to display perfect concordance with others. Unlike the other four guilds, Surface-foraging Carnivores, a collection of raptors, herons, and gulls, reached maximal diversity on large lakes that were deep, clear, less productive, and contained large-bodied fishes.

Conclusions

Our study demonstrates that concordance of aquatic birds with the environmental characteristics of lakes that they inhabit during the breeding season extends to the level of the ecological (foraging) guild. The concepts of foraging guild and concordance work well to describe assemblage-wide patterns and suggest possible mechanisms behind patterns. Standard measurements of lake morphometry, water chemistry, and the surrounding landscape can be related to patterns of species composition both for individual guilds and suites of guilds. The relationships that we found between basin morphometry and guild composition, in particular, offer a promising tool for

predicting guild structure or the presence of species of interest on unsurveyed lakes, as lake area and catchment slope are readily extracted from topographic maps or air photos. Use of "remote sensing" information is attractive to managers and conservation biologists when visiting sites is difficult and expensive, as is true in the boreal forest of western Canada. Such information might be used to identify candidate lakes for protection from activities such as logging (Hannon et al., 2002).

Our results also have relevance to conservation strategies for birds on lakes in the Boreal Plains of western Canada, and possibly in other geographical settings as well. The high degree of concordance among the different foraging guilds demonstrates that a lake displaying a complex or simple structure for one guild will typically support complex or simple structures for other guilds because of common links to the lake environments existing among guilds and their food resources. Government or conservation organizations that preserve or improve habitat to maintain a diversity of game species, such as dabbling or diving ducks, will likely preserve or enhance other aquatic birds with different foraging strategies and thus the entire avian assemblage. Similarly, monitoring the status of one guild could also give good indications of the status of other guilds of aquatic birds, and the condition of the lake ecosystems of which these birds are an integral part.

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Water bird guilds and their feeding connections in the Bodrogzug, Hungary

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Abstract

Species composition, number, species diversity, and evenness of nesting bird communities were surveyed in 2001 and 2002 in north-east Hungary. The survey was aimed at foraging birds. A higher number of species and species diversity was observed in the oxbows compared to that of the eupotamon-type areas, and was correlated with the more luxuriant vegetation covering the water surface. The species evenness value of the oxbows was lower than that of the flowing river. The number of species and species diversity in riparian areas covered with trees were higher than those in areas covered only by bushes. There was a negative correlation between evenness and the diversity of species for habitats covered with water, and habitats covered with trees and bushes along the banks. The following highly protected bird species nested in the study areas: black stork (*Ciconia nigra*), lesser spotted eagle (*Aquila pomarina*), saker falcon (*Falco cherrug*), red-footed falcon (*Falco vespertinus*), and corncrake (*Crex crex*). Compared to the total bird fauna of the investigated area, the highest ratio of aquatic bird species was present in the oxbow areas covered with aquatic vegetation. Considering the role of aquatic birds in material and energy cycles, three main species groups were distinguished: the material-transporting group (highest number of specimens); the bioturbating group (lowest number of specimens); and the decomposition-accelerating group (intermediate numbers).

Introduction

The Bodrogzug region is situated in the northern part of the Carpathian Basin, and its ecosystem values are attributed largely to its rivers.

It is generally unacceptable to compare aquatic invertebrates in river systems to those of standing water systems and assume the prevalence of the physical and chemical conditions of the latter. The most sensitive and ancient groups of aquatic insects tend to inhabit mainly areas in the upper part of the watershed. On the lower reaches, low diversity insects, and more developed holometabolic insects and maritime invertebrates (mainly

molluscs) can be found. Big rivers can carry a great amount of fine detritus.

In recent decades experts have emphasized that the river continuum concept (Vanotte et al., 1980) can only be applied to big rivers (including the Rivers Duna and Tisza) with restrictions. The regular, seasonal flooding of rivers should also be taken into account when it comes to the classification of rivers (Ward, 1989). Accordingly, the following units of rivers can be distinguished:

1. The river-bed in the *eupotamon* zone is rocky, graveled, and sometimes sandy. The water has the lowest salt content in the watershed, and

there are no rooted plants. This unit includes the main riverbed site and the area of lateral tributaries with constant flow.

2. Rocky, sandy and sometimes silty river-beds, as well as higher salt content, rich phyto- and zooplankton are typical of the *parapotamon* zone. This is the area where the river's dead arms connect to the main branch.
3. In *plesiopotamon* zones, the riverbed is sandy, covered with clay, and has abundant macrophyte stands. This is the unit of short-cut lateral arms.
4. Finally, *paleopotamon* zones are characterized by the dominance of standing water habitats, temperature-related layering might be substantial, and the salt content of water is often high. Topographically, this is the zone of bends and oxbows that have been disconnected from the main riverbed for a long while. After river flow was regulated in Hungary (about the middle to 19th century) wetlands almost disappeared from the Carpathian Basin. Currently we know of historically rich fish stocks and waterbird populations only from ethnographic literature (Borsos, 2000).

It is an interesting paradox that no study has been conducted yet on the effects of waterbirds on the ecosystems of shallow ponds and rivers. Today, the number of aquatic birds may be so high on the remaining small wetlands that they have a significant impact on material cycling (Báldi, 2001; Gere & Andrikovics 1992a, 1992b, 1994). The aim of this study was to investigate the role of aquatic birds in a complex of eu-, para- and plesiopotamon systems as that is found in Bodrogzug.

Study area

The Bodroglók is a small, young, floodplain enclosed by the Zemplén Mountains, Nyírség and Rétköz. It is surrounded by the Bodrog River in the West, the Tisza River in the East and South, and the inner range of the Carpathian Mountains in the North. The part of this area located on Hungarian territory reaches to the Slovakian border between Záhony and Felsőberecki. The Tisza and Bodrog Rivers bending at the foot of the mountains showcase the natural beauty of the

area. In the northeast, the area extends beyond the border into neighboring Slovakia (approximately 1/3 of the area). The waters running through this region have changed their course frequently and thus have created a system of ponds and oxbows. Based on the differences of surface forms, Bodrogzug can be divided into three sub regions: the central part of Bodrogzug, the alluvial plain along the Tisza, and Bodrog. Before the regulation of rivers, a large part of the area was covered with temporary standing water. Although these are seemingly standing waters, subsoil water and artificial channels connect them with the main branch of the river, thereby rheophile species may be present in the oxbows. In general, the original and more or less untouched vegetation of Bodrogzug can today be found only on the extensive river flood plains. The northernmost part is the alluvial plain along the Bodrog, running along the river in a 4 km-wide band. During its flooding, the Bodrog carries mainly clay and mud to this region. This large amount of fine-grained sediment is formed principally as a result of the denudation of wet soils and pyrogenic rocks. Deserted oxbows, riverbed sections and pleistocene sand islands ensure the diversity of the area. The monotonous landscape of the central part of Bodrogzug is broken by several of these sand islands of larger and smaller sizes. Most sand-hills are covered with sand containing loess. Among the sand-hills one can find several deserted riverbeds and oxbows, the majority of which are filled with water even today. The alluvial plain along the Tisza is covered by the youngest formations (alluvial sand, mud and sometimes clay) that constitute a completely plain formation. Its material is far coarser than that of the alluvial plain along the Bodrog. Summer is moderately warm; the average temperature in July is 20 °C and the number of sunny days is 65–70. In the fall, in the middle of October, the temperature drops below 10 °C. The dominant wind comes from the northeast, and the annual rainfall is 550–600 mm. Most of the rain falls in June (65–75 mm), whilst the area gets the lowest amount of rain in January (18–35 mm). Drought in early spring is typical of the distribution of rain in Bodrogzug. The authors have studied the Bodrogzug area, where eight study sites have been marked out as follows (Fig. 1):

- Berek dead arm, 52 ha (48° 18'N; 21° 35'E),
- Vajdácska dead arm, 51 ha (48° 16'N; 21° 38'E),
- Hosszú-rét dead arm, 9 ha (48° 17'N; 21° 37'E),
- Török oxbow, 48 ha (48° 14'N; 21° 30'E),
- Bodrog River at Sárospatak (48° 19'N; 21° 34'E),
- Görbe, oxbow 5 ha (48° 11'N; 21° 32'E),
- Remete dead arm, 5 ha (48° 11'N; 21° 35'E),
- Tisza River, at Balsa (48° 10'N; 21° 32'E)

Methods

Water chemistry was studied in eight characteristic stands of the area. The following data were recorded: air and water temperature, conductivity, pH, dissolved O₂ and redox potential. In addition, the composition of animal and plant species and aerial coverage of dominant plant stands were also surveyed.

Microcrustaceans were collected five times between May and September, 2002. The Tisza and Bodrog rivers and six dead arms were sampled. Zooplankton samples were taken by plankton net of 85 micron mesh size. The samples were collected near the shoreline in May and June, where it was usually covered by dense macrophyte stands. The samples in the other months were taken from

a boat in open water areas using a Sebestyén collecting device (Sebestyén, 1960).

Invertebrate macrofauna and aquatic insects were collected monthly from September 1, 2001 until late 2002. Qualitative and quantitative invertebrate samples were taken from typical aquatic plant stands. The quadrat method of sampling (50×50 cm bottom surface) was used for the collection of macrofauna, and, in parallel with this, comparative zooplankton and benthos samplings were performed. In order to identify seasonal dynamics, sampling took place in the relatively better-known Bodrogzug area between the spring of 2002 and October 2002. Both qualitative and quantitative sampling of reed-grass and emergent plant stands were conducted. Plants were picked from a half or a quarter square meter area, and animals were washed off.

The investigations covered the spatial and temporal patterns of the aquatic invertebrate macrofauna, a group constituting the food of aquatic birds. Macrofauna of 5–10 mm size, living in the benthic region of eutotamion and in pleiototamion (metafiton) were investigated. For the qualitative sampling, a hand net of 0.8 mm-mesh size was used and in some cases quantitative samples were also taken from the flora of oxbows. Qualitative sampling was carried out applying the “kick and sweep” method in the main rivers (the

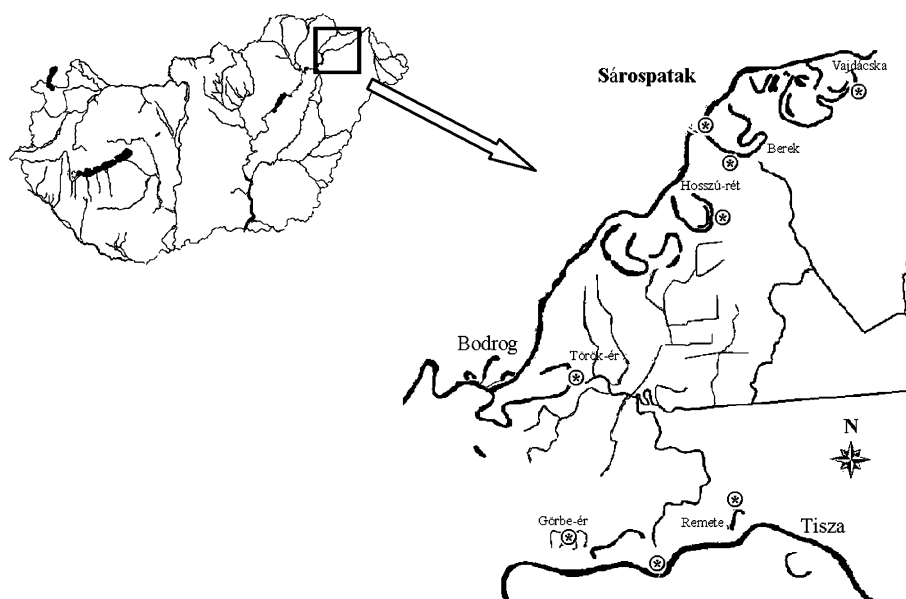


Figure 1. Sketch map of the Bodrogzug with the sample sites (*: sample sites).

Tisza and Bodrog). Fish were investigated in the spring, using a fish net (10 m long \times 1 cm mesh size).

Bird song monitoring was used for mapping the habitat of reed songbirds and corncrakes. During the nesting period (May–June) the presence of foraging birds was recorded along a 1000–1500 m long and 100 m wide area along the water, half of which was in the water and half on the shore. Surveys took place 10 times a year, during the breeding season at the following times: 7.00 a.m.–10.00 a.m., 10.00 a.m.–1.00 p.m., 1.00 p.m.–4.00 p.m. and 4.00 p.m.–7.00 p.m. In the same localities, water chemistry, botanical, macrofaunal and fish studies were carried out. Density was given per hectare, and – following the practice of the evaluation of other investigations – diversity was assessed based on the Shannon Weaver formula (Podani, 1993).

Results and discussion

Hydrochemistry

The Tisza and the Bodrog are well-aerated waters with relatively low conductivity, and, consistent with large water bodies, are characterized by significant thermal stability (Table 1).

The redox potential varies between 173.6 and 186.0 mV in the rivers. The slightly higher salt content and greenish color in the summer are conspicuous in the case of the Bodrog, which reflects the rather eutrophic nature of the bottom section of the river. Among the oxbows of the Bodrog, the Török oxbow represents the most diverse hydrochemistry, with considerable heterogeneity among various plant stands.

Salinity is relatively high and an oxygen deficiency is rather frequent in the heavily silted waters of the Hosszúrét and Vajdáciska. Among the oxbows of the Tisza (Remete, Görbe oxbows) the water of the Görbe oxbow has undergone eutrophication. Its salinity is high, silting is occurring, the dissolved oxygen changes rapidly, and the oxygen level was very low. The Remete oxbow had dried out, and the dissolved oxygen and redox potential were very low – hundred order with extremely reductive ecological characters (Table 1).

Hydrobotany

The typical water plant communities of Bodrogzug belong to the groups of floating reedgrass, reeds, and sedges. Species assemblages found silt, marsh fields, bush willows, fenwood, and ash–elm forests. The willow–poplar gallery forest is the dominant forest community of the alluvial plain, whereas ash–elm gallery forests are restricted to one or two localities only and sporadically bush willow stands can be found along the rivers. The cross-sectional figures show differences between the vegetation of the river banks and that of the oxbows (Fig. 2).

- Bodrog main channel (Figs. 1, 2a): Alluvial softwood forests follow the river. The dominant soft tree is the black poplar, *Populus nigra* (L.). The area covered by foliage in the upper layer is about 80–85%. The shrub layer is not dense with 2–5 m average height and only 2% covering. The herbaceous layer is dense covering 80–100%. The bottom is periodically flooded and is comprised of quickly accumulating fine sediments.

Table 1. Water chemistry along the rivers and at the oxbows (2002 summer, 10 days average and SD)

	River Bodrog		Vajdáciska		Hosszúrét		Berek oxbow		Török oxbow		River Tisza		Remete dead arm	Görbe oxbow		
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	Mean	SD	
Water temperature (°C)	24.6	1.2	23.8	1.0	27.4	3.4	27.9	0.9	23.8	1.1	25.2	1.0	34.9	28.5	1.0	
Conductivity ($\mu\text{S cm}^{-1}$)	340.6	18.2	240.5	2.8	208.5	1.6	206.6	16.2	320.3	72.1	149.4	68.0	566	339.5	10.5	
Total salt (mg/l)	188.2	25.1	121.7	2.7	117.2	0.4	132.0	1.9	124.2	6.2	126.7	72.2	180.3	327.7	19.7	
pH		7.14	0.19	7.56	0.25	6.92	0.11	6.94	0.15	8.78	0.36	7.54	0.23	6.2	8.84	0.42
Dissolved O ₂ (mg/l)		9.0	0.3	6.6	0.6	6.9	0.5	7.5	0.6	9.3	0.2	7.8	0.4	0.2	8.0	0.8
Redox potential (mV)		186	14.9	140	38.3	116	18.2	-98	44.1	133.6	15.1	173.6	23.5	-149.7	112.4	51.1

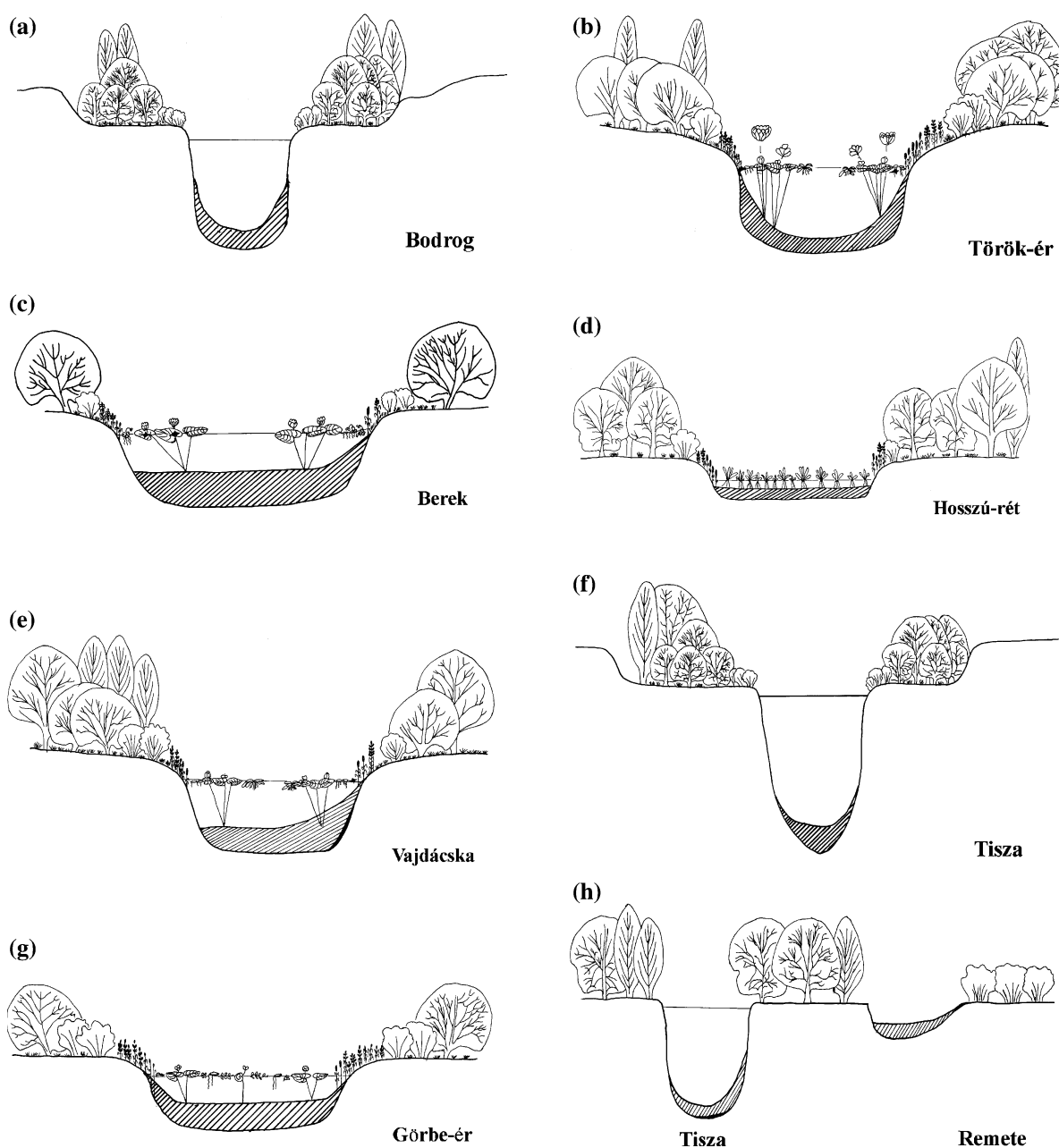


Figure 2. Cross-sectional view of the study areas and their dominant vegetation (a. The River Bodrog; b. Török oxbow; c. Berek; d. Hosszú-rét dead arm; e. Vajdácska dead arm; f. The River Tisza; g. Görbe oxbow; h. Tisza and Remete dead arm).

- Török dead arm (Figs. 1 and 2b): The floating vegetation: duckweeds [Lemnaceae], and hornworts [Anthocerotea], and *Salvia natans* (L.) can be seen. From here towards the edge of the water different pondweeds (*Trapa natans*, L.) and rooted aquatic plants with floating leaves

(water-lily, *Nymphaea alba* (L.), and yellow water-lily, *Nuphar lutea* (L.)) can be found. The water-lily stands can be found with 70% coverage and the yellow water-lily stands can be seen with 60% coverage. On the bank bur reed, *Sparganium erectum* (L.), managress,

- Glyceria* spp. and great bulrush, *Scirpus tabernaemontani* (Gmelin), stands occur with 10–15% coverage.
- Berek dead arm (Figs. 1 and 2c): In the floating vegetation, *Lemna trisulca* (L.), *Salvinia natans* (L.), and *Hydrocharis morsus-ranae* (L.) occur with 15–20% coverage. Because of its high trophic level, hornwort, *Ceratophyllum demersum* (L.), stands occur with 40–50% coverage. Along the bank, cattail, *Thypha angustifolia* (L.), stands can be seen with low (5–10%) coverage. In the mud vegetation there are *Sparganium erectum*, *Alisma plantago aquatica* (L.), and *Carex* spp. with 15–25% coverage. On the bank, poplar softwood forest can be seen.
 - Hosszúrét dead arm (Figs. 1 and 2d): In the water there is a water-soldier (*Stratiotes aloides* (L.)) stands with 80% coverage. Around the water, willow–poplar softwood alluvial forest can be seen. In the mud vegetation, *Nanocyperion* spp., *Juncus atratus* (Krock), *J. effusus* (L.), *J. conglomeratus* (L.), *Schoenoplectus lacustris* (L.), and *Carex* spp. can be found.
 - Vajdáska oxbow (Figs. 1 and 2e): In the floating aquatic vegetation, *Hydrocharis morsus-ranae*, *Lemna minor* (L.), and *L. trisulca* (L.), scarcely occur with coverage of 10–15%. In the rooted plant vegetation, *Trapa natans*, *Nymphaea alba*, *N. lutea*, *Myriophyllum verticillatum* (L.), *Polygonum amphibium* (L.), *Potamogeton lucens* (L.), *P. natans* (L.), and *P. pectinatus* (L.), can be found. There is a large water-chestnut, *Trapa natans*, stand with 40% coverage 3–4 m away from the bank. It is interesting that the common reed, *Phragmites communis* (L.), cannot be found in the Phragmiton association. The other characteristic species of the reed vegetation (e. g. *Typha angustifolia* (L.), *T. latifolia* (L.), *Glyceria maxima* (Hartm.), *Sparganium erectum*, *S. simplex* (Hudson), and *Schoenoplectus lacustris* form emerging vegetation stands with coverage of 25–30%.
 - Tisza main channel, at Balsa (Figs. 1 and 2f): Only the willow alluvial forest, (*Salicetum triandrae* –Noirf.) is characteristic inside the dike along the river.
 - Görbe oxbow (Figs. 1 and 2g): Around the water the dense aquatic reed can be seen. Before the reed stands in the water dense water-chestnut occurs. In the middle of the bed, scarce water-lily and yellow water-lily vegetation can be found. At the bank, willow forest occurs with *Salix alba* (L.), *Salix triandra* (L.), *Salix fragilis* (L.), and *Salix purpurea* (L.). In the herbaceous layer, there are *Carex vulpina* (L.), *C. elata* (All.), and *C. riparia* (Curtis) in larger stands. At the outer side of the reed, the liana *Calystegia sepium* (L.) is found.
 - Remete oxbow (Figs. 1 and 2h): There is willow–poplar softwood floodplain forest, which is dominated by autochthonous tree species (*Salicetum albae-fragilis*) with 20–25% coverage in the deepest part of the river bed. The most valuable forest type of the territory is the elm–ash hardwood floodplain forest [Fraxino-pannonicae– Ulmetum], with 35–40% coverage. There is no pondweed vegetation in the water. Water-lily association (*Nyphaetum albae-lutea*) with 35–40% coverage can be found in the deeper part of the backwater. The water-lily associations and common reed stands occur with 20–25% coverage near to the main channel. Mud plant association (Nanocyperion) and willow stands (*Salicetum albae-fragilis*) can be found with high (40–45%) coverage near the water. There are *Acer campestre* (L.), together with *Quercus robur* (L.), *Ulmus laevis* (Pall.), *Populus nigra* and *Fraxinus angustifolia* (Vahl.) ssp. *pannonica* (Soó et Simon) with coverage of 60–70% in the upper tree stratum. The average height of the trees here is 25 m with 30–40 cm trunk diameters. The upper tree stratum is usually followed by the lower tree stratum with 5–10 m high trees (with trunk diameters of 5–20 cm). The *Quercus* and *Ulmus* spp. occur but the *Fraxinus angustifolia* ssp. *pannonica* very seldom can be found in this stratum. There are *Quercus robur*, *Crataegus oxyacantha* (L.), *Ulmus laevis*, *Cornus sanguinea* (L.), and *Rosa gallica* (L.) in the shrub layer. The coverage of the shrub layer is 20% and its height is 1–5 m. The herbaceous layer is 20–40 cm tall and dense with 30% covering. *Vitis riparia* is characteristic along the edges and openings as a liana.

Zooplankton studies

A total of 32 (Cladocera) and 14 (Copepoda) species were found in the two rivers and in the dead arms. All species occurred in the dead arms,

while only five, three Cladocera and two Copepoda, were found in the river samples.

The number of species found in the samples varied between 1 and 14 in the river samples 1–3, whereas 3–14 species occurred in the dead arms. The species number was the greatest in May and June and it decreased towards September in each locality.

Generally, the number of Cladocera species was greater than that of the copepods in the samples from dead arms. Only a few planktonic species were detected (e.g. *Diaphanosoma brachyurum* (Liévin), *Bosmina longirostris* (O. F. Müller), *Mesocyclops leuckarti* (Claus)), while most of them are characteristic in the littoral, among macrophytes (e.g. *Sida crystallina* (O. F. Müller), *Simoccephalus* (Schoedler) and *Alona* (Baird) species, *Macrocyclus* (Claus), *Eucyclops* (Claus), *Cryptocyclops* (G.O. Sars) species). Some mud living species were also recorded (e.g. *Ilyocryptus sordidus* (Liévin), *Ectocyclops phaleratus* (Koch)).

Only a few individuals (one to eight per liter) were found in the river samples. The lowest density in both rivers was observed in September. Another important feature of the river samples was that small sized species and their juvenile stages were mostly dominant. In most dead arm samples, the copepods also dominated numerically; however, usually the juvenile stages occurred in high numbers. From July onwards, the density was slightly decreasing in these samples also. It was between 3–12 individuals (one to eight per liter) in September.

Macroinvertebrates

Both rivers were inhabited by typical invertebrate macrofauna specific to potamon-type systems. Mayfly (Palingenia) colonies were typical on the hard loess bottom. Mayfly can also be observed in the Bodrog (Andrikovics & Turcsányi, 2001). The prevalence of Ponti-Caspian fauna elements could be observed in the Tisza. Some oxbows subject to investigation dried out in 2002, which had a completely destructive effect on aquatic invertebrates and a large part of the nekton as well. Oxbows along the River Bodrog were hypertrophic. In addition to the water lily stands, only water soldiers were found in several oxbows. The metaphytic assemblages of the latter were made up of

only few species. According to our findings, macrofauna density is greater in oxbows than in eutopotamon-type systems. Large numbers of Diptera larvae were observed in oxbows along the Bodrog (1152 juvenile specimens of Chironomida were collected in the Berki oxbow), as well as Culicidae larvae, which were found in especially high numbers in the Tisza. Ephemeroptera larvae found in oxbows along the Tisza are also noteworthy (*Caenis* spp., and *Cloeon dipterum* (L.)), in the Görbe oxbow), and the ratio of certain Odonata larvae was also relatively high in the oxbows along the Bodrog (for instance, Coenagrionidae juveniles, *Erythromma najas* (Hansemann)). In the oxbows and in the rivers five main invertebrate taxa were found. Among the aquatic insects, the non-biting midges colonized in the largest individual number (Fig. 3). In the oxbows, a lot of non-native clam, the *Anodonta woodiana* (Lea), were collected (Table 2).

Fish

Altogether 18 species of fish were caught, of which 4 were adventives. The number of adventive species made up 69% of the 877 specimens caught. The deterioration of the ecological condition of the oxbows can be observed based on the decreasing number of native fish species and the increasing number of adventives. This has resulted in a decreasing number of food specialists and the increasing number of generalists.

Birds

The physical and chemical characteristics of water influence primarily the invertebrate macrofauna and the zooplankton that might be considered as a main food source for the nekton and the aquatic birds.

We used the guilds, in a broader sense, as subjective units (Körner, 1993) and we employed the groupings primarily upon the feeding habits of birds (Daily & Ehrlich, 1994; Weller, 1995; Roshier et al., 2002; Paszkowski and Tonn, in this volume). Since we were not able to find data for groupings based on energy transfer, we developed further the feeding-based bird guilds towards functional energy transfer guilds (material transporters, decomposition accelerators, bioturbating

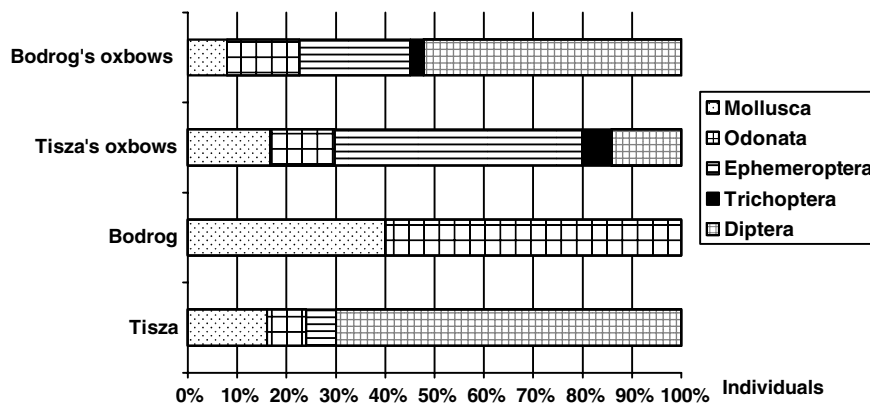


Figure 3. Distribution of the more significant invertebrate macrofauna in the rivers and oxbows alongside the rivers (between 2001 and 2002).

birds, Table 3). In the oxbows the number of bird species and their diversity were higher than in the flowing river. This is correlated with the richer vegetation covering the water surface. At the same time, the species evenness of oxbows was lower when compared to that of eutotamon-type systems (Tables 4 and 5). The number, density and evenness of bird species of riparian areas covered with trees were higher than those of open water and fields covered with reed and water soldiers. Species diversity and evenness reflected was negatively correlated with area covered with water and fields covered with trees. Black storks, an increasingly threatened species, nested in the study areas and corncrakes nested in tall grass communities. The number of raptors (*Aquila pomarina*; *Falco vespertinus*; *Falco cherrug*) was extremely high. The large species number and high diversity of birds of prey are indirect signs of the abundance of food. The highest ratio of aquatic birds compared to the total number of species was found in the oxbows. As to the role of aquatic species in the material and energy cycles, all three material-cycle guilds of these species were observed in all water habitats. The dominant members of transporter and metabolism accelerator guilds have been investigated by gut content analysis (Andrikovics and Gere, unpublished data; Ponyi, 1994). The feeding activity of the dominant waders as the members of bioturbating accelerators in sodic pools have been also studied by regurgitation gut analysis in our territory (Boros et al., 2006). With the help of these data and our field observations, the

aquatic birds were grouped into three main trophic guild groups (Oláh 2003).

The material-transporting guild represented the highest number, whereas the bioturbating group accounted for the lowest number of specimens, and the group involved in the acceleration of decomposition was intermediate in number. The specimen number and diversity of the material-transporting guild group in the oxbows exceeded those measured in flowing waters. Decomposition accelerators in eutotamon-type systems were represented by one single species: mallards, *Anas platyrhynchos* (L.). Only three bioturbating species were present in the oxbows: redshank, *Tringa totanus* (L.), black-tailed godwit, *Limosa limosa* (L.), and little ringed plover, *Charadrius dubius* (Scopoli). The diversity of songbird species foraging in water habitats was also higher than that of the living river sections. The difference, however, was lower than in the case of aquatic species other than songbirds. The diversity of aquatic species (not songbirds) and within that the diversity of the material-transporting group showed a positive correlation with evenness, contrary to the negative correlation observed in the relation of total species diversity and total species evenness (Tables 3, 4 and 5).

Conclusions

The eutotamon was well aerated, with high dissolved oxygen, pH. Its redox potential varied between 186–173 mV. Conductivity was generally

Table 2. Density and diversity of the invertebrate macrofauna in the Bodrogzug (between 2001 and 2002)

Sample site Taxa	Török oxbow <i>Density</i>	Görbe oxbow <i>Density</i>	Berek <i>Density</i>
Annelida	16	–	–
Mollusca			
<i>Anodonta woodiana</i>	*	*	*
<i>Bithynia tentaculata</i>	–	64	–
<i>Gyraulus albus</i>	16	224	–
<i>Lithoglyphus naticoides</i>	–	–	192
<i>Lymnaea peregra</i>	32	–	64
<i>Lymnaea peregra ovata</i>	–	48	64
<i>Lymnaea stagnalis</i>	16	–	–
<i>Physa fontinalis</i>	–	16	128
<i>Valvata piscinalis</i>	–	80	–
Odonata			
<i>Coenagrionidae juv.</i>	112	96	384
<i>Coenagrion puella</i>	256	–	320
<i>Erythromma najas</i>	32	–	192
<i>Sympetrum sp. juv.</i>	32	–	–
Ephemeroptera			
<i>Caenis sp. juv.</i>	1664	60	288
<i>Cloeon dipterum</i>	240	60	–
<i>Cloeon sp. juv.</i>	16	–	–
Coleoptera adults	16	32	–
Trichoptera			
<i>Holocentropus picicornis</i>	96	–	–
<i>Oecetris ochracea</i>	–	–	64
<i>Polycentropus sp. juv.</i>	–	32	–
Lepidoptera	–	–	–
<i>Nymphaea sp. juv.</i>	–	–	64
Diptera			
<i>Tipulidae juv.</i>	48	–	–
<i>Tabanidae juv.</i>	48	–	–
<i>Culicidae juv.</i>	16	–	–
<i>Chironomidae juv.</i>	336	112	1152
\sum Spp:	17	11	11
$\sum D$	171	164	182
H'	2.21	2.32	2.79
H_{\max}	4.09	3.46	3.46
J	0.540	0.672	0.808

\sum Spp: number of species, $\sum D$: density (ind/m²), H': diversity, H_{\max} : Max. Diversity, J: Evenness, *: Presence of *Anodonta woodiana* empty shells in great quantities.

low (340.6 and 149.4 $\mu\text{S cm}^{-1}$). Both River Tisza and the River Bodrog were rather stable systems during the hot summer days. The plesiopotamon Görbe and Remete dead arms have undergone heavy eutrophication. The amount of dissolved

oxygen was low or deficient in winter or at night. Conductivity was relatively high (300–550 $\mu\text{S cm}^{-1}$). Redox potential sometimes was about –100 mV. The Remete dried out in 2001 and 2002. The Török oxbow was characterized by

Table 3. Population parameters of aquatic bird guilds seeking food in the Bodrogzug area

	The River Tisza		Remete dead arm		Görbe oxbow		The River Bodrog		Török oxbow		Hosszú-rét dead arm	
Aquatic bird												
Spp.	4		6		21		3		8		19	
<i>D</i> (ind./ha)	1.6		3.6		9.0		1.3		5.5		15.6	
<i>H'</i>	1.008		1.366		2.737		0.79		1.705		2.009	
<i>J'</i>	0.727		0.762		0.899		0.720		0.820		0.682	
<i>Material transporters</i> ^a												
Spp.	3		4		10		2		6		16	
<i>D</i> (ind /ha)	1.2		2.9		5.5		0.9		3.1		9.6	
<i>H'</i>	0.781		0.994		1.877		0.437		1.322		2.417	
<i>J'</i>	0.718		0.717		0.815		0.631		0.738		0.872	
<i>Decomposition accelerators</i> ^b												
Spp.	1		2		10		1		2		11	
<i>D</i> (ind /ha)	0.4		0.7		3.1		0.4		2.4		4.4	
<i>H'</i>	0		0.507		1.917		0		0.557		1.912	
<i>J'</i>	0		0.732		0.832		0		0.804		0.797	
<i>Bioturbing birds</i> ^c												
Spp.	–		–		1		–		–		2	
<i>D</i> (ind /ha)	–		–		0.4		–		–		1.6	
<i>H'</i>	–		–		0		–		–		0.416	
<i>J'</i>	–		–		–		–		–		0.6	
Songbirds*												
Spp.	r	s	r	s	r	s	r	s	r	s	r	s
Spp.	0	5	4	3	9	9	0	3	4	5	11	8
<i>D</i> (ind /ha)	1.8		5.2		13.5		1.8		8.2		21.7	
<i>H'</i>	1.195		1.338		2.011		0.718		1.780		2.009	
<i>J'</i>	0.743		0.688		0.659		0.655		0.810		0.682	

Spp: number of species, *D*: density, *H'* diversity, *J'*: Evenness value; *: **r**: reed birds and other **s**: songbirds taking food on aquatic areas.

^aMaterial transporters: *Phalacrocorax carbo*, *Nycticorax nycticorax*, *Ixobrychus minutus*, *Egretta alba*, *Egretta garzetta*, *Ardea cinerea*, *Ardea purpurea*, *Ardeola ralloides*, *Anser anser*, *Ciconia ciconia*, *Larus ridibundus*, *Sterna hirundo*, *Chlidonias nigra*, *Chlidonias leucopterus*.

^bDecomposition Accelerators: *Botaurus stellaris*, *Anas platyrhynchos*, *Anas querquedula*, *Rallus aquaticus*, *Fulica atra*, *Gallinula chloropus*, *Porzana parzana*, *Vanellus vanellus*, *Podiceps ruficollis*, *Podiceps cristatus*.

^cBioturbing birds: *Gallinago gallinago*, *Tringa totanus*, *Limosa limosa*.

Table 4. Characteristics of the bird population in the Bodrogzug area

	The River Tisza		Remete dead arm		Görbe oxbow		The River Bodrog		Török oxbow		Hosszúrét dead arm	
	a	b	a	b	a	b	a	b	a	b	a	b
Spp.	10	33	14	30	40	10	8	38	19	30	49	25
<i>D</i> (ind/ha)	3.6	27.6	9.1	22.8	24.2	11	3.3	32.4	14.4	27.5	38.2	20
<i>H'</i>	2.053	2.576	2.158	2.686	2.545	1.992	1.905	2.540	2.267	2.702	2.506	1.644
<i>J'</i>	0.891	0.737	0.742	0.789	0.690	0.865	0.917	0.698	0.770	0.655	0.644	0.891

a: open water, reed, and area covered with water soldier's; b: riverside areas covered with bushes, trees; Spp.: number of species; *D*: density; *H'*: Diversity; *J'*: Evenness. Correlation between the *H'* and *J'*: referring to "a": $r = -0.80$, referring to "b": $r = -0.86$.

Table 5. Functional guild groups of aquatic birds in the Bodrogzug

	The River Tisza (%)	Remete dead arm (%)	Görbe oxbow (%)	The River Bodrog (%)	Török oxbow (%)	Hosszú-rét dead arm (%)
Spp.	40	43	53	38	42	59
Mt	64	72	51	79	83	57
Da	36	28	45	21	17	36
<i>B</i>	0	0	4	0	0	7

Spp: % of total number of species, Mt: % of material-transporters, Da: % of decomposition accelerators, *B*: % of the bioturbating group.

chemical heterogeneity determined by different aquatic plant stands. Heavy siltation was typical of the Hosszúrét, Vajdáciska and Berek, and redox potential was approximately 120 to -98 mV. These habitats (near the bottom) were not suitable for aerobic aquatic life. Altogether 32 Cladocera and 14 Copepoda were recorded. All species occurred in the dead arms. Only a few true planktonic species were recorded. Most species were characteristic of the littoral zone. The species number was greatest in the spring. The lowest density was observed in both rivers in September. Another important feature of the river samples was that mostly small-sized species and their juvenile stages were dominant. The species composition and size structure may indicate intensive predation by fish. The decrease in September was perhaps caused by the feeding activity of planktivorous fishes. These results for the rivers indicate similar conditions as found by Gulyás et al. (1995).

In contrast to the well-documented, rich fish stocks in eutotamion-type systems (Györe, 1995; Hoitsy, 2002), there were only 18 fish species in the oxbows. The numbers of individuals from non-native species accounted for 69% of the total. The decreasing number of food specialist fish and the increasing number of generalists also indicate a deterioration of water quality in the plesiopotamon.

In spite of the small size of aquatic habitats, the number and density of aquatic birds were very high. The extremely high density and number of species of raptors indicate an abundance of food items at all trophic levels. The relative abundance of European endangered bird species (e.g. black storks, corncrake, lesser spotted eagle) show the global importance of this area (Nagy, 1998). It is

an interesting paradox, that the disappearance of wetlands in the Bodrogzug and the decreasing amount of food (phytobenthos and nekton) were not followed by the decrease of aquatic bird guilds. The autochthonous ancient food types (burrowing mayflies, river inhabiting fishes) were impacted by new invader species. The position of species within aquatic bird guilds can change between ecological range and the holometabolic insects, and landbirds can colonize drier habitats.

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Effects of small-bodied fish on invertebrate prey and foraging patterns of waterbirds in Aspen Parkland wetlands

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Abstract

Competition between large-bodied fish and waterbirds for aquatic invertebrates is well documented in oligotrophic lakes. Recent evidence suggests that small-bodied fish that colonize eutrophic, hypoxia-prone wetlands such as prairie potholes can also reduce aquatic invertebrates, but the effects of these reductions on breeding waterbirds have so far not been directly documented. We added brook stickleback (*Culaea inconstans*) and fathead minnow (*Pimephales promelas*) to a fishless wetland in Aspen Parkland potholes in central Alberta, Canada. We monitored invertebrate biomasses and the foraging effort of blue-winged teal (*Anas discors*) and red-necked grebe (*Podiceps grisegena*) before and after the addition, relative to reference wetlands with and without fish. Fish reduced the biomass of gastropod prey of blue-winged teal, and teals increased foraging effort when fish were added. When the fish failed to overwinter due to hypoxic conditions, gastropod biomass increased, but teal foraging effort did not return to pre-treatment levels. Amphipods and chironomids increased following fish addition, possibly due to indirect positive effects of fish. Red-necked grebes did not exhibit any changes in foraging effort as a result of the fish addition or the subsequent fish extirpation. Grebes in Aspen Parkland appear to treat fish and invertebrates as equivalent prey. This study suggests that small-bodied fish in eutrophic systems can reduce some important invertebrate prey and change foraging behaviour of blue-winged teal and other waterbirds that rely on those invertebrates. Land-use practices that encourage survival of colonizing fish through drought years in Aspen Parkland wetlands, such as wetland consolidation, should not be encouraged.

Introduction

Competition between large-bodied fish and waterbirds for invertebrate prey is well documented in North American and European oligotrophic lake systems. Perch, *Perca fluviatilis* (L.), yellow perch, *Perca flavescens* (Mitchill), and roach, *Rutilus rutilus* (L.), show substantial diet overlap with common goldeneye, *Bucephala clangula* (L.), American black duck, *Anas rubripes* (Brewster), mallard, *Anas platyrhynchos* (L.), and teal, *Anas crecca* (L.), (Eriksson, 1978; Eadie & Keast, 1982; DesGranges & Rodrigue, 1986; Giles et al., 1990).

However, waterbird-fish competition is poorly understood in shallow eutrophic systems (but see Giles et al., 1990), such as prairie potholes or Aspen Parkland potholes. These systems often experience winter hypoxia that leads to mortality ('winterkill') of intolerant, often large-bodied fish species (Robinson & Tonn, 1989; Tonn et al., 1995).

Fishes reduce invertebrates even in eutrophic, hypoxia-prone systems like prairie potholes that only support small-bodied fishes (Hanson & Riggs, 1995; Zimmer et al., 2000; Zimmer et al., 2001). Waterbirds' use of eutrophic wetlands can also increase when fishes are removed in

biomanipulations (Hanson & Butler, 1994; Andersson & Nilsson, 1999). It may therefore benefit breeding waterbirds that rely on invertebrates if small fishes are removed or excluded from such systems (e.g., Bouffard & Hanson, 1997). But fish removals do not always result in an increase in invertebrate prey for waterbirds, because the methods used can kill invertebrates (e.g., toxaphene; Miskimmin & Schindler, 1994). Predatory invertebrates such as *Chaoborus obscuripes* (van der Wulp) can also occupy the trophic positions of small fishes after removals (Benndorf et al., 2000). Small-bodied fishes also frequently colonize and disappear from eutrophic hypoxia-prone wetlands in wet and dry years, respectively (Peterka, 1989). Thus, simply removing fish to enhance habitat for waterbirds may not be the most appropriate management action for systems like Aspen Parkland or prairie potholes that are strongly influenced by precipitation and evapotranspiration and undergo a 5–20 year wet–dry cycle (Mitsch & Gosselink, 2000). Where small wetlands are anthropogenically consolidated into larger, deeper, more permanent waterbodies, colonizing fish are more likely to survive drought years than they would in the original configuration of small, shallow wetlands – thus reducing the invertebrates available to waterbirds. Therefore, it might be useful to complement the findings of the aforementioned fish removal/extirpation-based studies by studying the effects on invertebrates and waterbirds of colonization of eutrophic, hypoxia-prone wetlands by small-bodied fishes.

The effects of colonization of such wetlands by small-bodied fishes have only been studied in prairie potholes. Cox et al. (1998) found that chironomid densities and mallard duckling growth rates were lower in prairie pothole mesocosms with high fish densities. Zimmer et al. (2001) observed reductions in amphipods and planorbid snails following a natural colonization of prairie potholes by fathead minnow, *Pimephales promelas* (Rafinesque). It is not clear whether these reductions are limited to highly omnivorous fish species such as fathead minnow (Keast, 1985), or can be exerted by species of a more restricted diet, such as brook stickleback, *Culaea inconstans* (Kirtland). The objective of this study, therefore, was to document changes in

invertebrate assemblages and waterbird foraging activities after a simulated colonization by small-bodied fishes of eutrophic pothole wetlands of a previously poorly studied ecoregion: North America's Aspen Parkland.

We added fathead minnows and brook sticklebacks to a fishless Aspen Parkland wetland, monitoring invertebrates and foraging activities of blue-winged teal, *Anas discors* (L.), and red-necked grebe, *Podiceps grisegena* (Boddaert), before and after that addition. These two species are common in Aspen Parkland and use the same wetlands in different ways, the grebe being a diver and the teal being a dabbler. Based on previous studies of bird foraging in the presence/absence of fishes (DesGranges & Rodrigue, 1986; Giles, 1990), we predicted that blue-winged teals would spend a greater proportion of observed time foraging after fish addition than before, due to a reduction in the availability of their invertebrate prey. Red-necked grebes, being opportunistically piscivorous (Stout & Nuechterlein, 1999), would spend the same amount of time foraging before and after fish addition, particularly since they eat larger invertebrates that may not be negatively affected by small-bodied fish. This prediction is particularly likely to hold true if the added fish reduce some of the invertebrate prey available to grebes, effectively replacing invertebrate food sources for grebes (see below). Since fathead minnows reduce the biomass of planorbid snails, amphipods and chironomids (Cox et al., 1998; Zimmer et al., 2001), we predicted that amphipods and chironomids (omnivores) would be reduced following fish addition, as would planorbids and other gastropods (herbivores). Corixids, notonectids and dytiscids are predators, some of which can attack adult fish or at least eat fry (Clifford, 1991) would increase in biomass following the addition of these fishes since their prey base has been added to. Finally, we predicted that if the introduced fishes failed to overwinter due to hypoxic conditions, their effects on invertebrates and birds would be reversed.

Study area

North America's Aspen Parkland, a transitional zone between prairies and boreal forest (Nicholson

& Vitt, 1994), contains many shallow meso- to hypertrophic freshwater potholes ($\sim 30 \mu\text{g/l}$ to $>400 \mu\text{g/l}$ total phosphorus; Nicholson, 1995; C. McParland, unpubl. data) that support many species of waterbird (Savard et al., 1994). Most parkland wetlands are rarely deeper than 1.5 m (Savard et al., 1994; C. McParland, unpubl. data). The fish fauna often consists only of fathead minnow and brook stickleback, which are very tolerant to low oxygen levels (Nelson & Paetz, 1992). We focused on Elk Island National Park (EINP) and Blackfoot Provincial Recreation Area (BPRA), two adjacent reserves that comprise a 292 km^2 remnant of the Aspen Parkland in central Alberta, Canada (Lat 53°N , Long 112°W).

Materials and methods

In June–August 2000, we monitored invertebrates and foraging activity of red-necked grebes and blue-winged teals on one wetland with fishes and two fishless wetlands in the Aspen Parkland. We measured average depth (using a marked rope), total phosphorus and chlorophyll-*a* (Table 1) in each of these wetlands in June 2000, since earlier studies of Aspen Parkland wetlands showed that these factors were important determinants of waterbird assemblage composition (C. McParland, unpubl. data; Savard et al., 1994).

In early June, late June, mid July and early August 2000, we sampled nektonic invertebrates using bottle activity traps placed for 24 h at 25 m intervals along 100 m transects within 2 m of

shore. Each wetland had 2–3 transects (10–15 traps). In deeper lakes, this technique would only be appropriate for sampling the littoral invertebrate community. In shallow parkland systems, however, the entire wetland shows little differentiation in depth, chlorophyll-*a* concentrations or invertebrate communities between the edges and centres of open water areas (C. McParland, pers. obs.). Using activity traps in such shallow wetlands provides a quick and readily employed index of invertebrate abundance. Benthos was sampled using a combination of Ekman grabs and kick-sampling along shore with a D-net.

Since birds do not select invertebrate prey based on taxonomic identity, we chose to sort invertebrates into guilds rather than employing fine taxonomic resolution. Invertebrates smaller than $250 \mu\text{m}$ were excluded from our analyses, since it was unlikely that the birds would consume them (Nudds & Bowlby, 1984; Stout & Nuechterlein, 1999). We sorted invertebrates as follows: omnivores (Chironomidae, Amphipoda), herbivores (Gastropoda), small predators (Glossiphoniidae), medium predators (Corixidae, Notonectidae, Dytiscidae except *Dytiscus alaskanus* (Balfour-Browne)), and large predators (*Dytiscus alaskanus*, Erpobdellidae and Hirudiniidae). Zooplankton was not sampled as some wetlands were too shallow at times to trawl a plankton net. All invertebrates were identified at least to family, counted, and some samples were preserved (frozen) for biomass estimation. Frozen samples were of beetles: up to five *D. alaskanus* and 10 smaller dytiscids per wetland; up to 10

Table 1. Some limnological features of the experimental wetland and references, as sampled each of the 3 years of the experiment. EW, Experimental Wetland; FW, Fish Reference; NW, Fishless Reference

	Year	Avg depth (m)	Chlorophyll- <i>a</i> ($\mu\text{g/l}$)	Total phosphorus ($\mu\text{g/l}$)
EW	2000	1.0 ± 0.07	22.0	104
EW	2001	0.59 ± 0.11	71.6	147.1
EW	2002	0.63 ± 0.09	2.3	95.2
FW	2000	1.22 ± 0.12	18.3	133
FW	2001	0.81 ± 0.23	3.0	100.8
FW	2002	0.87 ± 0.17	2.8	84.1
NW	2000	1.53 ± 0.05	10.2	37
NW	2001	1.06 ± 0.2	2.4	34.0
NW	2002	0.94 ± 0.25	1.6	38.0

glossiphoniid leeches per wetland, up to 10 chironomids and up to 10 amphipods per wetland. We converted counts of invertebrates to catch per unit effort (CPUE, number of individuals per litre of sampling device per hour; time for grab samples was taken as time to process grab contents) to account for the different types of collection methods. We summed the CPUE values obtained from each collection method to get a single CPUE value for each guild. In calculating CPUE as numbers/l/h, the time for grab and net samples was taken as time to process grab or net contents. Time for activity trap samples was taken as the duration the traps were set (24 h). We then used either direct measurement of wet mass or wet mass data from the literature (Wrona, 1982; Benke et al., 1999) to convert numbers of invertebrates to biomass for all guilds.

During the same four periods described above, we collected activity data on teal and grebe from all wetlands. We focused on up to three individuals of each species on each wetland per sampling session. As far as possible, we focused on females since they generally require more invertebrates than males during breeding, and hence are more likely to compete with fish (Krapu & Reinecke, 1992). Each activity budget lasted for 20–25 min and was conducted between 0500 and 1000. Activities for each individual were recorded every 30 s, to allow calculation of the proportion of total observed time spent in each activity. We then calculated the average proportion of observed time spent foraging (dabbling for teals, diving for grebes) by all grebes and teals on each wetland from these data. In the wetland with fishes, we used standard wire mesh traps (6 mm mesh) to collect fathead minnows and brook sticklebacks. Since the study area entered a severe drought period in 2000, we wished to be certain that fish had not disappeared from this wetland early in the study. These traps were set at 25 m intervals along the same 100 m transects used for the invertebrate activity traps. Fishes were counted and returned to their wetlands. Fish sampling was performed once a month in May–August 2000.

In late May 2001, we collected 8000 brook stickleback and fathead minnow (4000 of each species) from a lake in the same watershed as the study wetlands. We added 2000 individuals of

each species to one of the wetlands that had been fishless in 2000. This wetland, about 10 ha in area, was designated Experimental Wetland (EW). The other two wetlands from 2000 were used as references: a fishless reference (NW) and a fish reference (FW). In 2001, we sampled bird activity, fishes and invertebrates in the three wetlands as described for 2000, and repeated the sampling in 2002. We did not find fish in EW in 2002. Thus, we could determine whether any changes in invertebrates and birds' foraging effort that followed fish introduction in 2001 were reversed when fish were eliminated, presumably due to winterkill.

Data analysis

We used Randomized Intervention Analysis (RIA; Carpenter et al., 1989) to assess changes in bird foraging activity and invertebrate biomass in the experimental wetlands after fish addition. RIA assesses whether there is a non-random change in the average difference between an experimental system and a reference system following manipulation of the experimental system. Series of parallel observations of the data of interest are collected on experimental and reference systems before and after manipulation, and the series of intersystem differences (experimental-reference) is used to calculate average intersystem difference, \bar{D} , pre- and post-manipulation. The absolute value of the change in average intersystem difference following the manipulation, $|\bar{D}_{\text{pre}} - \bar{D}_{\text{post}}|$, becomes the test statistic, with a distribution determined by random permutations of the sequence of intersystem differences (Carpenter et al., 1989). Then, $|\bar{D}_{\text{pre}} - \bar{D}_{\text{post}}|$ is calculated for each of these permutations to estimate the exact p -value of the test statistic. We followed the graphical approach of Carpenter et al. (1989), where plots of RIA show changes in the difference between systems, rather than the changes in the raw data of interest (Carpenter et al., 1989). Wallace et al. (1999) show plots of changes in the raw data of interest rather than changes in intersystem difference. This approach does not always clearly depict changes within the experimental system relative to its reference (which RIA directly tests), due to the large within-system variation that is a common feature of single-system studies.

Results

Invertebrate responses to fish addition within the experimental wetland

Within EW, wet biomasses of small predators (glossiphoniids) and herbivores (gastropods) decreased following addition of fish (Table 2a). After the 2002 winterkill, herbivore biomass increased, whilst small predators continued to decrease. Medium-sized predators (hemipterans and dytiscids except *Dytiscus alaskanus*) remained at almost the same biomass after fish addition in 2001, but increased in 2002 (Table 2a). Biomasses of large predators (*D. alaskanus*, large leeches) and omnivores (amphipods/chironomids) increased in 2001 and remained elevated in 2002. Catch per unit effort of all guilds except large predators increased in EW across the period 2000–2002 (Table 2b).

Invertebrate wet biomasses in experimental wetland compared to fish reference

Randomized Intervention Analysis (RIA) assessed changes in intersystem differences in invertebrate wet biomasses between EW and FW pre- and post-manipulation. The absolute values of those changes in intersystem differences, $|\bar{D}_{pre} - \bar{D}_{post}|$, and their associated *p*-values, are shown in Table 3. Wet biomass of all invertebrate guilds was similar between EW and FW in 2000, the year before fish addition, and remained similar between these two ponds following the 2001 manipulation, despite changes in biomass within each pond (Table 2a, Fig. 1a–e). RIA reflected this lack of change, revealing no significant changes in intersystem differences for invertebrate biomasses between EW and FW for the period 2000–2001 (Table 3).

Table 2. (a) Biomass (mg/l/h), (b) CPUE (#/l/h) of invertebrate omnivores, larger herbivores, and predators in Experimental Wetland, Fish Reference, and Fishless Reference before (2000), after (2001) and one year after (2002) the fish addition. Values are averages (\pm SD) based on sampling in early June, late June, mid-July and early August of each year

	Experimental wetland (EW)				Fish reference (FW)				Fishless reference (NW)		
	2000	2001	2002		2000	2001	2002		2000	2001	2002
<i>(a) Biomass (mg/l/h)</i>											
Herbivores	1.4 (1.5)	0.7 (1.0)	1.1 (1.7)	Herbivores	4.4 (4.9)	1.3 (0.5)	7.0 (6.6)	Herbivores	1.1 (1.1)	5.5 (10.7)	14.0 (9.8)
Small predators	1.3 (1.6)	0.6 (1.0)	0.10 (0.03)	Small predators	1.0 (1.1)	0.2 (0.3)	2.8 (3.5)	Small predators	0.0 (0.0)	4.8 (9.7)	5.5 (5.9)
Medium predators	1.2 (1.7)	1.2 (1.2)	5.6 (0.4)	Medium predators	0.2 (0.3)	3.5 (1.7)	14.4 (19.8)	Medium predators	29.8 (57.4)	0.9 (1.3)	2.2 (3.0)
Large predators	1.3 (1.0)	14.1 (16.8)	23.6 (37.7)	Large predators	0.1 (0.2)	15.2 (12.8)	84.2 (54.0)	Large predators	4.3 (5.3)	14.0 (27.2)	6.6 (5.2)
Omnivores	0.1 (0.1)	0.6 (1.1)	0.6 (0.6)	Omnivores	0.8 (0.8)	0.2 (0.1)	4.8 (2.0)	Omnivores	0.2 (0.2)	0.15 (0.3)	1.8 (2.7)
<i>(b) CPUE (#/l/h)</i>											
Herbivores	3.4 (2.8)	14.2 (24.1)	392 (279)	Herbivores	1.8 (1.8)	70.4 (75.4)	4524.7 (1001.7)	Herbivores	1.1 (0.7)	9.3 (16.9)	7896.3 (9053.9)
Small predators	4.8 (4.8)	21.3 (42.5)	69.5 (127)	Small predators	0.2 (0.4)	15.8 (27.3)	174.3 (140.4)	Small predators	0.3 (0.4)	270.6 (522.0)	177.2 (202.1)
Medium predators	9.0 (4.2)	10.6 (18.6)	98.9 (64.5)	Medium predators	5.0 (6.8)	5.9 (4.5)	138.8 (165.9)	Medium predators	19.9 (17.6)	20.8 (33.7)	383.6 (587.2)
Large predators	23.5 (30.0)	5.7 (7.6)	259 (200.8)	Large predators	6.2 (7.3)	55.9 (80.3)	174.0 (193.6)	Large predators	3.9 (5.9)	2.5 (5.0)	17.4 (21.9)
Omnivores	9.1 (13.8)	21.4 (24.1)	561.7 (466)	Omnivores	31.3 (24.5)	173.3 (56.7)	5989.6 (7107.3)	Omnivores	42.7 (47.2)	23.1 (26.8)	2032.6 (1453.1)

Table 3. The absolute values of the changes in average intersystem differences, $|\bar{D}_{pre} - \bar{D}_{post}|$, between Experimental Wetland (EW) and references for RIA on wet biomass (mg/l) of five invertebrate guilds

Comparison	EW/FW			EW/NW		
	2000/2001	2001/2002	2000/2002	2000/2001	2001/2002	2000/2002
Herbivores	2.4 (0.648)	5.3 (0.044)	2.9 (0.462)	0.04 (0.971)	13.5 (0.561)	13.5 (0.619)
Small predators	0.03 (0.790)	3.1 (0.000)	3.0 (0.120)	0.7 (0.384)	1.7 (0.000)	2.4 (0.000)
Medium predators	3.3 (0.100)	6.5 (0.137)	9.7 (0.000)	1.1 (0.000)	3.7 (0.158)	4.8 (0.113)
Large predators	2.3 (0.975)	59.5 (0.147)	61.8 (0.000)	16.7 (0.193)	45.5 (0.150)	28.8 (0.382)
Omnivores	1.0 (0.224)	4.5 (0.000)	3.5 (0.000)	0.1 (0.969)	0.4 (0.680)	0.3 (0.673)

Comparisons with Fish Reference (FW) and Fishless Reference (NW) are shown. *p*-Values are shown in parentheses. A significant result (boldface) indicates a non-random change in the difference between the experimental and reference system.

Between 2001 and 2002, average intersystem differences between EW and FW in wet biomass of herbivores, small predators and omnivores changed significantly, following winterkill events in both wetlands (Table 3, Fig. 1a, b and e). For herbivores and small predators, intersystem differences between EW and FW in 2002 converged upon the original differences in 2000. Medium and large predator biomasses became less similar between EW and FW over the period 2001/2002, and the intersystem differences in biomass of these guilds diverged significantly from 2000 values (Fig. 1c and d). For medium predators, the change in intersystem difference in biomass post-winterkill was driven by a massive increase in the biomass of this guild in FW during 2002 (from 3.5 mg/l in 2001 to 14.4 mg/l; Table 2a, Fig. 1c). Intersystem differences in omnivore biomass (Fig. 1e) in 2002 diverged from both 2000 and 2001.

Invertebrate wet biomasses in experimental wetland compared to fishless reference

Wet biomass of all five guilds was similar between EW and NW in the pre-treatment year, 2000. None of the changes in intersystem difference between EW and NW in wet biomass of herbivores, large predators or omnivores were statistically significant across any pair of years. For small predators, the increase in intersystem difference in wet biomass between EW and NW

was significant for 2001 vs. 2002, when the added fish were lost from EW, and for 2000 vs. 2002 (Fig. 1b). This change was due to an increase in biomass of small predators in NW and a decrease in biomass in EW during 2002, i.e., changes in intersystem differences of small predators for EW vs. NW were driven by events in 2002. Wet biomass of medium predators between EW and NW became more similar in 2001 and diverged again in 2002. These changes were primarily driven by a large increase in biomass of this guild in NW during 2001 and 2002 (Fig. 1c).

Bird responses to fish addition

Within EW, the proportion of observed time spent foraging by blue-winged teals and red-necked grebes increased after addition of fish in 2001, and did not return to pre-treatment levels in 2002. The values in Table 4 are the averages of the four measures of foraging activity calculated in early June, late June, mid July and early August for EW and the references in each year. Foraging activity by both species also increased within each of the two references in 2001.

The intersystem difference in teal foraging effort between EW and FW increased between 2000 and 2001 ($|\bar{D}_{pre} - \bar{D}_{post}| = 28\%$, $p = 0.105$), decreased by nearly 14% between 2001 and 2002 ($p = 0.684$), and decreased by approximately 15% when comparing 2000–2002 ($p = 0.662$). Thus, teal

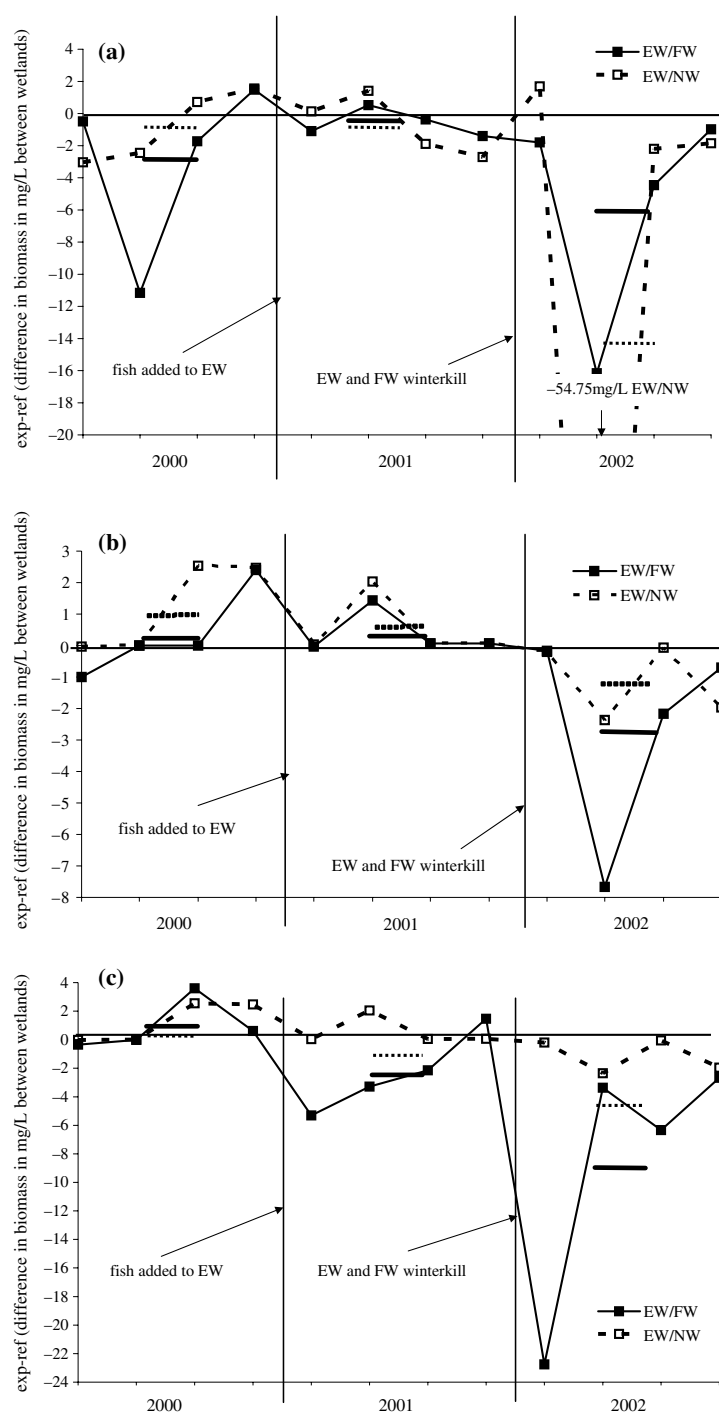


Figure 1. Intersystem differences in invertebrate biomass between experimental wetland (EW) vs. fish (FW) and fishless (NW) references. Solid horizontal bars = mean difference in biomass (mg/l/h) between EW and FW; dashed horizontal bars = mean difference between EW and NW, as calculated from the series of intersystem differences (exp-ref) in each year. RIA tests changes in these average intersystem differences ($|\bar{D}_{pre} - \bar{D}_{post}|$) between years. Invertebrate guilds: (a) herbivores (gastropods), (b) small predators (glossiphoniid leeches), (c) medium predators (hemipterans, beetles except *D. alaskanus*), (d) large predators (large leeches, *D. alaskanus*), and (e) omnivores (amphipods, chironomids).

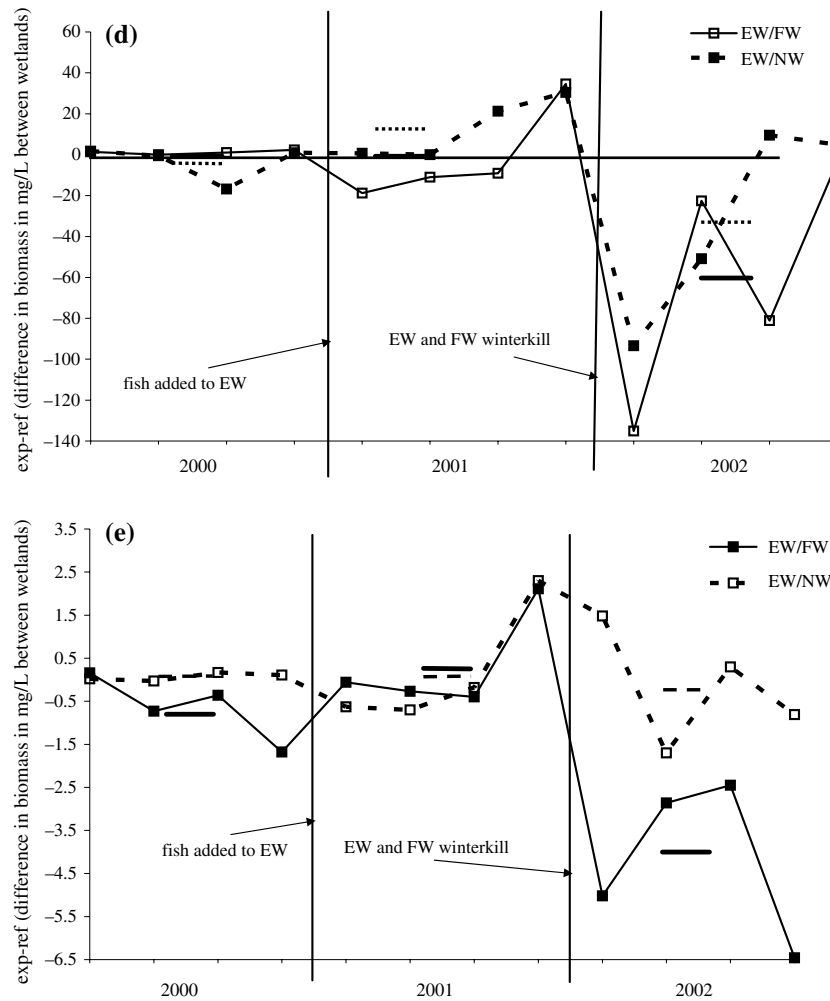


Figure 1. (Continued)

foraging effort tended to be less similar between EW and FW after fish addition than it was before fish addition or after fish extirpation (Fig. 2). The largest change in the intersystem difference in red-necked grebes foraging effort between EW and FW (Fig. 2) occurred when comparing 2000–2002 ($|\bar{D}_{pre} - \bar{D}_{post}| = 25\%$, $p = 0.184$), but the change in intersystem difference in foraging effort for grebes was only 5% between 2000 and 2001, the year when fish were present in EW ($p = 0.678$).

Average intersystem difference in teal foraging effort between EW and fishless reference NW increased significantly between 2000 and 2001 (the change in difference, $|\bar{D}_{pre} - \bar{D}_{post}|$, was 27%; $p = 0.000$), so that blue-winged teals spent a greater

Table 4. Average foraging effort (\pm SD) of red-necked grebes (RNGR) and blue-winged teals (BWTE) within the experimental and reference wetlands EW, FW and NW. Values are average % of time spent foraging during 4 observation sessions over the period early June–early August each year

BWTE	2000	2001	2002
EW	3.8 \pm 4.4	51.4 \pm 8.2	53.3 \pm 29.9
FW	11.3 \pm 14.9	34.5 \pm 29.2	50.1 \pm 28.1
NW	0.3 \pm 0.6	20.7 \pm 17.9	29.8 \pm 14.5
RNGR	2000	2001	2002
EW	14.0 \pm 6.1	21.1 \pm 14.9	28.7 \pm 42.2
FW	6.8 \pm 8.1	19.3 \pm 18.2	46.9 \pm 24.0
NW	15.9 \pm 6.6	30.9 \pm 20.0	36.1 \pm 13.2

proportion of the observed time foraging in EW than in NW after fish were added to EW (Fig. 3). This difference changed very little between 2001 and 2002, when fish in EW were extirpated ($|\bar{D}_{pre} - \bar{D}_{post}| = 7\%$, $p = 0.727$). Comparing 2000–2002, the years in which the fish status of EW and NW were the same, $|\bar{D}_{pre} - \bar{D}_{post}|$ was 20% ($p = 0.290$). For red-necked grebes, foraging effort was always very similar between EW and NW (Fig. 3), the largest value of $|\bar{D}_{pre} - \bar{D}_{post}|$ being less than 8% ($p = 0.950$) for 2000 vs. 2001.

Discussion

The addition of fish to fishless Aspen Parkland wetlands produced mixed results. We predicted that adding fish would result in decreased biomass of omnivores (amphipods, chironomids) and herbivores (gastropods), and that predatory invertebrates would increase, based on Cox et al. (1998) and Zimmer et al. (2001). We predicted that, since blue-winged teals consume large amounts of herbivorous and omnivorous invertebrates (Taylor, 1978; Swanson et al., 1979), the presence of fish would trigger increased foraging effort by blue-winged teals. Thus, if they were to maintain similar levels of food intake, teal foraging effort in EW

would be expected to become more similar to FW and diverge from NW. A similar response has been seen in black ducks foraging in lakes with and without fish in eastern Canada (DesGranges & Rodrigue, 1986). We predicted that red-necked grebes would not change their foraging effort since they eat fathead minnow and brook stickleback, and breed successfully on North American wetlands with or without fish (Stout & Nuechterlein, 1999).

Only herbivores responded as predicted within EW itself, decreasing after fish addition and increasing after fishes were extirpated (Table 2). Comparing EW to FW, only herbivore and small predator biomasses in the two wetlands converged in 2001 and diverged in 2002 as expected, and the changes in intersystem differences in biomass of these two invertebrate guilds between 2000 and 2001 were not statistically significant (RIA). Comparing EW to NW, none of the invertebrate biomass values in EW diverged from those of NW between 2000 and 2001 as predicted, nor did the EW invertebrate biomasses converge on NW biomasses post-winterkill (2001/2002). In fact, biomass of large predators and herbivores in EW diverged from NW biomasses in 2002. The herbivores' response is consistent with Zimmer et al.'s (2001) study of invertebrate communities in prairie pothole wetlands colonized by fathead minnow.

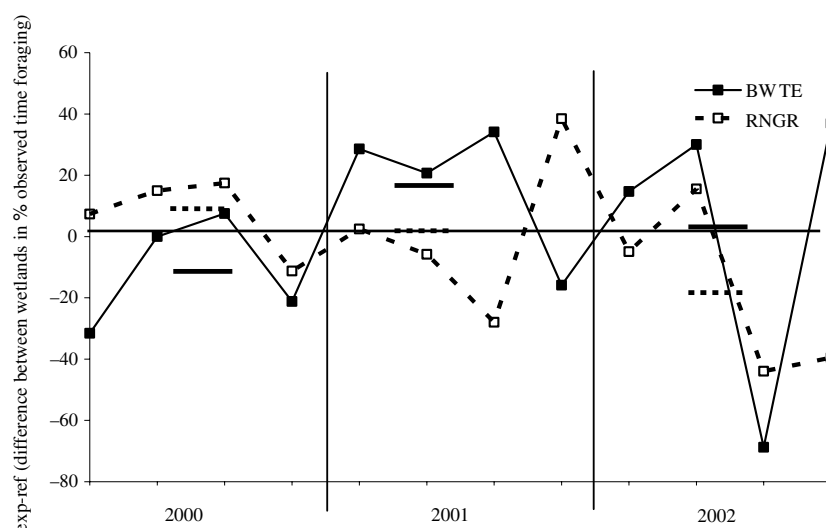


Figure 2. Intersystem differences in bird foraging (estimated as % of observation period spent foraging) between experimental wetland (EW) and fish reference (FW). Solid horizontal bars represent average intersystem difference for blue-winged teals foraging in each year, as calculated from the series of intersystem differences (exp-ref). Dashed horizontal bars represent average intersystem difference for red-necked grebes foraging in each year. Zero difference line shown by horizontal bar across entire graph. RIA tests changes in these average intersystem differences ($|\bar{D}_{pre} - \bar{D}_{post}|$) between years.

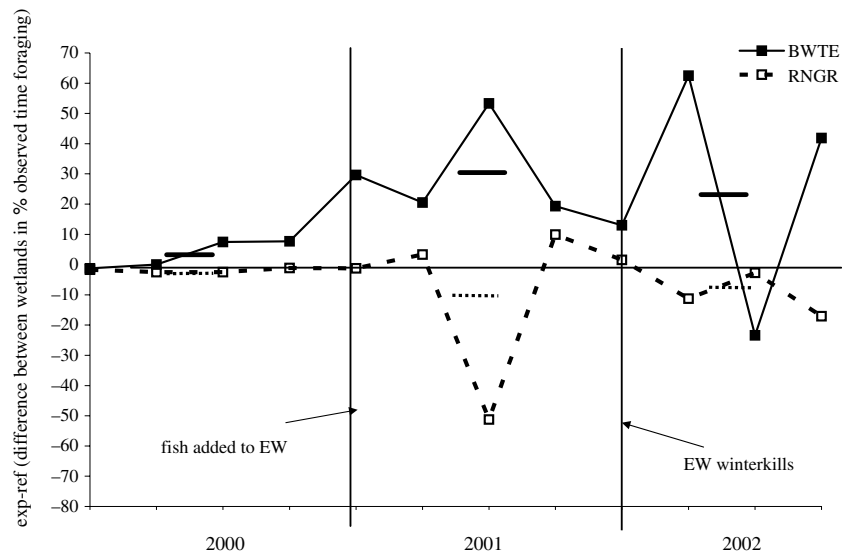


Figure 3. Intersystem differences in bird foraging (estimated as % of observation period spent foraging) between experimental wetland (EW) and fishless reference (NW). Solid horizontal bars represent average intersystem difference for blue-winged teals foraging in each year, as calculated from the series of intersystem differences (exp-ref). Dashed horizontal bars represent average intersystem difference for red-necked grebes foraging in each year. Zero difference line shown by horizontal bar across entire graph. RIA tests changes in these average intersystem differences ($|\bar{D}_{pre} - \bar{D}_{post}|$) between years.

Zimmer et al. (2001) also removed the colonizing fish with rotenone and found a reversal in the decreases in invertebrates that occurred when the fish colonized, similar to the response of herbivores to a natural 'removal' (via winter hypoxia) of fathead minnow and brook stickleback in our study.

The responses of omnivores (amphipods, chironomids) to fish addition within EW and relative to the references are more consistent with the findings of Batzer (1998) and Batzer et al. (2000), in which chironomids were more abundant in the presence of fishes in New York marsh systems. Pumpkinseed sunfish, *Lepomis gibbosus* (L.), and brown bullhead, *Ictalurus nebulosus* (LeSuer), consumed chironomids but they also suppress invertebrates that compete with chironomids for food, e.g., planorbid snails and other gastropods. This effect may outweigh the negative effect of predation on omnivores by colonizing fish and may be beneficial to blue-winged teals and other dabbling ducks since it results in an increase in biomass of important prey.

As for predatory invertebrates, the largest of these attack small-bodied fish (Clifford, 1991), whilst medium-sized predators (hemipterans, smaller dytiscids) may consume amphipods, copepods, cladocerans and chironomids (Scudder, 1976;

Clifford, 1991). Thus, large and medium predators may occupy the same or higher trophic positions as the fish in our study (Benndorf et al., 2000). If small-bodied fishes were a minor part of the diet the largest predatory invertebrates, their addition would not necessarily lead to an increase in large predator biomass. Competition between the added fishes and the medium-sized predators for omnivores and zooplankton may also inhibit any potential increases in biomass of that guild in the presence of fish, despite reports of positive associations between hemipterans and the presence of fathead minnow in prairie potholes (Zimmer et al., 2001).

CPUE data showed that numbers of individuals of all guilds of invertebrates within EW except large predators increased over the period 2000–2002 (Table 2b), so that any decreases in biomass of a particular guild, such as the herbivores in this study, would mean that that guild was composed of more and smaller individuals. Brook sticklebacks are very gape-limited even for small fish (Tompkins & Gee, 1983) and would be expected to consume smaller prey, leaving larger individuals in the invertebrate populations sampled. The main fish effect may therefore have been due to fathead minnows, which can take a wide variety of invertebrates (Price et al., 1991; Cox et al., 1998; Zimmer et al., 2001) and may

thus affect abundance and population characteristics of invertebrates. Pehrsson (1984) found more and larger invertebrates in the absence of larger fish such as perch (i.e., fewer and smaller in their presence). Thus, fish presence results in reduction in the average sizes of individuals in invertebrate populations in systems that support both large- and small-bodied fishes. The main difference with our study is that the biomasses did not change with respect to fish status, resulting in more and smaller individuals rather than fewer and smaller individuals.

RIA on bird foraging effort data (Table 4, Figs. 2 and 3) supported our prediction that blue-winged teal foraging effort in EW became less like NW when fish were added. When fish were extirpated from EW, there was however no reversal in teal foraging patterns. This suggests that the effect of fish colonization on teal foraging effort was longer-term than we expected, even in a dynamic system like Aspen Parkland (Nicholson & Vitt, 1994), where fish colonizations and extirpations are frequent events. There is little evidence for long-term effects of fish removals on birds in eutrophic systems (Bergman et al., 1999), and none at all on the long-term effects of fish colonizations on birds. The response of teals in EW relative to NW is consistent with oligotrophic systems in which Ephemeroptera were reduced in lakes with fish and black duck and common goldeneye ducklings showed greater foraging effort than they did in lakes from which fish were extirpated due to acidification (DesGranges & Rodrigue, 1986; Hunter et al., 1986). In our study, increased teal foraging effort is apparently linked to a decrease in biomass of herbivores (gastropods), an important food of breeding blue-winged teals and other ducks (e.g., Lesser Scaup, *Aythya affinis* (Eyton), and Buffleheads, *Bucephala albeola* (L.)) of the Prairie Pothole Region and Aspen Parkland of North America (Taylor, 1978; Austin et al., 1998). Teal foraging effort did not, however, reflect the rebound in herbivore biomass in 2002. This suggests that teal, being fairly generalist despite their heavy reliance on gastropods (Taylor, 1978), may be responding to changes in the overall invertebrate community that we were unable to detect by examining the guilds we chose. Although not all our RIA results were statistically significant for blue-winged teals, if we consider that laying females can spend 66% of their time feeding when

off the nest (Krapu & Reinecke, 1992), the increase in foraging effort within EW between 2000 and 2001 (Table 4) and in EW relative to FW and NW was substantial.

Red-necked grebes behaved as predicted, with no major change in foraging effort in EW relative to either FW or NW in any year. This supports the suggestion that adult red-necked grebes in Aspen Parkland treat fish and invertebrates as equivalent prey. Although young grebe chicks rely mostly on invertebrates even in lakes with fish (Stout & Nuechterlein, 1999), this may be due to gape limitation. For example, young black-throated diver, *Gavia arctica* (L.), chicks reject items above a certain size (Jackson, 2003), but eat a more 'adult' diet (including fish) when older. Energetically, invertebrate prey of red-necked grebes are similar to fathead minnows: 22.14 J/mg dry weight for *Dytiscus* nymphs and 22.37 J/mg dry weight for large leech, *Nepheleopsis obscura* (Verrill), (Driver, 1981; data converted from calories/g), compared to 25.04 J/mg dry weight for fathead minnow (Gingras, 1997).

Conclusions

Our study suggests that small-bodied fish can reduce invertebrate prey and change the foraging effort of blue-winged teals in meso- to eutrophic systems, much as large-bodied fish reduce invertebrates for waterbirds in oligotrophic systems. At the densities of fish used in this study, the major change in invertebrates seems to lie in relative abundance rather than biomass, with invertebrates generally being smaller and more abundant in the presence of fish than in their absence. In this study, typical fish CPUE values were much lower than in other studies: 0.39 ± 0.13 fish/trap/h compared to nearly 30 fish/trap in the Batzer et al. (2000) study of fish-invertebrate interactions in New York marshes (which, since Batzer et al., 2000 set their traps for 24 h, would be about 1.25 fish/trap/h). Prairie potholes also can have several orders of magnitude more fish in them during wet years than we found in our study (K. Zimmer, pers. comm.). This low density of fish may be behind the limited effects on invertebrate biomasses that we observed.

Although not all our results for blue-winged teals were statistically significant, Carpenter et al.

(1989) emphasize the importance of interpreting the results of RIA in terms of their ecological significance rather than solely relying on their statistical significance – particularly since studies such as ours deal with very low sample sizes and thus lack power (a point somewhat missed by Murtaugh (2002) in his critique of RIA). Jennions & Møller (2003) recently suggested that meta-analyses of studies in behavioural ecology might be a useful way to address these problems. This approach depends on the existence of a sufficient number of studies available for meta-analysis. Using foraging effort to document waterbird–fish competition is a simple, non-invasive method, unlike traditional analyses of oesophageal or gut content. For Aspen Parkland, a poorly studied ecosystem that provides prime breeding habitat for many of North America’s breeding waterbirds (Ducks Unlimited Canada’s Institute for Wetland and Waterfowl Research, unpubl. data; Puchniak, 2002), more studies of foraging patterns are needed to determine if other waterbirds besides blue-winged teals exhibit changes in foraging behaviour in the presence of small-bodied fishes. Our results suggest that land management practices such as consolidation of small wetlands in larger wetlands, which may enhance survival of colonizing fish through drought years and thus reduce invertebrates available to birds, should be discouraged.

Acknowledgements

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A comparison of three methods to investigate the diet of breeding double-crested cormorants (*Phalacrocorax auritus*) in the Beaver Archipelago, northern Lake Michigan

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Key words: alewife, cormorant, crayfish, pellets, regurgitate, stomach contents

Abstract

In order to understand the role of waterbirds in aquatic food webs it is important to first get an accurate depiction of their diet. Three methods of dietary assessment (pellets, regurgitate and stomach contents) are compared here for breeding double-crested cormorants (*Phalacrocorax auritus*) of the Beaver Archipelago, northern Lake Michigan. By numerical frequency (percent number), each method yielded different depictions of the diet. However, in terms of presence and absence (percent frequency) of possible prey types, stomach content data did agree with both pellets and regurgitate data. However, differences were noted between regurgitate and pellets. In terms of biomass measured (percent biomass) in regurgitate and stomachs, data gathered agreed. In essence, pellets underestimate the importance of alewife (*Alosa pseudoharengus*) and overestimate the importance of crayfish (*Orconectes* sp.) in the diet when compared to both regurgitate and stomach analysis. The non-lethal method of regurgitate collection and analysis appears most practical in assessing cormorant diet in this system. In combination with information on avian foraging ecology and prey populations, these data may be used to investigate the relationships among cormorants and their prey, and lead to a better understanding of Great Lake food web dynamics.

Introduction

Research suggests that waterbirds play central roles in marine food webs (Cairns, 1992), and this probably holds true in North American Great Lakes community dynamics. Several studies have been conducted investigating the influence of piscivorous birds on fisheries in Europe (Suter, 1995; Warke & Day, 1995) and the Great Lakes (Maruca, 1997; Neuman et al., 1997; Schiavone, 2001). Interactions between piscivores and their prey can lead to cascading direct and indirect effects at many trophic levels within lake communities (Kerfoot, 1987). To gain insight into the impact avian predators have on fish populations, it

is necessary to integrate quantitative data collected on many aspects of the biology and behavioral ecology of the avian populations in question, as well as an accurate account of the prey populations they may influence. In the Beaver Archipelago, data of this sort are being collected in order to facilitate the reconstruction of fish communities and to determine the extent of the role the double-crested cormorant [*Phalacrocorax auritus* (Lesson)], or DCCO, resurgence may have had in recent fishery declines in the region. Similar approaches have been successfully used in Lake Erie to assess the impact DCCOs have on fish populations (Madenjian & Gabrey, 1995; Hebert

& Morrison, 2003). Central to gaining an understanding of the role of piscivorous birds in aquatic systems is the acquisition of accurate dietary data.

The DCCO is an opportunistic fish predator that often feeds in shallow waters (Lewis, 1929; Birt et al., 1987). Over the past several decades, the population of cormorants inhabiting the interior of North America has increased and expanded (Hatch & Weseloh, 1999). High densities of birds combined with their observed fish-eating behaviors have led some natural resource biologists as well as the general public to implicate cormorants in declines of both commercial (Ludwig et al., 1989; Neuman et al., 1997) and recreational fisheries throughout the Great Lakes region (Neuman et al., 1997; Lantry et al., 1999). Although cormorants may have only small and localized effects on fish populations during migration (Kirsch, 1995), Birt et al. (1987) documented that this species may deplete fish prey around their breeding colonies in a marine environment. Cormorant diets often include species that are of little commercial value but may be important to community trophic dynamics (Craven & Lev, 1987). Therefore, cormorants may have a secondary effect on sport fisheries by competing with desired species for forage fish. Although the effects on forage fish numbers may be limited and only occur in localized areas (Madenjian & Gabrey, 1995), combined with direct sport fish depredation, cormorants may impact sport fish distributions and/or numbers.

Studies assessing DCCO diet have used several methods including the analysis of pellets, regurgitate, and stomach contents of harvested birds. Pellets may easily be collected in large numbers at breeding colonies. In addition, pellet analysis is relatively inexpensive and fairly easy to complete (Carss et al., 1997). However, pellets have been shown less effective at determining cormorant diet in some studies (Duffy & Laurenson, 1983; Johnstone et al., 1990; Blackwell & Sinclair, 1995; Trauttmansdorff & Wassermann, 1995; Zijlstra & van Eerden, 1995; Carss et al., 1997) and these limitations are discussed below.

Analysis of stomach contents and regurgitated food items can be useful tools to investigate cormorant diet because both methods allow for study of relatively fresh material (Carss et al., 1997). Bones and scales of partially digested fish can be used to determine fish age classes, as well as esti-

mate lengths and widths by utilizing fish reference collections (Blackwell et al., 1995; Ross & Johnson, 1995). There are drawbacks to stomach analysis, including the necessity of killing birds, potential small samples that may not be representative of breeding population diet, and presence of highly eroded biomass (Wires et al., 2003). However, stomach content analysis is useful because such dietary data are accompanied by age, sex and other information for each bird (Carss et al., 1997). Regurgitate samples, like pellets, are easily collected from breeding colonies because both nestling and adult birds will regurgitate stomach contents when disturbed (Lewis, 1929). However, these regurgitate samples may not be complete and also show varying levels of digestion (Wanless et al., 1993; Carss et al., 1997). Because good sample sizes are easily collected, regurgitated food items are considered a rigorous method for estimating of nestling diet, but not necessarily adult diet (Wires et al., 2003).

This study analyzes the use of each method (pellets, regurgitate and stomach contents) to assess the diet of DCCOs at breeding colonies in the Beaver Archipelago in northern Lake Michigan. The goal of this study is to ascertain which method(s) yields the most accurate portrayal of DCCO diet in northern Lake Michigan. This work is part of a larger study investigating cormorant foraging ecology and fish population dynamics in the Beaver Archipelago. These data have guided efforts in estimating DCCO diet in the study area.

Study area

The Beaver Archipelago is located in Michigan waters of colder, northern basin of Lake Michigan. The islands and surrounding mainland areas are primarily forested, sparsely populated, and considered the Northern Lacustrine-Influenced Ecoregion (Fuller et al., 1995). Inshore areas consist of sand, cobble, rock and occasional small wetlands (EPA, 2000). Open water areas around the islands include areas that exceed 80 m (262 ft) in depth (EPA, 2000). Fish communities, although changed and degraded compared to pre-settlement conditions, are still developed within this aquatic ecosystem. Nearshore areas provide habitats for warm water fish, including Centrarchids, and

pelagic prey fish, including alewife [*Alosa pseudoharengus* (Wilson)], dominate open water areas (EPA, 2000). Overall, the northern basin of Lake Michigan is characterized as a “typical phosphorus-limited lake ecosystem” (Chen et al., 2002).

The Beaver Archipelago consists of about 10 islands. Three of the larger islands (Gull, Hog and Hat Islands) and one small island (Pismire Island) contained nesting colonies of DCCOs that ranged in size from 277 to 4918 nests in 2000. The Hog Island colonies were located on two peninsulas known as Grape Spit and Timms Spit. For this work the diet of cormorants on Pismire Island (987 nests) and Grape Spit (2431 nests), because of their close proximity to each other (approximately 2 km or 1.25 miles), were examined together.

Methods

Pellets and regurgitates

Pellets and regurgitate samples were collected by hand from the ground adjacent to individual nests in the Pismire Island and Grape Spit colonies on 24 June 2000. In addition, regurgitates were collected from areas away from nests. Adults were observed regurgitating as they left the colony while young chicks remained in their nests. Therefore, adults likely produced samples collected within the colony but not immediately adjacent to nests. Each sample was placed in a plastic Whirl-pak[®] bag (510 g) and returned to the lab within 1–3 h of collection in a cooler. Pellets were subsequently dried at 43 °C in an oven for 24 h and then stored in plastic bags inside a plastic container. Pellets were kept at room temperature. Regurgitate samples were frozen immediately.

Sixty pellets (30 from each colony) were rehydrated using warm water. Rehydration allowed for manual removal of the mucous using rinse water and forceps. Pellet contents were further rinsed with cold water and sorted using a No.16 Standard Sieve (1.19 mm opening) and a No. 35 Standard Sieve (0.5 mm opening). All otoliths and some bones, including jaws, pharyngeal bones, operculae, cleithra and vertebrae, were removed and placed in vials containing 70% ethanol to retard any bacterial or fungal growth. Later, using a reference collection (University of Michigan

Museum and personal collection), the number and prey species (or genera) were recorded for each pellet. Because most bones and otoliths were eroded, no attempts were made to calculate original length and fresh mass of prey. These methods are similar to those outlined in Carss et al. (1997).

A total of 44 regurgitate samples, 31 from Pismire Island and 13 from Grape Spit, were thawed and analyzed. Each prey item was identified to species when possible and recorded. In addition, all identified prey items, including partially digested prey, were individually weighed. Complete fish were measured to the nearest 0.5 mm. Regurgitate samples were then preserved in 70% ethanol.

Stomach contents

Twenty-five birds used for the stomach analysis were collected using shotguns on 23 June and 06, 15, 23 July 2000 (USFWS Permit No. MB022886). These birds were harvested as they returned to their breeding colonies. After birds were collected, they were placed in plastic bags and frozen. Later, the birds were thawed and examined as outlined in Carss et al. (1997). The esophagus, crop and complete stomachs (proventriculus and pylorus) were removed from each bird and total mass of these organs and their contents were recorded. These organs were then dissected and all prey items were removed and identified to species when possible. All prey items, including partially digested prey, were individually weighed. Complete fish were measured to the nearest 0.5 mm. Stomach contents were then preserved in 70% ethanol. In addition, each bird was sexed by examining reproductive organs.

Analysis

Numerical frequencies of prey items in the samples were calculated for each method and were converted to percentages (also referred to as percent numbers). Wires et al. (2001) defines percent number as the number of specimens of a taxon as a percent of all specimens in a sample. Raw data from each method for both alewife and crayfish [*Orconectes* sp. (Hagen)] were analyzed using contingency tables for 3×2 and 2×2 comparisons and χ^2 goodness-of-fit tests (Sokal & Rohlf, 1995).

Data were also examined by comparing the number of samples that contained a particular prey item for each method. These data, converted to percentages, are referred to as percent frequencies by Wires et al. (2001). The values for both alewife and crayfish were compared for each method using 3×2 and 2×2 contingency tables and χ^2 goodness-of-fit tests (Sokal & Rohlf, 1995). All other prey items were found rather infrequently within the samples and were not further analyzed.

Biomasses of prey items for both regurgitate and stomach content data were converted to percents. Percent biomass is defined as the biomass of a taxon as a percent of total biomass (Wires et al., 2001). Because there was a large range of sample masses (2.0 g to 136.7 g for regurgitates and 1.4–413.7 g for stomach contents), these data were converted to proportions; an arcsine transformation was performed to normalize data (Sokal & Rohlf, 1995). Transformed data for alewife and crayfish were then analyzed using a Mann–Whitney test (Minitab 13 for Windows).

Results

Analysis of pellets, regurgitate and stomachs shows that in late June–July 2000 the diet of DCCOs in the Beaver archipelago included alewife (*Alosa pseudoharengus*), crayfish (*Orconectes* sp.), sculpin [*Cottus* sp. (L.)], nine-spine stickleback

[*Pungitius pungitius* (Cuvier)], sucker [*Catostomus* sp. (Luseure)], johnny darter [*Etheostoma nigrum* (Rafinesque)], trout-perch [*Percopsis omiscomaycus* (Walbaum)], and spottail shiner [*Notropis hudsonius* (Clinton)]. Birds harvested for stomach contents included nine males and sixteen females.

Percent number data indicated that pellets produced by Beaver Archipelago cormorants comprise 82.29% crayfish and only 2.54% alewife (Fig. 1). Regurgitate samples indicate, by percent number, crayfish constitute 39.54% of the samples, while alewife comprise 28.60% (Fig. 2). Stomach content data, by percent number, indicated that crayfish comprised 31.96% of the stomach contents and alewife made up 46.80% (Fig. 3).

The 3×2 contingency table (Table 1) and χ^2 goodness-of-fit tests for the raw numerical frequency data indicate that values differ from expected and therefore, each method differed from each other in estimating the diet of DCCOs for both alewife ($\chi^2 = 387.06$, critical value = 5.99 at $\alpha = 0.05$, $df = 2$) and crayfish ($\chi^2 = 119.02$, critical value = 5.99 at $\alpha = 0.05$, $df = 2$). The 2×2 contingency tables (not shown) also indicate that each method differed from the other two in describing the DCCO diet.

Table 2 shows the number of samples that contained a particular prey item for each method of dietary assessment. The 3×2 contingency table (Table 3) indicated that these data differed from expected and therefore, each method differed from

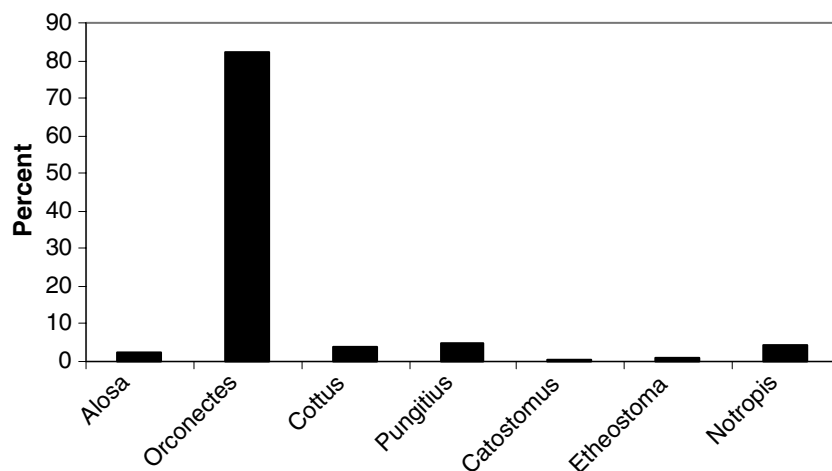


Figure 1. Pellet numerical frequency data showing the diet of Beaver Archipelago cormorants as percentages.

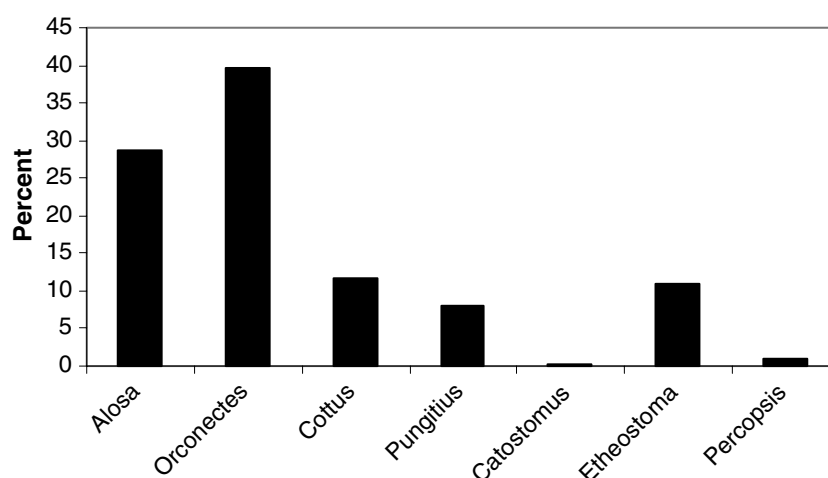


Figure 2. Regurgitate numerical frequency data showing the diet of Beaver Archipelago cormorants as percentages.

each other in estimating the diet of DCCOs for both alewife ($\chi^2 = 9.53$, critical value = 5.99 at $\alpha = 0.05$, $df = 2$) and crayfish ($\chi^2 = 6.46$, critical value = 5.99 at $\alpha = 0.05$, $df = 2$). However, pairwise comparisons using 2×2 contingency tables (not shown) indicate that pellets and stomach content data for both alewife ($\chi^2 = 3.35$, critical value = 3.84 at $\alpha = 0.05$, $df = 1$) and crayfish ($\chi^2 = 1.50$, critical value = 3.84 at $\alpha = 0.05$, $df = 1$) were statistically similar. The type of method had no effect. In addition, regurgitate and stomach content data, when analyzed using 2×2 contingency table (not shown), were

also statistically similar for both alewife ($\chi^2 = 0.61$, critical value = 3.84 at $\alpha = 0.05$, $df = 1$) and crayfish ($\chi^2 = 0.74$, critical value = 3.84 at $\alpha = 0.05$, $df = 1$).

Regurgitate samples indicate that, by percent biomass, crayfish constituted 15.83% of the DCCO diet, while alewife comprised 68.82% of their diet (Fig. 4). Stomach content data, by percent biomass, indicate that crayfish comprised 19.74% of the diet and alewife made up 69.24% of the diet (Fig. 5). The Mann-Whitney test (Fig. 6) indicates that biomass of alewife (confidence intervals = 0.01 to 36.21, $W = 1652.0$,

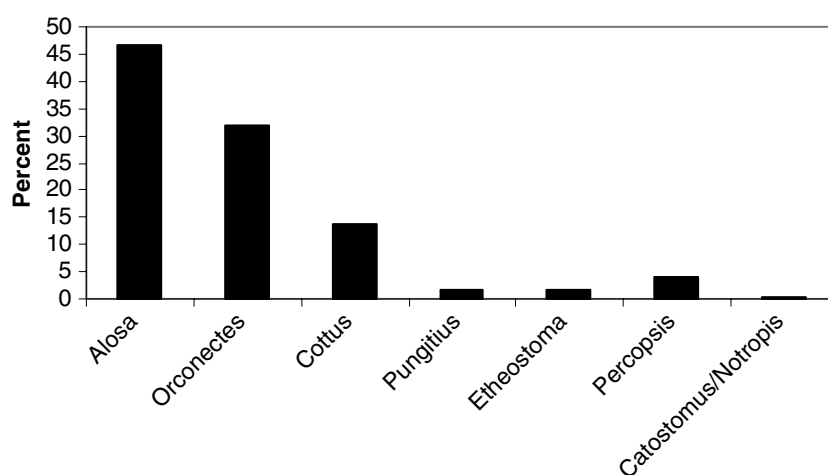


Figure 3. Stomach contents numerical frequency data showing the diet of Beaver Archipelago cormorants as percentages. Percent values for *Catostomus* and *Notropis* are small (both 0.23%) and were combined for clarity.

Table 1. 3×2 contingency table showing the actual (and expected) values of the numerical frequency data for alewife (*Alosa pseudoharengus*) and crayfish (*Orconectes*) in pellets, regurgitates and stomachs

Sampling method	<i>Alosa</i>	<i>Orconectes</i>	Total
Pellets	26 (204)	841 (663)	867
Regurgitate	123 (68.9)	170 (224.1)	293
Stomachs	205 (81.1)	140 (263.9)	345
Totals	354	1151	1505

Chi-square tests indicate that values differ from expected for both alewife ($\chi^2 = 387.06$, critical value = 5.99 at $\alpha = 0.05$, $df = 2$) and crayfish ($\chi^2 = 119.02$, critical value = 5.99 at $\alpha = 0.05$, $df = 2$).

$p = 0.1207$, adjusted for ties) and crayfish (confidence intervals = -36.20 to -0.01 , $W = 1428.0$, $p = 0.1207$, adjusted for ties) estimated by each method are not significantly different from each other at $\alpha = 0.05$. Both dietary assessment methods appear to be equal predictors of the alewife and crayfish biomass in the DCCO diet.

Discussion

Different methods of investigating the diet of DCCOs can lead to different estimations of prey abundance and occurrence in the diet. By numerical frequency, each method yielded different results. However, in terms of presence and absence of possible prey types, each method agreed, with some exceptions. Spottail shiner appeared in both pellets and stomachs, but not regurgitate samples. Likewise, pellets did not show any evidence of trout-perch in the diet of DCCOs, while the other two methods showed they are captured in small numbers. In addition, stomach content data did agree with both pellets and regurgitate data in terms of number of samples in which alewife and

Table 3. 3×2 contingency table showing the actual (and expected) values of the number of samples that contained alewife (*Alosa pseudoharengus*) and crayfish (*Orconectes*) in pellets, regurgitates and stomachs

Sampling Method	<i>Alosa</i>	<i>Orconectes</i>	Totals
Pellets	18 (29.5)	55 (43.5)	867
Regurgitate	29 (19.4)	19 (28.6)	293
Stomachs	14 (12.1)	16 (17.9)	345
Totals	61	90	1505

Chi-square tests for 3×2 comparison indicate that values differ from expected for both alewife ($\chi^2 = 9.53$, critical value = 5.99 at $\alpha = 0.05$, $df = 2$) and crayfish ($\chi^2 = 6.46$, critical value = 5.99 at $\alpha = 0.05$, $df = 2$). Comparisons using 2×2 contingency tables show that pellets and stomach contents data for both alewife ($\chi^2 = 3.35$, critical value = 3.84 at $\alpha = 0.05$, $df = 1$) and crayfish ($\chi^2 = 1.50$, critical value = 3.84 at $\alpha = 0.05$, $df = 1$) were statistically similar. Also, regurgitate and stomach contents data were statistically similar for both alewife ($\chi^2 = 0.61$, critical value = 3.84 at $\alpha = 0.05$, $df = 1$) and crayfish ($\chi^2 = 0.74$, critical value = 3.84 at $\alpha = 0.05$, $df = 1$).

crayfish occur. Regurgitate and pellets, however, differ from one another. Finally, in terms of biomass measured in regurgitate and stomachs, values for alewife and crayfish are not significantly different from each other.

Historically there have been several studies documenting diet of cormorants in the upper Great Lakes, including Lakes Huron, Michigan and Superior (Craven & Lev, 1987; Ludwig et al., 1989; Ludwig & Summer, 1997; Maruca, 1997; Neuman et al., 1997). Ludwig et al. (1989) documented food items ($n=8512$) in regurgitates of adults and chicks at several locations in Lakes Huron, Michigan and Superior from 1986 to 1989. By number, alewife and nine-spine stickleback accounted for 41% of the diet. By biomass, the important species included alewife (57%), yellow perch [*Perca flavescens* (Mitchill)] (13%), rainbow smelt [*Osmerus mordax*

Table 2. Number of analyzed samples where individual prey items were found in pellets, regurgitates and stomachs ($n = 60$ for pellets, $n = 44$ for regurgitates, and $n = 25$ for stomachs)

Sampling method	<i>Alosa</i>	<i>Orconectes</i>	<i>Cottus</i>	<i>Pungitius</i>	<i>Catostomus</i>	<i>Etheostoma</i>	<i>Percopsis</i>	<i>Notropis</i>
Pellets	18 (30)	55 (92)	25 (42)	20 (33)	7 (12)	9 (15)	0	11 (18)
Regurgitate	29 (66)	19 (43)	9 (20)	8 (18)	1 (2)	6 (4)	2 (5)	0
Stomachs	14 (56)	16 (64)	7 (28)	5 (20)	1 (4)	4 (16)	4 (16)	1 (4)

The percent frequencies of each prey item are shown in parenthesis.

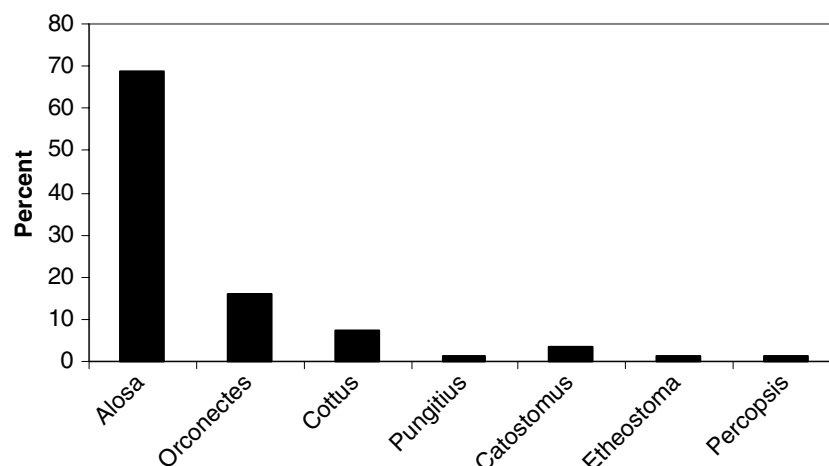


Figure 4. Regurgitate biomass data showing the diet of Beaver Archipelago cormorants as percentages.

(Mitchill)] (8%), and white sucker [*Catostomus commersoni* (Lacepède)] (7%). Diet varied seasonally, and by August, the diet of cormorants in each study area surveyed contained 100% alewife (Ludwig et al., 1989). In addition, Ludwig & Summer (1997) documented food items ($n = 6293$) in the regurgitates of adults and chicks at nesting colonies in the Les Cheneaux Islands of northern Lake Huron in 1995. By weight, alewife constituted 72% of the diet. As part of the same study, Maruca (1997), examined 373 stomachs and documented that adult cormorant diet contained approximately 48% yellow perch during the

perch spawning season. In July, however, adults fed primarily on alewife. With the exception of Lake Superior, throughout the Great Lakes region, open water fish species, including alewife, are important in DCCO diet (Wires et al., 2001). Weseloh & Ewins (1994) have suggested that cormorant reproductive success may be intimately linked to alewife population dynamics. In this study, it appears that in late June and July alewife is an important prey item in Beaver Archipelago DCCOs when analyzing both regurgitate and stomach samples. However, pellet analysis does not support this finding.

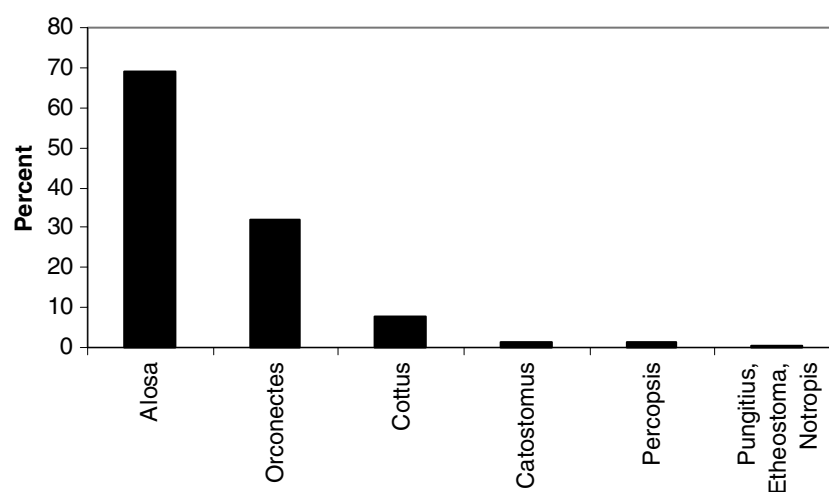


Figure 5. Stomach contents biomass data showing the diet of Beaver Archipelago cormorants as percentages. Percent values for *Pungitius*, *Etheostoma* and *Notropis* are small (1.48, 1.43 and 1.48%, respectively) and were combined for clarity.

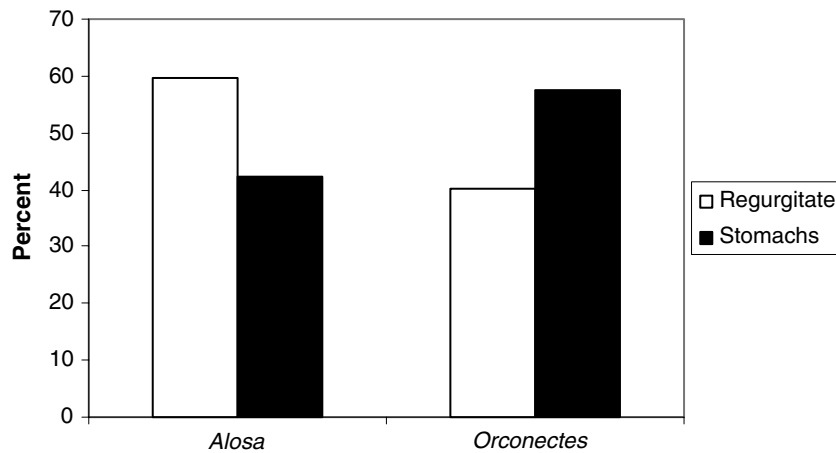


Figure 6. Means of arcsine transformed biomass data. The Mann–Whitney test indicated that biomass of alewife (confidence intervals = 0.01 to 36.21, $W = 1652.0$, $p = 0.1207$, adjusted for ties) and crayfish (confidence intervals = -36.20 to -0.01 , $W = 1428.0$, $p = 0.1207$, adjusted for ties) estimated by each method are not significantly different from each other at $\alpha = 0.05$.

The limitations of pellet analysis have been demonstrated in other works, including studies with captive birds (Johnstone et al., 1990; Trauttmansdorff & Wassermann, 1995; Zijlstra & van Eerden, 1995) and in the field (Duffy & Laurenson, 1983; Blackwell & Sinclair, 1995). However, several studies (Ross & Johnson, 1995, 1999; Warke & Day, 1995; Johnson et al., 1999, 2001a, b, 2003) have relied on pellets as indicators of the diet. In the Beaver Archipelago, evidence of some prey types was not apparent in pellets. This has been documented in other systems, as well (Brown & Ewins, 1996).

Pellets have been shown less effective at determining cormorant diet in some studies because of species-related differential recovery of prey types (Johnstone et al., 1990). In essence, small prey and soft-bodied species may be under represented (Brugger, 1993). Also, otoliths and bones may be eroded in pellets (da Silva & Neilson, 1985; Jobling & Breiby, 1986), thus the estimation of prey length and fresh mass are often in error (Carss et al., 1997). Prey found in pellets may also represent secondary consumption by cormorants (Blackwell & Sinclair, 1995). The assumption that pellets reflect the remains of prey taken during the previous 24-h period has been shown to be invalid in some species. Thus, pellets are less useful in estimating daily food intake and energy requirements (Russel et al., 1995). Additionally, DCCO nestlings digest bones, possibly due to minerals

needed for rapid growth (Dunn, 1975), and do not produce pellets until about seven weeks of age (Trauttmansdorff & Wassermann, 1995; Zijlstra & van Eerden, 1995). Therefore, pellet analysis does not reflect nestling diet. However, pellets have proved more useful in describing cormorant diets than feces (Johnson & Ross, 1996).

In northern Lake Michigan (Ludwig et al., 1989) and in similar systems such as northern Lake Huron (Ludwig & Summer, 1997; Maruca, 1997), alewife have been shown to be important prey. Because alewife remains are only detected at low levels in the samples, pellet analysis does not appear to accurately depict the importance of these fish in the diet of Beaver Archipelago cormorants. This could indicate different digestion of prey types. However, in eastern Lake Ontario, Johnson et al. (1999, 2001a, b, 2003) have used pellets to detect the presence and the importance of alewife in the diet of DCCOs. Yet, Derby & Lovvorn (1997), when comparing pellets and stomach contents, found that each sampling technique did lead to different estimates of fish and crayfish in the diet of DCCOs in an area with known changes in prey availability.

Regurgitate and stomach contents analyzed in this study more accurately depict the importance of alewife in the diet of DCCOs in the Beaver Archipelago, especially in comparison to the work by Ludwig et al. (1989). However, both methods have weaknesses and limitations, including the

probability of under- and over-estimating daily food intake (Carss et al., 1997). Therefore, caution should be used when using either method to estimate daily food intake, because some digestion has inevitably occurred prior to sample collection (Wanless et al., 1993). However, with addition of other information (e.g., feeding observations, foraging patch location), use of both regurgitate and stomach content data can be applied to bioenergetics models, and contribute to the understanding of relationships among waterbirds and their prey.

Other concerns include the accuracy of both regurgitates and stomach samples in describing the diet of both adults and chicks. However, Lewis (1929) noted by observation at breeding colonies that both male and female birds feed nestlings and adults appear to feed older chicks the same prey types consumed by adults. Therefore, regurgitate samples may provide a more complete assessment of cormorant diet during the breeding season. In addition, collection of regurgitates when nestlings are young may allow examination of seasonal and age-related diet differences, especially because young birds do not produce pellets. Such data are valuable in assessing important prey in the diet, the relative abundance of these prey, how these prey populations may be influenced by cormorants, and if these predator-prey relationships may vary as the breeding season progresses.

Choice of dietary assessment method used when investigating the diet of DCCOs may lead to different inferences in prey abundance and importance. According to Derby & Lovvorn (1997), daily changes in bird foraging behavior and time of data collection may account for some of these discrepancies. Such discrepancies may be reflected in this study, for birds were harvested for stomach contents over a month long time period, while both pellets and regurgitates were collected in one day. However, regurgitate and stomach content data do suggest that DCCOs in the Beaver Archipelago feed on alewife during the breeding season. During 2000 and 2001, a total of 1128 regurgitate samples (10,600 individual prey items) were collected. Each year, samples were collected on three dates during the breeding season in an attempt to determine seasonal changes in the diet. When regurgitated food items are compared by mass, alewife comprised 72.00% of the samples (57,073 g of 79,230 g) (unpublished data). Of the

150 stomachs (3363 individual prey items) collected during the breeding seasons of 2000 and 2001, alewife mass comprised 72.83% of the samples (18,603 g of 25,550 g) (Seefelt & Gillingham, unpublished data). This supports the findings of previous studies in the Upper Great Lakes (Ludwig et al., 1989; Ludwig & Summer, 1997; Maruca, 1997), where alewife become increasingly more important in the diet of DCCOs as the breeding season progresses.

Under the current Lake Management Plan, Lake Michigan is to be managed by an ecosystem approach (EPA, 2000). Seabirds, such as DCCOs, that occupy high trophic levels are an integral part of aquatic food webs because they are very mobile and can integrate ecosystem processes over wide spatial and temporal scales (Hebert & Sprules, 2002). Avian piscivores may be valuable environmental indicators in lake systems (Hebert & Sprules, 2002) and, therefore, accurately estimating seabird diet may prove imperative in monitoring ecosystem health and processes.

Conclusions

Regardless of limitations, pellets can be useful in qualitatively documenting what prey types occur in the diet of DCCOs and other waterbird species. Both regurgitate and stomach analyses appear to be more useful in both qualitative descriptions and quantitative analyses of prey importance in the diet of breeding Beaver Archipelago DCCOs. Because it is a non-lethal method, regurgitate collection and analysis is the most practical way to assess cormorant diets in this system. Regurgitates can be collected in good numbers, can be analyzed quickly, and provide information on prey type, length and mass. Information on size and age class of fish taken by birds, as well as total biomass, is important in determining the influence cormorants may have on a fishery (Wires et al., 2001). In a lake ecosystem, predation on fish can have complex effects on other trophic levels and help determine community structure (Vanni, 1987). The ability to estimate cormorant diet more accurately will strengthen attempts to understand the importance of these birds as predators in this study area. Diet studies alone cannot answer complex questions as to the relationships among DCCOs

and their prey. However, it is an important step, in combination with more detail information on avian foraging ecology and prey population dynamics, in investigating community level interactions.

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Pattern of natural ^{15}N abundance in lakeside forest ecosystem affected by cormorant-derived nitrogen

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Abstract

Waterbirds are one of the most important groups of organisms inhabiting the land–water interface, especially with regard to mediating the transport of materials from the aquatic to the terrestrial environment. The great cormorant (*Phalacrocorax carbo*) is a colonial piscivorous bird that transports nutrients from fresh water to forest. We measured cormorant-derived nitrogen at two nesting colonies on the Isaki Peninsula and Chikubu Island at Lake Biwa, Japan, and analyzed the long-term effects of cormorant colonization on the forest nitrogen cycle, and the mechanisms of nitrogen retention. Three sites were examined in each colony: a currently occupied area, a previously occupied but now abandoned area, and a control area never colonized by cormorants. High nitrogen stable isotope ratios of cormorant excreta, the forest floor, mineral soil, and living plants showed cormorant-derived nitrogen in both occupied and abandoned areas. The relationship between $\delta^{15}\text{N}$ and N content showed that the high $\delta^{15}\text{N}$ of the excreta and N turnover in the soil were important at the occupied sites, whereas high $\delta^{15}\text{N}$ of litter was important at the abandoned sites. Physiological changes of various organisms are also important for the N decomposition process. In conclusion, cormorant-derived nitrogen remains in the forest ecosystem as a result of two cormorant activities: heavy deposition of excreta and collection of nitrogen-rich nest material. Colony stage (occupied, abandoned, or never inhabited) and historical change of N decomposition process of an area can be identified from the relationship between $\delta^{15}\text{N}$ and N content.

Introduction

Waterbirds are among the most important organisms bridging the land–water interface, especially as concerns nutrient flow from aquatic to terrestrial habitats. Many researchers have been interested in the effects of seabird nesting on nutrient levels and vegetation on colony islands (Gillham, 1956; Ishizuka, 1966; McColl & Burger, 1976). Also, marine ecologists and biogeochemists, recognizing

the role of seabirds as a vector for the transport of nutrients from marine to terrestrial areas, have studied nutrient flow through food webs and the effects of alteration of this flow on the nutrient status of seabird colonies (Lindeboom, 1984; Mizutani & Wada, 1988). Such studies have usually been conducted at isolated marine islands, especially in arctic or antarctic settings (Erskine et al., 1998).

More recently, attention has been paid to the land–water interface in theoretical food-web studies

(Polis & Winemiller, 1996; Polis et al., 1997). Allochthonous input frequently may not be a negligible component in maintaining a system, especially when the recipient system does not have a higher productivity than the donor system; arid islands and their surrounding seas provide a good example (Polis & Hurd, 1996). From this point of view, transportation from water to land by animals has been recognized as nutrient transfer from a rich system to a poor one.

Although the effects of allochthonous input on nutrient status, vegetation, and food webs have been well studied in nutrient-poor systems such as polar areas and isolated islands, animals sometimes transport nutrients to nutrient-rich systems, with great effects. Egrets, herons, cormorants, shearwaters, and prions roost in colonies in forests and thereby affect the forest vegetation (Maesako, 1997) and the nutrient status of the forest soil (Hobara et al., 2001). Although effects of bird colonization on the forest are apparent, the entire mechanism and the relationship between nutrient dynamics and vegetation change have not been clarified yet.

Long-term effects of bird excreta on nutrient levels and vegetation have been reported (Ishizuka, 1966; Mizutani et al., 1991). In particular, Ishizuka (1966) suggested that effects of seabird colonization on nitrogen and phosphorous levels, and on vegetation lasted 20, or even 60 years after the birds had disappeared. These studies did not demonstrate a mechanism for such long-term effects of colonization. In a forest, long-term effects and a time lag of changes should be more important than in grasslands because trees live longer and store nutrients in their tissues. Moreover, nutrients transported by birds to land return to the water and have effects on aquatic plants (Powell et al., 1991) or food webs (Erskine et al., 1998) around the colony. Thus, it is important to know the nutrient dynamics on land to understand the effects of bird transportation of nutrients on aquatic ecosystems and watersheds.

The great cormorant, *Phalacrocorax carbo* (L.), is a colonial piscivorous bird that is distributed almost all over the world (Johnsgard, 1993). They dive and catch fish in lakes, rivers, and coastal areas and build nests in trees in forests. Because cormorants deposit a lot of excreta beneath their nesting trees, these birds play a role in transporting

nutrients from water to land. Great cormorants have a direct impact on the forest ecosystem and directly damage vegetation through their breeding activities and excreta deposition (Ishida, 1996a; Fujiwara & Takayanagi, 2001). The nutrient status of the forest soil is also greatly changed not only beneath active colonies but also in previously occupied areas abandoned by the birds (Hobara et al., 2001).

We have studied the effects of cormorant-derived nutrients on the nutrient cycle, including the functioning of microorganisms and plants, in a lakeside forest ecosystem, not only during but also after the cessation of allochthonous nutrient supply. We analyzed nitrogen as one of the important nutrients transported by the cormorants. Studies on nitrogen deposition caused by human activities or global environmental change (Aber et al., 1998) have demonstrated the effects of nitrogen on the nutrient status of both forest and aquatic ecosystems. For example, the effects of nitrogen leaching have been well documented (Ohruai & Mitchell, 1997; Carpenter et al., 1998). We expected, therefore, that the deposition of bird-derived nitrogen on land should cause noticeable changes in the nutrient dynamics in the whole watershed, including the lake.

We used nitrogen stable isotopes as natural tracers. Generally, $\delta^{15}\text{N}$ increases with soil depth because of decomposition of organic nitrogen (Nadelhoffer & Fry, 1988) and there is thus usually a negative correlation between $\delta^{15}\text{N}$ and organic nitrogen content with soil depth (Koba et al., 1998; Amundson & Baisden, 2000). Using this phenomenon, change of the nitrogen decomposition process in the forest soil can be examined. Nutrient decomposition and nutrient cycle in a forest is also affected by physiological characteristics of organisms there. We analyzed the role of microfungi in soils in nitrogen decomposition and the ability of plants to use decomposed nitrogen. Nitrogen mineralization rates of microfungi and nitrate reductase activity (NRA) of the dominant plants were examined. NRA shows the ability to use nitrate in a soil, and if NRA is high, plants use more nitrogen in a soil. The aims of this study are to identify the nitrogen pathway of cormorant-derived nitrogen in a forest and analyze the nitrogen decomposition process in forest soil by measuring the nitrogen stable isotope ratio, and to

clarify the function of related organisms on the nitrogen cycle in a forest.

Materials and methods

Study sites

Lake Biwa is located in Shiga Prefecture, in the west-central part of mainland of Japan (Fig. 1). It is the largest lake in Japan (area, 674 km²; volume, 27.5 km³; mean depth, 41 m; maximum depth, 104 m) and is divided into a northern basin and southern basin. The northern basin is mesotrophic and much larger and deeper than the southern basin, which has become eutrophic because of

human activities. Limnological characteristics of each basin are shown in Table 1.

In Lake Biwa and its watershed there were no breeding records of the great cormorant between World War II and 1982 (Kameda et al., 2003). Its population rapidly increased in the 1990s and the maximum number (17,532 cormorants) was recorded in Shiga Prefecture in September, 2003 (Shiga Prefecture, per. comm.). At present, ca. 17,000 cormorants are observed during the breeding season from January to August. There are two large colonies in Shiga Prefecture: Isaki Peninsula (35°12' N, 136°5' E) and Chikubu Island (35°25' N, 136°9' E) (Fig. 1). Almost all the cormorants observed in the prefecture during the breeding season roost in one or the other of these colonies, where the bird density is ca.

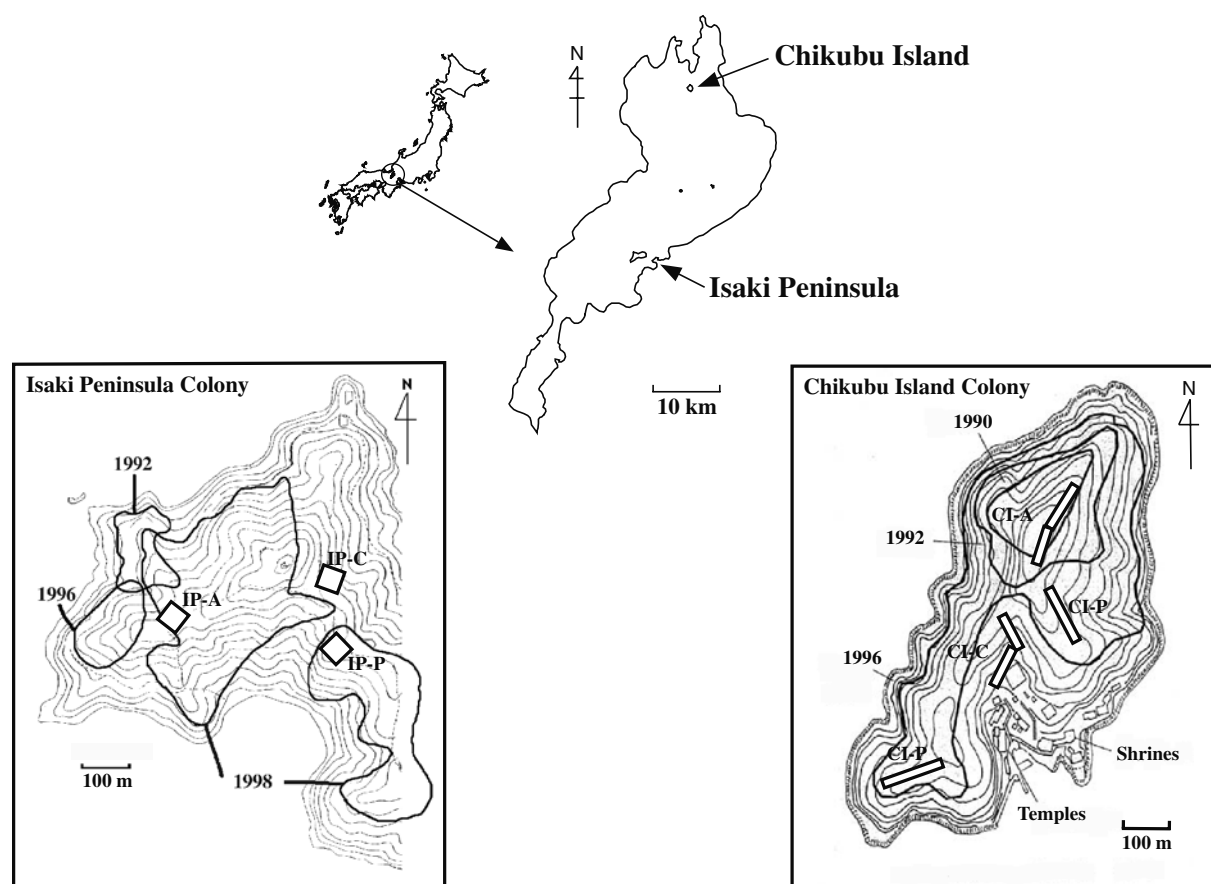


Figure 1. Study sites in the Isaki Peninsula and Chikubu Island cormorant colonies at Lake Biwa, Shiga Prefecture, Japan. The area colonized by nesting cormorants (*Phalacrocorax carbo*) in three specified years is indicated. Site abbreviations: IP, Isaki Peninsula; CI, Chikubu Island. C, control areas not yet colonized by cormorants; P, area colonized at present; A, previously colonized area abandoned by cormorants a few years before. The year and each area pointed by the number is the colonized area at that year.

Table 1. Physical characteristics of Lake Biwa, Japan

	Northern basin	Southern basin
Area (km ²)	616	58
Mean depth (m)	44	3.5
Water temperature (°C)	6.4–27.2	5.5–27.8
Transparency (m)	4.2–8.7	1.5–2.4
pH	7.4–8.9	7.5–8.9
Chlorophyll ($\mu\text{g/l}$)	1.7–7.2	3.4–17.2
T-N (mg/l)	0.18–0.31	0.25–0.45
T-P (mg/l)	0.005–0.009	0.012–0.023
Trophic state	Mesotrophic	Eutrophic

Limnological data are averages for 1982–1986 (ILEC, 1995).

510 cormorants per hectare (Shiga Prefecture, per. comm.).

Our study was mainly conducted at Isaki Peninsula colony. The Isaki Peninsula (57 ha) is situated in the southern part of the northern basin. It is covered with forest, the dominant tree species being Japanese cypress, *Chamaecyparis obtusa* (Sieb. et Zucc.), and chinquapin, *Castanopsis cuspidata* (Schottky var. *sieboldii* Nakai). Cormorant nests were first discovered there in 1988. The area of the colony expanded from 1.3 ha in 1992 to 19.3 ha in 1999 (Fujiwara & Takayanagi, 2001), and the number of the nests from 30 to 40 in 1989 to 5300 in 1999. We chose three study sites on the Isaki Peninsula according to use by cormorants: Site IP-C, the control area, has not been colonized by cormorants, Site IP-P was currently occupied at the time of the study (i.e. at “present”), and Site IP-A was in a previously occupied area last occupied by cormorants in 1998, 2 years previously, but now “abandoned”. One 50 m \times 50 m site was chosen at each site, where dominant tree species was Japanese cypress (Fig. 1). Within each of the three sites, we established three 5 m \times 5 m subplots for soil sampling.

In order to compare the site differences of nitrogen decomposition process, we also chose three sites in the Chikubu Island Colony (Fig. 1). Chikubu Island (14 ha), situated northern part of the northern basin, is one of four islands in the lake. Its dominant trees are the camphor tree, *Machilus thunbergii* (Sieb. et Zucc.), and Japanese cedar, *Cryptomeria japonica* (D. Don). Cormorants colonized Chikubu Island earlier than the

Isaki Peninsula: five cormorant nests were discovered in a nesting colony of egrets and herons in 1982. The number of nests and the area of the colony have been expanding there as well, to 1439 nests and 9.1 ha in 1996 (Shiga Prefecture, 1997). On Chikubu Island, two 3 m \times 10 m subplots were chosen within each of three sites, categories called CI-C, CI-P, and CI-A (control, currently occupied, and abandoned, respectively). Due to topographical limitations, two CI-P sites were chosen, each with one subplot (Fig. 1). CI-C was the only site where the cormorants had never nested on the island, but cormorants were observed briefly resting in this area; thus, while CI-C is considered not to have been affected by the cormorants’ breeding activities, it did receive at least small amounts of their excreta.

Sample collection

We collected samples of fish from Lake Biwa, cormorant liver, cormorant excreta, the forest floor (Oe+Oa layer), mineral soil, fungi, and leaves of living plants for nitrogen stable isotope analysis and quantification of nitrogen content (Table 2). In order to examine the nitrogen stable isotope ratio in the lake, some species of fish from Lake Biwa were analyzed. Fish were obtained from fishermen using an “eri” trap (large-scale labyrinth trap for fisheries in Lake Biwa (Kawanabe, 1999)) on the west coast of the southern basin of Lake Biwa in May, 1999. Ten species of fish were collected, nine of which had been reported as part of the cormorants’ diet in Lake Biwa (Kameda et al., 2002). Muscles of these were used for stable isotope analysis. Livers of cormorants were collected from the birds shot near the Isaki Colony in May and June, 1999, in a prefectural government cull. The stable isotope ratio of bird’s liver reflects the bird’s recent (about one week) diet (Hobson & Clark, 1992), so we used liver analysis to assess the nitrogen flow between the bird’s food and excreta. Cormorant’s excreta was collected in the Isaki Colony for 24 h in June, 1999, using 20 50 cm \times 50 cm cotton cloth traps. In order to examine decomposing process of cormorant-derived nitrogen, materials from the forest floor (organic layer) and mineral soil (0–5 cm depth beneath the organic layer) were collected from each subplot in the Isaki and

Table 2. Sampling dates and sites of samples for nitrogen stable isotope analysis

Sample type	Sampling date	Sampling sites
Fish	May 1999	Southern basin of Lake Biwa
Cormorant (liver)	May and June 1999	Around Isaki Colony
Cormorant excreta	June 1999	Isaki Colony (IP-P & others)
Forest floor (Oe + Oa layer)	June 2000	Isaki Colony (IP-C, IP-P, IP-A)
	June 2000	Chikubu Colony (CI-C, CI-P, CI-A)
Mineral soil	June 2000	Isaki Colony (IP-C, IP-P, IP-A)
	June 2000	Chikubu Colony (CI-C, CI-P, CI-A)
Leaves of living plants	June 2000	Isaki Colony (IP-C, IP-P, IP-A)
	June 2000	Chikubu Colony (CI-C, CI-P, CI-A)

Chikubu Colonies in June, 2000 (Hobara et al., 2005). Plants also play an important role in nutrient cycle in the forest ecosystem. In order to examine the interaction between nitrogen status of the forest soil and the plants, leaves of the following dominant trees and herbs in the shrub layer at each site were also collected in June, 2000: Japanese cypress and Japanese cedar (conifers), chinquapin and camphor tree (evergreen broad-leaved trees), and pigeonberry, *Phytolacca americana* (L.), Japanese knotweed, *Reynoutria japonica* (Houtt var. *japonica*), and bamboo grass, *Sasa palmata* (Nakai) (herbs).

The mechanisms of nitrogen dynamics were also investigated in relation to biotic activities of the Isaki Colony. We collected forest floor and mineral soil in the Isaki Colony in August, 1999, for samples, as above, and for a nitrogen mineralization experiment, described in the next section. In order to analyze nitrogen utilization of the dominant trees to analyze NRA, in 2002, we collected leaves and roots of Japanese cypress in the Isaki Colony. This is the dominant species at all the sites there (Fujiwara & Takayanagi, 2001). The samples were collected from IP-C, IP-P, and IP-A between 10:00 and 14:00 on a sunny day in order to avoid diurnal changes in NRA. Samples were refrigerated until laboratory treatment.

Since our preliminary work had shown that understories respond to cormorants' nesting by a quick increase in $\delta^{15}\text{N}$, we collected leaves of herbs all over the Isaki Peninsula in July, 2002, to estimate how widely the effect of the excreta can be detected by increases in the background abundance of $\delta^{15}\text{N}$. GPS mesh code (the peninsula is

located from 598,900 to 599,900 and from 3,895,600 to 3,894,500 in UTM units) was used to set 46 sampling points at lattice intersections of 100×100 UTM grids. Leaves of understory herbs (basically pigeonberry, but other species if pigeonberry was absent) were collected at each point, the position of which was confirmed by GPS (GPS III, Garmin Ltd.).

Laboratory treatment

For stable isotope analysis, animal samples (fish, cormorant liver, and excreta) were vacuum-dried and powdered before lipid extraction with chloroform-methanol (2:1) (Bligh & Dyer, 1959). Materials from the forest floors and mineral soil were passed through a 2-mm sieve to exclude plant roots and coarse fragments, then air-dried and powdered. Other samples were also dried and powdered for stable isotope analysis. Nitrogen stable isotope ratios of all the samples were analyzed on a mass spectrometer (Finnigan Mat Delta S) coupled with an Elemental Analyzer (Fisons EA1108) in the Center for Ecological Research, Kyoto University, Japan. Isotopic composition is expressed in permil (‰) deviation from atmospheric nitrogen, as defined by the following equation:

$$\delta^{15}\text{N} = \left[\frac{{}^{15}\text{N}}{{}^{14}\text{N}}_{\text{sample}} / \frac{{}^{15}\text{N}}{{}^{14}\text{N}}_{\text{standard}} - 1 \right] \times 1000$$

Total N content of forest floor, mineral soil, and plant leaves was analyzed by the combustion method (Bremner, 1996) with a NC analyzer

(Sumigraph NC-900, Sumigraph Corp., Japan) using the powdered samples (Hobara et al., 2005).

At Site IP-C, one of the dominant species of soil microfungi was *Penicillium restrictum* (Gilman & Abbott). It was also isolated at Site IP-P. On the other hand, the dominant microfungi at IP-P, *Penicillium herquei* (Bainier & Sartory), was isolated only there, not at IP-C (Osono et al., 2002). In order to know the role of these fungi in the mineralization rate of nitrogen at each site, we isolated these two species from the forest floor and mineral soil samples, and analyzed the net nitrogen mineralization rate in various kinds of soil typical of the study area. Five grams of organic soil samples collected from IP-C and IP-P were auto-claved at 120° C for 20 min after soil moisture had been adjusted to 60% of field capacity. Then the soil was inoculated with a species of microfungus or a piece of soil from IP-P and incubated at 30° C for 28 days. The net N mineralization rate for the period was calculated as the difference between total inorganic N ($\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N}$) concentration in the inoculated soil and that in the uninoculated control soil.

NRA analysis of leaves and roots of Japanese cypress was conducted with a modified version of the in vivo test according to Koyama & Tokuchi (2003). Leaf discs of 2.5 mm diameter and small pieces of roots were obtained and 0.1 g (dry weight) of each were rinsed with deionized water. After vacuum infiltration with 5 ml of incubation buffer, the samples were incubated for 1 h at 30° C in the dark. Enzyme activity was stopped by placing sample vials in hot water (80 ° C). Finally, nitrite concentration in the incubation buffer was measured.

Results

Nitrogen stable isotope ratios and nitrogen content in two colonies

Figure 2 shows nitrogen stable isotope ratio of each sample at each colony stage in the Isaki and Chikubu Colonies. Although there was no stable isotope data of nitrogen input in control area in the colonies, we could refer to the data in other forests in the same prefecture (about 27 km apart

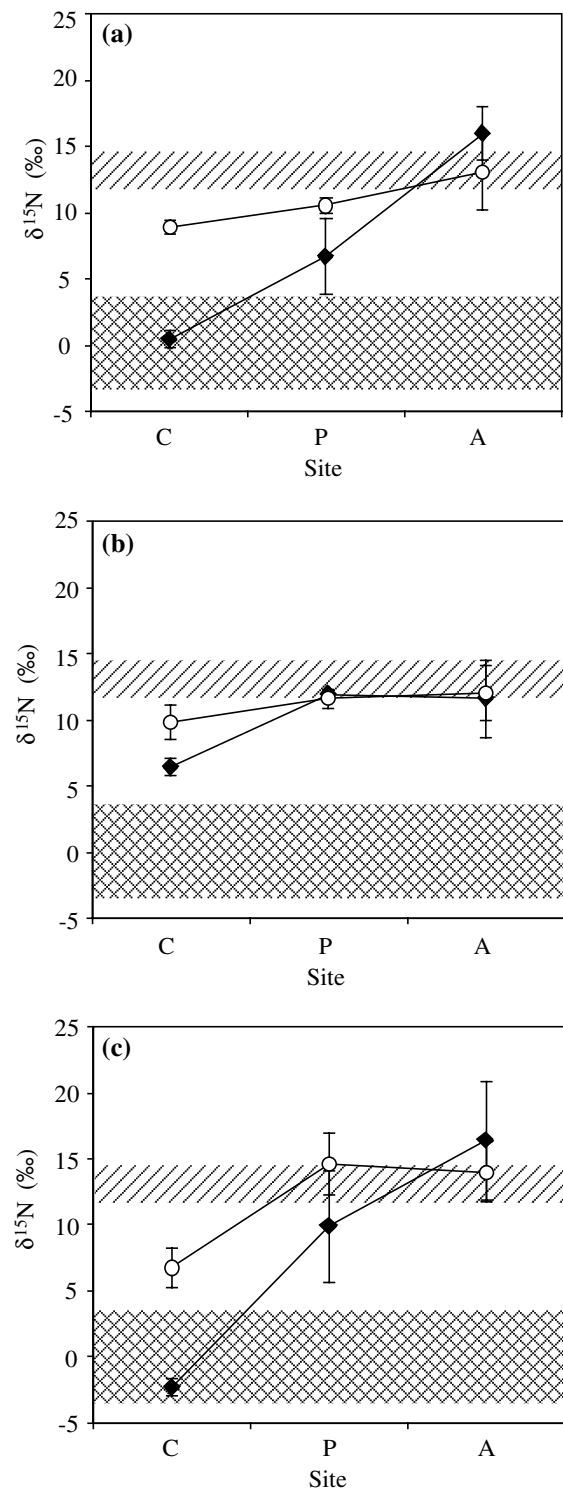


Figure 2. Nitrogen stable isotope ratios of (a) forest floor, (b) mineral soil, and (c) leaves of living plants in control (C), presently colonized (P), and abandoned (A) sites at the Isaki and Chikubu cormorant colonies. Solid diamonds show the Isaki Colony; open circles show the Chikubu Colony in (a), (b), and (c). Cross-hatched areas show the range of the nitrogen stable isotope ratio of precipitation in Shiga Prefecture, and diagonal-hatched areas, the same for cormorant excreta.

from the study sites: Koba et al., 1997). $\delta^{15}\text{N}$ of excreta was significantly higher than that of precipitation in other site in Shiga Prefecture, which was similar to that of atmospheric N_2 (Table 3).

Two-factor factorial analysis of variance (ANOVA) indicates that nitrogen stable isotope ratios of the forest floor and leaves of living plants were affected by the interaction between study site and colony stage (Table 4). Thus, the colonization of the cormorants affected the forest floor and plant leaves in the Isaki and Chikubu colonies differently. $\delta^{15}\text{N}$ of the forest floor increased with colony stage in both colonies while $\delta^{15}\text{N}$ of the plant leaves at Site A was not significantly higher than at Site P. At Site C and P, $\delta^{15}\text{N}$ of the forest floor and the plant leaves were higher in the Chikubu Colony than in the Isaki Colony, but Site A had an opposite trend: $\delta^{15}\text{N}$ of the forest floor and the plant leaves was higher in the Isaki Colony

than the Chikubu Colony. On the other hand, $\delta^{15}\text{N}$ of mineral soil was only affected by colony stage: $\delta^{15}\text{N}$ at Site P and A was significantly higher than at Site C.

Nitrogen content indicated different trends from $\delta^{15}\text{N}$ (Table 3, Fig. 3). N content of the mineral soil was affected by study site, colony stage, and the interaction between study site and colony site, while that of the forest floor was significantly higher in the Chikubu Colony than the Isaki Colony (Table 4). N content of the leaves of living plants was not significantly different among study sites or colony stages.

Relationship between $\delta^{15}\text{N}$ and N content

In order to know nitrogen decomposition process from forest floor to mineral soil in each colony stage, we analyzed the relationship between $\delta^{15}\text{N}$ and N content at each site in Isaki and Chikubu Colonies (Fig. 4). There was significant correlation between $\delta^{15}\text{N}$ and N content in the Isaki Colony and slight tendency of correlation at Site CI-C and CI-A (Table 5). Negative correlation between $\delta^{15}\text{N}$ and N content was found at control and occupied sites and positive correlation was observed at the abandoned site in both Isaki and

Table 3. Nitrogen stable isotope ratios and nitrogen content of forest floor, mineral soil, and leaves of living plants at Site C, P, and A in Isaki and Chikubu colonies

Sample type	$\delta^{15}\text{N}$ (‰) avg. \pm SD (n)			N content (%) avg. \pm SD (n)		
	Site C	Site P	Site A	Site C	Site P	Site A
<i>Nitrogen input from outside forest</i>						
Precipitation*	0.2 \pm 3.4 (5)					
Throughfall*	-1.1 \pm 1.3 (4)					
Fish in Lake Biwa	14.3 \pm 1.0 (49)					
Cormorant liver	17.1 \pm 0.6 (14)					
Cormorant excreta	13.2 \pm 1.3 (12)					
<i>Forest floor (Oe + Oa layer)</i>						
Isaki Colony	0.4 \pm 0.8 (9)	6.7 \pm 2.6 (9)	16.0 \pm 1.9 (9)	1.85 \pm 0.34 (9)	1.79 \pm 0.21 (9)	1.79 \pm 0.19 (8)
Chikubu Colony	8.9 \pm 0.8 (6)	10.6 \pm 0.7 (7)	13.1 \pm 2.8 (6)	2.23 \pm 0.09 (6)	2.00 \pm 0.06 (7)	2.33 \pm 0.45 (6)
<i>Mineral soil</i>						
Isaki Colony	6.4 \pm 1.5 (8)	12.0 \pm 1.6 (9)	11.6 \pm 2.7 (9)	0.30 \pm 0.06 (9)	0.32 \pm 0.09 (9)	0.42 \pm 0.03 (9)
Chikubu Colony	9.9 \pm 1.2 (6)	11.6 \pm 1.2 (6)	12.0 \pm 2.2 (6)	0.63 \pm 0.00 (6)	0.85 \pm 0.03 (6)	1.21 \pm 0.22 (6)
<i>Leaves of living plants</i>						
Isaki Colony	-2.3 \pm 0.7 (11)	9.9 \pm 4.2 (6)	16.4 \pm 4.5 (8)	1.31 \pm 0.12 (8)	2.68 \pm 0.96 (5)	3.25 \pm 2.53 (8)
Chikubu Colony	6.7 \pm 1.5 (9)	14.6 \pm 2.4 (27)	14.0 \pm 2.3 (23)	2.83 \pm 1.25 (9)	3.20 \pm 1.78 (27)	3.30 \pm 1.88 (23)

*Data of other forest in Shiga Prefecture (Koba et al., 1997)

Table 4. Two-factor factorial ANOVA for study site and colony stage (C, P, A) on nitrogen stable isotope ratio and nitrogen content of forest soil and plants

	Forest floor		Mineral soil		Leaves of living plants	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
$\delta^{15}\text{N}$ (‰)						
Study site	9.46	<0.05	1.80	0.21	114.81	<0.0001
Colony stage	40.29	<0.0001	9.70	<0.01	135.68	<0.0001
Study site \times colony stage	10.47	<0.01	1.74	0.23	27.93	<0.0001
<i>N</i> content (%)						
Study Site	7.63	<0.05	125.35	<0.0001	3.38	0.07
Colony stage	0.42	0.67	14.24	<0.01	1.94	0.15
Study site \times colony stage	0.48	0.64	7.08	<0.05	0.90	0.41

Chikubu Colonies (Table 5). Fractionation factor (ϵ) was significantly different at Site A but not affected by study sites and interaction between study site and colony stage (Table 6). However, intercept of y axes was affected by study sites, colony stage, and the interaction. In the Isaki Colony, the intercept increased with colony stages, while the value at Site A did not increase in the Chikubu Colony (Table 5).

Net mineralization rate of dominant microfungi

The dominant soil microfungi at Site IP-C and IP-P in the Isaki Colony showed different net mineralization rates in laboratory experiments (Fig. 5). *P. herquei* (the dominant species at IP-P) showed a higher net mineralization rate than *P. restrictum* (the dominant species at IP-C) on soil from IP-P (Fig. 5, Turkey's HSD test). *P. restrictum* showed a higher mineralization rate on the soil from IP-C than from IP-P, but the rate was lower than that of *P. herquei* in soil from Site IP-P.

NRA of the dominant tree

NRA of Japanese cypress was different between leaves and roots, and the latter had an approximately one order of magnitude higher value than leaves at IP-C (Table 7). Although leaves showed no significant difference among sites in the Isaki Colony (One-way ANOVA, $F=1.7$, $df=14$, n.s.), NRA of roots differed significantly among sites ($F=4.0$, $df=14$, $p<0.05$). The activity was higher in roots from IP-P than from IP-C (Scheffe's test,

$0.05 < p < 0.1$) and even those from IP-A showed higher activity than those from IP-C.

Nitrogen stable isotope map of the Isaki Cormorant Colony

Fifty-one measurements of $\delta^{15}\text{N}$ of plant leaves, ranging from -3.3 to 17.3 ‰, were plotted on a map of the Isaki Peninsula (Fig. 6). Comparing isotopic data between pigeonberry and other herb species (e.g., ferns, bamboo grasses, *Lactuca raddeana* (Maxim.), *Commelina communis* (L.), *Commelina benghalensis* (L.), *Pyrrosia lingua* (Thunb.) (Farw.), and *Tubocapsicum anomalum* (Makino)) at the same sampling points showed only tiny differences (average difference in means of 1.7 ‰); we therefore used the data without any calibration for species. The northeastern part of the peninsula showed the lowest $\delta^{15}\text{N}$ values, less than 0 ‰. Although $\delta^{15}\text{N}$ was high in presently occupied areas ("1998" in Fig. 6), past-occupied areas had even higher $\delta^{15}\text{N}$ values ("1992" and "1996" in Fig. 6).

Discussion

Factors affecting high nitrogen stable isotope ratios in a Cormorant Colony

Main nitrogen inputs of usual forests are precipitation and N fixation (Nadelhoffer & Fry, 1994; Koba et al., 1999). In temperate forest, $\delta^{15}\text{N}$ of forest floor and plants is close to 0 ‰ reflecting the

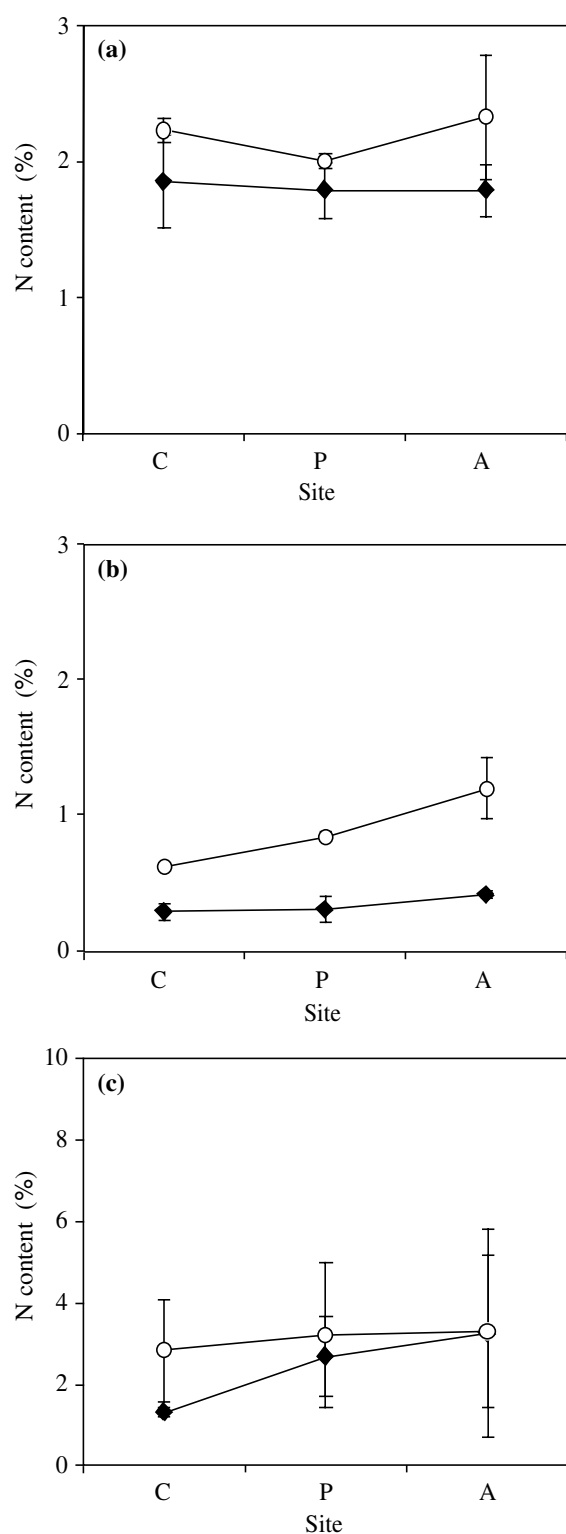


Figure 3. Nitrogen contents of (a) forest floor, (b) mineral soil, and (c) leaves of living plants in control (C), presently colonized (P), and abandoned (A) sites at the Isaki and Chikubu cormorant colonies. Solid diamonds show the Isaki Colony; open circles show the Chikubu Colony in (a), (b), and (c).

value of atmospheric nitrogen (Garten, 1993). In IP-C, we could find nearly 0‰ of $\delta^{15}\text{N}$ of forest floor and leaves of living plants (Table 3). Therefore, $\delta^{15}\text{N}$ in IP-C (control site in the Isaki Colony) showed typical values of a temperate forest when precipitation and N fixation is the main nitrogen input.

High nitrogen stable isotope ratios in a seabird colony has been explained from trophic enrichment and ammonia volatilization, one of the nitrogen decomposition process (Lindeboom, 1984; Mizutani et al., 1986). As piscivorous birds are one of the top predators in aquatic food webs (Hobson et al., 1994), $\delta^{15}\text{N}$ of their tissue and excreta is expected to be high. Excreta showed similar $\delta^{15}\text{N}$ to fish in Lake Biwa although several permil lower than cormorant itself (Table 3). This value was significantly higher than those of nitrogen from precipitation and N fixation (Table 3). From our investigation, averaged N input was $24 \text{ g m}^{-2} \text{ month}^{-1}$ in the Isaki Colony, which is several thousand times higher than nitrogen input from precipitation. Thus, high $\delta^{15}\text{N}$ values at Site P are probably attributable to the large amounts of high $\delta^{15}\text{N}$ excreta, transported by one of the lake's top predators.

In addition to high $\delta^{15}\text{N}$ of excreta, ammonia volatilization can change $\delta^{15}\text{N}$ of an ecosystem (Mizutani & Wada, 1988; Erskine et al., 1998). It produces both low $\delta^{15}\text{N}$ as ammonia gas and high $\delta^{15}\text{N}$ of remaining nitrogen in soil because isotopic fractionation during ammonia volatilization is large (Robinson, 2001). Erskine et al. (1998) showed that volatilized ammonia had -3 to -6 ‰ of nitrogen isotope ratio, while $\delta^{15}\text{N}$ of soil became heavier by volatilization process. Moreover, bird-derived nitrogen also affects plants in and around bird nesting areas. Lindeboom (1984) referred to volatilized ammonia as an "ammonia shadow" and found that it affects plant growth in a large area around a penguin rookery. $\delta^{15}\text{N}$ of plants reflected the change of $\delta^{15}\text{N}$ of soil, and leaves of the common plants had high $\delta^{15}\text{N}$ in the penguin rookery and low $\delta^{15}\text{N}$ around the rookery

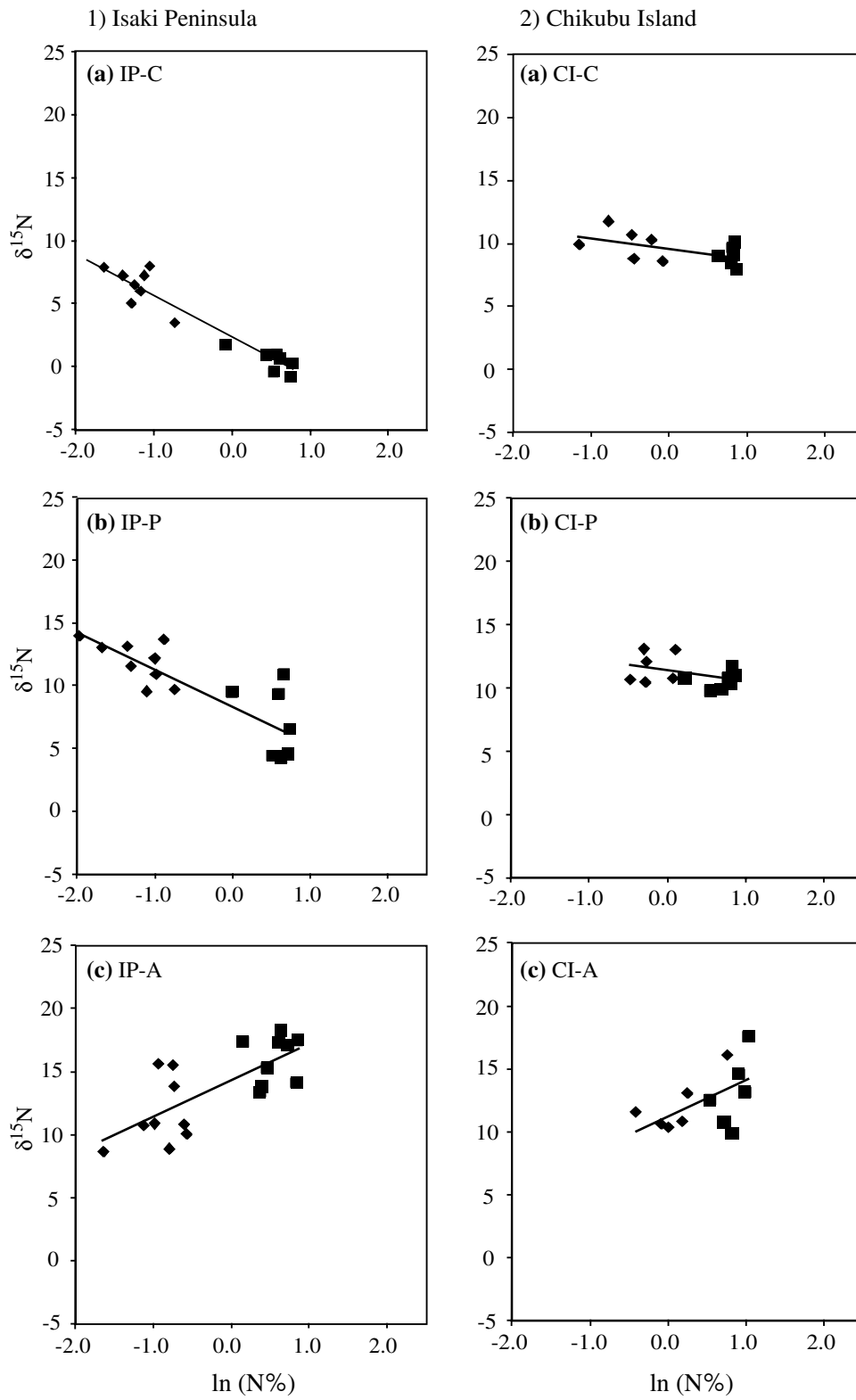


Figure 4. Relationship between ln-transformed N content and $\delta^{15}\text{N}$ of forest floor (solid squares) and mineral soil (solid diamonds) in the IP-C, IP-P, and IP-A sites at the Isaki Colony and the CI-C, CI-P, and CI-A sites at the Chikubu Colony.

(Erskine et al., 1998). However, we could find no evidence of lower $\delta^{15}\text{N}$ of plants around a cormorant colony (Fig. 6). The plants of colonized areas had similar $\delta^{15}\text{N}$ values to those observed in healthy, uncolonized temperate forests (Koba et al., 2003), which indicates that the plants do not greatly rely on ammonia with low $\delta^{15}\text{N}$. Previous studies were conducted on the isolated marine islands without forests. In this research, however, cormorants directly drop the excreta on the forest, where the soil should be better developed than isolated marine islands. pH of the surface of the soil on Isaki Peninsula and Chikubu Island was 3–4 (Ishida, 1996b), whereas pH in and around a penguin rookery on Marion Island was 6.5–9.0 (Lindeboom, 1984). In the soil conditions of the cormorant colonies, ammonia volatilization would be minimal even if large amounts of nitrogen are deposited.

Nitrogen decomposition processes such as mineralization and nitrification also cause high $\delta^{15}\text{N}$ in the soil (Nadelhoffer & Fry, 1988) because of a large isotopic fractionation during nitrification (Koba et al., 1998). When nitrate leaches out from the forest soil, remaining N becomes heavier. In this research, $\delta^{15}\text{N}$ of the forest floor significantly increased with colony stage in both colonies

Table 5. Correlation between ln-transformed nitrogen content and nitrogen stable isotope ratio of forest floor and mineral soil in the Isaki and Chikubu colonies

	Correlation line $\delta^{15}\text{N} = k + \epsilon \ln[\text{N}\%]$			<i>F</i> -test
	ϵ	<i>k</i>	<i>R</i> ²	
<i>Isaki Colony</i>				
IP-C	-3.00	2.22	0.83	<i>p</i> < 0.05
IP-P	-2.91	8.20	0.63	<i>p</i> < 0.05
IP-A	2.91*	14.31	0.54	<i>p</i> < 0.05
<i>Chikubu Colony</i>				
CI-C	-0.78*	9.52	0.29	<i>p</i> < 0.1
CI-P	-0.77*	11.30	0.13	<i>p</i> = 0.23
CI-A	2.88*	11.18	0.31	<i>p</i> < 0.1

Asterisks of slope (ϵ) indicate significant difference from the slope at IP-C.

Table 6. Two-factor factorial ANOVA for study site and colony stage on fractionation factor (ϵ) and *y* intercept (*k*) of nitrogen decomposition in forest soil

	Correlation between $\delta^{15}\text{N}$ and N Content	
	<i>F</i>	<i>p</i>
<i>Fractionation factor (ϵ)</i>		
Study site	2.26	0.17
Colony stage	25.80	< 0.001
Study site \times colony stage	4.14	0.05
<i>y Intercept (<i>k</i>)</i>		
Study site	10.15	< 0.05
Colony stage	35.50	< 0.0001
Study site \times colony stage	12.11	< 0.01

(Tables 3 and 4). The values of the forest floor were lower than those of excreta at Site P while they were higher than those of excreta in Site A (Table 3, Fig. 2). $\delta^{15}\text{N}$ of leaves of living plants also showed the same trends. If the effects of ammonia volatilization on $\delta^{15}\text{N}$ of the soil are significant, $\delta^{15}\text{N}$ of the forest floor would probably become higher than that of excreta at Site P. Therefore, N turnover in the soil (mineralization, nitrification and immobilization) is the important factor of high $\delta^{15}\text{N}$ in the forest soil.

Besides trophic enrichment and N decomposition in the soil, litter should be another N input for forest soils. Hobara et al. (2001) analyzed litterfall input and its N content in the occupied site in the Isaki Colony. 7–22 tons of litterfall (2.6 t ha⁻¹ - month⁻¹) was supplied to the forest floor in the occupied site, and N content increased with colony stage. Although N content of leaves of living plants did not differ significantly (Table 4), a slight increase of N content was observed in the Isaki Colony. Because leaves of living plants had high $\delta^{15}\text{N}$ at Site P and A (Table 3), litter should have high $\delta^{15}\text{N}$ in the occupied and abandoned sites. Thus, fallen leaves and woods should also be important N input and cause high $\delta^{15}\text{N}$ in a cormorant colony.

In summary, $\delta^{15}\text{N}$ of soil and plants becomes higher in cormorant colonies in forests than in uncolonized forests because of a change in the nitrogen cycle caused by large amounts of cormorant excreta and litter with high $\delta^{15}\text{N}$ and nitrogen decomposition processes such as

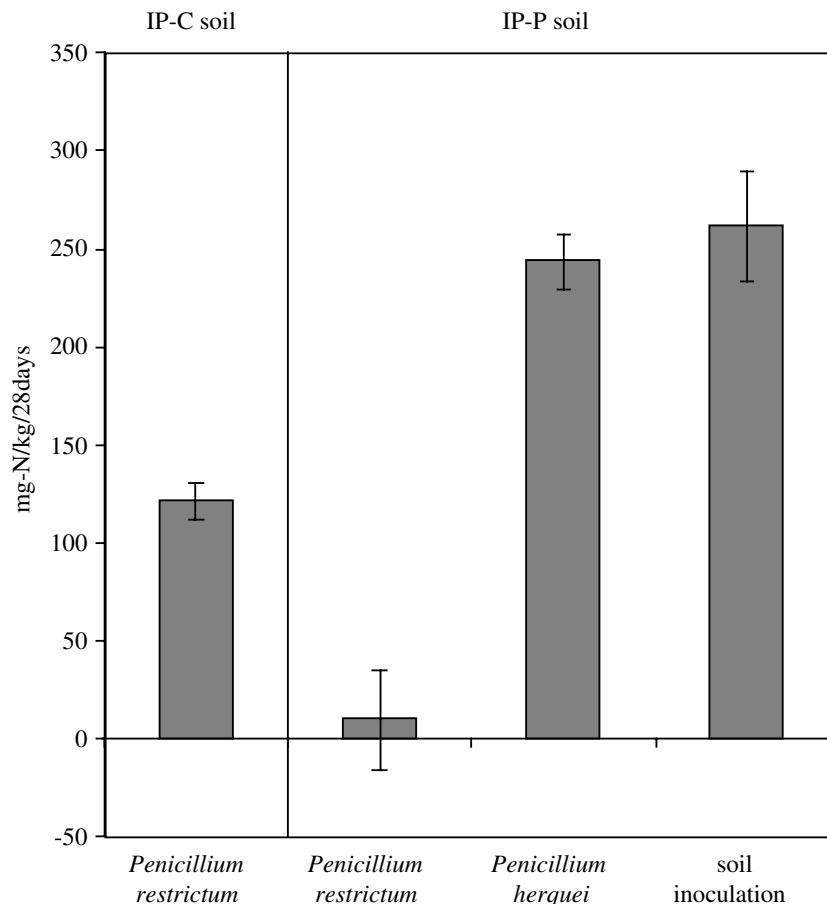


Figure 5. Net nitrogen mineralization rate of soil inoculated with two dominant fungi (*Penicillium* spp.) and a soil inoculum (mean \pm SE, $n = 3$).

mineralization and nitrification. All these processes are closely related, and show the effects of the cormorant reproductive activities on local nitrogen dynamics (Fig. 7).

Change of nitrogen decomposition process through colony stage

Evans & Ehleringer (1993) showed a negative correlation between $\delta^{15}\text{N}$ and N content in the forest

floor and the mineral soil. The isotopic fractionation factor, given as a slope of the regression, usually showed similar values in the forest soils: 1.7 to 3.3‰ (Koba et al., 1998), -1.5 to 4.8‰ (Nadelhoffer & Fry, 1988). At Site C and P, fractionation factors were similar to previous studies (Tables 5 and 6). Thus, the nitrogen decomposition process of the control and occupied sites is similar to normal forests never occupied by birds. At the Site P, k (intercept of y axis) was larger than

Table 7. NRA of leaves and roots of Japanese cypress at sites IP-C, IP-P, and IP-A in the Isaki Colony

Samples	NRA ($\text{NO}_2^- \text{N}$ $\mu\text{mol/g(DW)/h}$) mean \pm SD ($n = 5$)			One-way ANOVA
	IP-C	IP-P	IP-A	
Leaves	0.006 \pm 0.006	0.001 \pm 0.002	0.005 \pm 0.005	n.s.
Roots	0.08 \pm 0.03	1.2 \pm 1.1	0.4 \pm 0.3	$p < 0.05$

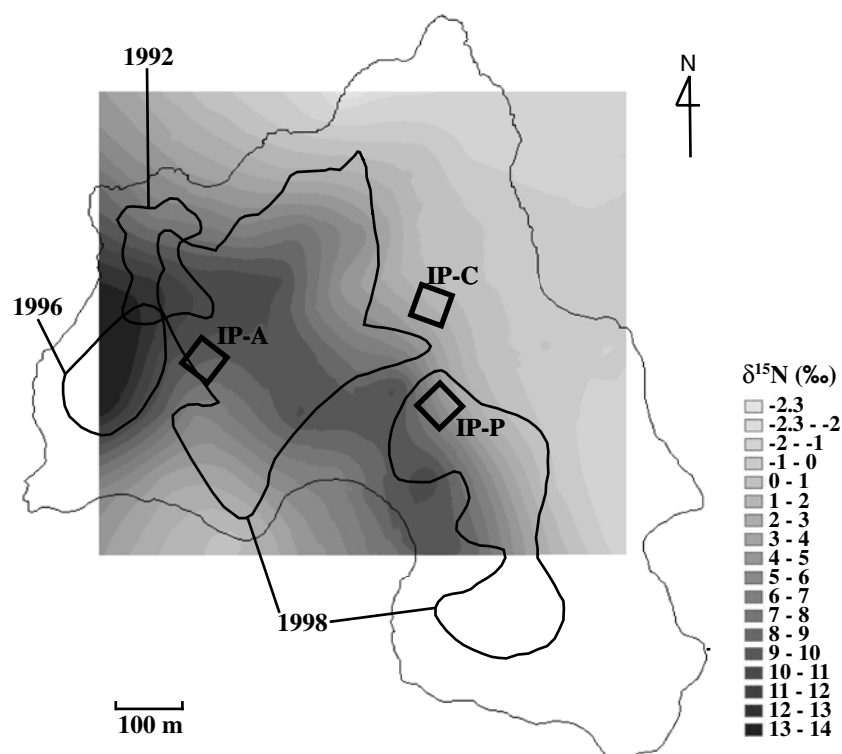


Figure 6. Nitrogen stable isotope map of the Isaki Colony. The cormorant colony boundaries in 1992, 1996, and 1998 are also shown (Fujiwara & Takayanagi, 2001).

that of control sites (Table 5). This means that each value of $\delta^{15}\text{N}$ of the forest soils at the occupied sites is higher than that of the control sites. Therefore, nitrogen decomposition process (or the balance between input and output in a closed soil system) at the occupied site does not change from that of the control site, and nitrogen with high $\delta^{15}\text{N}$ from excreta would be decomposed in the same way as the forest soils unoccupied. Because large amounts of excreta with high $\delta^{15}\text{N}$ is deposited to the forest floor at the occupied site, it increases $\delta^{15}\text{N}$ of the forest floor and $\delta^{15}\text{N}$ of the decomposed inorganic nitrogen in the mineral soil also increases parallel to the forest floor.

The slopes at Site A were different from those at the control sites: $\delta^{15}\text{N}$ and nitrogen content are positively correlated (Table 5). Possible factors affecting the change of the slopes are (1) relative increase of $\delta^{15}\text{N}$ of the forest floor compared with that of the mineral soil, and/or (2) relative decrease of $\delta^{15}\text{N}$ of the mineral soil compared with that of the forest floor. In this research, $\delta^{15}\text{N}$ of the forest

floor at Site A was significantly higher than those at Site C and P, and $\delta^{15}\text{N}$ of the mineral soil at Site A was not higher than those at Site P (Table 3). Thus, relative increase of $\delta^{15}\text{N}$ of the forest floor compared with that of mineral soil would affect the change of nitrogen decomposition process at the abandoned site. Rapid turnover of N in the forest floor stimulated by excreta (Hobara et al., 2001) is responsible for this pattern: nitrogen mineralization and nitrification is facilitated at the occupied and abandoned site (Fig. 5, Hobara et al., 2005), and it results in the increase of inorganic nitrogen for plant nutrients. Actually, the plants used cormorant-derived nitrogen and showed the similar values of $\delta^{15}\text{N}$ to the forest floor (Table 3). At the same time, a large amount of litter was supplied to the forest floor at the occupied site because of the cormorant's nesting activity (Hobara et al., 2001). Although the amount of litter soon decreases to the control level at the abandoned site (Hobara et al., 2001) and no cormorant excreta is deposited, the litter

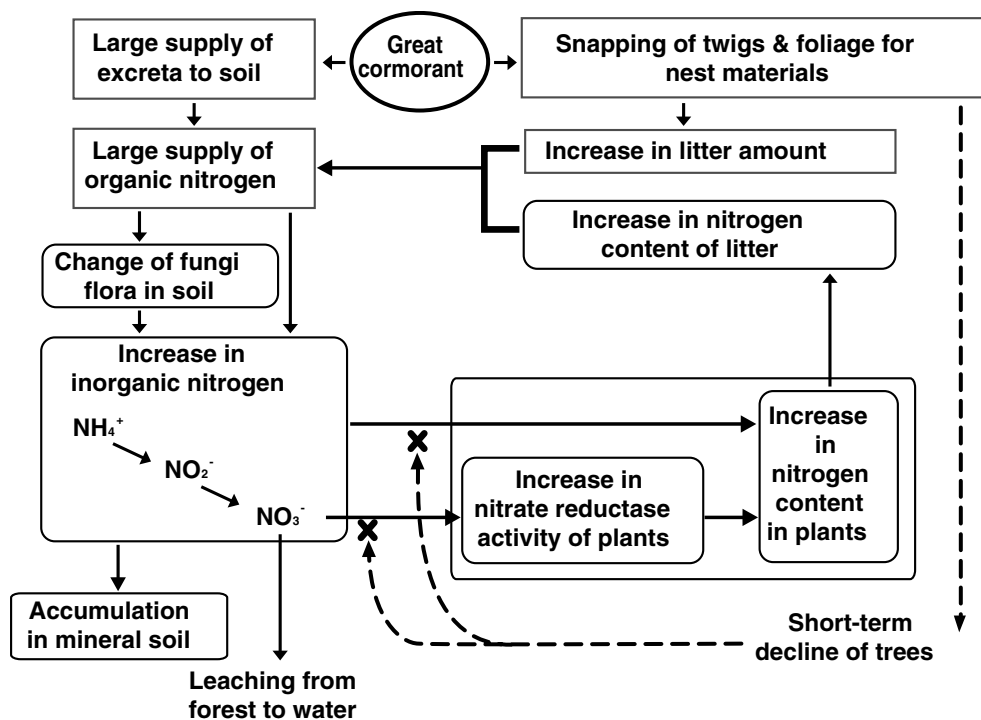


Figure 7. Model of the effects of cormorant colonization on nitrogen cycle in a forest ecosystem.

with high $\delta^{15}\text{N}$ is still supplied to the forest floor at the abandoned site. However, $\delta^{15}\text{N}$ of the mineral soil did not change greatly compared with that of the forest floor at the abandoned site (Table 3). Therefore, nitrogen with high $\delta^{15}\text{N}$ in the forest floor has not reached into the mineral soil at the abandoned site. Observation of the study sites also indicates that there was still thick forest floor by large amount of litter at the abandoned site.

Because soil organic matter and soil micro-organisms in the forest floor are important for nitrogen retention in a heavy nitrogen deposition site (Aber et al., 1998), the forest floor at the occupied and abandoned sites should be a large N sink. Therefore, nitrogen with high $\delta^{15}\text{N}$ is prevented from leaching down to the mineral soil at the abandoned sites. As decomposition of the forest floor proceeds, nitrogen with high $\delta^{15}\text{N}$ can be moved down to the mineral soil via leaching, diffusion, or advection (Amundson & Baisden, 2000). Slight increases in nitrogen content at the abandoned sites in this research probably indicates the start of the nitrogen moving down to the mineral soils.

The cormorants, egrets, and herons have been nesting on Chikubu Island longer than Isaki Peninsula (Ishida et al., 2000). Even at the control site in the Chikubu Colony (CI-C), high $\delta^{15}\text{N}$ was observed (Table 3) because of the birds' perching above the control site. Nitrogen content of the forest floors and mineral soils at all sites in the Chikubu Colony was significantly larger than those in the Isaki Colony (Table 3 and 4). Thus, the results of Chikubu Colony indicate the effects of cormorants on the nitrogen-rich forest. Nitrogen decomposition processes were not different between the Chikubu and Isaki Colony (Table 6). However, $\delta^{15}\text{N}$ of the forest floors and leaves of living plants and nitrogen content of the mineral soils were differently affected with colony stage between the Chikubu and Isaki Colony (Table 4). The change of the $\delta^{15}\text{N}$ with colony stage was moderate in the Chikubu Colony, especially from the occupied site to the abandoned one (Table 3, Fig. 2). On the other hand, nitrogen content of the mineral soils increased in the Chikubu Colony more than that of the Isaki Colony (Table 3, Fig. 3). These results indicate that the effects of cormorant-derived nitrogen on the nitrogen

decomposition process are moderate in the forest floors but that cormorant-derived nitrogen has great effects on nitrogen accumulation in the mineral soils in the nitrogen-rich forest. All the areas in Chikubu Island would be affected by the bird excreta due to the long-term colonization. Higher nitrogen content of mineral soils in the Chikubu Colony also shows that it takes a long time for mineral soils to be affected by large amount of excreta deposition (Fig. 3).

From these results, we conclude that large amounts of nitrogen deposition to the forest soils increased $\delta^{15}\text{N}$ of the forest floor and the mineral soil through nitrogen decomposition processes. For a long period of time, nitrogen decomposition process is altered and a relative increase in N-decomposition processes are observed. Using these data, it would be possible to identify the colony stage and the nitrogen decomposition process in forests. $\delta^{15}\text{N}$ of plants would increase by large amount of nitrogen supply at first, and then, $\delta^{15}\text{N}$ of the forest floor would become heavier by nitrogen decomposition process in the forest floor. After this stage, nitrogen with high $\delta^{15}\text{N}$ would increase in the mineral soil gradually.

These relationships among $\delta^{15}\text{N}$ of plants, forest floor, and mineral soil would tell us the effects of cormorant colonization on forests even after bird abandonment. A $\delta^{15}\text{N}$ map of the Isaki colony showed the highest $\delta^{15}\text{N}$ of shrub at the abandoned site 3–7 years before and this also indicates the possibility of identifying colony stage from stable isotope data (Fig. 6). Mizutani et al. (1991) showed that $\delta^{15}\text{N}$ is a good indicator of deserted seabird colonies. In their study, $\delta^{15}\text{N}$ of the soils in penguin's colonies decreased with time after desertion up to 10 years, but was almost constant after 10 years. In our research, however, $\delta^{15}\text{N}$ of shrub in the cormorant colonies increased with the time after desertion for at least several years. Because there are few plants on penguin's colonies, the nitrogen cycle would not be developed and nitrogen would easily leach from the colonies. Thus, constant high $\delta^{15}\text{N}$ after abandoned by the birds might be one of the characteristics of the colonized forest, although more studies are needed. Anyway, this is the first research to identify the colony stage and nitrogen decomposition process of the bird-nesting forest by $\delta^{15}\text{N}$ and nitrogen content.

Role of organisms in the nitrogen cycle in forest ecosystems

Figure 7 shows the model of the effects of cormorant colonization on the nitrogen cycle in a forest ecosystem. The great cormorant mainly affects the forest in two ways: large supply of excreta and snapping twigs for nest materials. This cycle is facilitated by not only the cormorant's roles but also the change of the function of various organisms.

Large supply of excreta caused drastic changes to species composition of the fungi community in forest soil (Osono et al., 2002). As dominant fungi *P. herquei* in the occupied site in the Isaki Colony (IP-P) showed high mineralization ability, large amount of excreta would be mineralized soon (Fig. 5). This facilitates ammonium production in the occupied site as well as ammonia volatilization. Thus, *P. herquei* should play an important role in nitrogen mineralization in the occupied site. The great increase of $\text{NH}_4^+\text{-N}$ and mineralization rate of forest floor in the occupied site supports this (Hobara et al., 2005).

At the abandoned site, *P. herquei* was not found (Osono et al., 2002). At the same time, $\text{NH}_4^+\text{-N}$ concentration in soil decreased but $\text{NO}_3^-\text{-N}$ was still high (Hobara et al., 2005). Therefore, relative importance of mineralization and nitrification was changed through colony stage. Hobara et al. (2001) illustrated the decrease in C/N ratio of forest floor from the control site (IP-C) to the abandoned site (IP-A). Nitrification is generally low at high C/N ratio (Schlesinger, 1997), thus the change of N cycle pattern in soil can be attributed to the change of soil C/N by the proceeding of decomposition of litter produced in colonized time. So far, the importance of $\text{NO}_3^-\text{-N}$ has not been studied in the occupied area because nitrate concentration was low during colonization (Lindeboom, 1984; Erskine et al., 1998). However, nitrate would be a more important N source for nitrogen cycle and plants at the abandoned site, as well as cause N leaching from soils. Thus, nitrate should be paid more attention to when we analyze long-term effects of nitrogen supply from birds.

On the other hand, high ability of mineralization and nitrification in soil produces large amounts of $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ (Fig. 7). $\text{NO}_3^-\text{-N}$ easily leach out from soils, but they are also used by plants.

Although some plants cannot use NO_3^- -N as N source (Koyama & Tokuchi, 2003), NRA in the roots of Japanese cypress was significantly high at the occupied site and still high at the abandoned site in the Isaki Colony (Table 7). The cormorant has colonized for about 6 years in IP-P and most Japanese cypresses were planted before cormorant colonization. Therefore, they probably started to exert the ability of nitrate use after the cormorant colonization. This facilitates the increase of N content of plants and maintains nitrate-rich condition of a forest (Fig. 7). These result in the increase of N content of the litter (Hobara et al., 2001).

The activity of nest material collection by the cormorant also increases the amount of litter because the birds remove foliage from living trees around a nest. It causes a greater supply to the forest floor of organic nitrogen for the forest soil. Moreover, litter also supplies carbon with nitrogen and this facilitates N retention in forest soil, although C/N ratio of litter decreases in the occupied and abandoned sites. As a result, long-term remaining and recycling of cormorant-derived nitrogen is realized (Fig. 7). Although Mulder & Keall (2001) pointed out the effects of nest material collection on bird flight, this is the first time to connect the bird behavior itself to the nutrient dynamics.

In this research, vegetation remained in the abandoned site and we could find the long-term effects of bird excreta on nitrogen cycle in "living" forest. If the nesting effects are severe, trees were damaged in a short-term (Ishida, 1996a; Fujiwara & Takayanagi, 2001). In that case, nitrogen uptake by trees decreases and nitrate leaches out from a forest. Although large amount of nitrate flow in soil solution also indicates the nitrate leaching even "living" forest in the abandoned site (Hobara et al., 2005), NO_3^- -N uptake by trees plays a role in retaining the nitrogen in a forest for a long time.

Conclusion

Effects of waterbird colonization on nutrients or vegetation are apparent during colonization and many studies have concentrated on the present or continuous effects of bird-derived excreta on nutrients and vegetation (Lindeboom, 1984; Mizutani & Wada, 1988; Erskine et al., 1998).

However, this research showed that even the abandoned site that seems to recover from the effects of colonization still has a great difference in nutrient cycle. Long-term effects would be greater in forest than grassland because trees store nutrients and supply a lot of litter for soil again. Although there are some studies pointing out the negative effects of bird colonization on trees (Ishida, 1996a; Mulder & Keall, 2001), this is the first study to analyze the mechanism of the long-term effects of waterbird colonization on a forest ecosystem.

Changes to nutrient dynamics in a forest ecosystem would also affect aquatic ecosystems around a colony. The cormorant feeds on fish in a broad area and brings nutrients into a colony near water. Thus, nutrients are concentrated in small areas around a colony. Moreover, forest retains large amounts of nitrogen for a long time after abandonment, and after that, nitrogen would leach out to the watershed after tree decline. It would have great effects on aquatic ecosystems (Carpenter et al., 1998). Phosphorous is another important nutrient transported by waterbirds and it would also retain in a forest for a long time after colonization. Hobara et al. (2005) shows that N/P ratios relatively increase in the leach out from the cormorant nesting forest because forest soils retain phosphorous more than nitrogen. Thus, nutrient transportation by waterbirds and nutrient dynamics in forest ecosystems are also related to allochthonous input to an aquatic ecosystem.

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Part II
Waterfowl – Habitat Use, Foraging Behaviour and Limnology

Temporal processes and duck populations: examples from Mývatn

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Key words: waterfowl, reproductive output, food resources, breeding density, population limitation

Abstract

Studies of temporal processes at Lake Mývatn, Iceland, on three scales, millennial, centennial and decadal, are reviewed and a summary is presented of the main results of waterfowl population monitoring studies conducted during the past three decades. The characteristics of shallow, subarctic Lake Mývatn and its volcanic environment, are outlined, as well as recent conflicts between development and conservation. Mining of the bottom sediment of Lake Mývatn has been a major agent causing habitat destruction and damage to the food web. Population limitation of waterbirds at Mývatn is discussed, as three research questions and emerging answers: (1) How is reproductive output determined? All species studied showed positive correlations of production of young with levels of aquatic insects, catastrophic weather was rarely important; (2) How is the dispersion of breeding ducks determined? Densities of migratory species are determined mainly by resource levels on the breeding ground in the year before they return to the breeding area; a year-round resident species, *Bucephala islandica*, adjusts its density to the current availability of insect food in each of two main habitats used; (3) How are flyway populations of ducks determined? For most species, there is not enough information on total numbers and the state of the habitat on a flyway scale. In *B. islandica*, there are indications that the total population is limited by resources in winter. The Mývatn study area is dominated by a single, shallow and eutrophic lake and for many waterbird species the area seems to form a single functional unit. This leads to significant correlations when comparing demography with environmental conditions, such as food resources.

Introduction

In this paper I review studies of temporal processes and waterbird populations that have been conducted over the past three decades at Mývatn, Iceland. To do this, I first describe in some detail the characteristics of Lake Mývatn and its surroundings, as well as a broad selection of studies relating to this area, especially temporal processes that have been studied at the lake on various time scales. Finally, I discuss some current ideas about explaining population change of waterbirds at Mývatn.

Lake Mývatn is a unique study site, and those who have worked there are often reminded of this by

colleagues who sometimes hint that processes of population limitation might be different at Mývatn than elsewhere. The uniqueness of Mývatn is explained mainly by the unusual situation of Iceland, a large (103,000 km²), remote, subarctic, oceanic and volcanic island. This situation has several consequences, including an impoverished terrestrial fauna. Many animal groups are entirely absent, for instance mosquitoes (Diptera, Culicidae) and most land mammals, including microtine rodents. Iceland was one of the very last lands on earth to be reached by man, *Homo sapiens* L. Several species of seabirds, waterbirds and shorebirds occur in relatively large numbers, but only a few passerine species are present.

At Mývatn, as everywhere in the central volcanic zone of Iceland, bedrock, soil and freshwater systems are shaped by volcanic activity. Ecological research at Mývatn has been conducted with a number of quite different purposes. First, Mývatn is a unique place where a biologist cannot fail to be confronted with challenging questions. Second, it is a rich natural resource, subject to constant change and threatened by the consequences of human activity. Third, as data accumulate, knowledge of temporal change has advanced, increasing the scope of questions that can be asked about the populations of the lake and how they are limited.

Research and modern development

Although known to naturalists already in the 18th century for its wealth of waterfowl, midges and fishing, the Mývatn area was long a rather remote and undeveloped part of Iceland (Table 1). Industrial interest in the 20th century at first centred on harnessing the outlet river of Lake Mývatn, the Laxá, for the production of electricity. The first power station was completed in 1939; new dams were added and plans to develop the river further gradually emerged. In the late 1960s, these developments led to serious political conflict which was resolved by an agreement in 1973 (Olafsson, 1981). The region was protected by law

Table 1. A chronological list of some major events that have occurred in recent centuries at Mývatn, Iceland, and that are thought to be of potential significance to ecological systems. Also listed are some major sources of information. Based largely on Gardarsson & Einarsson (2000) and references therein

Year	Events
1712	Land registry (Jardabok by Arni Magnusson and Pall Vidalin)
1724–1729	Eruptions in Krafla, lava flow reaching the lake ('Mývatn fires')
1746	Eruption in Krafla
1747	First description of natural history (Jón Benediktsson)
1819	First scientific account of avifauna (F. Faber)
1895	First record of tufted duck (<i>Aythya fuligula</i>), now the most abundant duck species at Mývatn
1913–1918	Large peak in egg harvest of long-tailed duck (<i>Clangula hyemalis</i>) and scoter (<i>Melanitta nigra</i>)
1922–1924	Large peak in charr (<i>Salvelinus arcticus</i>) catch
1926–1931	Peak in egg harvest of red-breasted merganser (<i>Mergus serrator</i>)
1930	First vehicle highway (a gravel road) reaches Lake Mývatn
1939	First hydropower plant on the River Laxá
1950s	Introduced mink spreads to Mývatn via the Laxá valley. Rapid change in distribution of breeding ducks, which abandoned islands
1950s	Rapid expansion of gill net fisheries, shore seining stopped
1950s	Transition in haymaking from meadows and irrigation marshes to fertilized fields
1950s on	Increase in tourism
1967	Beginning of diatomite extraction (strip mining) from bottom sediment of Lake Mývatn
1967	First geothermal power plant NE of Mývatn
1970	First recorded widespread crash in Mývatn duck populations and charr fishing; several crashes occurred later, in 1976, 1983, 1988 and 1997
1971–1974	Basic limnology studies (Jónasson, 1979)
1974	Mývatn region protected by law; research station established, beginning of monitoring studies
1975–1984	Eruptions in Krafla ('Krafla fires')
1978	The Mývatn–Laxá region becomes Iceland's first Ramsar Wetland of International Importance
1984	First published report suggesting that change in sediment transport caused by strip mining is harming the Mývatn ecosystem
2004	End of diatomite extraction

in 1974. Basic limnological studies of Mývatn were carried out in 1971–1974 and published as a collection of papers in *Oikos* (Jónasson, 1979). In 1974, the Mývatn Research Station was established, its aims included the monitoring of the Mývatn–Laxá ecosystem. When Iceland acceded to the International Wetland Convention in 1978, the Mývatn–Laxá became a Ramsar site.

Meanwhile, other developments were initiated. The bottom mud of the lake turned out to be mostly composed of diatomaceous earth which is used for filters and as an adsorbent in many products. Mining of the bottom sediment of Lake Mývatn commenced in 1967. A crash in both the charr, *Salvelinus alpinus* (L.), fishery and the breeding success of ducks followed within a few years. This was associated with changes in food as recorded in stomach contents, in particular the large chydorid crustacean, *Eurycercus lamellatus* (Müller), became very scarce in stomach contents (Gardarsson, 1979). The charr fishery has not recovered and the duck species that seem to be most dependent on *E. lamellatus* have remained at low levels.

Recent plans to expand sediment mining in Lake Mývatn have stimulated several environmental impact studies. The present mining area in the North basin is already gathering about 20% of the annual accumulation of sediment in the lake, mining pits in the South or East basin would accumulate as much as 34–64% of the estimated annual accumulation of sediment in the lake (Einarsson et al., 2004; Kjarran et al., 2004). Although the excavated area is still relatively small, about 10% of the total area of the lake, sediment transported into the area is in effect removed from the detritus-driven ecosystem. Thus, mining has a major impact on the benthic invertebrate community, and through the food web mining affects waterfowl and fish populations of the lake. Strip mining has also been shown to affect waterbirds of Mývatn directly by destroying the shallow feeding habitat of moulting whooper swans, *Cygnus cygnus* (L.). Their number at Mývatn has declined linearly with the area of available habitat (Gardarsson et al., 2002). The mining operation has led to remobilization of nutrients with an estimated 7% increase in the P-loading and 80% increase in the N-loading of Lake Mývatn (Ólafsson, 1979, 1991).

To conclude this overview of environmental issues, there seems to be no doubt that mining of the lake bottom reduces feeding habitat and disturbs the detritus-based food web. Mining and production of diatomite at Mývatn ended in 2004, but this will hardly mean that conflict between conservationists and developers and their political collaborators will end. Results of new and ongoing research projects were presented at a conference on Mývatn held in May 2001 and published in *Aquatic Ecology* (Vol. 38, no. 2), 2004.

The study area

The shallow eutrophic Lake Mývatn and the upper parts of its outlet river, the Laxá, are situated in North Iceland (65° 40' N, 17° 00' W) at an altitude of 278 m a.s.l. (Fig. 1). The area is near the northern limit of human habitation, with mean monthly temperatures varying between 10 °C (July) and –4 °C (February). Annual precipitation is close to 400 mm. Detailed descriptions of the Mývatn ecosystem are given by, among others, Jónasson (1979), Gardarsson & Einarsson (1994, 2000), Gíslason (1994) and Einarsson et al. (2004). Water enters Lake Mývatn mainly by subterranean flow from a volcanic area of about 1400 km².

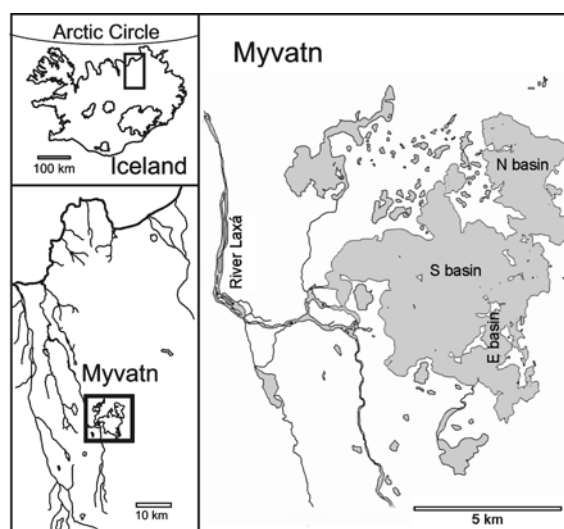


Figure 1. A map showing the study area and its location and the main place names mentioned.

Permanent surface waters cover about 50 km², of which Lake Mývatn comprises 37 km² and other lakes and permanent ponds some 9 km². Below a depth of about 2.5 m, much of the lake bottom is covered by a carpet of filamentous chlorophytes of the order Cladophorales. The algae are an important food for waterfowl and also form a substrate with which many epifaunal invertebrates are associated, notably *E. lamellatus* and orthocladiid chironomids. The infauna is dominated by chironomid larvae, mainly *Tanytarsus gracilentus* (Holmgren). Only three species of fish occur in Mývatn and the upper Laxá: three-spined stickleback, *Gasterosteus aculeatus* L., arctic charr, and brown trout, *Salmo trutta* L.; in the lower part of the river, Atlantic salmon, *Salmo salar* L., is plentiful. An average of 10,000–15,000 pairs of waterbirds of some 20 species, mainly diving ducks, breed at Mývatn (Table 2). The most abundant diving ducks are tufted duck, *Aythya fuligula* (L.), mean 182 birds km⁻², and greater scaup, *A. marila* (L.), 103 km⁻². Other important waterbirds include horned grebe, *Podiceps auritus* (L.), whooper swan, Eurasian wigeon, *Anas penelope* L., gadwall, *Anas strepera* L., common scoter, *Melanitta nigra* (L.), Barrow's goldeneye, *Bucephala islandica* (Gmelin), and red-breasted merganser, *Mergus serrator* L. Winter densities of adult waterbirds (mainly Barrow's goldeneye, mallard, *Anas platyrhynchos* L., and whooper swan) are similar to summer densities, if only open, ice-free water is taken into account.

The uppermost parts of the River Laxá support high densities of *Simulium vittatum* Zett. (blackfly) larvae, which contribute about two-thirds

of the total benthic production, usually between 40 and 150 g ash-free dry weight m⁻² year⁻¹. At the lake outlet, *Simulium* emerges twice annually, in June and August. Further downstream, *Simulium* densities and production decrease, and only a single generation is produced annually. Brown trout are the most abundant fish in the upper Laxá; Barrow's goldeneye and harlequin duck, *Histrionicus histrionicus* (L.), are the main waterbirds. The main paths of the food web of the ducks of Lake Mývatn and the Laxá are shown in Figure 2.

Temporal change at Mývatn

In its present form, Lake Mývatn is a young lake, only 2300 years old. Cores from the lake's sediment have revealed much about the lake's history and global or large-scale influences on the biota (Einarsson, 1982; Einarsson & Haflidason, 1988; Einarsson et al., 1993). The cores have been studied with a resolution in time of about 40 years. They reveal long-term fluctuations and trends that I have called millennial or Order 3 processes (Fig. 3a). The most evident of these is succession as the lake became shallower with time. Reduced depth can confidently be listed as the cause of decrease of profundal benthic species, such as the chironomid *T. gracilentus*, and of zooplankton such as *Daphnia longispina* (Müller). The sediment record also shows long-term fluctuations in benthic chlorophytes and the associated epifaunal chydo-rid *E. lamellatus* and chironomid *Psectrocladius barbimanus* Edwards. These fluctuations are

Table 2. Mean spring numbers and numerical trends of the eight most abundant ducks at Mývatn in 25 years, 1975–1999

	Mean spring number (<i>n</i> = 25)	C.V.	Trend in 1975–1999	<i>p</i>
Eurasian wigeon <i>Anas penelope</i>	2256	34	Increase	<0.01
Tufted duck <i>Aythya fuligula</i>	7386	32	Increase	<0.01
Greater scaup <i>Aythya marila</i>	3261	19	No ¹	NS
Common scoter <i>Melanitta nigra</i>	587	24	No ¹	NS
Longtailed duck <i>Clangula hyemalis</i>	302	27	No ¹	NS
Harlequin duck <i>Histrionicus histrionicus</i>	293	46	Increase	<0.001
Barrow's goldeneye <i>Bucephala islandica</i>	994	22	Decrease	<0.001
Red-breasted merganser <i>Mergus serrator</i>	738	26	Increase	<0.01

¹Current low numbers follow earlier declines.

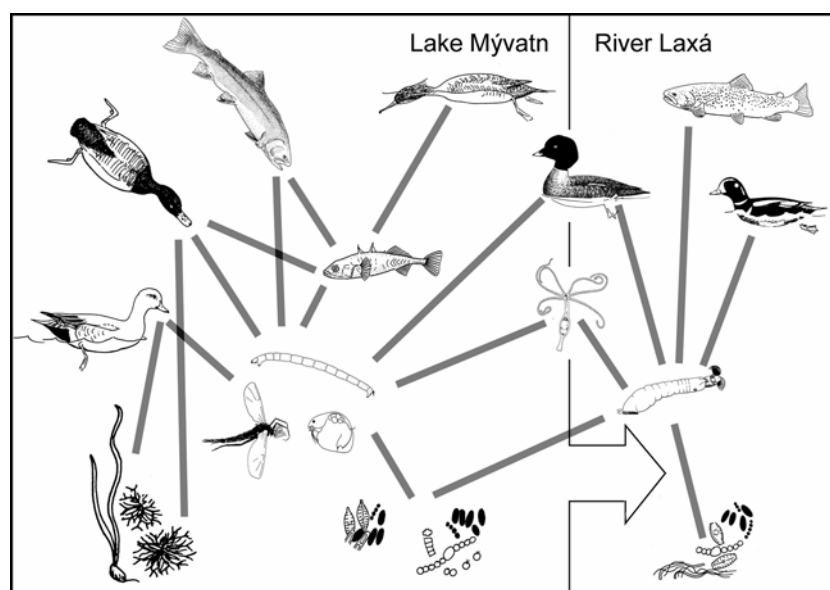


Figure 2. A simplified food web of Mývatn with particular reference to ducks and their benthic food base. Not to scale.

correlated with variation in volcanic ash (tephra) fallout (Einarsson et al., 1993). Finally, in the period 100–600 AD, the variety *venter* of the diatom *Fragilaria construens* (Ehr.) Grun. occurred in unusually high proportions and several species of chydorids had a concurrent low; this has tentatively been interpreted as due to reduced geothermal activity and consequent low levels of silica in the groundwater input (Einarsson et al., 1993).

More recent changes are sometimes accessible through naturalists' records and catch or harvest statistics. I have termed these centennial or Order 2 changes (Fig. 3b). At Mývatn, as elsewhere, very large population changes are often recorded by members of the general public who notice appearances and disappearances or drastic declines of species. For instance, the last breeding of the white-tailed eagle, *Haliaeetus albicilla* (L.), at Mývatn seems to have taken place shortly before 1900 (Nielsen, 1921); the first specimen of the tufted duck was collected in 1895, and it is now the most abundant duck species at Mývatn, having displaced the greater scaup from this position between 1971 and 1973. A huge decline in numbers of red-necked phalarope, *Phalaropus lobatus* (L.), took place some time between 1952 and 1975, but went unrecorded.

Around 1940, Finnur Gudmundsson collected records of fish catches and the harvest of wild duck eggs at Mývatn. The results showed some interesting long-term trends (Gudmundsson, 1979). The most remarkable of these is a large peak seen to pass sequentially through several populations: high numbers of Barrow's goldeneye occurred in the first years of the 20th century, peak numbers of common scoter and long-tailed duck, *Clangula hyemalis* (L.), followed about 1915–1918, a very large peak was seen in the catch of salmonids (mainly Arctic charr) in 1922–1924, and finally a peak in red-breasted merganser (a stickleback specialist) in 1926–1931. Analyses of stomach contents suggested that the large early 20th century fluctuation was causally related to change in crustacean populations, but direct evidence is lacking (Gardarsson, 1979; Gardarsson & Einarsson, 2000). Ducks of the genera *Anas* and *Aythya* did not show evidence of this large fluctuation; in the light of later research on food and population limitation, these species were probably mainly affected by chironomid levels (Gardarsson & Einarsson, 1994). Also, the largest peak in *Anas* and *Aythya* egg harvest, in 1942, coincided with a locally famous high in midges.

At present, Order 2 changes are difficult to study except in retrospect; available data are

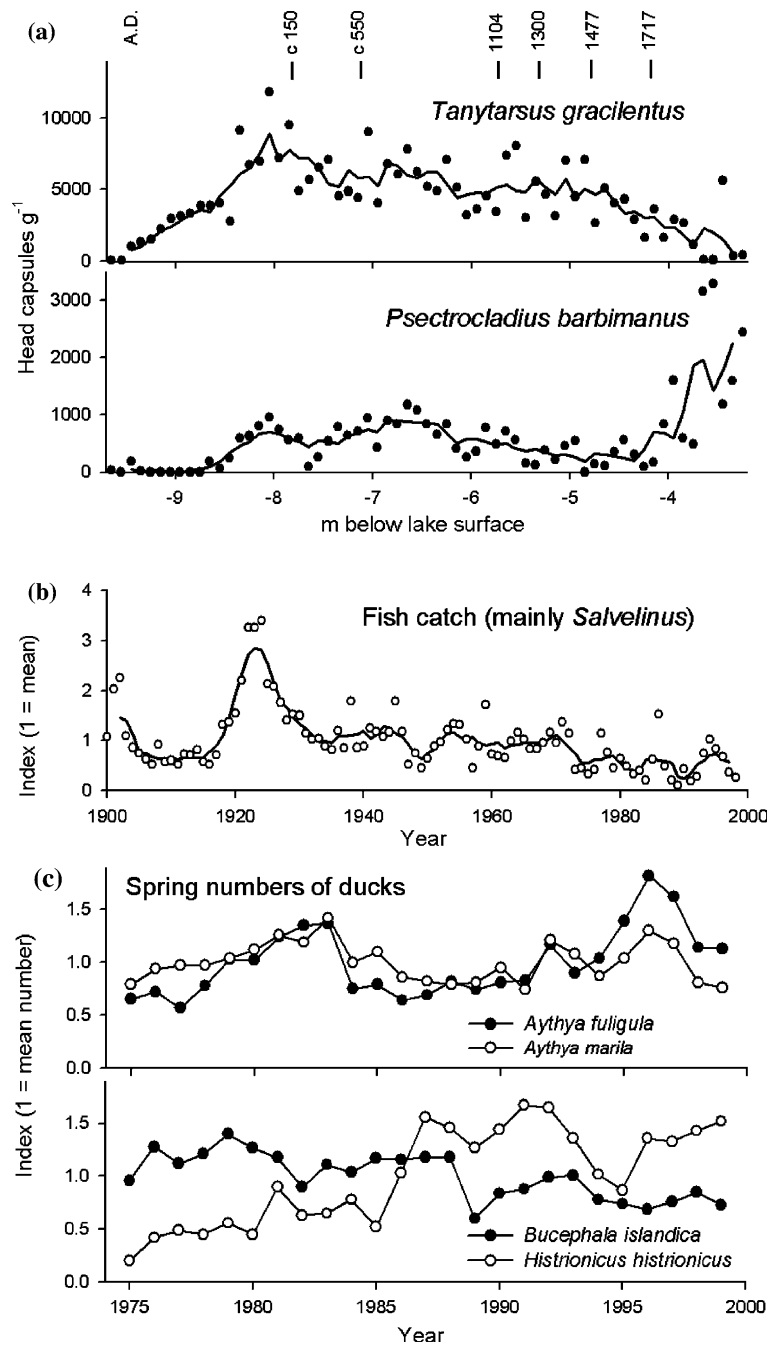


Figure 3. Some examples of temporal change at Mývatn at three different scales. (a) Order 3, millennial change, studied in sediment cores with a resolution in time of about 40 years. Shown are densities (numbers of head capsules per g dry weight organic sediment) of two chironomid species, the dominant *Tanytarsus gracilentus* and the important food species *Psectrocladius barbimanus* (based on Einarsson et al., 1993). Scale is in cm below lake surface, dates are determined from known volcanic eruptions that have produced layers of ash (tephra) in the sediment. Lines show five-point moving averages, dots are single samples. (b) Order 2, centennial change, based on catch data (Gudbergsson, 2004). Line shows five-point moving averages, dots are annual catches. (c) Order 1, decadal change, spring numbers of ducks from monitoring work beginning in 1975.

limited and new data accumulate slowly in comparison with the working lifetime of a scientist. Only teamwork and continued monitoring are likely to provide data sometime in the future that will suffice to explain some of these fluctuations satisfactorily. It seems likely that the Order 2 trends that can be seen in the long-term record at Mývatn may be related to the extent of the mat of filamentous green algae (Cladophorales) on the lake's bottom and its epifauna, especially *E. lamellatus* and certain chironomids. The changing cover of green algae can be estimated from aerial photographs and has also been studied by ground surveys. An early survey, by Finnur Gudmundsson in 1939, showed similar distribution of Cladophorales as the earliest available aerial photographs, from 1963, a far more extensive cover of the algae (1540 ha) than later photographs, the next dating from 1979 (852 ha). Since then, values from 452 to 1356 ha have been recorded (Einarsson et al., 2004).

Monitoring of various populations at Mývatn was begun in 1975, with the aim of estimating every year certain basic statistics on as many species as possible, of those that were either abundant or easily counted, or both. We started with waterbirds (Fig. 3c), and at least annual indices of numbers have been collected for 21 regularly breeding species (18 anatids, 2 loons, 1 grebe), leaving only phalaropes (1 species) and larids (2 species) unaccounted for. Monitoring the food resources of the waterbirds was an obvious priority. A window trap was developed for the purpose of catching aquatic insects in flight (thus avoiding more time-consuming and labour-intensive sampling methods) and these traps have been in operation annually in May–September since 1977 (Jónsson et al., 1986). The traps have successfully recorded Order 1 or 'short term' changes in many species of aquatic insects (e.g., Gardarsson et al., 2004). Of particular interest has been the demonstration of resource limitation in the dominant chironomid species of Lake Mývatn, *T. gracilentus*, the larvae of which form mats on the bottom (Einarsson et al., 2002). Population cycles of *T. gracilentus* also affect other benthic invertebrates (Einarsson & Örnólfsson, 2004; Gardarsson et al., 2004). Ducklings of most species depend on Chironomidae for food, but benthic crustaceans, especially *E. lamellatus*, are also of great importance,

and their abundance is now being monitored in specially developed traps (Einarsson & Örnólfsson, 2004).

Questions about population limitation

The limitation of animal populations is a wide-ranging subject that has been of particular interest to ornithologists (e.g., Lack, 1954, 1966; Newton, 1998). Questions of population limitation often revolve around breeding populations, their reproductive output, density and the interannual variation in these variables. Detailed studies of population ecology are usually carried out in relatively restricted areas in which emigration and immigration play a role (Baillie et al., 2000). In some cases, environmental aspects have been studied concurrently, but variation in food resources has not often been included (see review in Newton, 1998). In resident, well-demarcated populations, observed limitation may sometimes approximate that of a whole population. Often, however, the local breeding 'populations' commonly studied are only small fractions of larger flyway populations, approximating metapopulations (Levins, 1970; Gilpin & Hanski, 1991; Hanski & Simberloff, 1997; Wiens, 1997), which outside the breeding season may be subject to totally different limiting factors (Esler, 1998). Only in a few cases has limitation on the flyway scale been shown to take place, for instance in populations of North American ducks and coots which track the variation in the surface area of wetlands (Boyd, 1981; Kaminski & Gluesing, 1987; Raveling & Heitmeyer, 1989; Alisauskas & Arnold, 1994).

Lake Mývatn is a comparatively remote and isolated area with high densities of waterbirds and a well-known aquatic environment, which has been monitored for relatively long periods. In comparison with other studies of breeding waterbirds, the studies at Mývatn cover relatively large proportions of several flyway populations. Hence the birds of this lake provide an unusual opportunity to examine general questions about population limitation. For clarity, I have reduced these to three questions which I shall examine in a hierarchical order, starting with the simplest.

How is reproductive output determined?

Most losses of ducklings seem to occur in the first 1 or 2 weeks of life (Sargeant & Raveling, 1992). The availability of nutritious food, usually in the form of aquatic arthropods, is generally considered to be very important (Martin, 1987), although the proximate, observed cause of death is most often predation or weather (see review by Johnson et al., 1992). At Mývatn, we did not attempt to follow reproductive success through the stages of nesting and brood survival. Rather, we have used one extensive survey each summer when the ducklings were 2–4 weeks old (for details, see Gardarsson, 1979; Gardarsson & Einarsson, 2004).

The reproductive output of all the duck species studied at Mývatn shows close correlations with levels of aquatic insects (Gardarsson & Einarsson, 1994, 1997, 2004). The closest relationships with chironomids are shown by the Eurasian wigeon and the tufted duck. Greater scaup and common scoter show somewhat lower correlations, perhaps related to their greater use of crustacean food. Barrow's goldeneye ducklings tracked chironomid midges on Lake Mývatn and showed a weaker correlation with blackflies on the River Laxá. Numbers of young harlequin ducks produced each year on the Laxá were correlated with the abundance of blackflies. Only in one exceptional year was weather shown to depress the production of young. Indeed, the overriding importance of food, and not weather or other environmental influences, is underlined by the lack of correspondence between duckling production of the river and that of the lake in the same year.

How is the dispersion of breeding ducks determined?

Local densities of birds are a function of the total number available to disperse over the landscape and the characteristics of habitat patches, such as the availability of resources (usually food, cover or nest sites) or the relative freedom from predators or other disturbance. Most duck species breed on inland waters where usable wetland habitat is distributed as patches in a matrix of unsuitable habitat. Although patchily distributed and widely dispersed in the breeding season, many duck

species are migratory to a greater or lesser extent and the non-breeding distribution of subpopulations breeding in widely separated regions often overlaps broadly to form flyway populations. Pairing takes place on the wintering grounds, where ducks from widely separated breeding patches may meet; unlike most other birds, the female of most duck species is the philopatric sex (Sowls, 1955; McKinney, 1986). Breeding subpopulations of ducks are not independent and one would expect tradition (including philopatry), memory and information transfer to be of importance in determining the dispersion (Gardarsson & Einarsson, 1997). In a breeding subpopulation, density and changes in density are useful terms, but these variables may be determined largely through immigration and emigration (dispersion) rather than the balance of births and deaths.

Examples from the Mývatn monitoring studies indicate that change in the breeding densities of most migratory duck species is determined mainly by food abundance on the breeding grounds in the year that the ducks leave the breeding area. Resource abundance probably influences the adult bird directly, by improving its body condition (rather than through the actual breeding success which also responds to food abundance) or perhaps by altering its behaviour. This interpretation is supported by 1-year lag responses in pre-breeding densities of diving ducks which attain sexual maturity when 2 years old and do not return to the breeding area until then (Gardarsson & Einarsson, 1994, 2004). In the Eurasian wigeon, it seems that adult females are the decision makers and that their choice of mates on the wintering grounds is affected by the quality of feeding in the previous summer (Gardarsson & Einarsson, 1997).

The density of the resident Barrow's goldeneye in its two main habitats, the river and the lake, is adjusted to the concurrent availability of insect food in each (Einarsson et al., 2004). As a sample of breeding birds approaches the size of the flyway population, greater influence of conditions operating outside the breeding season is to be expected. At the same time, the information available varies between species for technical reasons, some estimates of population parameters are easier to make with one species, other parameters may be available for a different species. Another 'resident' (actually

short distance migrant) species that has been studied, the harlequin duck, probably winters almost entirely on the Icelandic coast. Variation from year to year in its numbers on the Laxá (about 5% of the Icelandic population) is apparently influenced by the situation in winter, although local mink, *Mustela vison* Schreber, may play a part in determining its dispersion on the river (Gardarsson & Einarsson, 2004; Einarsson et al., 2006).

Very large fluctuations in chironomid populations characterize Lake Mývatn and affect the production of wigeon, tufted duck and several other species. In years of high chironomid numbers, the lake may act as a source (*sensu* Pulliam 1988), whereas in years of low chironomid levels a rapid decline takes place, perhaps caused by emigration. Hence, local breeding density at Mývatn is correlated both with the previous food level and with the number of young produced in the year before. It seems likely that in other, less productive, wetlands that perhaps are sinks (Pulliam, 1988), this direct relationship of reproductive output and density does not occur. Detailed observations in Finland during 1985–2001, of wigeon breeding at low and decreasing densities (4–20 pairs km⁻²; 5–25 pairs counted each year on numerous small waterbodies, totalling 1.3 km² in a study area of 96 km²) showed no relationship between reproductive output (as number of broods) and change in density in the following year (Pöysä & Pesonen, 2003). In comparison, densities at Mývatn (9–35 pairs km⁻²; 500–1900 pairs, 54 km² of water) showed strong positive correlation between production of young and change in numbers from year to year; and an even stronger relationship between insect food available in late summer and return rates (Gardarsson & Einarsson, 1997). The Mývatn study area, which totals 54 km² of freshwaters, is dominated by a single lake (37 km²) and its ecosystem processes. Food resources of most waterbirds are dependent on this lake, the main exceptions being those that primarily utilize surrounding ponds and marshes, including Eurasian teal, *Anas crecca* L., and pintail, *Anas acuta* L. Interannual variation in the food resources that appear to be critical to reproductive success are usually synchronized over the whole study area. The striking difference between the Icelandic and Finnish studies seems to be best explained by differences in habitat mosaic patch size (Wiens, 1989, 2002), rather than by the

Mývatn population being more ‘closed’ in contrast to the ‘open’ population structure of the Finnish sample, the explanation favoured by Pöysä & Pesonen (2003).

How are (flyway) populations of ducks determined?

Most of the ducks of Mývatn are migratory, spending the winter in a large distant area, western Europe, where they mingle with ducks from other western palaeartic populations; the Icelandic, or more particularly the Mývatn, subpopulations constitute minority units in the western European flyway. For this reason, the relationship between numerical change at Mývatn and global or regional western European population levels is difficult to disentangle. However, three of the Mývatn populations are thought to be resident within Iceland, mallard, harlequin duck and Barrow’s goldeneye, and it may be easier to find evidence of population limitation in these than among the migratory species. The Barrow’s goldeneye winters exclusively on fresh waters and almost 90% of the Icelandic population is found wintering on the Mývatn–Laxá system (Gardarsson, 1978). Its total numbers are remarkably stable and its density on the ice-free parts of Mývatn in winter is similar to the density attained by all ducks of the lake in summer, suggesting that it is limited in a straightforward manner by the carrying capacity of the habitat.

Concluding remarks

To sharpen the focus on the interpretation of the waterfowl population work at Mývatn, it is useful to compare the results with other studies, taking advances in general ecological theory into account. A long-term ecological study starting in the late 20th century inevitably is affected by progress in methods, especially in computation and multivariate statistics, and progress in the framing of general theory, especially landscape ecology and meta-population ecology (e.g., Hanski & Gilpin, 1997).

Three aspects of the Mývatn waterfowl studies are of particular interest and deserve further study:

- (1) The question of limitation of breeding numbers in an array of related species, varying in

dispersal or migratory habits and other life history details. Food resources strongly influence the production of young. Expressed as the total number or density of young produced in a breeding area. There is a linear correlation with estimated food availability on an area basis, rather than the more commonly used per capita productivity which leads to an asymptotic relationship. A response of adult breeders to food resources, rather than to the production of young or recruitment of locally produced birds to the breeding population, seems to determine return rates or interannual change in density of adult breeding ducks. Significant recruitment responses were found in greater scaup (lag 3 years), common scoter (lag 3 years) and harlequin duck (lag 2 years) in the first 15 years of this study (Gardarsson & Einarsson, 1994), but after extended monitoring in the period 1975–1999, only the common scoter continued to show a significant recruitment response.

- (2) The spatial pattern of the Mývatn study area differs radically from many other sites where breeding ducks have been studied. Being dominated by processes in a single, relatively large lake, population change of both ducks and some of their most important foods are synchronized on approximately the scale of study area. On the River Laxá, the Barrow's goldeneye, which utilizes both Lake Mývatn and its outlet river by dispersing in accordance with the current resource situation in each habitat, and the harlequin duck, which is restricted to the river, are indirectly dependent on processes in Lake Mývatn since their presence on the river is governed by the availability of suspension feeding blackfly larvae (Einarsson et al., 2004; see also Fig. 2). In practice, the coarse habitat mosaic leads to more significant results; it so happens that the study area as demarcated nearly coincides with one functional landscape unit. In contrast, a more typical study area of many small lakes or wetlands is likely to contain a number of subunits; if the food resources in each waterbody fluctuate independently, strong effects on breeding waterbirds may not show up in an area large enough to yield a quantitative sample of duck density and production.

- (3) Although resources in the breeding area seem to account for most of the reproductive success and much of the dynamics in annual density of breeding adults, the flyway population (or metapopulation) may be thought of as being a more appropriate scale when looking for population limitation in ducks, in the sense of determining how densities of populations are maintained in the long term (see Krebs, 2002). Using the flyway scale as a basis, relative breeding densities in any one locality may be limited by resources in that locality and the number of breeders in the total area occupied by a flyway population would be set by limits in the whole range or perhaps only the winter range.

The question where in the total range population limitation takes place was especially important at the onset of this study when it was debatable whether negative changes observed at Mývatn were caused by environmental change at Mývatn (including mink and strip mining of the lake bottom) or in the winter range (including habitat destruction and hunting pressure, but also climate-induced hydrological change). After almost three decades of research and monitoring, it has now become quite clear that habitat destruction and damage inflicted on the Lake Mývatn ecosystem by mining was a major agent causing population decline in both waterfowl and fish of the lake. Mining was brought to a halt in 2004, but rough calculations of sedimentation rates suggest that the recovery of the Mývatn ecosystem may take decades or even centuries. Management of the waterfowl populations will, however, continue to be a task where the whole flyway must be under consideration.

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Effects of water quality on habitat use by lesser scaup (*Aythya affinis*) broods in the boreal Northwest Territories, Canada

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Abstract

Populations of lesser scaup (*Aythya affinis*), an abundant duck in the northwestern boreal forest of Canada, have declined markedly over the past few decades. The limnological characteristics of northern wetlands used by lesser scaup and other waterfowl are inadequately documented and the possible effects of habitat quality or other factors on the use of water bodies by scaup are poorly understood. Waterfowl and limnological data, collected on a 38 km² area roadside study area near Yellowknife, Northwest Territories, were used to describe the characteristics of ponds and evaluate potential variables influencing use of water bodies by lesser scaup (and might therefore limit the growth of the lesser scaup population). The specific objectives of this study were to (1) describe and compare the water quality of natural ponds and roadside borrow pits created during highway construction; and (2) evaluate habitat preferences of lesser scaup broods by comparing water quality, physical features and invertebrate abundance in natural ponds and borrow pits that were used or avoided by brood-rearing lesser scaup. Twenty eight water quality, physical and biotic characteristics of ponds were measured in the field or from water samples collected at 48 water bodies. Waters are weakly alkaline, hard, non-saline, and meso-eutrophic. Natural ponds and artificial borrow pits created during highway construction had statistically significant differences ($p < 0.05$) in ten water quality variables, many of which can be attributed to the origin of the water bodies. Water bodies used by brood-rearing lesser scaup had significantly higher particulate organic carbon ($p = 0.01$), particulate organic nitrogen ($p = 0.01$), dissolved potassium ($p = 0.04$), and density of amphipod crustaceans ($p = 0.01$) than those water bodies without lesser scaup. Multiple regression analysis indicated that pond area and depth had a dominant effect on the presence of scaup broods but the effects of other water quality or biotic variables were unclear.

Introduction

The boreal forest region accounts for the largest expanse of wetlands and lakes in the world and is an important breeding ground for a diverse assemblage of waterfowl and other aquatic birds.

In Canada, as elsewhere in the world, the boreal region faces ever growing threats from developmental pressures (Senate Sub-committee on the Boreal Forest, 1999). In North America, lesser scaup (*Aythya affinis*, Eyton) are a waterfowl species of special interest because of recent

population declines (Afton & Anderson, 2001; Austin et al., 2000), particularly in the western boreal forest where more than half the population breeds. The cause of the decline is uncertain.

In the western boreal region near Yellowknife, Northwest Territories, Canada, nesting and brood-rearing lesser scaup and other waterfowl frequently use some water bodies in preference to others, although the reasons for such preferences are not entirely apparent (Fast et al., 2004). Selection of wetlands could be influenced by many factors including water chemistry, vegetation, invertebrates and physical features (McNicol, et al., 1987; DesGrange & Houde, 1989). Lesser scaup feed primarily on amphipods, other crustaceans, and aquatic insects (Austin et al., 1998) so any factor which influences the abundance of these invertebrates could influence scaup numbers as well.

One factor that could limit invertebrate abundance, and by extension, the suitability of habitat for scaup, is water quality (Scheuhammer et al., 1996). Water quality is influenced by many factors including surface runoff, ground water infiltration, precipitation, geology of underlying substrate, time of year, drainage, and size and depth of water bodies (Halliwell et al., 2002).

The purpose of our study was to gain a better understanding of wetlands in the boreal forest near Yellowknife, Northwest Territories, and determine how the features of those wetlands might influence their use by lesser scaup. Specific objectives were to describe the water quality of natural ponds and borrow pits, and to evaluate the possible influence of physical features, water quality, and invertebrate abundance on use of ponds by lesser scaup broods.

Study area

A 38-km² area bordering Highway 3 near Yellowknife (62° N, 144° W), Northwest Territories, Canada was used as a waterfowl study area by the Canadian Wildlife Service (CWS) from 1989 to 2001. The Yellowknife Study Area (YKSA) extends 400 m on each side of the highway over a distance of 48 km. Approximately 575 water bodies, ranging in size from <0.1 to 18.2 ha, occur

within the area; 262 are natural ponds and 313 are borrow pits (man-made ponds resulting from the excavation of large quantities of earth during highway construction). The YKSA lies at the southern boundary of the Canadian Shield so much of the land surface is rock outcrop with sediments occurring mainly in low areas. Soils in this area are dominated by clay, sand and gravel (Trauger, 1971). The entire area is underlain by discontinuous permafrost (EMAN North, 2003). Drainage courses follow the bedrock structure in which the main lines follow long straight lineaments, major fracture zones, or dominant joint systems in massive rocks (Wedel et al., 1990). Flow rates vary greatly throughout the year, with the freshet beginning in mid-late May, recession occurring from mid July to mid October (when freeze-up occurs), and base flow occurring from October to May (EMAN North, 2003). Both upland and wetland vegetation are typical of that found near the northern edge of the boreal forest (Fournier & Hines, 1999).

Methods

Criteria for selection of study water bodies

There were four factors considered in selecting water bodies for study:

- (1) Size – In an effort to reduce the number of variables affecting waterfowl use it was decided that the study water bodies should, if possible, be similar in size. As a result, several extremely large ponds and lakes were excluded. Water body size was also restricted to simplify field logistics.
- (2) Origin (natural ponds or borrow pit ponds) – Of the 48 total water bodies selected, 24 were borrow pits and 24 were natural ponds.
- (3) Distribution – The study area was divided into three equal sections to discern any spatial trends over the YKSA. Sixteen water bodies were selected from each section based their origin and use by lesser scaup.
- (4) Use by breeding lesser scaup – Water bodies known to have been used by one or more lesser scaup broods during the 14 year period were identified as water bodies with lesser scaup. Water bodies without lesser scaup were

selected from those ponds that were never observed to have been used.

Water quality field sampling program

The 48 water bodies were each visited once in July of 1999–2002. Access to sampling sites was dictated by pond shoreline morphology and vegetation, but generally, sites near the largest open water portion of the lake or pond were chosen. Samples were obtained from the main water body from an inflatable boat or by wading as far from shore as possible. Areas with aquatic vegetation were avoided because of the presence of increased variability of meter readings. Depth was measured using an Eagle depth sounder and confirmed with a weighted line. Field measurements of pH, conductivity [(mS/cm) or (μ S/cm)], turbidity (Nephelometric Turbidity Units (NTU)), water temperature ($^{\circ}$ C), and salinity (%) were taken using a Horiba U-10 water quality meter. In many instances, a 3-m pole was used to extend the Horiba sensor further toward the centre of the water body to ensure that neither the water column nor the substrate was disturbed near the sample site. The pH and conductivity readings were augmented using Hanna Instruments Piccolo Handheld pH and Hanna Instruments ATC Conductivity and TDS meters. Dissolved oxygen was measured in the field using an YSI dissolved oxygen meter. Water temperature was measured using both the YSI and a hand held ethanol thermometer. With the exception of the 2002 season (no chemical analysis were performed that year), hand dipped grab samples were taken from each water body. These samples were taken from approximately 20 cm below surface. Grab samples were analysed by certified, accredited and periodically audited laboratories in Burlington, Ontario and Yellowknife, Northwest Territories using standard laboratory techniques documented in the Dictionary of Lab Codes (1996 Unpublished Report, Environment Canada, Ottawa, Ontario). Water samples from every water body were analysed for physical variables (conductivity, colour, turbidity, total suspended solids, total dissolved solids, alkalinity), nutrients (nitrate/nitrite, NH_3 , total phosphorus, dissolved phosphorus, dissolved nitrogen, dissolved organic carbon, particulate

organic carbon, particulate organic nitrogen), and major ions (calcium, magnesium, sodium, potassium, fluoride, chloride, sulphate, silica).

Aquatic invertebrates

A survey of aquatic invertebrates, modified after the sweep sampling and scoring method of Lindeman & Clark (1999), was conducted in 2002 only. One standardized sweep was taken at five different locations at each water body. Sample locations were chosen as randomly as logistics permitted but were influenced somewhat by accessibility and time. It was impossible to sample at standardized locations with regard to aquatic plant communities as some ponds were completely vegetated and others were devoid of vegetation. All samples were taken at a depth of approximately 1 m by the same sampler (Walsh). Sweeps were performed using a D-net (net mouth 0.3 m wide) by scooping the flat mouth of the net from the surface, down to the bottom, across the substrate, and back to the surface of the water body in a digging motion covering 2 m. Each sweep sampled an area of approximately 0.6 m², and passed twice through the water column. Invertebrates accepted to be primary foods for lesser scaup were identified to the level of taxonomic Order in the field with the help of Clifford (1991). Amphipods are considered to be the most important food source for lesser scaup (Bartonek & Murdy, 1970; Austin et al., 1998; Lindeman et al., 1999), and therefore the actual numbers of amphipods were recorded. Most specimens were released after identification but a sample of specimens were preserved in ethanol and brought back to the lab to confirm identifications. Phyla known to be primary foods of lesser scaup include Arthropoda, Mollusca and Annelida (Bartonek & Murdy, 1970).

Lesser scaup

Data collected over a 14-year period (1989–2002) by CWS were used to evaluate the use of water bodies by lesser scaup. The average number of lesser scaup broods sighted on each water body during standardized surveys carried out in July and August of each year (see Murdy, 1963; Fournier & Hines, 1998 for methods) was used as

an index of water body use. Water bodies where broods were never seen in the 14 years were classified as water bodies without lesser scaup and those where broods were sighted one or more times were treated as water bodies with lesser scaup. Brood density was calculated by dividing the average number of broods observed on the water body each year by the size of the water body in hectares.

Statistical analysis

Preliminary analyses indicated that many of the data were not normally distributed. As a result, water quality, sediment quality and amphipod density were compared between natural ponds and borrow pits, and between water bodies with and without lesser scaup, using the non-parametric Mann–Whitney U Test (Freund & Wilson, 1993). For these two-sample comparisons, statistical significance was determined at the $p < 0.05$ level using Statgraphics Plus 4.1 software (Manugistics, 1998).

A multiple regression analysis was used to further evaluate patterns previously identified with the two sample (Mann–Whitney U test) comparisons. The regression analysis allowed an assessment, in a relative sense, of the potential importance of different water quality, physical, and biotic characteristics of ponds on habitat use by scaup broods. The general approach was to use model selection criteria to simultaneously evaluate possible hypotheses or explanations of habitat use (Burnham & Anderson, 2002; Johnson & Omland, 2004). First, potential variables were selected for a broad or global model. Second, the fit of the global model to the data was tested (Littell et al., 2002) and, third, various sub-models of the most complex model were considered to test specific hypotheses that might explain pond use by scaup broods. Models were then ranked and assigned relative weights based on both their fit to the data and their degree of complexity. Best ranking models are expected to be the most parsimonious from a statistical viewpoint, achieving a good degree of fit to the data without including an excessive number of variables.

Potential explanatory variables for multiple regression were chosen by selecting those variables that showed possible statistical significance

($p < 0.10$) in the Mann–Whitney U test analysis. As well, variables known from other studies to have an effect on habitat use by scaup broods were selected (e.g., Fast et al., 2004; Lindeman & Clark, 1999). To reduce the number of variables and alleviate potential problems with spurious correlations (i.e., Freedman's paradox, Burnham & Anderson, 2002: 17), the only variables retained were those where $p < 0.25$ in a simple correlation with the dependent variable (Hosmer & Lemeshow, 1989). To check for potential multicollinearity problems, the variance inflation factor (VIF) of the variables was assessed following Rawlings et al. (1998). Only variables with a VIF < 5 were included in the global model.

Candidate models were built to test specific hypotheses about the effects of water quality, pond type (borrow pit and natural pond), and amphipod abundance on habitat use by scaup broods while controlling for the expected effects of pond size and depth on habitat use (Fast et al., 2004). Thus, models were developed to determine if the effects of amphipod abundance, pond type, and water quality on habitat use were independent of the physical characteristics of the pond, and each other.

Fit of the most complex or global model was assessed using a general linear model approach to multiple regression and by inspecting plots of standardized residuals against each explanatory variable (Collett, 2003). Each candidate model was evaluated using a generalized linear model that incorporated a log link function and assumed a Poisson distribution of the dependent variable (Nelder & Wedderburn, 1972; Littell et al., 2002). The analyses were done using PROC GENMOD in SAS statistical software (Littell et al., 2002).

Models were ranked by Akaike's Information Criterion corrected (AICc) for small sample size and a model weight was calculated for each candidate model (Burnham & Anderson, 2002: 75). All candidate models within 4 AIC values of the model with the lowest AICc were considered to be somewhat supported by the data. To further determine which variables had the greatest influence on pond use, model averaged regression coefficients ($\hat{\beta}$) and their 95% confidence limits were estimated for each variable based on model weights (Burnham & Anderson, 2002). Variables

where 95% confidence limits of $\hat{\beta}$ overlapped 0 were considered to be statistically ambiguous.

Results

Physical water quality variables

Water bodies in the YKSA were neutral to moderately alkaline, with pH values ranging from 6.5 to 9.8. Field and lab measurements for conductivity were highly variable, ranging from 81.4 to 868.5 S/cm depending on time of year and type of water body (natural pond or borrow pit). True colour ranged from 23 to 270 True Colour Units (TCUs) while turbidity varied from 1.0 to 17.7 Nephelometric Turbidity Units (NTUs). Non-filterable residue, also known as total suspended solids, ranged from 2 to 78 mg per litre (mg/l).

Nutrient water quality variables

Dissolved organic carbon levels from the YKSA ranged from 15 to 63 mg/l. Total phosphorus ranged from 0.017 to 0.165 mg/l and total dissolved nitrogen ranged from 0.004 to 0.046 mg/l. Particulate organic carbon (POC) and particulate organic nitrogen (PON) ranged from 0.187 to 12.585 mg/l and 0.021–1.478 mg/l respectively.

Major ions

YKSA waters ranged from soft to moderately hard, with total calcium concentrations ranging from 7.25 to 76.85 mg/l and total magnesium concentrations ranging from 5.6 to 50.5 mg/l. Waters were moderately alkaline (30.1–236.1 mg/l total alkalinity). Salinity varied greatly from water body to water body (range: 1.3–169.0 mg/l chloride depending on type of water body). Sulfate values ranged between 1.8 and 125.0 mg/l.

Natural ponds vs. borrow pits

Borrow pits ($N=24$) and natural ponds ($N=24$) differed significantly in 10 of the 27 physical and water quality variables (Table 1). Natural ponds were significantly larger and deeper than borrow pits. Borrow pits had significantly higher pH, conductivity and total dissolved solids than natu-

ral ponds. Borrow pits also had significantly higher alkalinity, salinity, dissolved chloride, calcium, and magnesium than natural ponds. Although statistically significant, the absolute differences in median values for three of the parameters (pH, salinity and chloride) were relatively small.

Amphipods were found in 92% of the natural ponds and 67% of the borrow pits. The densities of amphipods were similar in natural ponds and borrow pits, with means of 3.8 ± 0.8 SE and 2.5 ± 0.6 SE individuals per sweep respectively ($p=0.69$, Mann–Whitney U test). The median for both natural ponds and borrow pits was 0.0 individuals/sweep, with ranges of 0–62 and 0–63 respectively.

There was a median density of 2.5 broods/ha (range: 0.0–8.6) on natural ponds and 1.7 broods/ha on borrow pits (range: 0.0–50.0). The differences between the two water body types were not significant ($p=0.48$, Mann–Whitney U test).

Water bodies with lesser scaup vs. water bodies without lesser scaup

Water bodies with lesser scaup broods ($N=29$) were significantly larger than those without broods ($N=19$) (Table 2). Possibly as a function of area, water bodies with lesser scaup also tended to be deeper. The only other physical and nutrient variables that differed significantly between used and unused water bodies were particulate organic carbon and particulate organic nitrogen, both of which were higher in water bodies with lesser scaup. Dissolved potassium (here termed an ion although functionally a nutrient) was significantly higher in water bodies with lesser scaup, but all of the other major ions were similar in water bodies with and without lesser scaup.

The density of amphipods in water bodies with lesser scaup broods was significantly higher than in those without, with median values of 1.8 (0.0–25.4) and 0.2 (0.0–23.0) individuals/sweep in the two types respectively ($p=0.01$). Other taxa of invertebrates known to be important foods for lesser scaup were also observed in both types of water bodies, including daphnia (Cladocera), mayflies (Ephemeroptera), water mites (Parasitengona), snails (Gastropoda), caddisflies (Trichoptera), copepods (Copepoda), damselflies and dragonflies (Odonata).

Table 1. Medians, ranges and *p*-values of Mann–Whitney U Tests comparing aquatic quality in natural ponds and borrow pits near Yellowknife, Northwest Territories, Canada (1999–2001)

Variables	Ponds			Borrow pits			<i>p</i>
	Median	Min	Max	Median	Min	Max	
<i>Physical variables</i>							
Area (ha)	2.6	0.3	12.8	0.2	0.1	1.1	<0.01
pH (pH units)	7.6	6.5	9.1	8.1	7.0	9.8	<0.01
Conductivity (s/cm)	201.1	81.4	469.5	346.9	140.2	868.5	<0.01
Salinity (mg/l)	0.00	0.00	0.20	0.01	0.00	0.04	<0.01
Alkalinity (mg/l)	96.3	30.1	203.5	153.7	61.3	236.1	<0.01
Colour (TCU)	80	30	260	51	23	270	0.04
Total Dissolved Solids (mg/l)	186.3	106.0	395.7	254.0	147.0	737.5	0.01
Total Suspended Solids (mg/l)	9	2	62	8	2	78	0.94
Turbidity (NTU)	3.9	1.0	11.9	3.5	1.3	17.7	0.86
Depth (m)	2.0	0.3	4.8	1.5	0.7	3.6	0.69
Water Temperature (°C)	20.4	16.0	21.7	20.1	16.8	23.3	0.43
Ammonia (mg/l)	0.054	0.021	0.277	0.047	0.024	0.366	0.35
Nitrate/Nitrite (mg/l)	0.005	0.004	0.037	0.005	0.004	0.046	0.62
Dissolved Nitrogen (mg/l)	0.528	0.004	1.224	0.667	0.284	1.082	0.12
Dissolved Organic Carbon (mg/l)	35	20	62	30	15	63	0.18
Total Phosphorus (mg/l)	0.031	0.017	0.165	0.033	0.018	0.124	0.87
Dissolved Phosphorus (mg/l)	0.02	0.01	0.04	0.02	0.01	0.06	0.68
Particulate Organic Carbon (mg/l)	1.625	0.187	12.585	0.842	0.235	12.176	0.21
Particulate Organic Nitrogen (mg/l)	0.190	0.021	1.478	0.116	0.026	1.460	0.54
<i>Major Ions</i>							
Dissolved Potassium (mg/l)	2.94	0.22	5.75	3.74	0.81	8.65	0.26
Dissolved Fluoride (mg/l)	0.18	0.09	0.23	0.19	0.09	0.28	0.12
Sulfate (mg/l)	5.8	1.9	18.8	5.0	1.8	125.0	0.67
Reactive Silica (mg/l)	1.14	0.35	4.94	1.62	0.72	5.18	0.08
Chloride (mg/l)	11.67	1.27	92.35	21.15	3.54	169.00	0.04
Calcium (mg/l)	18.23	7.25	57.50	26.55	14.25	76.85	0.01
Magnesium (mg/l)	12.6	5.6	34.2	22.3	6.4	50.5	0.01
Sodium (mg/l)	9.54	3.61	20.39	12.05	3.25	59.67	0.27

Based on the results of the Mann–Whitney U tests, the following variables were screened in for the multiple regression analysis: Water body area, depth, turbidity, particulate organic carbon, particulate organic nitrogen, dissolved organic carbon, dissolved potassium, and dissolved sodium. In addition, amphipod abundance and water body type (borrow pit or natural) were included in the analysis because of their expected effect on scarp habitat use (Fast et al., 2004). Three of the variables (particulate organic carbon, dissolved potassium, and dissolved sodium) were subsequently removed from the analysis because they were poorly correlated with brood use ($p > 0.25$)

but no variables had to be eliminated based on collinearity problems (i.e., had a variance inflation factor > 5).

The resulting global model contained seven variables and fit the data well ($r^2 = 0.75$, $p < 0.001$). Twenty-five possible explanatory models, all derived from the global model were then considered (Table 3). The potentially best model included two variables (water body area and depth) but seven other models fell within four AICc of this model and therefore were considered to be somewhat supported by the data (Table 4). Water body area was included in all eight of the top-ranking models and depth, dissolved organic

Table 2. Medians, ranges and *p*-values of Mann–Whitney U Tests comparing aquatic quality in water bodies used or not used by lesser scaup broods near Yellowknife, Northwest Territories, Canada (1999–2001)

Variable	Water bodies without lesser scaup			Water bodies with lesser scaup			<i>p</i>
	Median	Min	Max	Median	Min	Max	
<i>Physical Variables</i>							
Area (ha)	0.3	0.1	1.3	0.8	0.1	12.8	<0.01
Depth (m)	1.2	0.3	3.4	2.6	0.9	4.8	0.01
pH (pH units)	7.62	6.51	9.82	7.81	7.43	9.41	0.40
Conductivity (s/cm)	269.7	127.0	757.0	286.2	81.4	868.5	0.90
Salinity (mg/l)	0.01	0.00	0.04	0.01	0.00	0.04	0.99
Alkalinity (mg/l)	112.5	30.1	231.0	118.0	35.8	236.1	0.58
Colour (TCU)	83	23	270	58	24	230	0.38
Total Dissolved Solids (mg/l)	203.3	147.0	663.3	234.3	106.0	737.5	0.51
Total Suspended Solids (mg/l)	8	2	21	9	2	77	0.33
Turbidity (NTU)	2.9	1.0	8.3	4.4	1.3	17.7	0.09
Water Temperature (°C)	20.2	18.6	23.3	20.4	16.0	22.2	0.74
<i>Nutrient Variables</i>							
POC (mg/l)	0.771	0.187	8.64	2.290	0.376	12.585	0.01
PON (mg/l)	0.113	0.021	0.808	0.354	0.038	1.478	0.01
Ammonia (mg/l)	0.053	0.024	0.367	0.050	0.021	0.277	0.61
Nitrate/Nitrite (mg/l)	0.007	0.004	0.017	0.004	0.004	0.046	0.19
Dissolved Nitrogen (mg/l)	0.540	0.284	0.832	0.581	0.004	1.22	0.91
Dissolved Organic Carbon (mg/l)	33	15	61	31	16	63	1.00
Total Phosphorus (mg/l)	0.033	0.018	0.094	0.031	0.017	0.165	0.81
Dissolved Phosphorus (mg/l)	0.02	0.01	0.03	0.02	0.01	0.06	0.80
<i>Major Ions</i>							
Dissolved Potassium (mg/l)	2.72	0.22	5.75	3.24	1.43	8.65	0.04
Dissolved Fluoride (mg/l)	0.18	0.09	0.27	0.18	0.10	0.28	0.94
Sulfate (mg/l)	5.1	1.8	18.8	5.3	1.9	125.0	0.63
Reactive Silica (mg/l)	1.59	0.76	5.18	1.13	0.35	4.94	0.21
Chloride (mg/l)	12.65	3.54	139.00	15.96	1.27	169.00	0.68
Calcium (mg/l)	21.25	8.34	74.65	22.95	7.25	76.85	0.65
Magnesium (mg/l)	15.95	5.56	43.75	16.56	5.62	50.5	0.78
Sodium (mg/l)	7.59	3.25	28.05	10.8	4.25	59.67	0.11

carbon, and particulate organic nitrogen occurred in four, three, and two of the models, respectively. Water body type and amphipod abundance each occurred in one of the eight top models.

The model averaging procedures indicated that water body size was an important variable explaining use by scaup broods. The 95% confidence limits of $\hat{\beta}$ for depth overlapped 0 very slightly (4.1%) suggesting this variable was possibly important as well. The confidence limits of $\hat{\beta}$ for other variables overlapped 0 and so their possible effects on water body use were statistically ambiguous.

Discussion

Water quality on the YKSA was typical of northern waters in Canada (Wedel et al., 1990) and easily met or exceeded the standards documented in the Canadian Environmental Quality Guidelines for freshwater aquatic life (Canadian Council of Ministers of the Environment, 1999). Conductivity was moderate to high; pH values were neutral to alkaline; and colour, turbidity and total suspended solids were low. According to guidelines of Vollenweider & Kerekes (1980), water bodies on the YKSA would be classified as

Table 3. The relative support for different models of physical, water quality, and biological features that might explain the use of ponds by lesser scaup broods near Yellowknife, Northwest Territories, 1989–2001

Variables in model	Number of parameters in model	AICc	Δ AICc	AICc Weight
<i>Area^a Depth^b</i>	3	53.15	0	0.2668
<i>Area DOC^cDepth</i>	4	55.0649	1.91492	0.1024
<i>Area Depth Type^d</i>	4	55.2461	2.09606	0.0936
<i>Area Depth Amphi^e</i>	4	55.4014	2.25144	0.0866
<i>Area</i>	2	55.9371	2.78711	0.0662
<i>Area DOC</i>	3	56.4353	3.28533	0.0516
<i>Area PON^f</i>	3	56.5469	3.39687	0.0488
<i>Area DOC PON</i>	4	56.9759	3.82589	0.0394
<i>Area DOC Type</i>	4	57.5694	4.41938	0.0293
<i>Area Depth Amphi Type</i>	5	57.6702	4.52018	0.0278
<i>Area Type</i>	3	57.6905	4.54045	0.0276
<i>Area Turb^g</i>	3	57.9032	4.75315	0.0248
<i>Area Amphi</i>	3	58.0546	4.9046	0.023
<i>Area PON Type</i>	4	58.1753	5.02531	0.0216
<i>Area DOC Turb</i>	4	58.4478	5.29781	0.0189
<i>Area DOC Amphi</i>	4	58.5986	5.44863	0.0175
<i>Area PON Amphi</i>	4	58.8996	5.74961	0.0151
<i>Area DOC Depth Amphi Type</i>	6	59.6499	6.49988	0.0103
<i>Area DOC Amphi Type</i>	5	60.006	6.85599	0.0087
<i>Area DOC PON Amphi Type</i>	6	60.0671	6.91705	0.0084
<i>Area PON Amphi Type</i>	5	60.6707	7.52065	0.0062
<i>Area DOC Turb Amphi Type</i>	6	61.9831	8.83307	0.0032
<i>Area Amphi DOC Depth PON Turb Type</i>	8	62.7293	9.57933	0.0022
<i>Pond Type</i>	2	70.1631	17.0131	0.0001
<i>Amphi</i>	2	78.5908	25.4408	0

Models are ranked by Akaike's information criterion adjusted for small sample sizes (AICc). All models within 4 AICc units (Δ AICc) of the top ranked model were considered to be somewhat supported by the data.

^aArea = area of pond (ha).

^bDepth = depth of pond (m).

^cDOC = dissolved organic carbon (mg/l).

^dType = estimate for borrow pits measured against ponds.

^eAmphi = amphipod density (individuals/sweep).

^fPON = particulate organic nitrogen (mg/l).

^gTurb = turbidity (nephelometric turbidity units).

meso-eutrophic with moderate to high levels of dissolved organic carbon, total phosphorous, dissolved nitrogen, particulate organic carbon and particulate organic nitrogen. Waters were moderately hard and alkaline. The relatively high pH is perhaps surprising, given the location of the study area on the edge of the Precambrian Shield. Shield lakes and ponds in other parts of Canada tend to be somewhat acidic and have pH values in the 5.0–7.0 range (Wedel et al., 1990). The neutral to slightly alkaline nature of our study ponds and other lakes in the Yellowknife region probably

reflects impacts of weathered Precambrian bedrock and surficial deposition from the Laurentide continental glaciation (Wedel et al., 1990).

Ponds vs. borrow pits

A comparison of the water quality of natural ponds and borrow pits showed some significant differences, many of which can be attributed to the origin of the water bodies. Borrow pits are located close to the unpaved, gravel highway, have substrates composed of sand and clay, and are small in

Table 4. Model averaged results for physical, water quality, and biological features that might explain the use of ponds by lesser scaup broods near Yellowknife, Northwest Territories, 1989–2001

Variable	Regression coefficient ($\hat{\beta}$)	Standard error	Lower 95% confidence limit	Upper 95% confidence limit
Intercept	-1.9956	1.0928	-4.1374	0.1462
Area^a	0.2304	0.0532	0.1260	0.3347
Depth^b	0.4418	0.2460	-0.0404	0.9239
DOC ^c	-0.0322	0.0309	-0.0928	0.0285
Type ^d	-0.5052	0.7263	-1.9288	0.9184
Amphipod ^e	0.0131	0.0383	-0.0621	0.0882
PON ^f	0.8785	0.6272	-0.3508	2.1078

Variables in bold are statistically unambiguous based on 95% confidence limit.

^aArea = area of pond (m²).

^bDepth = depth of pond (m).

^cDOC = dissolved organic carbon (mg/l).

^dType = estimate for borrow pits measured against ponds.

^eAmphipod = amphipod abundance (individuals/sweep).

^fPON = particulate organic nitrogen (mg/l).

size. The elevated levels of calcium and chlorine can possibly be attributed to the former use of calcium chloride for dust suppression on the highway. The inorganic substrate in borrow pits is more exposed than that of natural ponds, and is more porous and permeable to water which may permit better connectivity between surface and ground waters. Higher levels of conductivity and total dissolved solids might result as fine particles and associated ions are disturbed and become dissolved in the water column of the borrow pits. Although values for pH, salinity, and chloride were significantly lower ($p < 0.05$) in natural ponds than in borrow pits, the actual difference in median values were less than 45%. Thus, the difference is probably not biologically significant. The greater alkalinity in borrow pits is expected in light of the elevated pH levels. Higher pH levels indicate greater groundwater contribution relative to surface water as occurs in the nearby Yellowknife River basin in late winter (Wedel et al., 1990). Despite the differences in physical and chemical properties of water from natural ponds and borrow pits, amphipods appeared to be similarly abundant in the samples from the two types of ponds.

Water bodies with lesser scaup vs. water bodies without lesser scaup

Only a few water quality variables differed significantly between water bodies used by lesser scaup

broods and those never used by lesser scaup broods. These included particulate organic carbon, particulate organic nitrogen and dissolved potassium. Elevated particulate organic carbon and particulate organic nitrogen may be related to increased feeding by scaup on invertebrates and therefore increased disturbance of sediment and excrement. It is unknown if the invertebrates are present because of higher nutrient levels, or if the nutrient levels are higher because of invertebrates and their capability to recycle nutrients. In either case, lesser scaup use of water bodies can be more directly attributed to invertebrate densities than to water quality *per se*. Amphipods, considered to be primary food source for lesser scaup, were found to be present in significantly higher densities in water bodies used by lesser scaup. This finding is consistent with conclusions of other studies that amphipod abundance is an important factor influencing wetland use by some species of waterfowl (Joyner, 1980; Godin & Joyner, 1981; Pehrsson, 1984; Parker et al., 1992).

The multiple regression analysis was carried out to further evaluate the relative importance of different factors on the presence of scaup broods. The analysis indicated the dominant effect that area and depth of water bodies had on the presence of scaup broods and suggested possible but definitely much weaker effects of a few other variables on use by scaup. Our inability to detect a strong effect of water quality on use by scaup

broods possibly reflected the low among water body variability in some of these measurements. We suspect that the dominant effect that area and depth exerted on scaup use of water bodies probably reflected the greater amount of habitat and larger population of invertebrates available in the larger water bodies.

Acknowledgements

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Diurnal time-activity budgets of redheads (*Aythya americana*) wintering in seagrass beds and coastal ponds in Louisiana and Texas

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Abstract

Diurnal time-activity budgets were determined for wintering redheads (*Aythya americana*) from estuarine seagrass beds in Louisiana (Chandeleur Sound) and Texas (Laguna Madre) and from ponds adjacent to the Laguna Madre. Activities differed ($p < 0.0001$) by location, month, and diurnal time period. Resting and feeding were the most frequent activities of redheads at the two estuarine sites, whereas drinking was almost nonexistent. Birds on ponds in Texas engaged most frequently in resting and drinking, but feeding was very infrequent. Redheads from the Louisiana estuarine site rested less than birds in Texas at either the Laguna Madre or freshwater ponds. Redheads in Louisiana fed more than birds in Texas; this was partially because of weather differences (colder temperatures in Louisiana), but the location effect was still significant even when we adjusted the model for weather effects. Redheads in Louisiana showed increased resting and decreased feeding as winter progressed, but redheads in Texas did not exhibit a seasonal pattern in either resting or feeding. In Louisiana, birds maintained a high level of feeding activity during the early morning throughout the winter, whereas afternoon feeding tapered off in mid- to late-winter. Texas birds showed a shift from morning feeding in early winter to afternoon feeding in late winter. Males and females at both Chandeleur Sound and Laguna Madre showed differences in their activities, but because the absolute difference seldom exceeded 2%, biological significance is questionable. Diurnal time-activity budgets of redheads on the wintering grounds are influenced by water salinities and the use of dietary fresh water, as well as by weather conditions, tides, and perhaps vegetation differences between sites. The opportunity to osmoregulate via dietary freshwater, vs. via nasal salt glands, may have a significant effect on behavioral allocations.

Introduction

The northern and western coasts of the Gulf of Mexico provide important wintering areas for redheads, *Aythya americana* (Eyton) (Michot, 2000; Woodin & Michot, 2002; Woodin & Michot, 2005). The Laguna Madre and adjacent bays along the Texas coast (Fig. 1) support the highest concentration of wintering redheads (about

300 000 birds) in North America (Weller, 1964; Bellrose, 1980; Woodin, 1996). Chandeleur Sound, Louisiana (Fig. 1) is also an important redhead wintering area and supports about 20 000 birds (Bellrose, 1980; Michot, 1997). The estuarine study sites in Louisiana and Texas contained areas of dense shoalgrass, *Halodule wrightii* (Aschers.) (Michot & Chadwick, 1994; Onuf, 1996), the rhizomes of which are the primary constituent

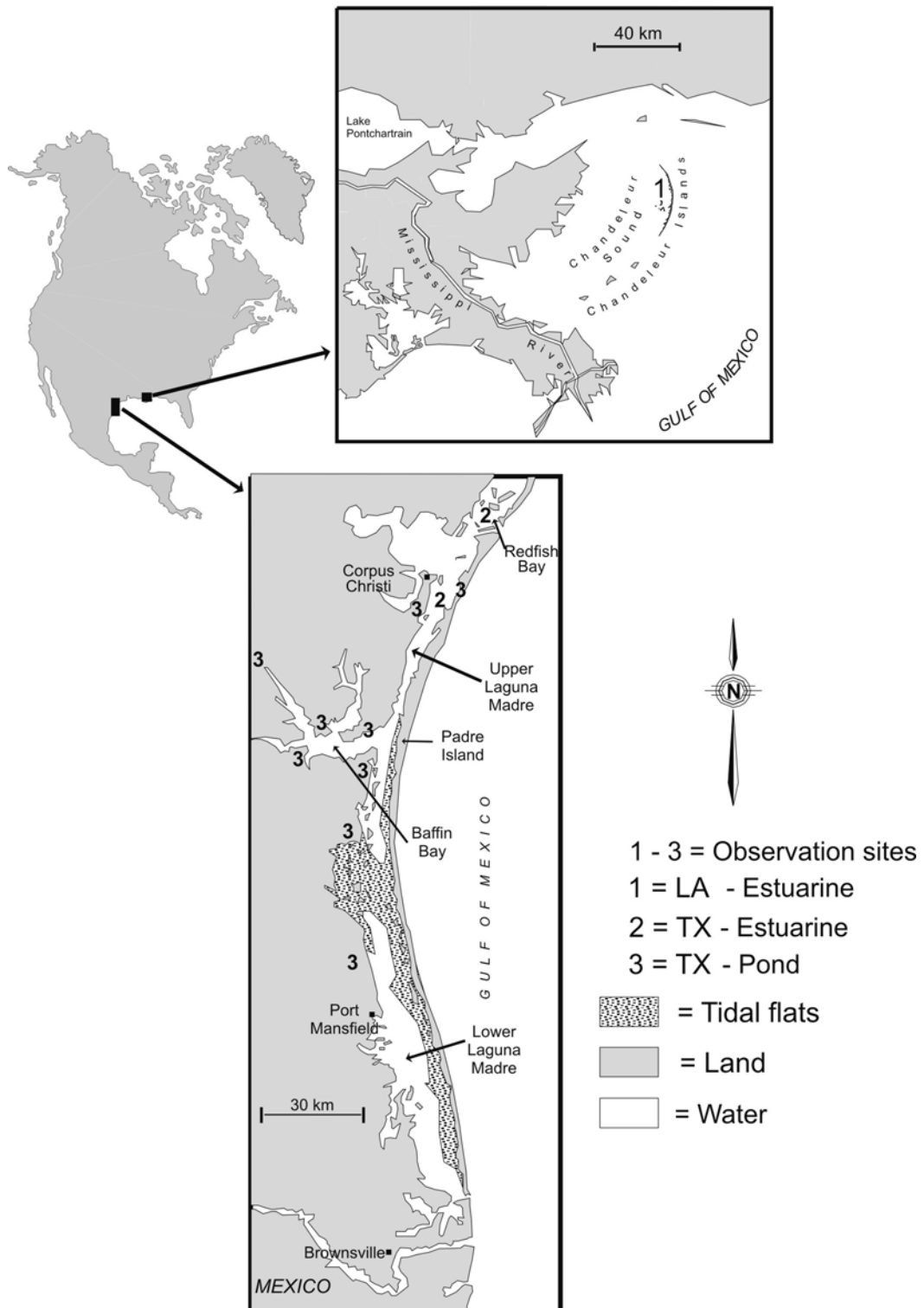


Figure 1. Map of study areas and observation sites for redheads in Louisiana and Texas, and locations on the North American continent. Observation sites: 1 = LA-E; 2 = TX-E; 3 = TX-P.

in the winter diet of redheads (McMahan, 1970; Cornelius, 1977; Michot & Nault, 1993; Michot & Woodin, 1997). The relatively stable food supply provided by shoalgrass rhizomes in the Laguna Madre area and at Chandeleur Sound has made them traditional wintering grounds for redheads.

Because of the frequently hyperhaline (> 35 ppt) conditions in the Laguna Madre and adjacent Redfish Bay, redheads in southern Texas typically fly to adjacent fresh or slightly brackish (0–12 ppt) wetlands to drink (Moore, 1991; Woodin, 1994; Adair et al., 1996; Michot, 2000; Skoruppa & Woodin, 2000). Supplementary fresh water is not used by redheads wintering at Chandeleur Sound, where waters are hypohaline (20–30 ppt) because of the outflow of fresh water from the Mississippi River and other rivers into coastal waters (Michot, 2000). We hypothesized that redheads in Texas, because of the increased energy expenditure associated with daily flights to obtain fresh water, would spend more time feeding and less time in other activities than birds in Louisiana. We further hypothesized that redheads were using the fresh-water ponds in Texas for drinking, resting, and other behaviors, but not for feeding. The objectives of our study were to compare time-activity budgets of wintering redheads from saltwater habitats in Louisiana and Texas and from low-salinity ponds in Texas, and to assess the effects of habitat, location, sex, month, time of day, year, and weather on those time-activity budgets.

Methods

We collected diurnal time-activity budget data from three areas: Louisiana estuarine areas (LA-E; estuarine [polyhaline] subtidal and intertidal aquatic bed and unconsolidated bottom habitat, classified according to Cowardin et al., 1979), Texas estuarine areas (TX-E; estuarine [hyperhaline] subtidal and intertidal aquatic bed and unconsolidated bottom habitat), and Texas ponds (TX-P; palustrine [oligosaline-mesosaline] aquatic bed and unconsolidated bottom habitat). In coastal Louisiana (29° 50' N, 88° 50' W) observations were taken from Chandeleur Sound, adjacent to the main island in the Chandeleur Island chain (Fig. 1), about 8–12 km south of the

Chandeleur Lighthouse. In coastal Texas (27° 30' N, 97° 30' W), observations of redhead flocks were taken from estuarine areas at Redfish Bay and the upper Laguna Madre, between Baffin Bay and Corpus Christi Bay, and from low-salinity ponds adjacent to (< 6 km from) the upper and lower Laguna Madre and Baffin Bay (Fig. 1). The portion of Chandeleur Sound (LA-E) used by redheads was approximately 6900 ha, and depth averaged 1 m (range 0–4 m). The Laguna Madre (TX-E) was approximately 75,550 ha and averaged about 1 m in depth as well (range 0–4 m). Most ponds (TX-P) were < 2 ha (range 0.1–12 ha) and average depths were usually < 0.3 m (range 0.1–1.5 m). Our study areas in Louisiana and Texas are described in detail in Hedgpeth (1947), Pulich (1980), Adair et al. (1990), Ritchie et al. (1992), Michot & Nault (1993), Michot & Chadwick (1994), and Michot et al. (1994).

We used spotting scopes to conduct scans (Altmann, 1974) every 15 min during daylight hours. We used scan sampling rather than focal bird sampling because of the difficulty of keeping track of an unmarked individual bird in large flocks, especially when birds were diving. At the estuarine sites, scans were conducted for 2 min and covered portions of flocks, and they were selected via random compass bearings, or complete flocks if the entire flock could be scanned in 2 min. At the pond sites, scans were conducted over the entire pond and lasted from 2–13 min. We conducted observations in half-day sessions (dawn to noon, noon to dusk). Within each half-day session, observations were divided into time periods as follows: 1 = early morning [06:00–08:59], 2 = late morning [09:00–11:59], 3 = early afternoon [12:00–14:59], 4 = late afternoon [15:00–18:00]. Observations began at 06:00 or as soon after that as there was adequate light, and they ended at 18:00, or before that if there was inadequate light.

Each month, November through March, we randomly assigned 10 half-day sessions (5 morning and 5 afternoon sessions) over 5 days per month per site (LA-E, TX-E, TX-P). From November 1987 through March 1988, we scanned redhead flocks at the TX-E sites only; from November 1988 through March 1989, we scanned flocks from the LA-E, TX-E, and TX-P sites. Flocks were observed from the shoreline at all sites. In LA-E, scans were conducted from four observation

blinds, spaced about 1 km apart, and flocks were selected at random from randomly selected blinds for observation. In TX-E we conducted observations from a vehicle, and we randomly chose flocks for observation from the shoreline. At TX-P, we selected ponds based on recent use by redheads. We assumed that locations chosen for observations (Fig. 1) were representative of the entire study area for each site (LA-E, TX-E, TX-P).

We placed all bird behaviors in one of five categories: REST, FEED, DRINK, SWIM, or OTHER. Sleeping or resting birds were classified as REST. FEED included all feeding behaviors identified by Mitchell et al. (1992) (i.e., head dip, dive, tip, glean, and peck) and waddle, a behavior very infrequently observed where the birds moved their feet under water along the substrate in a waddling fashion, apparently to expose submerged shoal-grass rhizomes. In a separate paper (Woodin & Michot, 2006) we reported on differences among feeding behaviors. The SWIM category included swim and alert swim. Birds that dipped their bill into the water and held the head in a bill-high posture were classified as DRINK. The OTHER category included primarily comfort movements (approximately 90%), as well as aggression, courtship, social, and alert behaviors. Flight behavior was not included in the study because the flock scan method is biased against detection of flying birds (i.e., only flocks on the water could be scanned). Sex was recorded for the birds observed during the 2-min scans at LA-E and TX-E. If light conditions prevented determination of sex, birds were classified as unknown. Sex of birds observed during the scans of redhead flocks at TX-P was not recorded. The number of birds in each flock was counted or estimated after each scan for all three sites.

At LA-E, automated instrumentation at the study site provided data recording, at 15 min intervals, for water level (tide), air temperature ($^{\circ}\text{C}$), wind velocity (km/h), and wind direction ($^{\circ}$ from true north), and ocular estimates were made for cloud cover (to the nearest 10%). For Texas scans, local climatological data were available from Corpus Christi (National Climatic Data Center, 1987–1989) at 3 h intervals for air temperature, wind velocity, wind direction, and cloud cover; we then used linear interpolation to estimate values for those four weather variables for each scan (15 min intervals). We transformed the two-

dimensional circular wind direction variable to the two orthogonal sine (east–west component) and cosine (north–south component) variables to remove the problem of circularity.

If we scanned the same flock more than once, we assumed that behaviors of birds in that flock were representative of behaviors of birds in different flocks had they been scanned during the same time periods. For each scan, the number of birds observed in each of the five behavioral categories was divided by the total number of birds observed during that scan to estimate the proportion of the time budget allocated to each activity. To remove the [0,1] bounds on proportions and to preserve the sum-to-1 constraint of proportions within a scan (i.e., an increase in the percentage of one behavior necessitates a decrease in one or more of the others), we used an additive log-ratio transformation (Aitchison, 1986). We simultaneously analyzed the five separate behavioral components of time budgets using multivariate analysis of variance (MANOVA). This was accomplished by using several different combinations of ratios, each of one behavior over another (e.g., $\log \text{FEED} / \log \text{OTHER}$) as dependent variables in the MANOVA. The Wilks' lambda criterion was used to determine significance for all multivariate tests, and Student's *t* test was used for all *a priori* pairwise comparisons. A conservative alpha level of 0.01 was used to reduce the experimentwise Type I error rate (Day & Quinn, 1989).

We tested for differences in time-activity budgets between the sexes by using a split-plot MANOVA model. We included only scans with at least 15 activities of males and females each for the LA-E ($n=475$, Year=2) and TX-E ($n=411$, Year=2) sites. Interactions of sex with location, time period, and month were considered in this model. In a separate MANOVA, we combined categories of male, female, and unknown sex for each scan to use the maximum amount of data ($n=2529$) for comparisons among sites, years, months, and time periods, under the assumption that interactions of sex with location, time period, and month were negligible for these comparisons, based on our results (see Differences in Activities between Sexes, below). For this model, time-activity budgets for winter 1988–1989 (Year 2) were compared among the three locations (i.e., LA-E, TX-E, and TX-P) by month (November

through March) and time period. Comparisons between years (1 = 1987–1988, 2 = 1988–1989) were possible only for the TX-E site, and this was done in a third MANOVA that also considered interactions of year with month and time period. We treated TX-E and TX-P as separate study locations, even though the birds using those two habitats undoubtedly shared the same time budgets.

We used ANOVA to compare weather variables (air temperature, wind direction, wind speed, cloud cover) between Louisiana and Texas for Year 2. We assessed the influence of weather conditions on feeding activity of redheads at the Louisiana and Texas estuarine sites (Year 2) by MANOVAs, with FEED as the dependent variable in four models. For that analysis we used a logit transformation (Aitchison, 1986) where $\text{logit} = \log (\% \text{FEED} / [100 - \% \text{FEED}])$. *A priori* pairwise comparisons among the four models were then made using general linear hypothesis tests to assess the relative contributions of weather and location on redhead feeding. The first of the four models, Model I, considered all main effects and all possible interactions (up to four-way) among the seven independent variables (location, month, time period, air temperature, wind direction, wind speed, cloud cover). Model II was the same as Model I, but with all location \times weather interactions removed. Model III included only the location, month, and time period variables (i.e., all weather variables removed), and Model IV included only the weather variables without location, month, and time period. Three pairwise comparisons were used to test hypotheses as follows: (1) Models I vs. II: H_0 = no difference in weather effects between locations; (2) Models I vs. III: H_0 = the addition of the weather variables to the model makes no contribution over and above that already contributed by location, month, and time period; (3) Models I vs. IV: H_0 = the addition of location, month, and time period to the model makes no contribution over and above that already contributed by the weather variables.

To test the effect of tide on SWIM activity at Chandeleur Sound, we first regressed the absolute value of change in tide height between observations (15 min) against SWIM to test the hypothesis that birds responded to tidal changes by swimming to stay located in optimal water depths. We also regressed water level change between observations

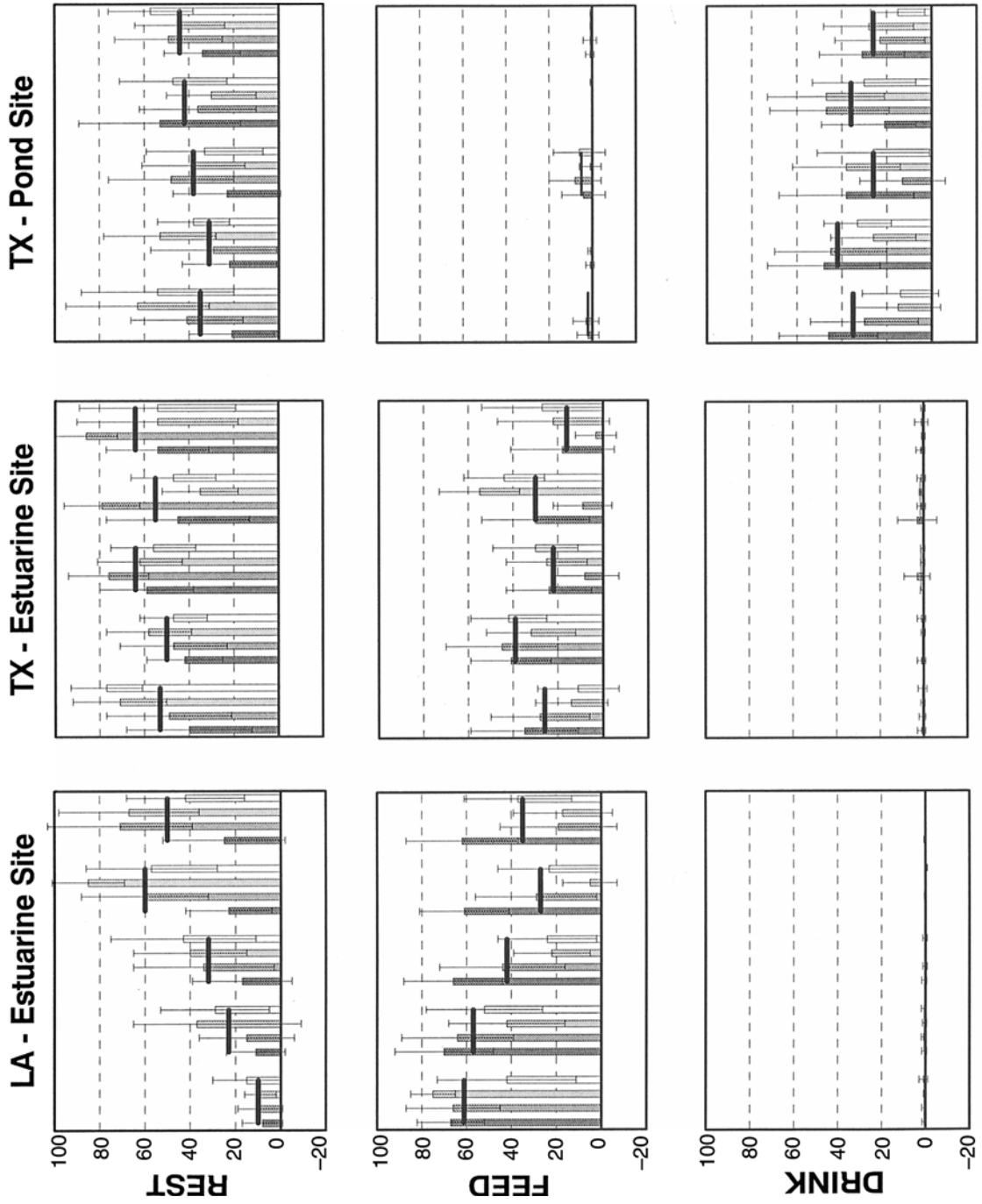
against month and time of day, then ran an analysis of covariance (ANCOVA) on SWIM with water level change, month, and time of day as the independent variables to determine if the water level effect would explain the variation attributed to month and time of day.

Results

We conducted a total of 2563 2-min scans from the LA-E ($n=747$), TX-E (Year 1: $n=759$; Year 2: $n=483$), and TX-P ($n=574$) sites; total observation time for all sites was 666 h. On TX-P, flocks were not recorded because individual birds moved on and off the ponds continuously during the scanning period; there we had 51 observation periods, with an average duration of 3.3 h each (range = 2–5 h). On the estuarine sites we observed a total of 215 flocks; each flock was observed for an average duration of 3.7 h (range = 1–8 h) with an average of 9.5 2-min scans per flock (range = 1–37). Behaviors were recorded on the estuarine sites for an average of 53 birds per scan (range = 15–142) and on the pond sites for an average of 201 birds per scan (range = 20–1820). The average flock size for scanned flocks was 315 birds (range = 20–1000) for LA-E and 846 birds (range = 30–10 000) for TX-E. Sexes were approximately equally distributed in scans from LA-E (50.0% males) and TX-E (62.6% males) sites.

Comparison of activities among study sites

The time budgets of redheads differed ($F=3.1$; $df=96$, 6765; $p<0.001$) among the three study locations according to month and time period (i.e., there was a significant 3-way interaction, study location \times month \times time). REST was the predominant behavior at all study locations (Fig. 2). Redheads at the TX-E site rested more than birds in the LA-E or TX-P sites (means: TX-E: 57%; LA-E: 40%; TX-P: 37%). Patterns of REST among months and diurnal time periods for redheads at the TX-E and TX-P sites tended to be similar, but LA-E differed in that a general increase was shown over the winter period (Fig. 2). FEED was a predominant behavior in both estuarine areas (TX-E: 26%; LA-E: 41%), whereas feeding was virtually nonexistent among redheads



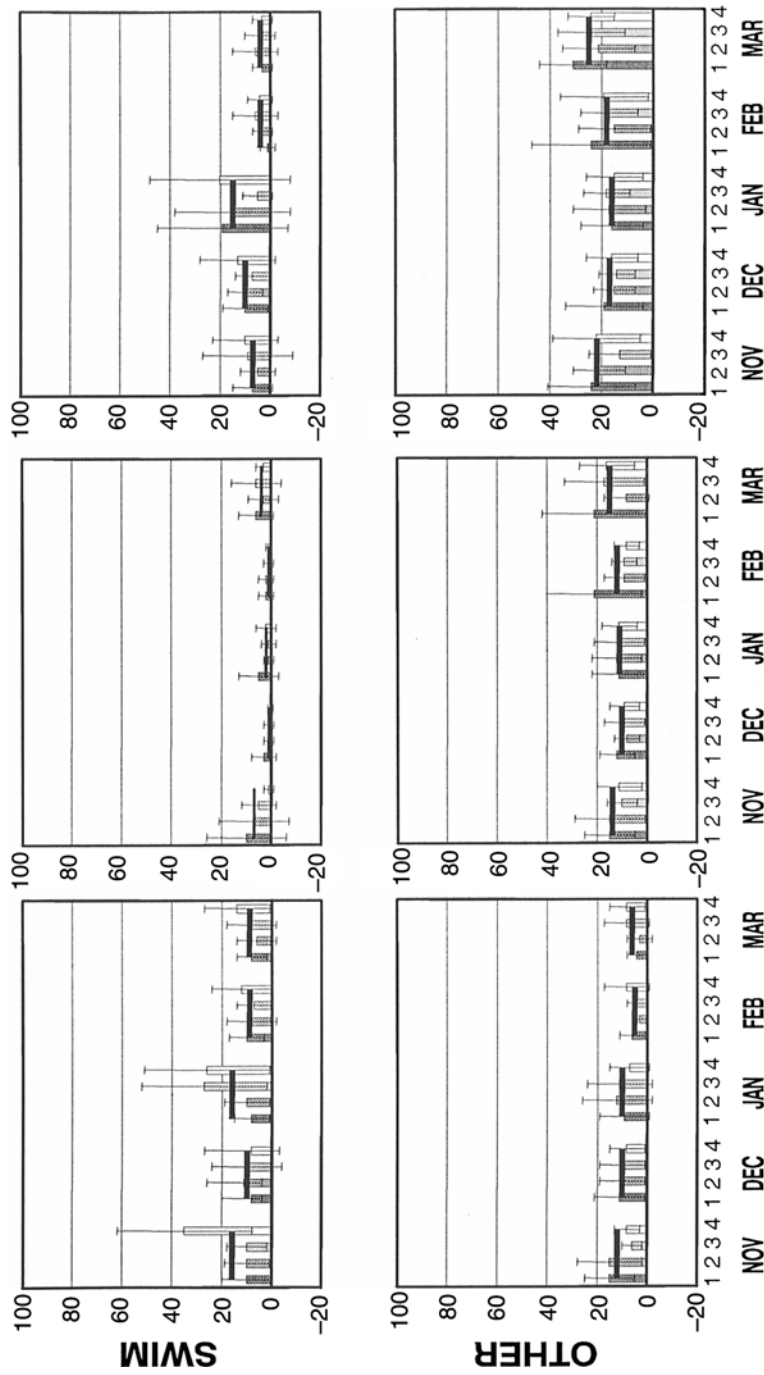


Figure 2. Time-activity budgets of redheads (sexes pooled) from the Louisiana estuarine ($n = 747$), Texas estuarine ($n = 483$), and Texas pond ($n = 574$) sites during winter 1988-1989 (Year 2). Values on y-axis are mean percentages, calculated on a per-scan basis, of birds observed exhibiting REST, FEED, DRINK, SWIM, or OTHER behaviors for all scans within a given time period \times month \times study site group. Vertical error bars indicate 1 SD, and horizontal bars indicate the monthly mean for that group. Numerals on x-axis indicate Time Periods (1 = early morning [06:00-08:59], 2 = late morning [09:00-11:59], 3 = early afternoon [12:00-14:59], 4 = late afternoon [15:00-18:00]).

at the Texas ponds (TX-P: 2%; Fig. 2). FEED by redheads at Chandeleur Sound (LA-E) was greater than for redheads at the Laguna Madre (TX-E). Virtually no drinking occurred at the saltwater areas (TX-E: 1%; LA-E: <1%), whereas DRINK was a frequent behavior of redheads at freshwater ponds (TX-P: 33%). Patterns of DRINK for birds on freshwater ponds resembled feeding patterns of redheads at the Laguna Madre (TX-E: Fig. 2). SWIM occurred on all three study sites, although birds at the Laguna Madre (TX-E) spent less time swimming than birds at the other two locations (TX-E: 3%; LA-E: 11%; TX-P: 9%). Birds on freshwater ponds spent more time in the OTHER category (primarily comfort movements) than did birds in either of the two saltwater areas (TX-E: 12%; LA-E: 8%; TX-P: 20%). When the Texas pond data were removed from the analysis, redheads from the two estuarine areas still differed ($F=2.2$; $df=48$, 4574; $p<0.001$) in their time budgets by month and diurnal time period. Redhead time budgets from the three areas are discussed separately below.

Louisiana estuarine sites

The two most frequent activities of redheads at LA-E were REST and FEED, which were inversely related by month and diurnal time period (Fig. 2). Birds showed a general increase in REST from early to late winter. The greatest REST activity occurred in the afternoon in all months but March, when the greatest REST activity occurred in time periods 2 and 3. The lowest REST occurred in the early morning period for all months.

Redheads showed a general decrease in FEED from early to late winter (Fig. 2). Percentage of feeding birds exceeded 40% for all time periods through December, whereas less than 40% of redheads were feeding in two or three time periods in January, February, and March. A high level of FEED (60–70%) was maintained during time period 1 (early morning) throughout the year, whereas the other diurnal time periods showed a decrease in FEED (to <40%) by late winter. The greatest FEED activity occurred in the early morning period for all months except November. The lowest FEED always occurred in the afternoon. Early afternoon showed the least amount of feeding activity for all months except November.

Redheads from LA-E showed decreases in both SWIM and OTHER activities in late winter (February and March; Fig. 2). They showed more OTHER activities in the morning during the early winter months, whereas those behaviors became more prominent in the afternoon by late winter. LA-E birds swam more in the afternoon than in the morning. A simple regression showed that SWIM was positively correlated with the absolute value of change in water level ($F=12.66$; $df=1$, 691; $p=0.0004$, $r^2=0.02$), so the birds generally swam more when tides were rising or falling, and less when tides were stable, but this relationship explained very little of the variation in SWIM. The change in water level was also associated with time of day and with month (ANOVA: $F=7.26$; $df=19$, 673; $p<0.001$), but SWIM was still significantly associated with month and time of day even when the water level effect on SWIM was adjusted for in the model (ANCOVA: $F=7.53$, $p<0.001$).

Texas estuarine sites

Like the Louisiana birds, the two most frequent activities of redheads at TX-E were REST and FEED, and there the two activities were also inversely related for month and diurnal time period (Fig. 2). While TX-E birds showed greatest REST in January and March, an overall pattern in REST through the winter was not apparent. TX-E birds showed a seasonal shift from peaks for REST in the afternoon in November and December to late morning (period 2) peaks for REST in January through March. Early morning (period 1) REST was relatively low for all months, and a subsequent low in resting activity occurred in the afternoon (time period 3 and/or 4) for all months except November.

Redheads at TX-E showed greatest FEED in December and February, but there was no discernible winter pattern in feeding activity (Fig. 2). FEED shifted from morning peaks in early winter, however, to afternoon peaks in late winter. Period 2 had the lowest FEED activity from January through March. SWIM in TX-E peaked in November and March, with very little swimming occurring in December through February. Laguna Madre redheads swam most in the morning. OTHER activities occurred at consistently modest frequencies (10–20%) from November through

January. Pronounced peaks in OTHER activities occurred in period 1 in February and in periods 1, 3, and 4 in March.

Texas pond sites

The one frequently occurring activity shared by redheads at TX-P with conspecifics at the two saltwater locations was REST (Fig. 2). There was no discernible seasonal pattern for birds resting at TX-P, although REST activity was slightly higher in February and March. Redheads showed the lowest REST levels in the early morning during all months except February. DRINK, the second most common activity of redheads at freshwater ponds, was inversely related to REST. There was no monthly pattern in drinking activity for pond birds although monthly peaks in DRINK occurred in December and February. Early morning was the time of highest drinking activity for all months except February. The very limited FEED activity by redheads at TX-P was concentrated in January, which was higher than other months. Birds showed a marked decrease in SWIM in late winter (February and March), but they showed no consistent effect by time period in swimming activity. No seasonal pattern for OTHER activities of redheads at TX-P was evident. With the exception of January,

OTHER activities were highest in the early morning, with a secondary peak in the late afternoon.

Differences in activities between sexes

At LA-E, sex was significant ($F=4.3$; $df=3, 453$; $p=0.0054$) as a main effect, but no interactions of sex with month or time period were detected ($p>0.40$). We found that differences in frequency of OTHER behaviors between males and females accounted for the significant main effect, but there was very little absolute difference between sexes in percent OTHER (males = 8.7%, females = 7.6%). Males and females from LA-E never differed by more than 2 percentage points among the combinations of months and time periods for any of the five behavioral categories used in this study.

At the TX-E, the year \times month \times sex interaction was significant ($F=3.46$; $df=6, 1240$; $p=0.0022$). The means of males and females differed by more than 2 percentage points only in November of both years (Fig. 3). In November, Year 1, males had higher values for FEED and OTHER and lower values for REST than females. In November, Year 2, however, males fed less and rested more than females, and the OTHER category did not differ between sexes. In Year 2, males were observed in the OTHER category more frequently

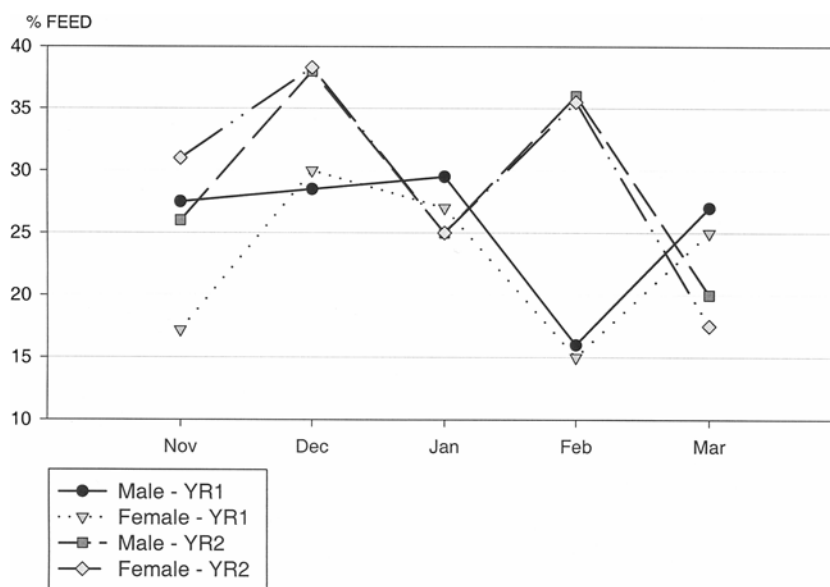
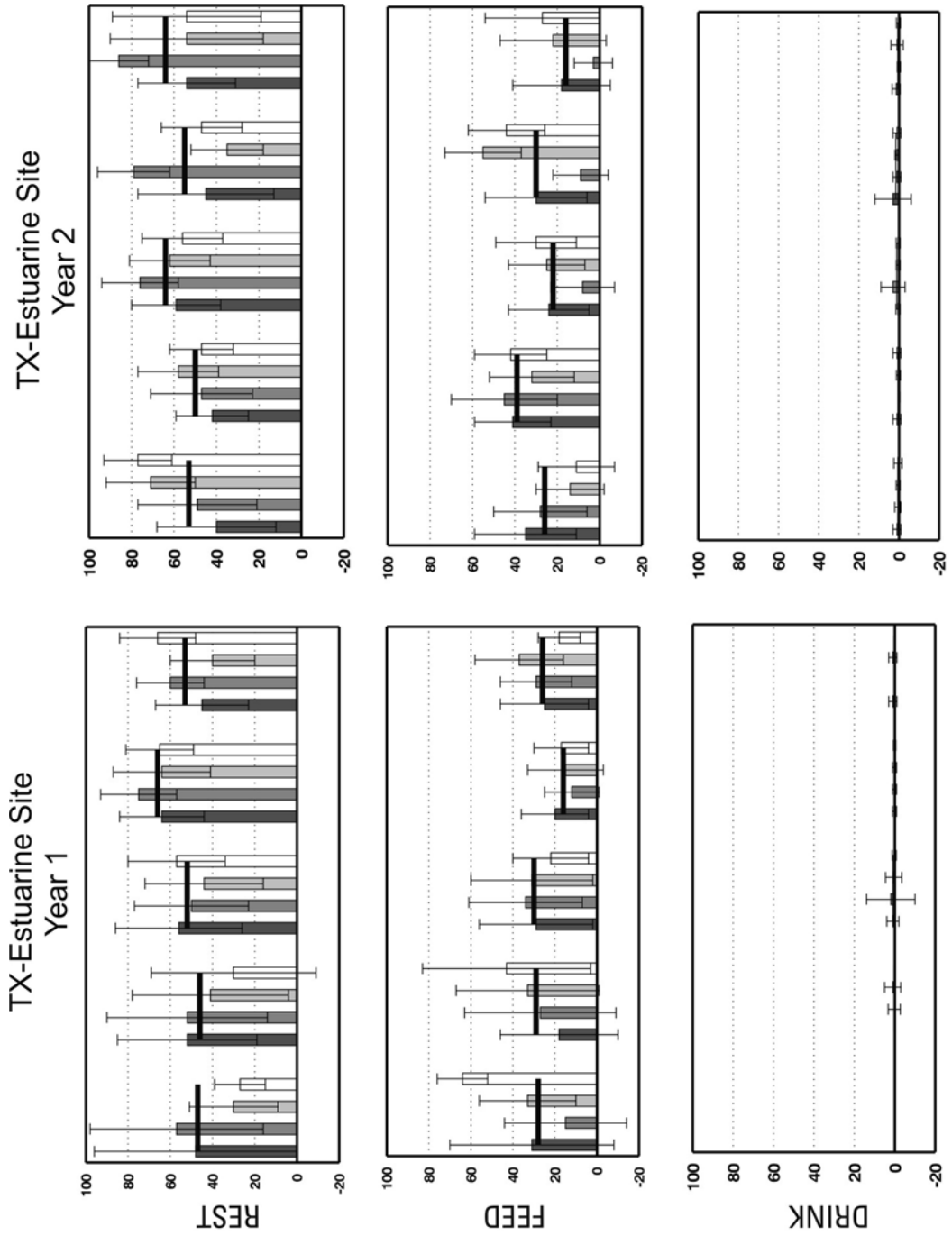


Figure 3. Comparison of feeding activity between male and female redheads from the Texas estuarine site during the winters of 1987–1988 (Year 1; $n=759$) and 1988–1989 (Year 2; $n=483$). Values on y -axis are mean percentages, calculated on a per-scan basis, of birds observed exhibiting FEED for all scans within a given year \times month \times sex group.



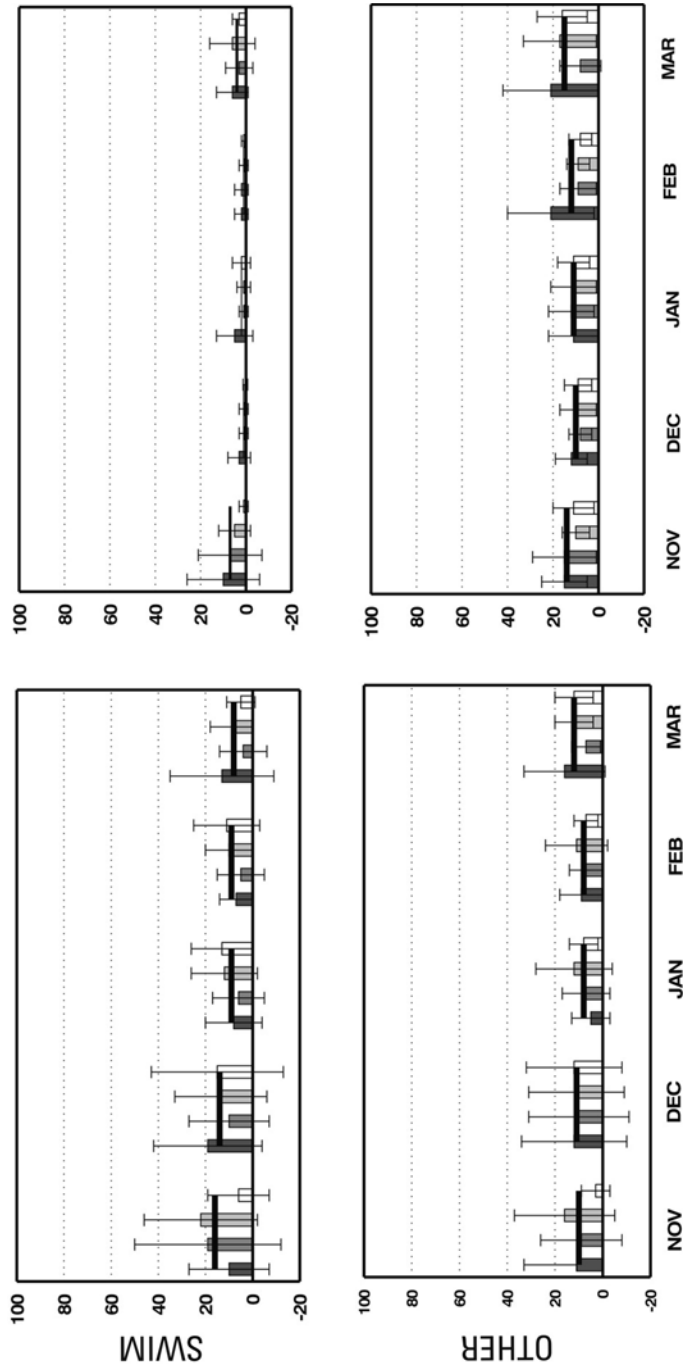


Figure 4. Time-activity budgets of redheads (sexes pooled) from the Texas estuarine site during the winters of 1987–1988 (Year 1; $n = 759$) and 1988–1989 (Year 2; $n = 483$). Values on y-axis are mean percentages, calculated on a per-scan basis, of birds observed exhibiting REST, FEED, DRINK, SWIM, or OTHER behaviors for all scans within a given time period \times month \times year group. Vertical error bars indicate 1 SD, and horizontal bars indicate the monthly mean for that group. Numerals on x-axis indicate Time Periods (1 = early morning [06:00–08:59], 2 = late morning [09:00–11:59], 3 = early afternoon [12:00–14:59], 4 = late afternoon [15:00–18:00]).

than females (but never >2% difference between sexes) for every month except March.

Differences in activities between years

TX-E birds showed different activity patterns during the 2 years of study; the year×month×time interaction was significant ($F=2.76$; $df=36, 3546$; $p<0.0001$). The birds showed a slight increase in REST and FEED (3% in each case) and a substantial decrease in SWIM (8%) from Year 1 to Year 2 (Fig. 4). DRINK and OTHER activities did not change in overall frequency. In Year 1 REST peaked in February, but in Year 2 it peaked in January and March (Fig. 4). February had less feeding activity than did all other months in Year 1, whereas in Year 2 peak feeding occurred in December and February. REST peaked in the morning, and FEED peaked in the afternoon during November and December of Year 1; in contrast, REST peaked in the afternoon and FEED in the morning in November and December of Year 2. The trend toward peaks in morning REST and afternoon FEED in late winter occurred only in Year 2. REST peaked in Period 2 more frequently than in any other time periods for both years.

Birds in Year 1 showed a pattern of decreased SWIM from early to late winter (Fig. 4). In Year 2 they showed very little swimming from December to February, with peaks in November and March. OTHER activities showed no consistent patterns between years.

Differences in activities associated with weather

During Year 2, air temperatures at the LA-E site were colder ($F=70.78$; $df=1, 821$; $p<0.001$) than temperatures at the TX-E site (means: LA-E: 12.9° C; TX-E: 18.7° C). Of the other weather variables, cloud cover was greater in Texas (mean=61%) than in Louisiana (43%); wind direction and wind speed showed no consistent patterns between the two sites. Our general linear hypothesis tests comparing the four models revealed that weather effects on feeding differed between Louisiana and Texas (Models I vs. II; $F=1.54$; $df=89, 974$; $p=0.0015$). We also found that weather effects on feeding are important and cannot be explained by location, time of day, or month (Models I vs. III; $F=4.260$; $df=185, 974$;

$p<0.001$) and that there are location effects on feeding that cannot be explained by using only information about the weather (Models I vs. IV; $F=2.237$; $df=109, 974$; $p<0.001$). In Texas, the mean temperature during the study was higher ($F=12.13$; $df=1, 252$; $p=0.0006$) during Year 2 (19° C) than in Year 1 (15° C). Cloud cover was greater ($F=8.70$; $df=1, 252$; $p=0.0035$) in Year 1 (78%) than in Year 2 (61%); wind speed showed no year effect, and wind direction showed no consistent pattern between years.

Discussion

Our hypothesis that redheads were using the freshwater ponds in Texas for drinking, resting, and other behaviors, but not for feeding, was supported by results from this study. We rejected, however, our hypothesis that redheads in Texas would spend more time feeding and less time in other activities than birds in Louisiana. We found the reverse to be true, i.e., that redheads in Louisiana spent more time feeding than birds in Texas. An alternative hypothesis is that the increased energy demand associated with daily flights by Texas redheads between the hyperhaline Laguna Madre and the adjacent hyposaline ponds is offset by the osmoregulatory benefits derived from increased consumption of fresh water, and that there is thus an overall savings in the daily energy budget. Because of the lower energy need for osmoregulation in birds using the ponds, less food would be required, and hence less time spent feeding. By contrast, redheads in Louisiana would have higher energy demands from osmoregulation because they do not use a supplemental fresh water source but rely solely on their salt glands to excrete excess salt ingested while feeding in salt water (Schmidt-Nielsen & Kim, 1964; Cornelius, 1982). Consequently, redheads in Louisiana must forage more to meet those increased energy demands.

Other possible explanations for the observed higher feeding frequencies of redheads in Louisiana compared to birds in Texas include dietary differences, thermoregulatory differences associated with climate effects, behavioral differences in foraging strategies, or annual cycle differences. Because diets of redheads in Louisiana and Texas have been shown to be virtually identical (T. C. Michot, M. C. Woodin & A. J. Nault, Submitted),

we ruled out any dietary effect on time budgets. Redheads in Louisiana winter approximately 270 km farther north than those in southern Texas. The colder temperatures at the more northerly latitude of Chandeleur Sound undoubtedly result in greater thermoregulatory costs for these birds (Brodsky & Weatherhead, 1984; Jorde et al., 1984). In addition, the Chandeleur Islands are situated approximately 30 km offshore from the Louisiana mainland, while the Laguna Madre is immediately adjacent to the Texas mainland. The largely open environment offered by Chandeleur Sound may account for the extent to which the behavior of Louisiana redheads may be affected by weather conditions in the Gulf of Mexico. Michot et al. (1994) found that redhead flocks in Chandeleur Sound do increase feeding and move in closer to shore to decrease fetch during periods of high winds and low temperatures. This also may account for the increased SWIM behavior in birds from Louisiana. In contrast, the environment of the Laguna Madre may present birds with sufficiently adequate shelter from prevailing southeasterly winds and occasional northern cold fronts to largely eliminate the need for them to alter their activities for thermoregulatory purposes. Our results showed that colder temperatures and other weather factors did indeed contribute to the time budget of redheads in Louisiana, but that weather alone does not fully explain the differences in feeding between the two locations. Mitchell et al. (1992) found that Texas redheads fed more as air temperature decreased.

The distribution or abundance of shoalgrass, *Halodule* (Endl.), could also be a factor in the behavioral differences shown. The nutritional quality and belowground biomass of *Halodule* during the wintering period was similar for Louisiana and Texas (Cornelius, 1975; Michot & Chadwick, 1994; Mitchell et al., 1994; Onuf, 1996; Michot, 1997), so it is unlikely that redheads in Louisiana had to spend more time extracting rhizomes from the substrate. In fact, redheads in Louisiana spent less time feeding by diving, as opposed to tipping and dipping, than redheads in Texas (Woodin & Michot, 2006), so the Louisiana birds would realize savings in energy and time by feeding in shallower waters. Average continuous patch size of *Halodule wrightii* was smaller at Chandeleur Sound (mean = 20 m, max = 152 m,

along transects perpendicular to shoreline; T. C. Michot & H. A. Neckles, unpublished data) than at the Laguna Madre, where typical *Halodule* patches were virtually continuous across the entire bay, or along a side, for hundreds of meters (Onuf, 1996). This may mean that, once established at a feeding site, redheads in Louisiana have to spend more time moving among patches. This should not, however, result in an increase in the time spent feeding once on a patch, assuming that the birds would spend as much time feeding as necessary to obtain the required nutrients (Perry et al., 1986). If SWIM is increased to facilitate movement between patches, that may partially explain the decrease in REST among Louisiana redheads, compared to Texas, assuming that FEED is held constant. The increase in SWIM at the expense of REST would also contribute to the increased energy demand among Louisiana birds, and thus to increased FEED overall (though not necessarily within a patch).

The daily flights to coastal ponds by redheads in Texas (Moore, 1991) are reflected in the similarity of monthly activity patterns shown for FEED at TX-E and DRINK at TX-P (i.e., peaks in December and February, but no upward or downward pattern over time). Redheads wintering at LA-E did not engage in this type of daily flight activity. The gradual decline through winter in FEED by redheads at LA-E could reflect decreased energetic needs and acclimation to osmoregulation by birds in a saltwater environment without the use of supplementary fresh water. Since supplementary fresh water will assist salt glands in osmoregulation (Cornelius, 1982), use of fresh water by redheads in the hyperhaline Laguna Madre could explain the lack of any overall winter pattern (i.e., increase or decrease) in feeding at that site, or in drinking in the adjacent ponds. The seasonal pattern (decreased feeding) shown for Louisiana, and not Texas, supports the role of osmoregulation over the other factors (diet, thermoregulation, plant differences) in the higher feeding levels in Louisiana.

Annual cycle events could contribute to the seasonal pattern of FEED and REST shown for LA-E. The high level of feeding activity in early winter could result from post-migratory hyperphagia to build up depleted body lipid reserves. Indeed, birds at Chandeleur Sound did arrive in a very lean con-

dition and continued to put on body fat through the winter (T.C. Michot, unpublished data). It could be that increased feeding was needed to replenish a lipid deficit, then feeding could be reduced in mid- to late-winter once an acceptable lipid level was achieved. Redheads in Texas, however, also showed the pattern of lean post-migratory arrival and increased body lipid levels through the winter (M. C. Woodin, unpublished data), yet they did not show the high levels of feeding in early winter that were shown in Louisiana birds. Therefore, it is unlikely that the pattern was associated with nutrient reserve levels or annual cycle differences, and more likely that local habitat factors played a greater role.

Redheads at LA-E showed a very high level of feeding in early morning throughout the winter, whereas redheads at TX-E showed either no diurnal pattern or increased feeding in the afternoon. Mitchell et al. (1992) found that redheads in the lower Laguna Madre, like those at LA-E, fed more during early morning. Early morning feeding peaks have been shown for several waterfowl species (Pethon, 1967; Minot, 1980; Madsen, 1988; Paulus, 1988b) and may indicate a lack of nocturnal feeding in that it would serve to overcome the deficit in energy intake from nocturnal inactivity. If so, this would mean that redheads feed at night more in Texas than in Louisiana. Saunders & Saunders (1981) speculated that redheads in the Laguna Madre de Tamaulipas, Mexico, were feeding at night based on observed signs of feeding activity (floating feathers and shoalgrass leaves). Adair et al. (1996) and Moore (1991) found that redheads continued to make flights between the Laguna Madre and the adjacent ponds at night, especially during moonlit nights, so night feeding may have been occurring then as well. At Chandeleur Sound, redheads were observed feeding at night on at least one occasion, and 24 of the 50 redheads collected at night had food in their esophagi, which would indicate recent feeding activity (T. C. Michot, unpublished data). Thus, because night feeding probably occurs to some extent on both areas, the higher morning feeding in Louisiana redheads is probably not related to a lack of night feeding there. Colder temperatures in the early morning in Louisiana may have contributed to the increased feeding during that time period.

Coastal ponds in Texas served redheads in other ways besides providing resting sites and

sources of drinking water, since redheads at the ponds exhibited greater frequency of OTHER activities (mostly preening and other comfort behaviors) than did birds at the estuarine sites in Texas and Louisiana. Increased occurrence of preening and other comfort activities for redheads on freshwater ponds have been noted by Woodin (1994) and Mitchell et al. (1992). The high degree of comfort movements and swimming behavior on the ponds could be displacement behavior in response to crowding caused by the high densities of birds and decreased spacing on the ponds (Adair, 1990). Cotgreave & Clayton (1994) found that the amount of time spent in maintenance behavior by birds was not correlated with morphology, molt, latitude, or season, but that it may be correlated with ectoparasite load; we have no knowledge of ectoparasite loads among wintering redheads, but endoparasite loads at LA-E were exceptionally low (Michot et al., 1995). Courtship behaviors may also be elevated among redheads at freshwater ponds of coastal Texas (Woodin, 1994).

The higher frequency of SWIM at LA-E vs. TX-E may have been due to the smaller *Halodule* patch size or to wind-related flock movements to reduce fetch, as discussed above, or to the greater tidal amplitude in Louisiana (about 1 m) vs. Texas (about 2 cm). As tide levels, and subsequent water depths, changed through the diurnal period at Chandeleur Sound, the redheads had to swim to stay in water that was the optimum depth for feeding (Michot et al., 1994; Mitchell, 1992). This was supported by our finding that SWIM was correlated with the change in water level for Louisiana redheads; however, the higher frequency of SWIM in early winter and in the afternoon was not explained by greater tidal amplitude at those times.

Effects on migratory water birds of recreational fishing and other types of human disturbance have been described by Pfister et al. (1992), Bell & Austin (1985), and Korschgen et al. (1985). It is unlikely, however, that the higher levels of SWIM at TX-E during Year 1 over Year 2 was caused by higher levels of disturbance. On the contrary, TX-E Year 2, which had the lowest SWIM, also had higher levels of disturbance (18.6% of the scans had potential disturbance factors such as boats, aircraft, or fishermen in proximity to the flocks) than the TX-E Year 1 or LA-E Year 2 sites (6.0%

and 5.9% potential disturbance factors, respectively; Michot & Woodin, unpublished data).

Although we discovered that there were significant differences between activities of males and females at both Chandeleur Sound and Laguna Madre, the absolute differences shown were slight and showed no consistent patterns. Therefore, we ascribed the detection of statistically significant differences in this study as a consequence of large sample size and probably not biologically important (Tacha, 1982).

Habitat types and variation in weather patterns have been related to time and activity budgets of ducks (Morton et al., 1989; Rave & Baldassare, 1989; Paulus, 1988a; Turnbull & Baldassare, 1987; Miller, 1985; Paulus, 1984). Often, variation in time and activity budgets is interpreted as a bioenergetic response to influences such as variable rate of food intake in different habitats, differential demand for nutrients among sex and age groups, or weather-induced changes in thermoregulation (Paulus, 1988b). Based on the results of this study, water salinity is also a factor which can influence time and activity budgets of waterfowl. Osmoregulatory strategies, seldom recognized as sources of variation in time-activity budgets of birds, should be considered in bioenergetics investigations of avian species inhabiting saline and hypersaline environments. We believe that diurnal time-activity budgets of redheads on the wintering grounds were influenced by water salinities and the use of fresh water, and by weather conditions, tides, and vegetation differences (patch size) between sites.

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Foraging behavior of redheads (*Aythya americana*) wintering in Texas and Louisiana

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Abstract

Redheads, *Aythya americana*, concentrate in large numbers annually in traditional wintering areas along the western and northern rim of the Gulf of Mexico. Two of these areas are the Laguna Madre of Texas and Chandeleur Sound of Louisiana. We collected data on 54,340 activities from 103 redhead flocks in Texas and 51,650 activities from 57 redhead flocks in Louisiana. Males and females fed similarly, differing neither in levels of feeding (percent of all birds in flock that were feeding) ($p > 0.90$) nor in percentages of birds feeding by diving, tipping, dipping, or gleaning from the surface ($p > 0.10$). The foraging level of redheads in the upper Laguna Madre region was relatively constant throughout two winters. Foraging of redheads in early winter in Louisiana was significantly greater than redhead foraging in the upper Laguna Madre, but by late winter, foraging by redheads in Louisiana had declined to the same level as that shown by redheads foraging in the upper Laguna Madre. The overall foraging level of redheads from Chandeleur Sound was greater (41%) than that of redheads in the upper Laguna Madre (26%), yet it was quite similar to the 46% foraging level reported for redheads from the lower Laguna Madre. Redheads in the upper Laguna Madre region of Texas fed more by diving than did those in the Chandeleur Sound and the lower Laguna Madre. Diving increased in frequency in late winter. Greater reliance by redheads on diving in January and February indicates that the birds altered their foraging to feed in deeper water, suggesting that the large concentrations of redheads staging at this time for spring migration may have displaced some birds to alternative foraging sites. Our results imply that the most likely period for food resources to become limiting for wintering redheads is when they are staging in late winter.

Introduction

In winter, approximately 80% of the continental redhead, *Aythya americana* (Eyton), population historically has occurred in a few relatively shallow coastal lagoons, bays, and nearshore waters along the coast of the Gulf of Mexico (Weller, 1964; Bellrose, 1980; Woodin, 1996; Michot, 2000). Total numbers of redheads wintering in the Gulf of Mexico region average 640,000 birds (Michot, 2000). Two of these traditionally important wintering areas are the Laguna Madre of Texas and Chandeleur Sound of Louisiana

(Fig. 1). Several hundred thousand redheads winter annually in the Laguna Madre (mean = 402,000), and about 15,000 annually spend the winter in Chandeleur Sound (Michot, 2000).

Redheads wintering in Texas use both freshwater and saltwater habitats, although redhead foraging essentially is limited to salt water (Adair, 1990; Mitchell et al., 1992; Woodin, 1994). Redheads in Louisiana also limit their feeding to saltwater habitats (Michot & Nault, 1993; Michot et al., 1994). Redheads wintering in south Texas and Louisiana consume primarily shoalgrass, *Halodule wrightii* (Aschers), rhizomes, although

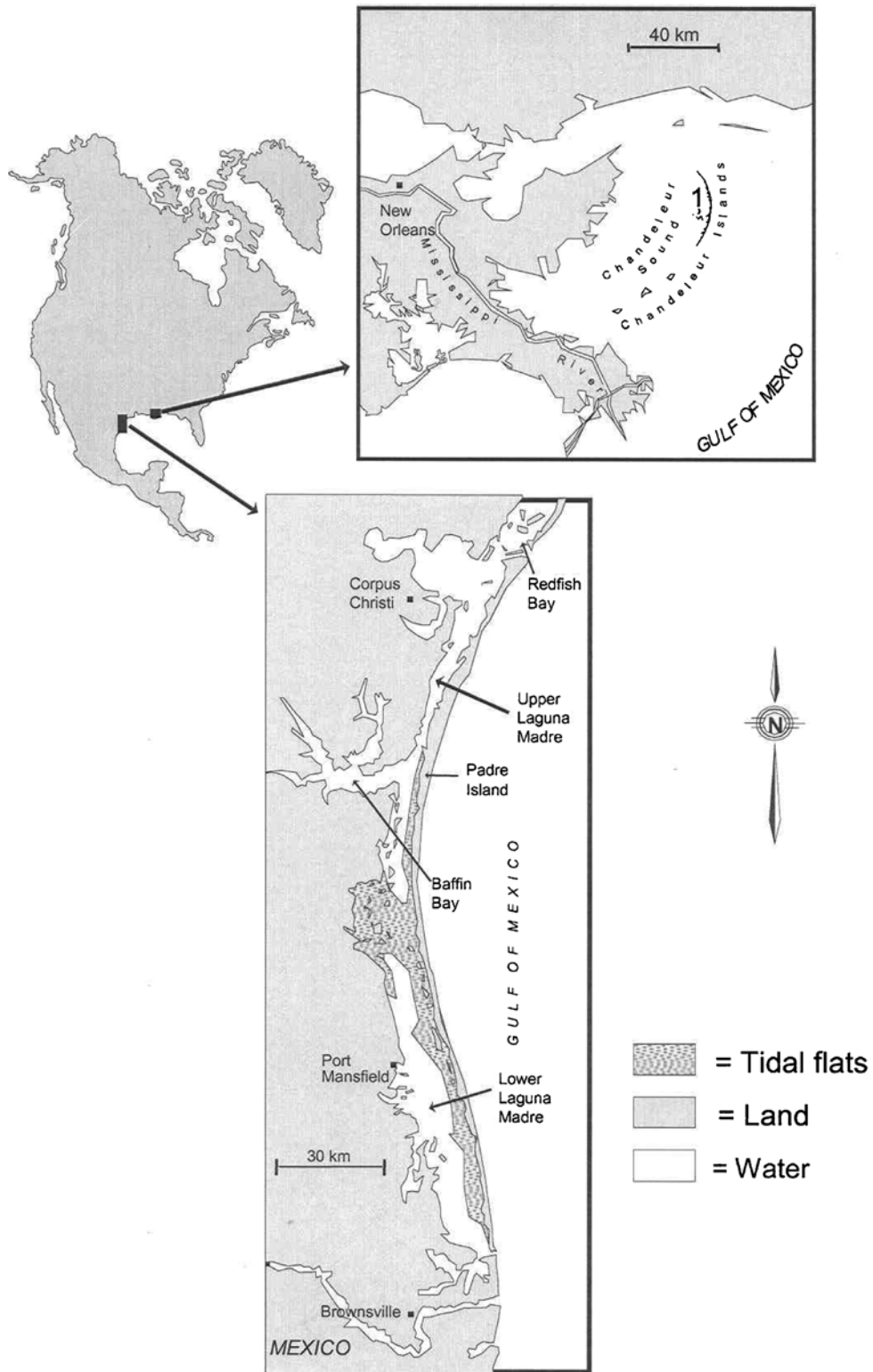


Figure 1. Locations of the Laguna Madre, Texas and Chandeleur Sound, Louisiana.

marine molluscs are also taken widely (McMahan, 1970; Cornelius, 1977; Michot & Nault, 1993; Woodin, 1996).

Time-activity budgets of waterfowl in winter can be used to produce data on differential habitat use, evaluate responses of waterfowl to environmental conditions, make inferences about energy budgets, and compare populations in different parts of the winter range (Paulus, 1988a). For example, variation in frequency of diving and other foraging behaviors is an indicator of variation in water depth and foraging efficiency. For redheads, feeding rates decline from 11 dips/min in shallow water, to 7 tips/min in intermediate depths, to but 3 dives/min in deeper water (Mitchell et al., 1992). Foraging flocks of redheads prefer shallow water (often only 12–30 cm deep), where the most commonly observed feeding behaviors are dipping and tipping (Mitchell, 1992; Mitchell et al., 1992). While redheads often forage by diving (Woodin & Michot, 2002), this is an energetically costly means of acquiring food (Lovvorn & Jones, 1991). Diving tufted ducks, *Aythya fuligula* (L.), for example, showed an average output of mechanical power nearly an order of magnitude greater (1.349 watt) than swimming tufted ducks (0.182 watt) (data from Stephenson et al., 1989). Foraging behavior and water depth are related, so patterns of foraging behavior in winter reflect differential habitat use (by depth) and, hence, variable foraging efficiency. These interrelationships can be useful in comparing birds in different parts of the winter range; nutrient reserves and foraging efficiency become especially important in areas such as Louisiana, where birds may be at or near carrying capacity (Michot, 1997). Our objectives in this study were to: (1) compare foraging of male and female redheads, (2) compare foraging behavior of redheads in Texas and Louisiana, (3) relate water depth to foraging behavior, and (4) interpret variation in foraging behavior of redheads relative to local bathymetry and energetics in winter.

Study sites

The Laguna Madre of Texas is one of only six large, hypersaline lagoons on Earth. The other large, hypersaline lagoons are the Laguna Madre

of Tamaulipas (Mexico), the Sivash (Crimean Peninsula, Ukraine), Laguna Ojo de Liebre (Baja California, Mexico), and Spencer Gulf and Shark Bay, both of which are in Australia (Tunnell & Judd, 2002). When combined, the Laguna Madre of Texas and the Laguna Madre of Tamaulipas (separated by the Rio Grande delta by only 75 km) are the largest hypersaline system in the world, with a combined surface area of 3800 km² Mean Sea Level (MSL) (Tunnell & Judd, 2002). The Laguna Madre of Texas extends 185 km from Corpus Christi Bay south to the delta of the Rio Grande at the Mexican border and is sheltered from the Gulf of Mexico along its entire length by Padre Island (Fig. 1). The Laguna Madre of Texas is shallow, with mean water depth of 1.2 m and maximum water depth of about 3 m; mean width is 7 km, and maximum width is 12 km (Tunnell & Judd, 2002). The Laguna Madre of Texas is composed of two distinct basins, the upper Laguna Madre and the lower Laguna Madre, separated by exposed tidal flats (Fig. 1). The upper Laguna Madre is oriented north-northeast by south-southwest, with surface area of 191 km² mean low water (MLW) and 277 km² mean high water (MHW). The lower Laguna Madre is oriented north-northwest by south-southeast and has a surface area of 727 km² MLW and 1364 km² MHW. The greater relative difference between MLW area and MHW area for the lower Laguna Madre is caused by the expanses of adjoining wind-tidal flats (Tunnell & Judd, 2002).

Based on the classification scheme of Vollenweider & Kerekes (1980), the Laguna Madre generally is eutrophic but ranges from mesotrophic to hypertrophic (Whitledge & Pulich, 1991). The limited number of channels connecting the Laguna Madre with the Gulf of Mexico results in exceptionally small (2–3 cm) daily amplitude of lunar tides (Smith, 1978). In contrast, wind-tides on the order of about 1 m are common in the Laguna Madre and can persist for several days. Because of the low relief within the basin of the Laguna Madre, wind-tides can flood or expose vast expanses of tidal flats very rapidly (Tunnell & Judd, 2002). Limited water exchange with the Gulf of Mexico, low freshwater inflow from the mainland, and a high evaporation rate from its shallow waters have in the past frequently caused the lagoon to become hypersaline (Pulich, 1980;

Tunnell & Judd, 2002). Quammen & Onuf (1993), however, documented that salinity levels there have moderated in recent decades because of improved water circulation, a consequence of the completion of construction in 1949 of the Gulf Intracoastal Waterway along the entire length of the Laguna Madre. Prior to 1949, the range of salinity in remote reaches of the Laguna Madre was 70–100 ppt. In more recent decades, the salinity has been typically 30–40 ppt, and only rarely has it exceeded 50 ppt (Hedgpeth, 1947; Quammen & Onuf, 1993; Tunnell & Judd, 2002). The Laguna Madre of Texas is vegetated by seagrasses, of which the dominant species are *Halodule wrightii* (61%), *Syringodium filiforme* (Kutz) (21%), and *Thalassia testudinum* (Koenig) (16%) (Onuf, pers. comm.).

Redfish Bay, located immediately north of Corpus Christi Bay (Fig. 1), is very shallow (mean depth < 1 m) and is approximately 20 km long and 10 km wide. The bay also supports dense stands of seagrasses, especially *Halodule wrightii* and *Thalassia testudinum* (Hoese & Jones, 1963).

In the northern Gulf of Mexico, redheads winter in the Chandeleur Sound of Louisiana, in the lee of the adjacent Chandeleur Islands (a barrier island chain, approximately 65 km in length, located about 40 km off the eastern coast of Louisiana) (Fig. 1). Water depth in the sound averages about 1 m at mean low water (MLW). Chandeleur Sound generally is oligotrophic but may range from ultra-oligotrophic to mesotrophic. Chandeleur Sound is characterized by a strong daily tidal cycle; maximum daily amplitude during the study was about 0.8 m (Michot et al., 1994). Moderated by freshwater effluent from the mouth of the Mississippi River, sound waters are saline (20–30 ppt) (Michot et al., 1994). The shallow Chandeleur Sound is characterized by seagrass communities, which are dominated by *Halodule wrightii* (20%), *Thalassia testudinum* (57%), and *Syringodium filiforme* (18%) (Michot, 2000).

Methods

We located flocks of redheads on the open waters of the upper Laguna Madre and Redfish Bay in Texas and in the Chandeleur Sound of Louisiana. We observed birds with a spotting scope from a

vehicle at 30 sites in Texas and from four permanent blinds in Louisiana. We gathered redhead behavioral data on microcassette tape recorders while scanning (Altmann, 1974) flocks of redheads for two minutes. We collected data on every bird in small flocks (≤ 60 birds) that could be scanned entirely within the two minutes. We divided larger flocks that could not be scanned completely within this time into three or four subunits and randomly selected one for sampling. We scanned a single flock at 15-min intervals from dawn to noon or noon to dusk, unless the flock moved beyond view. One of these two diel time blocks was chosen randomly for every other observation period, so that different times of day were represented for all months.

Major information gaps exist for the nocturnal activities of waterfowl (Jorde & Owen, 1988; Paulus, 1988a), and nocturnal foraging by redheads apparently is commonplace on both the winter range and breeding grounds (Low, 1945; Mitchell et al., 1992; Michot & Nault, 1993). We attempted to collect nocturnal data on behaviors of redheads (using a night vision scope), but roosting and foraging locations of redhead flocks at night on the open waters were not reliably predictable. Consequently, we were forced to limit our observations to diurnal redhead activities.

We recorded redhead activities instantaneously upon observation, assigning activities of feeding birds to the following categories of behavior: (1) diving, (2) tipping, (3) dipping, (4) gleaning, and (5) all others (Pöysä, 1986; Mitchell et al., 1992). When birds were diving, we slowed the rate of scanning across flocks to reduce the potential bias of missing submerged birds, aided in our efforts by behavioral characteristics of feeding redheads. Diving redheads typically are submerged for about 10–20 sec, and when they reappear on the surface, they seldom are more than 1 m from the point of entry (Siegfried, 1976; Mitchell et al., 1992). Further, while on the surface, feeding redheads (during a dive pause) can be recognized by characteristic bill movements (as they manipulate food items), subtle distinctions in head and neck positions, and by feather compression just before diving. We grouped all other activities of birds as nonfeeding behavior.

In Texas, we collected data on bird activities for two winters, November–March, 1987–88 and 1988–

89. In winter 1987–88 we gathered data in Texas on activities of redheads during 40 days (monthly minimum = 2 days in March, monthly maximum = 14 days in December). In winter 1988–89 we collected data on redhead activities in Texas during 33 days (monthly minimum = 6 days, monthly maximum = 8 days). In Louisiana, we collected data on activities of redheads during one winter for 22 days (3–6 days consecutively every month, between the 8th and 18th days of each month), November–March 1988–89. Water depths at 26 flock sites in Texas were measured with a meter stick at the end of the observation periods, while tide heights in Louisiana were measured with an automated digital data logger, which recorded data as mean low water (MLW) every 15 min throughout the observation period. We used MLW as a measure of water depth in Louisiana under the assumption that tide height is correlated with water depth at any given flock site.

To eliminate concern about inflating sample sizes artificially by scanning the same flocks repeatedly (i.e., pseudoreplication), we treated each flock as a sampling unit, rather than each individual scan. We summed numbers of feeding and nonfeeding males and females over all scans for each flock and calculated percentages of feeding birds for each sex by flock. For feeding birds within flocks, we determined percentages that were diving, tipping, dipping, and gleaning. We used the square root-arc sine transformation of percentages to approximate more closely the assumptions of normally distributed data with equal variances (Steel & Torrie, 1980). We used three-way analyses of variance (ANOVAs) of the transformed percentage data to test if overall feeding levels and percentages of feeding behaviors varied between sexes, among winters and locations (1987–88 and 1988–89 in Texas, 1988 in Louisiana), or among months (November–March) within a winter. If we found no significant differences in foraging behaviors between sexes in the initial three-way ANOVAs, we pooled the data over sexes and included birds of unknown sex. Then, to analyze for the effects of winters at different locations and months within a season, we ran a reduced model (two-way ANOVA) for each dependent variable. We report untransformed percentages to permit easy interpretation and comparison with other studies.

To determine if different feeding behaviors were associated with variable water depth (objective 3), we assigned flocks for which water depths or tide heights (MLW) were available to classes, based on the most common feeding behavior within flocks. We used only percentages of diving, tipping, and dipping in assigning flocks to one of three classes, since gleaning is a surface feeding activity and independent of water depth. Water depths for flocks were then compared in two separate one-way ANOVAs, one for Texas (using water depth as the dependent variable) and one for Louisiana (using MLW as the dependent variable). Statistical differences of mean water depths of flocks assigned to the three classes were determined using pairwise comparisons of least-squares means, via Student's *t*-test.

Results

We gathered data on redheads from 103 flocks in Texas and from 57 flocks in Louisiana. For the Texas flocks, we observed 54,340 redhead activities (34,011 male, 20,319 female, and 10 unknown sex), of which 14,148 (26.0%) were feeding activities. For the flocks in Louisiana, we observed a total of 51,650 redhead activities (15,879 male, 15,908 female, and 19,863 unknown sex), of which 20,147 (39.0%) were feeding activities.

Analysis of variance of transformed (square root-arc sine) percentages showed that males and females within a flock did not differ in levels of feeding or in foraging behaviors ($p > 0.10$ for sex as a main effect and in all interactions). Consequently, we pooled the data for males, females, and birds of unknown sex for subsequent analysis. We then conducted a two-way ANOVA of square root-arc sine transformed percentages of feeding birds in flocks, using winters and locations as one explanatory variable and months as the second explanatory variable. The results showed a significant ($F = 10.06$, $df = 2, 145$, $p < 0.0001$) difference in levels of feeding among the winter seasons in Texas and Louisiana. Percentages of redheads feeding in flocks were less in Texas in both winters (25.0% in 1987–88 and 28.6% in 1988–89) than in Louisiana in

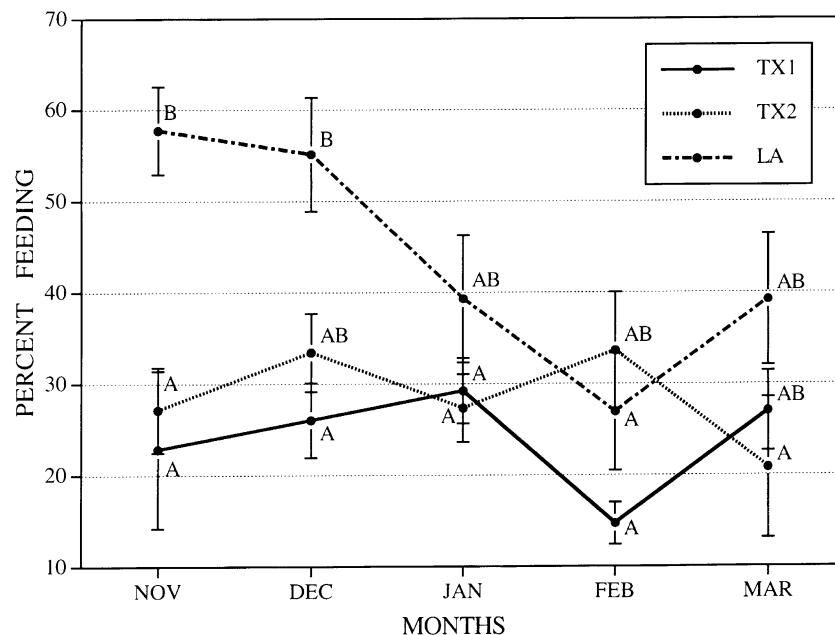


Figure 2. Monthly mean percentages (± 1 standard error) of feeding redheads in Texas during winters of 1987–89 (TX1 and TX2) and in Louisiana during winter of 1988–89 (LA). Data points which lack a common letter are significantly different ($p < 0.01$).

1988–89 (41.1%). There was also a significant ($F=2.04$, $df=8,145$, $p < 0.05$) difference in monthly feeding levels among winters and locations (Fig. 2). The monthly trend for redhead feeding levels in Texas was relatively stable for both winters. In contrast, feeding in Louisiana, after an early winter peak, declined to levels in January through March that were similar to levels found in Texas (Fig. 2).

There was a significant difference in diving among the winters in Texas and Louisiana ($F=8.09$, $df=2,138$, $p < 0.0005$). Redheads fed more by diving in Texas in both 1987–88 (24.9%) and 1988–89 (37.3%) than in Louisiana in 1988–89 (17.1%). There was also a significant ($F=4.33$, $df=4,138$, $p < 0.0025$) difference among months in percentages of diving birds, although this monthly variation did not differ ($F=1.15$, $df=8,138$, $p > 0.30$) among winters in Texas and Louisiana. Diving by redheads peaked in January and February, then declined in March to early winter levels (Fig. 3).

Tipping did not differ among winters in Texas and Louisiana ($F=2.73$, $df=2,138$, $p > 0.05$) or monthly among winters in the two states ($F=0.65$,

$df=8,138$, $p > 0.70$). We found a significant ($F=4.44$, $df=4,138$, $p < 0.005$) difference in tipping among months, but this monthly variation did not differ among winters in Texas and Louisiana. Tipping was bimodal, peaking in early and late winter (Fig. 4).

There was a significant ($F=12.39$, $df=2,138$, $p < 0.0001$) difference in dipping among winters in Texas and Louisiana. Redheads in Texas fed less by dipping in both winters (12.9% in 1987–88 and 12.7% in 1988–89) than did birds in Louisiana in 1988–89 (34.0%). There was also a significant ($F=5.71$, $df=4,138$, $p < 0.0003$) difference in redhead dipping among months, although monthly variation in dipping did not differ among winters in the two states ($F=1.88$, $df=8,138$, $p > 0.05$). Dipping by redheads was most frequent in early winter (Fig. 5).

Gleaning showed no significant ($F=2.20$, $df=2,138$, $p > 0.10$) difference among winters in Texas and Louisiana, but gleaning differed significantly among months ($F=17.22$, $df=4,138$, $p < 0.0001$), and monthly variation in gleaning differed among winters in the two states ($F=3.33$, $df=8,138$, $p < 0.005$). Gleaning by redheads

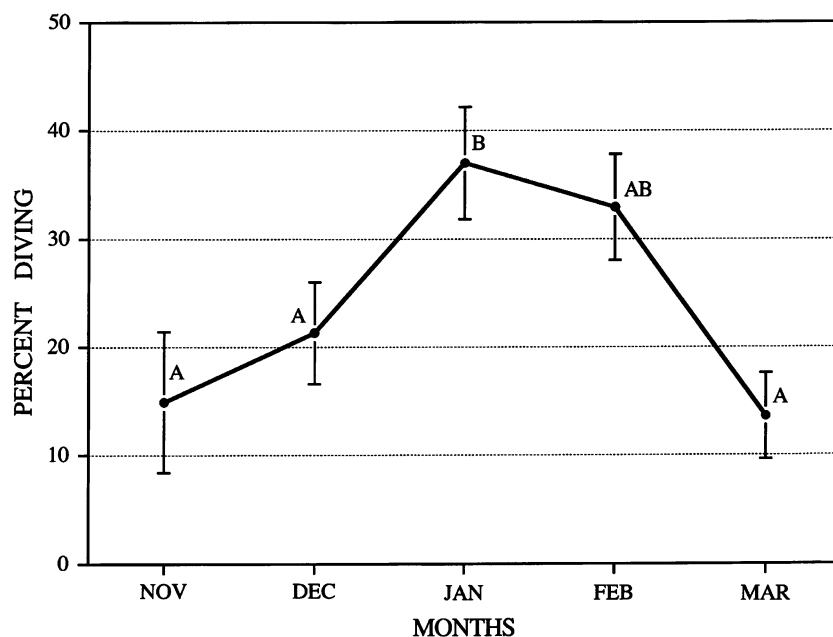


Figure 3. Monthly mean percentages (± 1 standard error) of diving redheads in Texas and Louisiana (data combined). Data points which lack a common letter are significantly different ($p < 0.01$).

generally was least in early winter and increased thereafter; differences among winters in Texas and Louisiana were not consistent within months.

Dominant feeding behaviors exhibited by flocks of redheads were related significantly to

water depths in Texas and Louisiana. In Texas, depths where diving predominated ($n = 7$ flocks, mean = 61.7 cm) were significantly greater than depths at flock sites where tipping ($n = 15$ flocks, mean = 37.6 cm, $p < 0.01$) or dipping ($n = 4$ flocks,

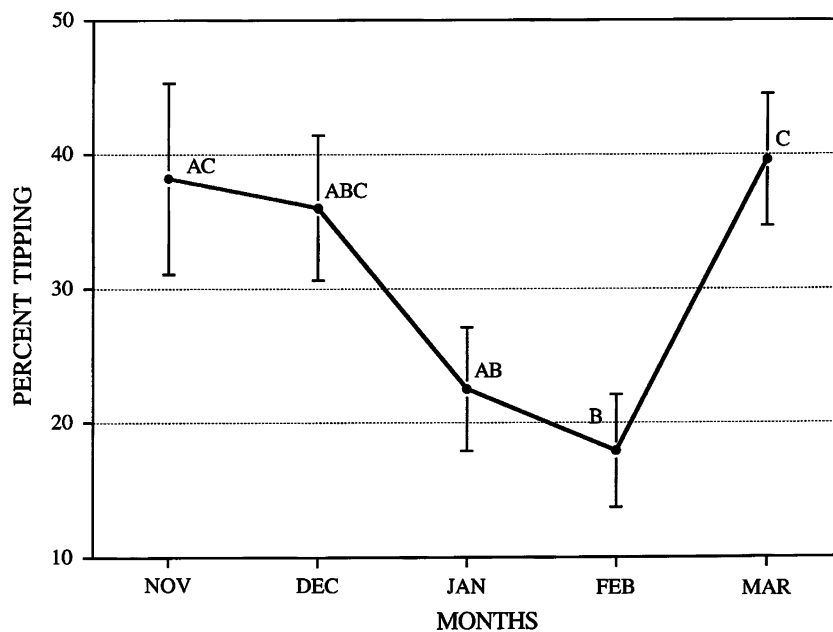


Figure 4. Monthly mean percentages (± 1 standard error) of tipping redheads in Texas and Louisiana (data combined). Data points which lack a common letter are significantly different ($p < 0.01$).

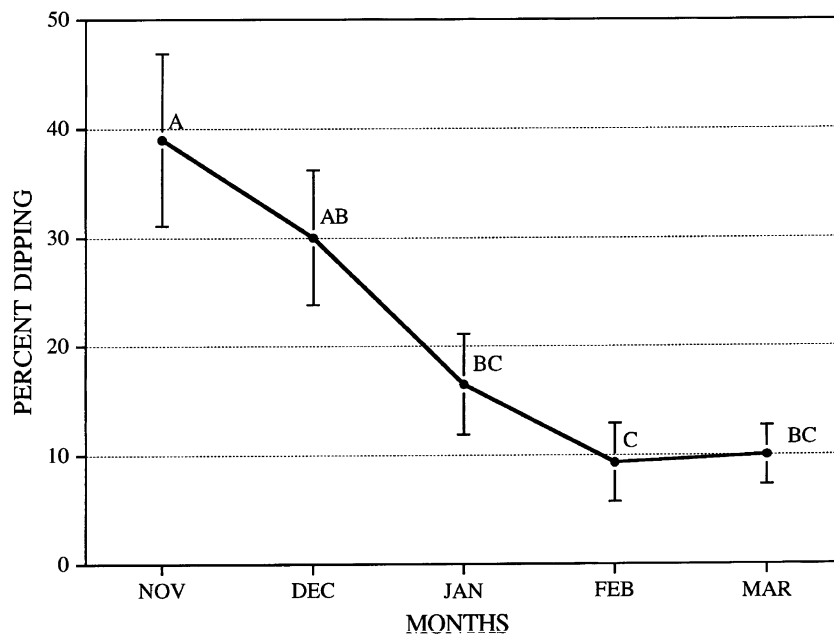


Figure 5. Monthly mean percentages (± 1 standard error) of dipping redheads in Texas and Louisiana (data combined). Data points which lack a common letter are significantly different ($p < 0.01$).

mean = 30.0 cm, $p < 0.02$) was dominant; the latter two were not significantly different from each other ($p > 0.45$). Tidal gauge readings in Louisiana for flocks in which diving predominated ($n = 5$ flocks, mean = 37 cm above MLW) were significantly greater than tidal heights for flocks in which tipping ($n = 18$ flocks, mean = 9 cm above MLW, $p < 0.0001$) or dipping ($n = 17$ flocks, mean = 3 cm below MLW,

$p < 0.0001$) was dominant; the latter two were also statistically different ($p < 0.005$).

Figure 6 compares percentages of diving, tipping, dipping, and gleaning in redhead flocks in the upper Laguna Madre (1987–88 and 1988–89) and Chandeleur Sound (1988–89) (this study) with similar foraging data from redhead flocks in the

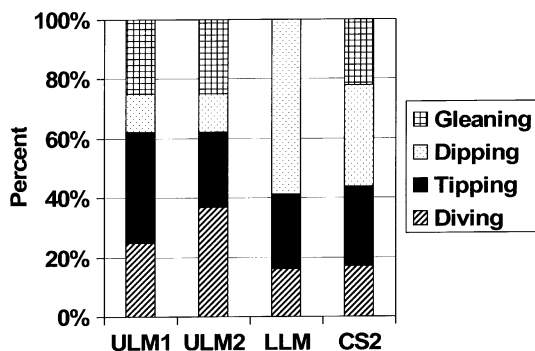


Figure 6. Percentages of diving, tipping, dipping, and gleaning for redhead flocks in the upper Laguna Madre in 1987–88 (ULM1) and 1988–89 (ULM2), lower Laguna Madre (LLM) (data from Mitchell et al., 1992), and Chandeleur Sound, 1988–89 (CS2).

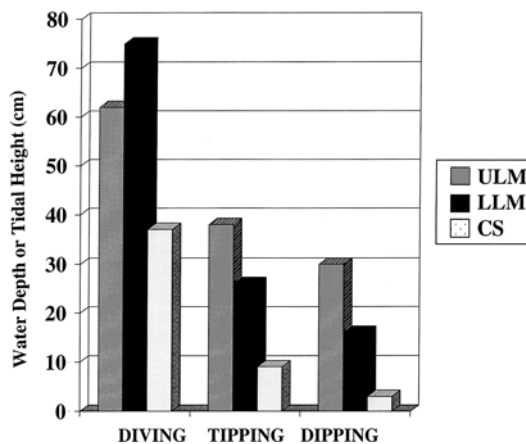


Figure 7. Mean percentages of dominant feeding behaviors by water depth (or mean water level) for redhead flocks in the upper Laguna Madre (ULM), lower Laguna Madre (LLM) (data from Mitchell et al., 1992), and Chandeleur Sound (CS).

lower Laguna Madre (Mitchell et al., 1992). Water depths (in Texas) or MWL (in Louisiana) and diving, tipping, and dipping in redhead flocks in the upper Laguna Madre and in Chandeleur Sound (this study) are contrasted with similar data for redhead flocks in the lower Laguna Madre (Mitchell et al., 1992) (Fig. 7). At all three sites, dominant flock feeding behaviors were associated with water depths ordered from deepest to shallowest (diving > tipping > dipping).

Discussion

The absence of any differences in foraging between males and females in this study was not unexpected. It is not uncommon for males and females of many species wintering in more southerly latitudes to forage similarly (Paulus, 1984; Quinlan & Baldassarre, 1984; Rave & Baldassarre, 1989; Thompson & Baldassarre, 1991; Migoya et al., 1994; Jeske & Percival, 1995). The implication is that energy demands, nutrient intake, and thermoregulation are so similar for males and females in mild winter climates that both sexes adopt similar foraging strategies.

Feeding of waterfowl in winter is affected by ambient weather conditions (Jorde et al., 1984; Hepp, 1985; Miller, 1985; Morton et al., 1989; Michot et al., 2005). Redheads increase foraging activity in response to increased thermoregulatory demands (Mitchell et al., 1992; Michot et al., 1994), as do many other species of waterfowl (Tamisier, 1974; Jorde et al., 1983; Paulus, 1988b; Bergan et al., 1989). The lower overall level of feeding by redheads in Texas in this study indicates that Louisiana birds were more exposed to harsh weather conditions, a consequence of either their more northerly latitude or the greater distance from the mainland of the Chandeleur Sound, relative to the Laguna Madre of Texas. Redheads wintering offshore in Chandeleur Sound are exposed to high winds, increased wind fetch, and elevated wave action (Michot et al., 1994). In addition, temperatures experienced by redheads in winter in the Chandeleur Sound are colder (mean = 13.0 °C) than those during winter in the upper Laguna Madre area (range of monthly means = 13.6–18.5 °C) (Tunnell & Judd, 2002). These conditions contribute to the elevated level of

feeding by Louisiana birds compared to redheads in the upper Laguna Madre region, immediately adjacent to the coast. It also offers an apparent anomaly, however, since 46% of activities of redheads wintering in the lower Laguna Madre during 1986–87 and 1987–88 were foraging (Mitchell et al., 1992), much more similar to the 41% of redheads foraging in Louisiana than to the 26% of redheads foraging in the upper Laguna Madre (this study). Winter temperatures in the lower Laguna Madre region are even warmer (range of monthly means = 15.7–20.2 °C) than those for the upper Laguna Madre (Tunnell & Judd, 2002). In the lower Laguna Madre of Texas, redheads increased feeding when faced with extreme cold (–1 to 6 °C in southern Texas) (Mitchell et al., 1992), which is rare and short-lived. This is consistent with observations of other waterfowl, which increase foraging with declining temperatures, down to about 0 °C (Paulus, 1988a). If thermoregulatory demands imposed by different winter temperature regimes are the primary factor influencing levels of feeding by redheads in Louisiana and Texas, then we would expect redhead foraging in Louisiana to exceed that for redheads in both the upper and lower Laguna Madre. The patterns of foraging levels shown by redheads wintering in the Chandeleur Sound and the upper and lower Laguna Madre do not demonstrate this.

Heavy use by redheads of coastal ponds along the entire length of the Laguna Madre is a widely reported phenomenon (Adair, 1990; Moore, 1991; Mitchell et al., 1992; Woodin, 1994; Adair et al., 1996; Skoruppa & Woodin, 2000; Michot et al., 2005), including the use of these ponds as sources of drinking water. Redheads begin arriving at coastal ponds at dawn, and exchange of birds between the Laguna Madre and coastal ponds occurs continuously until dusk, when the ponds largely are abandoned. Coastal ponds are not used by redheads for foraging, which occurs in the Laguna Madre. Mitchell et al. (1992) noted that 78% of activities of redheads on coastal ponds along the lower Laguna Madre were sleeping and resting, while drinking was minimal, an exception to the more normal pattern of heavy drinking by redheads on coastal ponds. This strongly implies that redheads use coastal ponds for reasons beyond securing drinking water. Indeed, resting consistently has been documented as a major activity for

redheads on coastal ponds along the entire length of the Laguna Madre of Texas (Moore, 1991; Mitchell et al., 1992; Woodin, 1996; Adair et al., 1996), occurring as the primary activity in three of the four studies. We believe that energy conservation is a second benefit of redhead use of ponds, as many of the ponds are small (Adair, 1990) and offer some measure of shelter from fetch and wave action on the open waters of the Laguna Madre. The differential use by redheads of coastal ponds along the upper (more drinking, less resting) and lower Laguna Madre (less drinking, more resting), along with the different levels of feeding exhibited by birds wintering in the two different basins, are consistent with the hypothesis that redheads are presented with different energy demands in the basins of the upper and lower Laguna Madre. This could be especially important for young birds, which continue in late winter to exhibit lower mean body masses than do adults (Moore, 1991). In fact, young birds form a disproportionately large percentage of birds on coastal ponds in late winter (Moore, 1991). Mean duration of pond visits by all sex and age classes of redheads increased dramatically in March (Moore, 1991), when all remaining birds are staging and undergoing hyperphagia and rapid increase in fat deposition. Prolonged resting on small coastal ponds probably assists these birds in minimizing pre-migration thermoregulatory costs while increasing body mass and fat prior to northward migration.

In comparison to redheads in Texas, redheads in the Chandeleur Sound seldom use freshwater ponds on the Chandeleur Islands. The prevailing salinity in the sound is below the threshold at which they must visit ponds to obtain drinking water to aid their salt glands in secreting excess salt. Excess salt (NaCl) ingested by birds is discharged from the nares by secretions from supra-orbital salt glands, which are extraordinarily effective at transporting sodium chloride ions (Schmidt-Nielsen, 1975; Holmes & Phillips, 1985). Salt glands of redheads are known to respond rapidly when the birds encounter saltwater habitats after their arrival in coastal areas (Cornelius, 1982). It is possible that the reduced levels of feeding by redheads in the upper Laguna Madre region are related to the availability of nearby freshwater ponds (Michot et al., 2005). To assist

their salt glands with flushing of excess salt, redheads in the upper Laguna Madre obtained drinking water at coastal ponds (Adair, 1990; Moore, 1991; Woodin, 1994), while redheads in the lower Laguna Madre apparently obtained most of their drinking water from agricultural drains (used heavily by redheads) entering the lagoon from the mainland; little drinking by redheads on coastal ponds along the lower Laguna Madre was observed (Mitchell et al., 1992). Because fresh water was available to birds wintering in both the upper and lower basins of the Laguna Madre, however, the large overall difference in feeding levels between redheads wintering in the upper (26%) and lower (46%) Laguna Madre probably cannot be attributed to salt loading and the metabolic costs of osmoregulation. In fact, since salinity in the upper Laguna Madre typically exceeds that in the lower Laguna Madre (in recent decades) (Tunnell & Judd, 2002), we would expect redhead foraging to be greater in the upper lagoon, if salinity and cost of osmoregulation were primarily responsible for foraging levels. We believe the single most plausible explanation for this dichotomy lies not with osmoregulation, but rather with the greater fetch (and resulting greater wave action) of the lower Laguna Madre, which subjects redheads wintering there to a harsher microclimatic regime than that experienced by birds wintering in the northern Laguna Madre area.

The long axis of the large basin of the lower Laguna Madre is oriented toward the south-southeast (Fig. 1) (toward the direction of the prevailing winds). Consequently, birds on the lower Laguna Madre are exposed to greater wind fetch (and greater wave action) than birds using the smaller basin of the upper Laguna Madre, whether it be from sustained southerly winds or during the passage of cold weather systems from the north. Redfish Bay, just to the north of the upper Laguna Madre (Fig. 1), is characterized by irregular stands of smooth cordgrass, *Spartina alterniflora* (Loisel.), and black mangrove, *Avicennia germinans* (L.), in coves and embayments scattered among tidal islets, offering redheads shelter from winds and wave action. Redheads wintering in Chandeleur Sound reduce fetch during cold weather and high winds by moving closer to shore for protection (Michot et al., 1994). Weather conditions affect redhead

feeding during winter (Michot et al., 1994). Variation in foraging in different parts of the winter range, however, was not explained satisfactorily by weather variables (Michot et al., 2005), but wind fetch and wave action were not included in the analyses. We believe that redheads wintering in the upper Laguna Madre region experience fewer extremes of wind fetch and wave action than do their counterparts wintering in the Chandeleur Sound of Louisiana and in the lower Laguna Madre of Texas. We suggest that the lower feeding levels exhibited by redheads in the upper Laguna Madre region are a response to reduced energetic demands in this relatively more benign environment.

Foraging activities typical of dabbling ducks, such as tipping and dipping (Pöysä, 1986), were common feeding behaviors of redheads in Texas and Louisiana (Fig. 6). Redheads feeding in Texas and Louisiana showed the same seasonal patterns in diving, tipping, and dipping. In early winter, diving was low, whereas tipping and dipping were high. In midwinter, the relative frequencies of these feeding behaviors were reversed. Redheads observed gleaning were seen feeding frequently in association with other dipping, tipping, or diving birds, usually other redheads or lesser scaup, *Aythya affinis* (Eyton). Presumably, the gleaning birds were exhibiting cooperative feeding on shoalgrass rhizomes brought to the surface by other foraging birds (Woodin & Michot, 2002).

Our results showed that the dominant feeding behaviors observed in flocks were associated with different water depths. The exception was that foraging flocks which fed mostly by tipping did not occur in water depths statistically different than for flocks which fed mostly by dipping, although the small number ($n=4$) of flocks characterized by dipping may have been insufficient to make this comparison. Mitchell et al. (1992) also found that water depths were greatest where diving was most prevalent, intermediate where tipping was common, and shallowest where dipping was most common among feeding birds (Fig. 7). Dipping was much more prevalent in the lower Laguna Madre than in the upper lagoon or in Louisiana (Fig. 6). This was probably because the lower Laguna Madre supports such extensive, shallow beds of shoalgrass (Cornelius, 1977; Mitchell,

1992) at relatively uniform depths. Mitchell (1992) concluded that water depths 12–30 cm were good predictors of redhead flock locations, presumably because such sites enhance redhead foraging efficiency (Stephenson et al., 1989; Mitchell et al., 1992). This basin bathymetry of the lower Laguna Madre presents large flocks of redheads with excellent opportunities for dipping, an energetically low-cost alternative to diving.

Diving was more frequent in the upper Laguna Madre than in the lower Laguna Madre or Louisiana (Fig. 6). This could have been an indication that redheads switched to alternative foods located at greater depths than their preferred food (*Halodule wrightii* rhizomes). We consider this unlikely, however, since redhead reliance on shoalgrass rhizomes in winter is consistent among years, geographic areas, and locations along the Gulf of Mexico (Stieglitz, 1966; McMahan, 1970; Cornelius, 1977; Michot & Nault, 1993; Woodin, 1996). A more likely explanation is that redheads in the upper Laguna Madre region were foraging for shoalgrass rhizomes in the deeper beds in Redfish Bay and the upper Laguna Madre, where dredging projects and channelization for recreational boats, development of natural gas fields, and construction of highway causeways have resulted in increased substrate relief. Increased diving in January and February, when redheads begin staging in larger concentrations prior to migration, indicated that redheads were feeding more in deeper water than earlier in the winter. This suggests at first that rhizomes in shallow beds of shoalgrass may have become depleted (Mitchell et al., 1994), making foraging at deeper sites relatively more profitable by late winter. By March, however, when most redheads have departed the winter range (Woodin & Michot, 2002), diving and tipping had reverted to levels first observed in early winter, and dipping remained low.

We believe this pattern of foraging behavior may have resulted because redheads staging for spring migration become increasingly concentrated in January and February; less dominant birds could have become displaced to lower-quality (i.e., deeper) habitats, resulting in the increased frequency of diving that we observed. This would also explain why most redheads remaining in March (after most had departed)

reverted to feeding primarily by tipping. Some displacement of birds to poorer habitats has been known to occur when birds mass in large concentrations (Frederick & Klaas, 1982; Paulus, 1984).

We suggest that if resource limitation of redheads occurs on the winter range, it will be experienced most likely at the end of winter, when shoalgrass rhizomes will be most depleted and when staging redheads become most densely concentrated within restricted areas.

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Macroinvertebrate abundance, water chemistry, and wetland characteristics affect use of wetlands by avian species in Maine

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Abstract

Our objective was to determine use by avian species (e.g., piscivores, marsh birds, waterfowl, selected passerines) of 29 wetlands in areas with low (<200 $\mu\text{eq l}^{-1}$) acid-neutralizing capacity (ANC) in south-eastern Maine. We documented bird, pair, and brood use during 1982–1984 and in 1982 we sampled 10 wetlands with a sweep net to collect invertebrates. We related mean numbers of invertebrates per wetland to water chemistry, basin characteristics, and avian use of different wetland types. Shallow, beaver (*Castor canadensis*)-created wetlands with the highest phosphorus levels and abundant and varied macrophyte assemblages supported greater densities of macroinvertebrates and numbers of duck broods (88.3% of all broods) in contrast to deep, glacial type wetlands with sparse vegetation and lower invertebrate densities that supported fewer broods (11.7%). Low pH may have affected some acid-intolerant invertebrate taxa (i.e., Ephemeroptera), but high mean numbers of Insecta per wetland were recorded from wetlands with a pH of 5.51. Other Classes and Orders of invertebrates were more abundant on wetlands with pH > 5.51. All years combined use of wetlands by broods was greater on wetlands with pH \leq 5.51 (77.4%) in contrast to wetlands with pH > 5.51 that supported 21.8% of the broods. High mean brood density was associated with mean number of Insecta per wetland. For lentic wetlands created by beaver, those habitats contained vegetative structure and nutrients necessary to provide cover to support invertebrate populations that are prey of omnivore and insectivore species. The fishless status of a few wetlands may have affected use by some waterfowl species and obligate piscivores.

Introduction

When we began this study in 1982 concerns about effects of acidification of wetlands and associated biological resources were rising. Loss of fish and aquatic invertebrates were being documented, but effects of acidification on aquatic avifauna in areas with low acid-neutralizing capacity (ANC) were less well known. Since 1982 knowledge of biologi-

cal, chemical, and physical characteristics of wetlands that affect water birds has increased substantially (DesGranges & Gagnon, 1994; Staicer et al., 1994; McNicol et al., 1998). Previous studies emphasized effects of acidification (McNicol et al., 1987; Parker et al., 1992), especially on fish (DesGranges & Darveau, 1985; Elmberg et al., 1994), that affect trophic levels (i.e., macroinvertebrates) (Eriksson et al., 1980; Mallory

et al., 1994), and subsequently duckling foods (DesGranges & Rodrigue, 1986; McNicol & Wayland, 1992). Adverse effects caused by acidification are toxicological and ecological. Effects range from loss of an essential mineral (i.e., calcium), changes in availability of trace metals (e.g., copper, nickel, zinc) and toxic metals (e.g., mercury, cadmium, lead) to long-term degradation of habitat through loss of species and modification of aquatic food webs (Scheuhammer, 1991; Longcore et al., 1993; McNicol et al., 1998; Doka et al., 2003). Just before we initiated our study in 1982, Norton (1980) had reported that 15 000 km² (17%) of the land area of Maine had low to no ANC and fell within sensitivity Class 1, wherein widespread effects of acidic deposits on aquatic ecosystems were expected. Furthermore, the New England region had been identified especially as the recipient of airborne acidic depositions (NAPAP, 1990, 1991). Our objective was to determine use by bird species (e.g., piscivores, marsh birds, waterfowl, and selected passerines) and use by broods on 29 wetlands during 1982–1984 in two areas of Maine with low ANC. We wanted to relate densities of pairs and broods to water chemistry and basin characteristics. Also, we sought to determine mean numbers of macroinvertebrate taxa in 10 of 29 wetlands with different water chemistry and basin features. We then sought to relate mean numbers of macroinvertebrate taxa to water chemistry and basin characteristics and to density of water bird broods on these 10 wetlands.

Methods

Study areas and collection of data

Study areas were in southeastern Maine, an area with bedrock classified as extremely sensitive (Class 1) to acidification (Norton, 1980). In the 66-km² Cherryfield study area (Township 10 SD, 68°5' W. Long., 44°40' N. Lat., ~20 km west of Cherryfield, Maine; 1957 U.S.G.S., Tunk Lake Quadrangle, 15-min Series) the bedrock is intrusive rocks of the Devonian located in the Plutonic rock metamorphic zone of the Eastport Formation (Osberg et al., 1985). The surficial geology of the Cherryfield site is a combination of extensive bedrock outcrop and glacial till with a heteroge-

neous mix of sand, silt, clay, stones, and large boulders, forming drumlins and stream-lined hills (Thompson and Borns, 1985). In the 25-km² Beddington study area (SE corner of Township 30 MD, 67°50' W. Long., 44°55' N. Lat.; 13 km east of Beddington, ME, 1941 U.S.G.S. Tug Mountain Quadrangle, 15-min Series) the area is underlain mostly by alkali feldspar granite-biotite rock. Both areas are within the Northern Hardwoods-Spruce Forest (2114) section of the Laurentian Mixed Forest Province (2110) (Bailey, 1978) wherein vegetation is transitional between deciduous forest and boreal forest zones.

Because chemical properties of water are only one component of aquatic environments that affect use by birds (Hilden, 1965), we measured several variables of wetland basins to explain differences in invertebrates and use by water birds. With 1980 black & white aerial photographs (RF 1:15 840) we sketched major wetland features and vegetative life forms (e.g., floating-leaved, emergent). For wetlands too small to map from aerial photographs, we measured them in the field with a parallax range-finder or by standard pacing. We used an electronic digitizer to measure wetland features of photographs or maps enlarged with a transfer scope.

We classified wetlands with criteria of Cowardin et al. (1979). We designated each wetland at System, Class, and Subclass level with each 'Class' recognizable according to the dominant (>30% areal coverage) vegetative life form. Identifying vegetative types was essential because life forms (e.g., emergent, floating-leaved, submergent) are different in their ability to support aquatic invertebrates (Moyle, 1961; Krull, 1970) and to provide concealing cover for waterfowl broods (Ringelman, 1980). Therefore, we determined area (ha) of each life form of aquatic vegetation and a measure of patchiness of life forms (i.e., index of life-form diversity) for each wetland (Lloyd et al., 1968: 258).

We collected water samples in mid-July from mid-pond or behind dams of American beaver, *Castor canadensis* (Kuhl); flowages at elbow depth (35 cm) directly into acid-washed bottles rinsed in deionized water. For deep ponds we used a plastic Van Dorn-type sampler at the pond's center. We iced samples during transport and completed analyses for pH, alkalinity, specific conductance,

and color within 24 h. We soaked all containers for 4 h in 10% nitric acid then rinsed them 3 times with glass-distilled, deionized, water. We measured acidity at ambient temperature of a 100-ml sample with a portable meter (Fisher Model 640) equipped with a gel-filled combination electrode. We standardized the meter with pH 7.0 and 4.0 buffers, and then verified electrode response by measuring pH of dilute sulfuric acid solutions of theoretical pH 4.0. We rinsed the electrode in deionized water, blotted it dry, and soaked it in the sample for 15 min or longer. When three successive readings at 1-min intervals were identical we recorded pH.

We determined alkalinity by titrating each 100-ml sub-sample with Fisher certified, 0.0200 N sulfuric acid to pH 4.0. We added acid with a 1-cc tuberculin syringe until pH 5.0 was reached, then we added acid in discrete 0.05-ml portions to attain pH 4.0. We gently stirred the sample to disperse acid and we recorded pH after equilibration (~10–30 s) following each addition of acid. We calculated alkalinity by Gran inflection point (Stumm & Morgan, 1970).

We measured specific conductance with a portable, calibrated meter (Markson Science, Inc., Model-10) and we determined color (Hazen units) by comparison of unfiltered samples with a platinum cobalt standard solution (Lamotte Chemical Co., Chestertown, MD). We converted color of water to total organic carbon (TOC) by the regression, $\text{TOC (mg l}^{-1}\text{)} = 1.32 + 0.0613 \times \text{color (Hazen Units)}$, $r^2 = 0.902$ (Haines & Akielaszek, 1983).

In 1982 C.S. Cronan, University of Maine, measured anion concentrations (fluoride, chloride, nitrate, sulfate) in water samples with a Dionex, Model 16, double-channel Ion Chromatograph following standard procedures. Quality Assurance and Quality Control included repeated precision and accuracy tests with EPA reference standards and inter-laboratory calibration standards. Multiple standards were run sequentially during a seven-hour run and replicates were analyzed for means, standard deviations, and coefficients of variation.

J.S. Kahl and S.A. Norton, University of Maine, measured cation concentrations (aluminum, calcium, magnesium, potassium, sodium, manganese, iron, zinc) for 1982 water

samples and all cations and anions for 1983 and 1984 water samples. Cations were determined from acidified, unfiltered samples with a Perkin-Elmer, Model 703, Atomic Absorption Spectrophotometer using standard methods (Perkin-Elmer, 1976, 1981). Analytical standards were made by combining single metal solutions to yield an artificial water of composition similar to the actual sample. Air-acetylene, nitrous oxide-acetylene, and graphite furnace atomic absorption spectrophotometry were used for cation measurements. Element standards were prepared from AC reagent-grade chemicals or from AA reference standards. The instrument was calibrated before analysis of each set of samples for each element. Standards were verified every 10–20 samples on flame and every 2–6 samples on furnace and recalibrated as needed. Ion Chromatography (IC) was used with filtered (0.45 μm Millipore filter) water samples to determine anions. Standards were prepared from reagent-grade chemicals and the instrument calibrated with 4–7 standards at the start of each run; 1–2 standards were run every hour of machine time. At least 3 EPA reference standards were run every day. Precision of individual elements ranged from $\pm 1\%$ (calcium) to 10% (aluminum) and the analytical ion balance (ratio, sum of cations to sum of anions) was used as a measure of overall validity of the analysis.

R.B. Davis, University of Maine, measured total reactive phosphorus. Each sample was digested in the sampling flask by adding 16 ml of 5% potassium persulfate solution then heating at 15 lbs pressure for 0.5 h in an autoclave. The sample was cooled and the reactive phosphorus produced by digestion was analyzed. These methods followed the procedure of Wetzel & Likens (1979), which is adopted from standard methods. A Cary 5 recording spectrophotometer was used to prepare standard absorbance curves at 800 nm over a range of concentration (1–500 ppb phosphorus). Standards, blanks, and water samples were read for absorbance in relation to distilled water, using 10 cm light path cuvetts. Phosphorus concentrations in water samples were determined from their absorbances by referring to known absorbencies on standard curves that were prepared each day. Water samples with perceptible color were divided before addition of reagents; the other portion was used as a color blank and treated

similarly except no composite reagent was added. Absorbance of blanks never exceeded 800 nm. All glassware was washed with acid and rinsed in glass-distilled water. Based on seven standard curves, accuracy is within 10% of true values.

Sampling and identification of invertebrates

We sampled 10 of 29 primary study wetlands to determine invertebrate abundance and diversity. We selected ponds to represent a range of pH (4.48–6.65) and two basin types (i.e., glacial vs. beaver-created). We chose 10 sampling sites within the littoral zone for each wetland with a clear, plastic, numbered grid that overlaid the wetland map from which we selected 10 grid numbers from a table of random numbers. At each site we used a sweep net (circular type with cross-sectional area of 0.036 m²; 11.8 meshes per cm) to make 2, 2-m-long sweeps, 1 each at water surface and near wetland bottom substrate while standing in the wetland. For Kerosene Pond, whose margin was bog-like and unstable, we sampled from a canoe. We made sweeps in emergent or floating-leaved vegetation because Reinecke (1977) and Ringelman (1980) have reported that invertebrates occur most commonly in these vegetation types in Maine. We collected samples during 21–28 June at Cherryfield and on 8 July at Beddington and stored samples in 70% ethanol before and after picking specimens from debris.

We identified macroinvertebrates, except for Chironomidae, to genus and occasionally to species primarily with keys of Hilsenhoff (1975) and Pennak (1953). We used keys of Clarke (1981) for mollusks and keys of Klemm (1982) for freshwater leeches. We identified Chironomidae larvae with keys of Simpson & Bode (1980) and Hilsenhoff (1975). We separated larvae into 4 major subdivisions (i.e., Tribes – Chironomini and Tanytarsini; Subfamilies – Tanypodinae and Orthocladinae). We separated the genus *Chironomus* from other Chironomini. We further subdivided specimens in these Chironomidae subfamilies, except *Chironomus*, into groups based on morphology. We did not further subdivide Orthocladinae based on morphology. For samples of fewer than 10 specimens we mounted all specimens. For samples with many specimens we sub-sampled and prepared 10 slides from each sample. We cut graph

paper with a cm² grid to fit a Petri dish. We separated each cm² grid into 4, 0.25 cm² squares and numbered them from 1 to 203. We placed Orthocladinae specimens in the Petri dish and dispersed them. We used a table of random numbers to select 10 specimens for mounting. Because we separated Chironomidae by gross morphological characteristics before they were mounted, some groups contained more than one genus. When this occurred we apportioned the total number of specimens in the group to each genus based on proportions observed among mounted specimens. We mounted Chironomidae specimens on glass slides with either polyvinyl lactophenol or Euparal[®]. We placed cover slips on slides after manipulating specimens to expose mouthparts and we ringed cover slips with polyvinyl lactophenol.

Fish status in ponds

Because fish can affect invertebrate communities we consulted Fish Stocking Reports for 1976–1981 (Maine Department of Inland Fisheries and Wildlife) and a regional fisheries biologist to determine status of fish in study wetlands. Two study wetlands (Kerosene Pond, Mud Pond) with low pH (4.5–4.7) were reported to be fishless. For these two wetlands and three others (Fueloil Pond, Foxtit Pond, Soft Shoulder) we set out 4 cylindrical minnow traps (1.0 m × 0.30 m long, 6 mm mesh wire, 40 mm opening) for 24 h. We baited traps with dog biscuits and bread on June 22, 1982 and either placed traps on the substrate or suspended traps 0.7–1.2 m below the water surface.

Surveys for bird, pair, and brood use of wetlands

We recorded three types of observations for birds on study wetlands: use (presence or absence), pair data, and brood data. We recorded bird presence for all species each time we visited a wetland beginning in late April during scheduled 2-h visits and during incidental visits. We collected pair data for territorial species that could be identified as an 'indicated' pair, namely anatids (i.e., waiting males) and the pied-billed grebe, *Podilymbus podiceps* (L.). Beginning in early May we initiated brood surveys (visits randomly assigned to wetlands) that extended through mid-July. For 1982–1983 we scheduled eight visits per wetland,

and for 1984 we scheduled only four visits because of logistics with another project. We recorded number of visits and hours of observation for each wetland. We repeatedly surveyed wetlands by quiet observation from elevated (12–15 m high) platforms in trees during 0400 to 0600 h or 1800 to 2100 h to identify females with broods and to record numbers of ducklings (Longcore & Ringelman, 1980) and age of broods based on plumage (Gollop & Marshall, 1954). We determined numbers of different broods by contrasting brood size and plumage changes between visits to wetlands and maintaining flow charts of broods for each wetland (see Longcore et al., 1998). Although we recorded all bird species observed, we monitored the following species for use, pairs, and broods that were included in analyses: pied-billed grebe, common loon, *Gavia immer* (Brünnich), double-crested cormorant, *Phalacrocorax auritus* (Lesson), common merganser, *Mergus merganser* (L.), hooded merganser, *Lophodytes cucullatus* (L.), American black duck, *Anas rubripes* (Brewster), mallard, *A. platyrhynchos* (L.), green-winged teal, *A. crecca* (L.), blue-winged teal, *A. discors* (L.), wood duck, *Aix sponsa* (L.), ring-necked duck, *Aythya collaris* (Donovan), common goldeneye, *Bucephala clangula* (L.), American bittern, *Botaurus lentiginosus* (Rackett), great blue heron, *Ardea herodias* (L.), sora, *Porzana carolina* (L.), common snipe, *Gallinago gallinago* (L.), spotted sandpiper, *Actitis macularia* (L.), osprey, *Pandion haliaetus* (L.), belted kingfisher, *Ceryle alcyon* (L.), common nighthawk, *Chordeiles minor* (Foster), chimney swift, *Chaetura pelagica* (L.), eastern kingbird, *Tyrannus tyrannus* (L.), and tree swallow, *Tachycineta bicolor* (Vieillot).

Analyses of data

We computed descriptive statistics to compare wetland components based on wetland origin (beaver-created vs. glacial). We used Student's *t*-test to detect differences in mean area of vegetation in wetland classes and life forms between these subsets of the 29 wetlands.

We collected two sets of water chemistry data; field measurements of pH, alkalinity, conductivity, and color, and laboratory determinations of selected anions and cations. We evaluated anion

and cation data for consistency before statistical analysis. Although screening was somewhat subjective, whenever possible we used quantitative guidelines (i.e., we calculated and compared the sum of anion and cation ionic equivalents). If the higher of these two totals was <1.5 times that of the lower, we accepted totals as consistent, but agreement was usually better than this criterion. When an individual sample value for an anion or cation was clearly an outlier, the corresponding anion or cation measurement for that sample was deleted from the data set. In some instances no single anion or cation value was clearly discrepant and if the other samples for this wetland were consistent, then the discrepant cation or anion sample was deleted from the data set. For some wetlands with highly colored water, none of the cation:anion ratios were within the criterion we set, but these data were included assuming that an unmeasured parameter (i.e., organic ions causing color) was substantially influencing ionic balance. These wetlands were Downing Bog, Kerosene Pond, Salmon Pond, and Snake Flowage. Although the anions and cations did not balance, the ratios were generally consistent among samples for each of these wetlands. We believe that resulting data represent a conservative description of ionic characteristics of these wetlands within constraints of our methodology for these dilute, ionic solutions, but we caution that measures of sulfate may be inflated in those wetlands with high levels of TOC. For water chemistry variables for all 29 wetlands we calculated means and 95% confidence intervals based on wetland origin (beaver-created vs. glacial) and on pH class (≤ 5.51 vs. >5.51).

For each taxonomic level (Class, Order, Family) of invertebrates with wetlands grouped by categories of pH (≤ 5.51 vs. >5.51) and wetland origin (glacial vs. beaver-created) we determined differences in category means for each taxon with Student's *t*-tests. When fewer than 50% of the ponds had non-zero values for a taxon, we constructed 2×2 contingency tables with presence and absence data for each of the categories. We performed tests of homogeneity of the proportion 'present' by category with methods of McDonald et al. (1977).

We used principal component analysis (PCA) and multiple-linear regression on principal components to examine the relationship between

mean numbers of invertebrates per taxon and wetland water chemistry and physical and vegetative characteristics of wetlands. Eight of 22 independent variables were used in the principal components analysis and the four largest components were used in the multiple regression analysis. We used varimax orthogonal rotation prior to regression analysis to aid in interpreting principal component and multiple regression analyses. We chose independent variables i.e., % water area vegetated, % water area with flooded timber, % water area with ericaceous vegetation, Mg, K, P, pH, and conductivity, to reduce redundancy and to produce 'good' multiple regression analyses (based on r^2 values) for as many taxa as possible, and to minimize number of independent variables and principal components used. To help interpret principal components we calculated correlations between rotated principal components and independent variables not used in generating the principal components. For taxa that occurred on >5 wetlands and with more than 35 specimens we regressed mean number of invertebrates per sample for each Class, Order, and Family on 4 principal component scores to determine which components accounted for variability in macroinvertebrate taxa abundance among wetlands.

Fish status

We assembled available information of fish status in wetlands, but we did not attempt to analyze because of the anecdotal nature of these data.

Avian surveys

We summed effort to observe birds as the mean number (SE) of visits and hours of observation per wetland per year and by wetland origin. For species observed >25 times in any year, but including chimney swift and eastern kingbird with fewer sightings, we used Chi-square tests of homogeneity to determine whether the proportion of visits to each wetland of each origin (beaver-created, glacial) was the same. We used frequency data to test for differences among functional foraging groups (i.e., species of a group that ate similar prey). A group was 'present' if at least one of the species of

the group was observed during a visit. We tested for differences between wetlands of different origin with Chi-square tests of homogeneity for five groups: 'Piscivore' (i.e., common loon, double-crested cormorant, common merganser, belted kingfisher, osprey, and great blue heron), 'Omnivore-1' (i.e., American black duck, green-winged teal, wood duck, ring-necked duck), 'Omnivore-2' (i.e., pied-billed grebe, American bittern, sora), 'Insectivore-1' (i.e., hooded merganser, common goldeneye, common snipe, spotted sandpiper), and 'Insectivore-2' (i.e., common nighthawk, chimney swift, eastern kingbird, tree swallow).

For combined years and species we tested (*t*-tests) for differences in mean number of pairs and broods per pond and per hectare of surface water area between beaver-created and glacial wetlands. We excluded Soft Shoulder Pond for pairs and broods because the pond's small size (0.02 ha) caused an extremely high density (e.g., 50–100 broods per ha) that we treated as an outlier. For individual species we constructed contingency tables with presence and absence data, and we used Chi-square tests of homogeneity to determine if the proportion of wetlands with pairs or broods of a species were different for glacial vs. beaver-created wetlands. We tested for differences among wetland vegetative classes for mean pair and brood densities (all waterfowl species plus pied-billed grebe) with one-way ANOVA; means were separated with the Least Significant Difference (LSD) procedure of Milliken and Johnson (1984).

We used principal component analyses (PCA) and multiple regressions on principal components to examine relations between pair and brood densities (all anatid species plus sora and pied-billed grebe) and water chemistry and wetland physical and vegetative characteristics. We used the following variables to generate the principal components: % of water vegetated (sum of floating-leaved and emergent), life form diversity, % of water unvegetated, water area, conductivity, Ca, pH, and TOC. We retained five principal components for use in the multiple regression analyses and we used varimax orthogonal rotation to aid in interpreting results. We correlated principal components with water chemistry and habitat variables not used to generate components to further assist in interpreting results. We regressed mean pair and brood densities on principal

component scores to determine which were related to use of wetlands.

To determine relations among wetland features, Insecta abundance, and duck brood density we examined data by principle components. In these analyses we used only data for the ten wetlands that we sampled for invertebrates. We had more variables than wetlands so we reduced water chemistry variables and morphometry/vegetation variables by performing PCA on each group. Standard deviations were not uniform across variables for each set so we ran each PCA with the correlation matrix. From each data set (i.e., water chemistry variables and morphometry/vegetation variables), four principal components emerged with eigenvalues ≥ 1.0 . Component loadings were used to create new variables as weighted combinations of original variables. Thus, the 14 chemistry variables were reduced to 4; PC1, 'overall chemistry'; PC2, 'acidity/organic carbon'; PC3, 'conductivity'; and PC4, 'aluminum/sulfate interaction'. The 10 morphometry/vegetation variables also were reduced to four principal components; PC1, 'wetland size/amount vegetated'; PC2, 'ratio of vegetated to open water'; PC3, 'beaver effects'; and PC4, 'forested wetland/emergents'. Four other variables (i.e., 'mean number of Insecta per pond', 'life-form diversity', 'origin of wetland', and 'order of wetland') were combined with the eight PCA-derived variables and examined for effect on brood numbers. Because brood numbers were counts from 0 to 37, we analyzed data by Poisson regression. Wetland size can influence numbers of broods, thus, we included wetland size as an offset in these analyses. An offset is a variable included in a regression analysis with a fixed coefficient of 1 that adjusts the analysis to a different scale. By applying wetland size as an offset in our analysis it adjusted the analysis such that we analyzed how the predictors affected brood density (i.e., broods per ha) instead of how they affected the number of broods directly.

Results

Characteristics of wetlands

Characteristics of study wetlands (163.8 ha of surface water in 12 beaver-created wetlands and 145.7 ha in 17 glacial wetlands) were diverse

(Table 1) relating to the unique bedrock and surficial geology of the region. Three features defined wetlands; size ranging from <1 to >100 ha, percentage of the wetland vegetated varying from 0 to 100%, and amount of littoral zone (<2 m deep), which averaged less ($1.6 \pm 0.6\%$) in glacial ponds ($n = 17$) than in beaver-created wetlands ($13.0 \pm 9.0\%$, $n = 12$) but not different ($p = 0.139$). For glacial ponds $82.5 \pm 7.2\%$ of the surface water was unvegetated, whereas only $19.5 \pm 9.9\%$ of beaver-created wetlands was in open water ($p = 0.0001$). Percentages of submergent aquatic plants ($40.8 \pm 11.6\%$ vs. $12.1 \pm 5.0\%$) and ericaceous vegetation ($13.7 \pm 6.0\%$ vs. $1.1 \pm 0.6\%$) were both greater ($p \leq 0.019$) in beaver-created wetlands. Percentage of emergent, herbaceous vegetation was greater in beaver-created wetlands ($26.3 \pm 8.4\%$ vs. $7.9 \pm 5.4\%$), but not different ($p = 0.062$).

Water chemistry

Mean water chemistry variables for the 29 wetlands were similar for beaver-created vs. glacial origin wetlands (Table 2). Except for pH, mean water chemistry variables were similar between the pH groups (i.e., ≤ 5.51 and >5.51). Mean alkalinity values did not exceed $43 \mu\text{eq l}^{-1}$ for any group of wetlands. Conductivity ($\mu\text{mhos cm}^{-1}$) was uniformly low, averaging from 23.0 (>5.51 pH group) to 25.2 (beaver-created wetlands). Beaver-created wetlands often contained colored water, wherein the Hazen units were twice as high as for glacial-origin wetlands. Color of water (Hazen units), converted to total organic carbon (TOC) (Haines & Akielaszek, 1983), was highly correlated with total phosphorus ($r = 0.86$, $p < 0.005$).

Invertebrates

Fewer Classes and Orders of invertebrates ($p < 0.05$) occurred on ponds grouped as $\text{pH} \leq 5.0$ as compared with ponds grouped as ≥ 5.5 (Fig. 1). Aquatic hemipterans (Hemiptera; Corixidae) were especially abundant in low pH wetlands such as Kerosene Pond, and Downing Bog and Fueloil Pond, which were also highly vegetated. Dipterans (Chironomidae) were most abundant in Downing Bog, Snake Flowage, and

Table 1. Wetland physical characteristics for study wetlands in Beddington and Cherryfield townships, southeastern Maine, 1982–1984

Study area, wetland name	Class ¹	Origin ²	Surface water area perimeter (ha)	Surface water area perimeter (m)	Water irreg. index ³	Percent surface water in life forms					Life form diversity	
						Littoral zone < 2 m	Open	Submergent	Floating leaved	Emergent		Ericaceous
<i>Beddington</i>												
Crooked River ⁴	PSSBLE	B	5.25	5659	6.47	0.4	93	93	7	0	0	0.81
Crooked Pond	PSSBLE	B	1.86	971	2.0	1.6	12	88	0	88	0	1.0
Fueloil Pond ⁴	PSSBLE	G	0.64	823	2.89	0.6	0	0	0	92	8	1.0
Kerosene Pond ⁴	PSSBLE	G	2.62	648	1.13	0.0	100	24	0	0	0	0.0
Lilly Lake	LUBGRA	G	11.6	1783	1.47	0.3	99	1	0	1	0	0.81
Peep Pond	LUBSND	G	14.38	2064	1.53	2.4	83	0	11	0	6	4.36
Pickrel Lake	PSSBLE	G	10.74	1625	1.28	2.6	76	6	8	16	0	1.44
Pickrel East	PABRVA	G	4.35	1120	1.51	1.7	59	6	36	3	2	3.27
Salmon Pond ⁴	PUBGRA	G	3.96	835	1.18	0.3	93	1	7	0	0	1.0
Soft Shoulder Pd	PEWNOP	G	0.02	89	1.96	0.0	100	0	0	0	0	0.0
<i>Cherryfield</i>												
Anderson Pond	LUBCOB	G	4.55	972	1.28	0.1	100	3	0	0	0	0.0
BFA Flowage	PFWDEA	B	3.45	1110	1.68	3.5	0	78	0	22	0	1.0
Downing Bog ⁴	PSSBLE	B	117.1	10936	2.85	110.5	6	22	20	22	46	2.21
Fox Pond	LRBRUB	G	23.91	3394	3.99	0.8	97	0	3	0	0	1.79
Foxtit Pond	PSSBLE	B	1.19	679	1.75	15.2	0	0	49	6	45	1.52
Gill Bog	PSSBLE	B	1.32	2245	5.51	1.2	91	0	9	0	0	0.97
Hatchery Pond	PSSBLE	B	4.39	1947	2.62	4.3	0	69	69	31	0	0.72
Hotdog Pond	PABRVA	G	2.89	1138	1.88	2.7	94	50	6	0	0	1.0
LittleA Flowage	PFWDEA	B	0.65	418	1.45	0.6	0	0	0	28	0	1.0
Little Long Pond ⁴	LRBRUB	G	21.75	2989	1.80	0.3	99	2	0	1	0	1.0
Myrick Pond	PABAMS	G	15.22	3413	5.69	3.8	75	75	25	0	0	0.99
Mud Pond ⁴	PUBORG	G	1.6	559	1.24	0.3	98	16	1	1	0	1.58
Rainbow Pond	PRBRUB	G	5.9	982	1.13	0.2	99	0	0	1	0	1.0
Salmont Pond ⁴	PUBCOB	G	2.45	633	1.13	0.1	97	3	0	3	0	0.91
Shillalah Pond	PABRVA	G	12.76	2250	1.79	10.4	18	18	64	15	3	1.9
Snake Flowage ⁴	PFWNLE	B	4.95	1245	1.57	4.5	10	10	0	28	21	1.95
Spring River Arm	PEWPER	B	10.1	2488	2.2	9.9	6	0	16	78	0	1.41
Tilden Pond ⁴	LRBRUB	G	12.26	1563	1.25	0.9	97	0	1	2	0	1.14
Tunk Stream Pd	PSSBLE	B	8.88	1375	1.3	0.1	11	38	27	13	49	1.76
Unnamed Pond	PSSBLE	B	4.68	2215	2.88	4.4	5	92	92	0	3	1.4

¹Wetland classification based on Cowardin et al. (1979). Systems: P = Palustrine, L = Lacustrine; Classes: AB = Aquatic bed, EW = Emergent wetland, FW = Forested wetland, RB = Rock bottom, SS = Scrub-shrub wetland, UB = Unconsolidated bottom; Subclasses: AMS = Aquatic moss, BLE = Broad-leaved evergreen, COB = Cobble, DEA = Dead timber, GRA = Gravel, NLE = Needle-leaved evergreen, NOP = Non-persistent, PER = Persistent, RVA = Rooted vascular, ORG = Organic.

²B = Beaver-created, G = Glacial basin or kettle pond.

³The ratio of surface water perimeter to the perimeter of a circle with an area equal to that of the surface water.

⁴Wetlands sampled for macroinvertebrates in 1982.

Table 2. July surface water chemistry data for all 29 wetlands by origin and those 10 wetlands sampled for invertebrates by pH classes in Beddington and Cherryfield townships, southeastern Maine, 1982

Variable	Mean ¹ 95% CI			
	Beaver-created, <i>n</i> = 12		Glacial, <i>n</i> = 17	
Al ($\mu\text{eq l}^{-1}$)	8.50	4.7–12.3	5.80	2.1–9.5
Ca ($\mu\text{eq l}^{-1}$)	56.70	46.4–66.9	50.75	36.5–65.0
Total phosphorus ($\mu\text{g l}^{-1}$)	36.44	5.3–67.5	9.65	5.9–13.3
Mg ($\mu\text{eq l}^{-1}$)	35.26	29.9–40.6	29.49	23.1–35.7
K ($\mu\text{eq l}^{-1}$)	8.10	5.5–10.6	7.11	5.5–8.7
Na ($\mu\text{eq l}^{-1}$)	101.97	74.2–129.7	114.76	81.3–148.2
Cl ($\mu\text{eq l}^{-1}$)	91.03	62.5–119.6	103.25	72.1–134.4
SO ₄ ⁻ ($\mu\text{eq l}^{-1}$)	39.22	23.4–55.1	50.08	39.1–61.1
NO ₃ ⁻ ($\mu\text{eq l}^{-1}$)	5.14	-2.7–12.9	1.75	0.49–3.0
pH	5.82	5.47–6.17	5.91	5.50–6.31
Alkalinity ($\mu\text{eq l}^{-1}$)	42.50	22.1–62.9	31.58	3.2–59.8
Conductivity ($\mu\text{mhos cm}^{-1}$)	25.25	20.9–29.6	27.35	22.2–32.4
Color (Hazen units)	75.58	32.4–116.8	37.35	16.8–57.9
Total organic carbon (TOC) (mg l^{-1})	5.89	3.3–8.5	3.61	2.3–4.9
		pH \leq 5.51, <i>n</i> = 6		pH $>$ 5.51, <i>n</i> = 4
Al ($\mu\text{eq l}^{-1}$)	10.88	0.5–21.2	5.95	-7.2–19.1
Ca ($\mu\text{eq l}^{-1}$)	36.95	17.7–56.2	51.62	41.1–62.1
Total phosphorus ($\mu\text{g l}^{-1}$)	22.61	-4.2–49.5	6.35	-2.1–14.8
Mg ($\mu\text{eq l}^{-1}$)	23.33	11.3–35.4	29.30	25.9–32.6
K ($\mu\text{eq l}^{-1}$)	5.85	0.8–10.9	7.15	3.6–10.7
Na ($\mu\text{eq l}^{-1}$)	73.31	20.9–125.7	85.80	79.8–91.8
Cl ($\mu\text{eq l}^{-1}$)	69.68	17.7–121.7	82.50	68.7–96.3
SO ₄ ⁻ ($\mu\text{eq l}^{-1}$)	33.75	-3.0–70.5	55.90	22.3–89.4
NO ₃ ⁻ ($\mu\text{eq l}^{-1}$)	4.15	1.8–6.5	0.75	-1.6–3.1
pH	4.91	4.55–5.27	6.29	5.68–6.91
Alkalinity ($\mu\text{eq l}^{-1}$)	-3.00	-37.6–31.6	34.25	5.8–62.7
Conductivity ($\mu\text{mhos cm}^{-1}$)	23.33	15.8–30.9	23.00	20.7–25.2
Color (Hazen units)	70.83	3.1–138.5	28.75	-36.3–93.8
Total organic carbon (TOC) (mg l^{-1})	5.66	1.5–9.8	3.08	-0.9–7.1

¹Means for 29 wetlands include data for May instead of July for one wetland and a deep instead of a surface sample for another wetland.

Kerosene Pond that all have pH \leq 5.51. At the Family level the mean number of taxa was greater (22.4 vs.18.8) on higher pH ponds, but not different ($p > 0.05$). Mean number per sample of Insecta was greater (119.1) for low pH ponds compared with high pH ponds (47.8), but not different ($p = 0.12$) (Table 3). Oligochaetes were more abundant in high pH wetlands, and although limited by low pH (Raddum, 1980), they also are influenced especially by substrate type and water depth. The Order Diptera and Families Chiro-

nomidae and Chaoboridae were more abundant in low pH wetlands. Aquatic Hemipterans (Family, Belostomatidae) also were more abundant in low pH wetlands as were Corixidae.

Invertebrate taxa related to wetland origin

Beaver-created wetlands are usually shallow (<2 m), densely vegetated, irregularly shaped basins with diverse vegetative life forms. In contrast, glacial ponds are usually deep basins,

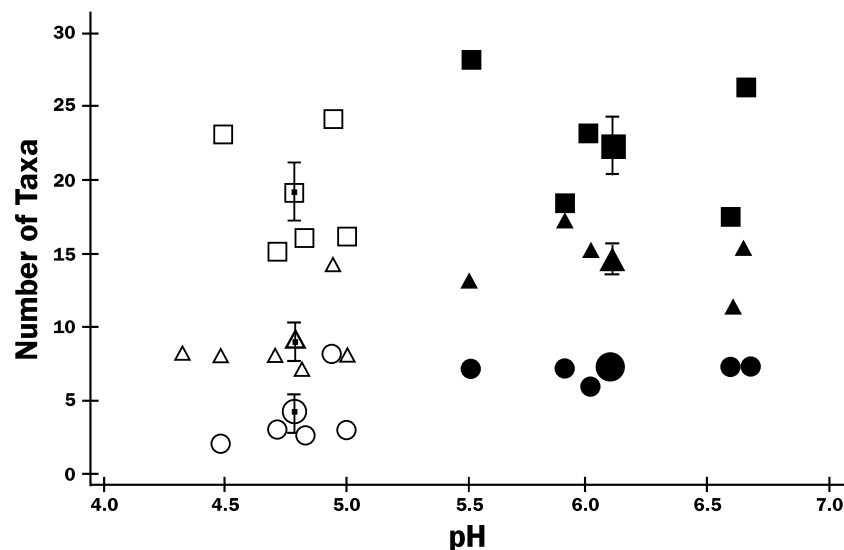


Figure 1. Mean (SE) difference in numbers of taxa for invertebrate Classes (O) (□), Orders (▲), and Families (■) between low (≤ 5.0) and high (≥ 5.5) pH wetlands. Mean numbers were different for Class and Order, $p < 0.05$.

with sparse vegetation, uniformly shaped, without macrophyte diversity. These glacial wetlands were mostly headwater ponds that are susceptible to acidification or are acidic. Mean counts per sample for all taxa were ≥ 2 times greater for beaver-created wetlands than for glacial wetlands (Table 3), although the observed significance levels (OSL) did not always indicate differences at ($p \leq 0.05$) for an individual taxon. For taxa that were tested with contingency tables, each taxon occurred more frequently in beaver-created wetlands. The mean number per sample of Ephemeropterans was greater ($p = 0.045$) in the higher pH wetlands. Mollusks are especially vulnerable to low pH (Okland, 1969; Raddum, 1980) and Gastropods (Ancyliidae) were less frequently collected ($p = 0.026$) in lower pH (≤ 5.51) wetlands. Crustaceans (Caldocera, Isopoda) also were less frequently collected in lower pH wetlands ($p = 0.026$) because they are more sensitive to low pH (Havas, 1981) than are insects.

We examined invertebrate densities by principal component and regression analyses. After rotation, the four principal components accounted for 81.6% of the total variance of the habitat variables (Table 4). The 4 components were interpreted as follows: PC1 explained 28.9% of the variance and represented 'eutrophication', PC2 explained 23.3% of the variance and was repre-

sentative of 'mineralization/buffering', PC3 explained 18.3% of the variance and represented 'potassium-vegetation interaction', and PC4, explained 11.0% of the variance and represented 'littoral zone vegetation'. Regressions of mean numbers of invertebrates for each Class, Order, and Family on principal components are presented in Table 5. Nearly 50% (19) of the significant regressions on taxa were associated with PC1 'eutrophication', including 3 of 5 Classes, 6 Orders, and 12 Families. Only Crustacea was associated with PC2 'mineralization/buffering', whereas 10 taxa were associated with PC3 'potassium-vegetation interaction', and 9 taxa were associated with PC4 'littoral zone vegetation'.

Fish status

Foxtit Pond contained pumpkinseed sunfish, *Lepomis gibbosus* (L.), creek chub, *Semotilus atromaculatus* (Mitchill), northern redbelly dace, *Phoxinus eos* (Cope), and golden shiner, *Notemigonus crysoleucas* (Mitchill). Kerosene Pond and Mud Pond were confirmed as fishless by R.M. Jordan (Maine DIF&W, pers. commun.) and we caught no fish in Kerosene Pond and Mud Pond or the kettle hole ponds (Fueloil Pond, Soft Shoulder Pond). Other wetlands were known to contain fish, except that no data were available on fish status for

Table 3. Mean numbers of invertebrates per sample related to pH and basin origin from 10 wetlands in southeastern Maine, 1982

Taxa	pH \leq 5.51 (<i>n</i> =6)	pH > 5.51 (<i>n</i> =4)	OSL ¹ <i>p</i>	Beaver (<i>n</i> =3)	Glacial (<i>n</i> =7)	OSL <i>p</i>
Mean number/sample or proportion (present/absent)						
<i>Class</i>						
Insecta	119.1	47.8	0.120	158.9	63.3	0.063
Crustacea				68.1	14.0	0.142
Hirudinea				3/0	2/5	0.035
Oligochaeta	0.2	1.6	0.044			
Gastropoda	2/4	4/0	0.026			
<i>Order</i>						
Diptera	48.1	23.0	0.083	57.8	29.6	0.065
Ephemeroptera	0.4	8.2	0.045			
Hemiptera	24.2	2.5	0.116	38.7	5.6	0.012
Pharynobellida				3/0	2/5	0.035
Basommatophora	2/4	4/0	0.026			
Cladocera	2/4	4/0	0.026			
Isopoda	2/4	4/0	0.026			
<i>Family</i>						
Chironomidae	40.3	22.7	0.120	48.3	26.8	0.067
Corixidae				33.2	2.3	0.005
Caenidae				3/0	2/5	0.035
Erpobdellidae				3/0	2/5	0.035
Hydrophilidae				3/0	2/5	0.035
Lestidae				3/0	2/5	0.035
Mesoveliidae				3/0	1/6	0.035
Ancylidae	2/4	4/0	0.026			
Belostomatidae	4/2	0/4	0.026			
Chaoboridae	4/2	0/4	0.026			

¹We used two-tailed *t*-tests to determine mean differences for taxa with > 50% non-zero values. We assumed equal variances because most variance comparisons did not suggest differences at the 1% level. If fewer than 50% of the samples were non-zero, but at least 4 non-zero values were available, we constructed a contingency table (McDonald et al., 1977) with presence and absence data and reported observed significant levels (OSL).

Gill Bog, Hatchery Pond, Hotdog Pond, LittleA Flowage, Pickerel East, Pickerel Lake, Shillalah Pond, Snake Flowage, Tunk Stream Pond, and Unnamed Pond. Although no sampling records exist for these latter ponds, neighboring wetlands within the study area contained 17 additional species of fish, which suggests that fish inhabited these wetlands as well because streams interconnected most wetlands.

Avian surveys

To determine use by birds we visited study wetlands 1077 times (1982, *n*=399; 1983, *n*=425; 1984, *n*=253) and we made observations during

1469 h (1982, *n*=482; 1983, *n*=622; 1984, *n*=365). Means (SE) for wetlands by year and all years combined are presented for beaver-created vs. glacial wetlands (Table 6).

Most (*n*=13) of the 21 monitored species and 4 of 5 designated functional foraging groups used beaver-created wetlands in greater proportion than wetlands of glacial origin, whereas common loon, common goldeneye and chimney swift were observed on or over glacial wetlands more often (Table 7).

For combined duck species plus sora and pied-billed grebe and 6 unknown broods on all 29 wetlands, most pairs (88.9%) and broods (87.9%) (Table 8) used beaver-created wetlands. Most

broods 77.4% used wetlands in the lower pH class (≤ 5.51) compared with the higher pH class (> 5.51) at 21.8%. The mean \pm SE number of pairs per beaver-created wetland (5.8 ± 3.7 , $n=12$), however, was not different ($t_{11}=1.40$, $p=0.187$) from that on glacial ponds (0.52 ± 0.11 , $n=16$) and neither was the mean number of broods per wetland (beaver-created, 6.03 ± 3.8 , $n=12$; glacial, 0.56 ± 0.17 , $n=16$; $t_{11} = 1.45$, $p=0.174$). The mean \pm SE density (pairs per ha of surface water) on beaver-created wetlands

(0.65 ± 0.15 , $n=12$) was different ($t_{26}=2.35$, $p=0.027$) from that on glacial ponds (0.18 ± 0.13 , $n=16$), but mean density of broods on beaver-created wetlands (0.635 ± 0.22 , $n=12$) was not different ($t_{26}=1.47$, $p=0.157$) from that of glacial wetlands (0.238 ± 0.16 , $n=16$).

We generated five principal components that accounted for 86.1% of total variation of mean pair or brood densities as related to wetland variables. PC1 'alkalinity-mineralization' explained 27.6% of the variance, PC2 'littoral zone vegetation' explained 20.1%, PC3 'eutrophication' explained 15.6%, PC4 'morphometry' explained 13.4% and PC5 'irregularity of water perimeter' explained 9.3% of the variance (Table 9). These components explained 54.8% of the variation in total pair density and 60.6% in brood density. Regression coefficients were different from zero for only two of the principal components, PC2 (mean pair density, $t_1=3.31$, $p=0.003$; mean brood density, $t_1=2.91$, $p=0.008$) and PC3 (mean pair density, $t_1=4.97$, $p=0.001$; mean brood density, $t_1=5.99$, $p=0.001$).

Mean pair densities ($F_{6, 20}=3.28$, $p=0.021$) and mean brood densities ($F_{6, 20}=3.29$, $p=0.020$) were different among some wetland classes. Densities of total pairs were higher ($p<0.01$, $t_{20} > 2.84$) on the Palustrine Forested Wetland class (1.26 ± 0.39) than all other classes except for Palustrine Scrub-Shrub (0.57 ± 0.17); means for other classes were 0.08 ± 0.008 for Palustrine Aquatic Bed, $0.05 \pm \text{nd}$ for Lacustrine Rubble Bottom, and < 0.02 for all other classes. Densities for broods were higher on Palustrine Forested Wetland (1.81 ± 0.46) than on all other classes (i.e., Palustrine Scrub-Shrub, 0.45 ± 0.22 ; Palustrine Rubble Bottom, 0.16 ± 0.16 ; Palustrine Aquatic Bed, 0.11 ± 0.06 ; and other classes averaged < 0.02 broods per hectare).

For the combined 10 wetlands sampled in 1982 for invertebrates we examined morphometry, Insecta abundance, and duck broods by principle components. In these wetlands numbers and densities (broods per ha) of duck broods in 1982 were: Snake Flowage 10 (2.02), Fueloil Pond 1 (1.56), Crooked River 2 (0.38), Downing Bog 37 (0.32), and Salmon Pond 1 (0.25). No broods were recorded for the other five wetlands.

The four principal components derived from water chemistry variables for these 10 wetlands

Table 4. Loadings for principal component analysis (PCA) for invertebrates and wetland variables, Cherryfield and Beddington townships, southeastern Maine, 1982

Variable ³	PC1	PC2	PC3	PC4
Water area (ha)				
Water irregularity index ¹				
Life form diversity ²				
% Water open				-0.6530 ³
% Submerged vegetation				
% Floating-leaved vegetation				
% Emergent vegetation				
% Ericaceous vegetation				0.9192
% Flooded timber	0.9757			
% Water vegetated			-0.4831	0.4704
Al ($\mu\text{eq l}^{-1}$)				
Ca ($\mu\text{eq l}^{-1}$)		0.9345		
Total phosphorus ($\mu\text{g l}^{-1}$)	0.9736			
Mg ($\mu\text{eq l}^{-1}$)	0.4659	0.8374		
K ($\mu\text{eq l}^{-1}$)			0.9145	
Na ($\mu\text{eq l}^{-1}$)		0.7208		
Cl ($\mu\text{eq l}^{-1}$)		0.7717		
SO ₄ ⁻ ($\mu\text{eq l}^{-1}$)				
NO ₃ ⁻ ($\mu\text{eq l}^{-1}$)	0.7166			
pH		0.7386		
Alkalinity ($\mu\text{eq l}^{-1}$)		0.8557		
Conductivity ($\mu\text{mhos cm}^{-1}$)		0.8366		
Total organic carbon (TOC) (mg l^{-1})	0.7784			

¹The ratio of surface water perimeter to the perimeter of a circle with an area equal to that of the surface water.

²Life form diversity index based on the formula $H = c/N \{\log_{10} N! - \sum \log_{10} n_i!\}$, where c is the scale factor (i.e., 3.321928) to convert logarithms from base 10 to base 2, N the sum of all life forms, and n_i the number of individual life forms (Lloyd et al., 1968).

³All variables with correlation coefficient ≥ 0.45 .

Table 5. Regressions of mean number of invertebrates for each Class, Order, and Family on principal components for habitat data from 10 wetlands, Cherryfield and Beddington, ME, June–July, 1982

Taxa	ANOVA Prob > <i>F</i>	Adjusted <i>R</i> ²	Prob > <i>T</i> Principal components ¹			
			PC1	PC2	PC3	PC4
Insecta	0.035	0.69	0.023	ns	ns	ns
Ephemeroptera	0.39 ns					
Baetidae	0.90 ns					
Leptophlebiidae	0.90 ns					
Caenidae	0.71 ns					
Ephemeridae	0.053 ns					
Trichoptera	0.46 ns					
Polycentropodidae	0.49 ns					
Hydroptilidae	0.0001	0.97	0.0001	ns	0.011	ns
Limnephilidae	0.80 ns					
Leptoceridae	0.18 ns					
Diptera	0.09 ns					
Chaoboridae	0.036	0.69	0.005	ns	ns	ns
Chironomidae	0.16 ns					
Ceratopogonidae	0.07 ns					
Odonata	0.59 ns					
Lestidae	0.0009	0.93	0.0003	ns	0.009	ns
Coenagrionidae	0.45 ns					
Aeshnidae	0.47 ns					
Libellulidae	0.005	0.86	0.0031	ns	ns	ns
Coleoptera	0.0001	0.98	0.0001	ns	0.0001	0.001
Gyrinidae	0.74 ns					
Hydrophilidae	0.0001	0.98	0.0001	ns	0.01	ns
Dytiscidae	0.0001	0.98	0.0001	ns	0.0003	0.002
Megaloptera	0.59 ns					
Sialidae	0.73 ns					
Hemiptera	0.0003	0.95	0.0012	ns	ns	0.009
Corixidae	0.0001	0.99	0.0001	ns	0.0005	0.000
Gerridae	0.0002	0.96	0.0001	ns	0.022	0.015
Notonectidae	0.14 ns					
Mesoveliidae	0.057 ns					
Crustacea	0.0007	0.94	0.0005	0.0068	ns	0.043
Isopoda	0.001	0.92	0.0007	ns	ns	ns
Cladocera	0.17 ns					
Arachnida	0.76 ns					
Hydracarina	0.99 ns					
Gastropoda	0.42 ns					
Basommatophora	0.58 ns					
Pelecypoda	0.045	0.66	0.028	ns	ns	ns
Eulamellibranchia	0.045	0.66	0.028	ns	ns	ns
Sphaeriidae	0.045	0.66	0.028	ns	ns	ns
Oligochaeta	0.20 ns					
Hirudinea	0.028	0.73	0.028	ns	0.014	0.006

Continued on p. 156

Table 5. (Continued)

Taxa	ANOVA Prob > <i>F</i>	Adjusted <i>R</i> ²	Prob > <i>T</i> Principal components ¹			
			PC1	PC2	PC3	PC4
Pharyngobdellida	0.0001	0.98	0.001	ns	0.0001	0.000
Erpobdellidae	0.000	0.98	0.001	ns	0.0001	0.000

¹PC1, 'eutrophication'; PC2, 'mineralization and buffering'; PC3, 'potassium-vegetation association'; PC4, 'littoral zone vegetation'.

were as follows: PC1 explained 41.5% of the variance and represented 'overall chemistry', PC2 explained 22.2% of the variance and represented 'acidity and organic carbon', PC3 explained 18.3% of the variance and represented 'conductivity', and PC4 explained an additional 10.9% of the variance and represented an 'aluminum/sulfate interaction'. PC loadings are presented in Table 10. For morphology and vegetation variables for the 10 wetlands sampled for invertebrates the following principal components emerged: PC1 explained 50.1% of the variance and represented 'wetland size/amount vegetated', PC2 explained 23.4% of the variance and represented 'ratio of vegetated to open water', PC3 explained 15.6% of the variance and represented 'beaver effects', PC4 explained an additional 9.0% of the variance and represented 'forested wetland/emergent' (Table 10).

The Poisson regression indicated that only the 'mean number of Insecta per pond' (INSECT), adjusted for wetland size significantly explained

mean numbers of broods ($t_8 = 4.50$, $p < 0.001$). Examinations of residuals and the Chi-squared goodness of fit indicated no departures from model assumptions. The estimate of the coefficient of INSECT was 0.012 with SE equaling 0.0027. Thus, mean numbers of broods on these wetlands were positively associated with mean number of Insecta per wetland.

Discussion

Characteristics of wetlands

The amount of habitat and its structure (vegetation development and interspersions) influence use by water birds. For two Iowa marshes, Weller & Spatcher (1965) reported that the maximum number and diversity of birds were reached when a well-interspersed cover-water ratio of 50:50 occurred. Later, Weller & Fredrickson (1974)

Table 6. Effort (visits, hours) expended per year per beaver-created vs. glacial wetlands in Cherryfield and Beddington townships in southeastern Maine, 1982–1984

Wetland origin	Mean ± SE, 95% CI			
	Number of visits		Hours of observation	
Beaver-created				
1982	15.6 ± 2.1	11.0–20.3	20.3 ± 3.4	12.8–27.8
1983	20.8 ± 8.3	2.5–39.2	35.6 ± 17.8	–3.5–74.7
1984	13.7 ± 6.9	–1.5–28.9	21.6 ± 12.5	–5.9–49.1
1982–1984	50.2 ± 17.0	12.6–87.7	77.5 ± 33.5	3.7–151.3
Glacial				
1982	12.4 ± 1.7	8.8–16.0	14.0 ± 1.2	11.5–16.5
1983	10.3 ± 0.98	8.2–12.4	11.5 ± 0.98	9.4–13.6
1984	5.2 ± 0.57	4.0–6.4	6.2 ± 0.42	5.3–7.1
1982–1984	27.9 ± 12.4	21.6–34.3	31.7 ± 2.2	27.0–36.4

associated bird use with increased diversity of vegetative types. Murkin et al. (1982) reported that the highest densities of dabbling duck pair use were associated with 50:50 plots (water: vegetation) in Manitoba. Nelson & Kadlec (1984: 263) stated that the distribution and pattern of emergent vegetation within wetland basins may be an important structural component influencing habitat suitability and determining reproductive effort of breeding waterfowl because inundated accumulations of litter affect macroinvertebrate abundance. Wetzel & Likens (1979: 146–147) emphasized the importance of complex wetland-littoral areas of lakes and stated that the littoral components and their metabolism regulated the productivity of most lakes. In our study, the amount and structure of the vegetation did influence use by birds (Table 1). The principal component, 'littoral zone vegetation', had a strong negative association with the percentage of unvegetated water and was important in explaining the variation in pair and brood densities. Although the total surface water area of beaver-created (163.8 ha) vs. glacial (145.7 ha) wetlands was similar, the amount of vegetated surface water in the beaver-created group (81.5%) was 4.8 times greater than in the glacial wetland group (19.5%). Furthermore, beaver-created wetlands contained many times the area of the life forms of submergent (2.6×), floating-leaved (2.2×), and emergent (8.0×) vegetation than that of glacial wetlands. Emergent herbaceous vegetation in Maine has dense invertebrate populations (Reinecke, 1977; Ringelman, 1980). The abundant ericaceous habitats in beaver-created ponds provide both nesting and brood cover for water birds, especially ducks.

The habitat structure (i.e., vegetation) largely dictates the production of macroinvertebrates in freshwater wetlands (Andrews & Hasler, 1944; Moyle, 1961; Keiper, 1966; Krull, 1970; Voigts, 1976). In our study, for most invertebrate taxa tested from 3 beaver-created and seven glacial ponds, the mean number of individuals per sample or the frequency of occurrence was greater on beaver-created ponds ($p=0.063$ to $p<0.005$) than on glacial ponds (Table 3), even though three of the sampled glacial ponds were fishless. Water bird use was concomitantly greater on wetlands (i.e., beaver-created wetlands) with abundant macroinvertebrates as reported by McKnight & Low

(1969) in Utah, Arner et al. (1970) in Mississippi, Voigts (1976) in Iowa, and Kaminski & Prince (1981) in Manitoba. Joyner (1980) concluded that principally invertebrate numbers in the 7 ponds he studied in Ontario regulated duck use. Murkin & Kadlec (1986) suggested that wetland use may not be influenced by invertebrate density during springs with above normal water depths when invertebrates are more widely dispersed, however, our data suggest bird use was related to invertebrate density and strongly influenced by the macrophytes available to support them.

Table 7. Use of beaver-created or glacial wetlands by 21 avian species and 5 designated functional foraging groups in Cherryfield and Beddington townships in southeastern Maine, 1892–1984

Species/foraging group	Percent use of Wetland type			
	Beaver-created	Glacial	χ^2_1	p
Common Loon * ¹	5.7	26.5	73.4	<0.0001
Double-crested Cormorant *	15.4	5.3	20.9	<0.0001
Common Merganser *	10.4	17.9	10.8	=0.0015
Great Blue Heron *	19.6	7.1	25.7	<0.0001
Osprey *	10.8	8.5	1.14	=0.2846
Belted Kingfisher *	31.3	32.1	0.53	=0.8183
American Black Duck ■	54.6	12.3	255.1	<0.0001
Green-winged Teal ■	22.1	0.6	80.9	<0.0001
Wood Duck ■	62.4	11.8	214.4	<0.0001
Ring-necked Duck ■	48.9	7.3	161.3	<0.0001
Pied-billed Grebe ◇	17.6	0.3	64.2	<0.0001
American Bittern ◇	13.3	0.6	43.7	<0.0001
Sora ◇	9.3	0.0	33.8	<0.0001
Hooded Merganser ●	38.3	13.5	61.8	<0.0001
Common Goldeneye ●	0.2	11.5	57.9	<0.0001
Common Snipe ●	9.4	0.0	33.8	<0.0001
Spotted Sandpiper ●	8.0	5.3	2.35	=0.1247
Common Nighthawk	19.4	14.4	3.24	=0.0716
Chimney Swift	7.6	11.8	4.14	=0.0419
Eastern Kingbird	14.9	1.8	40.2	<0.0001
Tree Swallow	44.2	28.8	20.5	<0.0001
Piscivore *	59.1	62.6	1.07	=0.2998
Omnivore-1■	81.8	25.9	264.8	<0.0001
Omnivore-2 ◇	30.3	0.8	116.1	<0.0001
Insectivore-1●	51.3	25.6	55.6	<0.0001
Insectivore-2	58.5	41.5	22.4	<0.0001

¹Species with the same symbol represent functional foraging groups.

Water chemistry

Limnological characteristics of freshwater wetlands also influence invertebrate density and waterfowl use. Phosphate and nitrite were highly correlated with levels of duck use in taiga ponds of Alaska (Murphy et al., 1984) and were useful predictors of duck species richness and duck density. In Ontario, Patterson (1976) reported that pairs were dependent only on the amount of surface water available, but that broods and fledged ducks aggregated on the more biologically productive ponds. Nilsson & Nilsson (1978) in Sweden reported that total numbers of species and

species diversity were correlated with shore development and pH. Furthermore, they concluded that both correlates of water bird density, along with fen area and total phosphorus, could be interpreted as a response of birds to lake productivity. Andersson (1981) stressed the importance of the effects of fish in changing freshwater ecosystems through eutrophication, wherein planktonic algae dominate, submerged plants are reduced, invertebrates become less abundant and water birds are adversely affected by the habitat change.

For all species combined, pair density and brood density were associated with fertile wet-

Table 8. Numbers of broods on all 29 wetlands by origin and pH class and on those 10 wetlands sampled for invertebrates in Cherryfield and Beddington townships, southeastern ME, 1982–1984

Pond group Species	Wetland Origin		Wetland pH	
	Beaver-created, <i>n</i> = 12	Glacial, <i>n</i> = 17	≤ 5.51, <i>n</i> = 9	> 5.51, <i>n</i> = 20
<i>All ponds</i>				
American Black Duck	62	5	58	9
Mallard	3	0	1	2
Green-winged Teal	10	0	10	0
Blue-winged Teal	3	0	3	0
Wood Duck	53	5	42	16
Ring-necked Duck	27	2	24	5
Hooded Merganser	38	8	35	11
Common Merganser	6	2	0	8
American Goldeneye	0	7	5	2
Pied-billed Grebe	9	0	9	0
Sora	2	0	2	0
Unidentified broods	6	0	6	0
	219 (88.3%)	29 (11.7%)	194 (77.4%)	54 (21.8%)
<i>Invertebrate sample ponds</i>				
	<i>n</i> = 3	<i>n</i> = 7	<i>n</i> = 6	<i>n</i> = 4
American Black Duck	56	0	55	1
Mallard	3	0	1	2
Green-winged Teal	10	0	10	0
Blue-winged Teal	3	0	3	0
Wood Duck	36	0	36	0
Ring-necked Duck	24	0	24	0
Hooded Merganser	26	7	30	3
Common Merganser	0	0	0	0
American Goldeneye	0	5	5	0
Pied-billed Grebe	9	0	9	0
Sora	2	0	2	0
Unidentified broods	6	0	6	0
	174 (93.5%)	12 (6.4%)	180 (96.8%)	6 (3.2%)

lands. Total pair density was correlated with PC3 'eutrophication' ($r=0.64$, $p<0.01$), as was total brood density ($r=0.72$, $p<0.01$). PC2, 'littoral zone vegetation' was next in importance in explaining the use of wetlands as total pair density was associated with this component ($r=0.42$, $p<0.05$) and total brood density nearly so

($r=0.35$, $p=0.069$). Both regressions of pair and brood density on PC2 and PC3 were significant.

Invertebrates

For the 10 wetlands, densities of invertebrate taxa were associated with wetland nutrients, tolerance of specific taxa to low pH, vegetation, absence of fish, and effects of beaver. Total phosphorus averaged 16.6 ppb (range 1.6–70), somewhat higher than in large headwater lakes of Maine where the mean value ranged from 2.4 to 27.8 ppb (Davis et al., 1978). Total phosphorus in Maine streams not receiving point-source pollution are among the lowest in the conterminous United States, but higher than in lake surface water (Davis et al., 1978: 22). Despite uniformly low phosphorus and conductance ($\bar{x}=23 \mu\text{mho cm}^{-1}$) compared with a mean of 3550 in prairie wetlands (Kadlec, 1986), for all 10 wetlands most variance (28.9%) in invertebrate densities, regardless of taxonomic level, was accounted for by PC1, 'eutrophication' (Table 4). Aquatic invertebrates are abundant in waters with 'nutrient or organic matter enrichment' (Likens, 1972), but fertility of wetlands in the northeast is inherently low (Reader, 1978; Richardson, 1979). As rooted macrophytes colonize nutrient-rich sediments, biological productivity may reach its greatest level (Westlake, 1963) and associated aquatic insects readily use macrophytes for food and concealment (McGaha, 1952). Even when pH is low (4.0–5.0) numbers of insects and Oligocheats (Kerekes et al., 1984) and Crustaceans (DeCosta et al., 1983) are increased with nutrient inflows. Mollusks (Gastropoda, Pelecypoda) are most plentiful in eutrophic lakes with hard water, less common in oligotrophic lakes and are absent from dystrophic waters with little calcium (Hunter, 1964), but Gastropod abundance correlated with total phosphorus concentrations in small Ontario lakes (Bendell & McNicol, 1993). Furthermore, beaver are a keystone species that alter hydrologic regimes (Naiman et al., 1986), influence biogeochemical cycles (Naiman et al., 1994), and enhance richness and abundance of macroinvertebrates in lentic wetlands they create (McDowell & Naiman, 1986; France, 1997; Rolauuffs et al., 2001).

Tolerance to low pH is extremely variable among invertebrate taxa. The median of minimum

Table 9. Loadings (correlation coefficients) of wetland variables for principal component analysis (PCA) of mean pair and brood densities, Cherryfield and Beddington townships, southeastern Maine, 1982–1984

Variable ¹	PC1	PC2	PC3	PC4	PC5
Basin area				0.7538 ¹	
Water area				0.8028	
Life form diversity				0.7772	
Water irregularity index					0.9452
Water area < 2 m				0.7317	
% Water open		-0.9159			
% Submerged vegetation					
% Floating-leaved vegetation		0.5946			
% Emergent vegetation		0.7081			
% Ericaceous vegetation					
% Flooded timber			0.5799		
% Water vegetated		0.9679			
Al ($\mu\text{eq l}^{-1}$)			0.6881		
Ca ($\mu\text{eq l}^{-1}$)	0.9465				
Mg ($\mu\text{eq l}^{-1}$)	0.8352				
K ($\mu\text{eq l}^{-1}$)					
Na ($\mu\text{eq l}^{-1}$)	0.7660				
F ($\mu\text{eq l}^{-1}$)					
Cl ($\mu\text{eq l}^{-1}$)	0.6316				
SO ₄ ⁻ ($\mu\text{eq l}^{-1}$)			-0.6284		
NO ₃ ⁻ ($\mu\text{eq l}^{-1}$)					
H ($\mu\text{eq l}^{-1}$)					
pH	0.7412		-0.5499		
Alkalinity ($\mu\text{eq l}^{-1}$)	0.9165				
Conductivity ($\mu\text{mhos cm}^{-1}$)	0.7620				
Total organic carbon (TOC) (mg l^{-1})			0.9141		

¹We included all variables with correlation coefficient ≥ 0.50 .

pH values for most aquatic groups is between 5.2 and 6.1 (Eilers et al., 1984; Doka et al., 1997). Furthermore, acid-neutralizing capacity (ANC) (i.e., alkalinity) was lacking (-37.7 to -1.2) or low (7.9 – 58.8) among the 10 wetlands. Thus, PC2, 'mineralization and buffering', was associated with Crustacea, which respond negatively to lack of buffering and low pH (Grahn et al., 1974).

Table 10. Loadings (correlation coefficients) of wetland variables for principal component analysis (PCA) of waterfowl brood densities, Cherryfield and Beddington townships, southeastern Maine, 1982

Variable ¹	PC1	PC2	PC3	PC4
<i>Water chemistry</i>				
Al ($\mu\text{eq l}^{-1}$)				0.7936
Ca ($\mu\text{eq l}^{-1}$)	0.8036	-0.5728		
Total phosphorus ($\mu\text{g l}^{-1}$)	0.7130		-0.5288	
Mg ($\mu\text{eq l}^{-1}$)	0.8724			
K ($\mu\text{eq l}^{-1}$)	0.7751			
Na ($\mu\text{eq l}^{-1}$)	0.6162		0.7484	
Cl ($\mu\text{eq l}^{-1}$)	0.5025		0.7944	
SO ₄ ⁻¹ ($\mu\text{eq l}^{-1}$)		0.5031		0.6109
NO ₃ ⁻¹ ($\mu\text{eq l}^{-1}$)	0.5410			
pH		-0.8817 ¹		
Alkalinity ($\mu\text{eq l}^{-1}$)	0.7910	-0.5267		
Conductivity ($\mu\text{mhos cm}^{-1}$)			0.7918	
Total organic carbon (TOC) (mg l^{-1})	0.7763	0.6011		
<i>Wetland morphometry</i>				
Water area	0.9291			
Water perimeter	0.9262			
Water irregularity index ²		0.5856	-0.7002	
Water area < 2 m	0.9535			
% Water open	-0.6470	0.6412		
% Submerged vegetation		0.7692	-0.5319	
% Floating-leaved vegetation	0.8984			
% Emergent vegetation		-0.6253	-0.5500	0.5080
% Ericaceous vegetation	0.9324			
% Flooded Timber		-0.5575		-0.7487

¹We included all variables with correlation coefficient ≥ 0.50 .

²The ratio of surface water perimeter to the perimeter of a circle with an area equal to that of the surface water.

Although Kerosene Pond is acidic (pH = 4.48), trichopterans can tolerate low pH (Bell, 1971; Eilers et al., 1984) and may have benefited from lack of fish. Chironomidae were twice as abundant in low pH wetlands but not different ($p = 0.12$) from high pH ponds; Chironomids are known to tolerate extremely acidic (\sim pH 2.8) environments (Wiederholm & Eriksson, 1977; Eilers et al., 1984) and elevated levels of aluminum caused by acidification (Havas & Likens, 1984). *Chaoborus* sp. (Chaoboridae) also tolerates low pH (Mossberg & Nyberg, 1979; Raddum, 1980) and they increase in acidified lakes (Stenson, 1978; Eriksson et al., 1980) when fish are eliminated. Aquatic Hemipterans (Corixidae and Belostomatidae) (Table 3) were especially abundant in the low pH wetlands (Downing Bog, Fueloil Pond, Kerosene Pond) as reported for these taxa in Sweden (Henrikson & Oscarson, 1978). The mean number per sample of Ephemeropterans was greater ($p = 0.045$) in the high pH ponds because mayflies are fairly sensitive to acid waters (Bell, 1971; Hendrey et al., 1976). In Pennsylvania the mayfly genus *Ephemerella* was not collected from water with a pH of < 5.5 (Dinsmore, 1968). Raddum (1980) reported that pH 5.5 was the tolerance limit of gastropods in lakes deficient in lime in acidified regions, but correlations between mollusk distribution and either water alkalinity or calcium were higher than correlations with pH (Macan, 1950). The mean amount of Ca ($21.7 \mu\text{eq l}^{-1}$) for the 5 low pH ponds was lower ($p < 0.05$) than for the five high pH wetlands (mean = $53.2 \mu\text{eq l}^{-1}$). According to Hunter (1964) calcium is the most important chemical parameter and several hard-water species are rarely found in water with $< 20 \text{ mg l}^{-1}$ calcium (Boycott, 1936). Crustaceans (Caldocera, Isopoda) were less frequently collected in low pH wetlands (Table 3) because of intolerance to acidic water (Havas, 1981). This phenomenon has been reported (Hendrey et al., 1976; Fryer, 1980), but the relationship is confounded because a decrease in crustaceans in acidified water may be from increased acidity or from increased predation by invertebrates when fish are eliminated (Eriksson 1980). Kenlan et al. (1984) reported that their Maine studies support the hypothesis that pH is more important than physical habitat as a factor affecting diversity of chydorid communities in lakes. Odonates, which were more abundant in

some acidic study wetlands (e.g., Snake Flowage, Kerosene Pond, Downing Bog), are known to prey on Cladocera (Pritchard, 1964) and other crustaceans. This scenario may apply to Downing Bog, in which effects of low pH may be offset by the dense aquatic macrophytes that support and conceal invertebrates from predators (Krull, 1970).

Development of vegetation in a wetland is affected by and confounded with nutrient levels, basin depth, and beaver activity. Abundance and diversity of vegetation are known to influence invertebrate numbers (Gerking, 1957; Moyle, 1961) and Krull (1970) reported that macroinvertebrates were more abundant in vegetated areas than in non-vegetated areas.

Newly flooded beaver-created wetlands (e.g., Snake Flowage) are known to harbor large populations of invertebrates (Keiper, 1966, Whitman, 1974) and in Maine recently impounded beaver flowages (<3 years) received greater brood use than older ones (Ringelman & Longcore, 1982). In Maine, herbaceous vegetation supports a higher biomass of aquatic invertebrates than other life forms (Reinecke, 1977: 86). The transition period in the wet-dry cycle of a prairie wetland, which is believed the period of maximum invertebrate diversity and abundance (Murkin and Ross, 1999), is functionally similar to reflooding of a beaver meadow in the northeast. Beaver create meadow and pond patches with high standing stocks of ions and nutrients in surface organic profiles, and for nitrogen, in plant-available forms (Naiman et al., 1986). Furthermore, Snake Flowage contained abundant organic debris (e.g., *Calamagrostis* sp. and *Carex* spp.), which likely contributed to high production (Street, 1982) when it was reflooded. Some variance also was accounted for by PC3, 'potassium-vegetation association' for the Order Coleoptera and for five insect Families. The role of potassium with PC3 may be related to the cyclic nature of K as influenced by the macrophyte growing season and the tendency of K to be lost from solution by adsorption and other processes (Hem, 1959: 91). PC4, 'littoral zone vegetation' explained some additional variance for leeches (Erpobdellidae), which search through vegetation seeking as prey other oligochaetes and larvae of Odonata, Coleoptera, Trichoptera, Ephemeroptera and Diptera (Sawyer, 1974). Conversely, a primary defense by prey species (Crustacea and

Insecta) is to seek refuge, frequently in high densities, in mineral or macrophyte substrates in the littoral zone of ponds (Macan, 1977; Peckarsky, 1984). The three relatively deep, glacial ponds (Salmon Pond, Little Long Pond, Tilden Pond) with the fewest mean number of Insecta had small littoral zones that were sparsely vegetated, which affects insect abundance (Andrews & Hassler, 1944; Krull, 1970). Wetlands with intermediate insect numbers (Salmon Pond, Mud Pond, Fueloil Pond, Crooked River) represented wetlands with mostly open water, which limits colonization by aquatic invertebrates; Mud Pond and Fueloil Pond also were acidic.

Fish status

Many of the effects of fish on macroinvertebrate communities are known (McNicol & Wayland, 1992; Bendell & McNicol, 1995). The three wetlands with the lowest mean number of Insecta (Salmon Pond, Little Long Pond, and Tilden Pond) all contained fish; feeding activity of fish is known to reduce invertebrate populations (Brooks & Dodson, 1965; Macan, 1977; Morin, 1984). In contrast, three wetlands in the low pH group (Kerosene Pond, Mud Pond, Fueloil Pond) were fishless; lack of fish allows some insect populations to increase (Healey, 1984). Kerosene Pond, which contained the highest number of Trichoptera, also was fishless and that may account for the higher mean number, because fish (brook trout, *Salvelinus fontinalis* Mitchell) prey on trichopteran larvae (Raddum, 1980; Hunter et al., 1986). Conversely, Snake Flowage was expected to have high trichopteran numbers but averaged only 2 per sample for the wetland. This small (5.0 ha) wetland probably contained fish, but it supported 10 female ducks with broods (i.e., 60-70 ducklings), and several molting wood duck males. American black ducks in Maine are known to feed heavily on trichopterans (Reinecke, 1979), thus, competition between ducks and fish for specific aquatic taxa, as suggested by Eriksson (1979), may have existed in Snake Flowage.

Avian surveys

Mean numbers of visits and hours of observation per year, except for 1982, were about twice as great

in 1983 as in 1984 and for all years combined when data for Downing Bog are included (Table 6). Excluding data for Downing Bog, however, results in beaver-created wetlands being visited on average only 1 or 2 times more, accounting for 3–6 h more observation effort than on glacial wetlands.

Among the 5 functional foraging groups, the 2 omnivore and the 2 insectivore groups that rely on invertebrates for food used beaver-created wetlands more than glacial wetlands (Table 7). In contrast, the combined piscivore species used these habitat types equally. Individually, common loon and common merganser used glacial wetlands more than beaver-created ones, whereas belted kingfisher and osprey used both wetland groups equally. DesGranges & Darveau (1985) reported that common loon and great blue heron used large, low altitude lakes with little vegetation, but we found that great blue heron rarely used un-vegetated, glacial wetlands. Because birds have mobility, effects of acidification on them may be subtle, except when increasing acidity eliminates prey, which is applicable to piscivores. Even then, acidity may briefly enhance foraging for some species (e.g., common loon, common merganser), by increasing transparency of surface of water or by allowing pelagic invertebrate numbers to expand thereby benefiting species (i.e., common goldeneye) that prefer fishless wetlands (Eriksson, 1979; Wayland & McNicol, 1990). Avian use of wetlands is influenced by a complex array of physical, chemical, and biological properties so that individual species need evaluation. Common loons, for example, use large wetlands (>250–1230 ha) more than small (<25–60 ha) ponds (Sawyer, 1979) because more area is needed to become airborne. Although common loons can raise broods on fishless lakes by eating alternative prey (Munro, 1945), studies in New York (Parker and Brocke, 1984), Ontario (Alvo, 1985) and Sweden (Almer et al., 1978) suggest losses of loons that use acidic wetlands. Recent data of loon breeding success on 292 lakes in Ontario from 1987–1999 depict a significant negative trend (McNicol et al., 1995). Common mergansers in Sweden emigrated from acid lakes (Almer et al., 1978) where fish populations declined. We observed that females with newly hatched broods on glacial ponds, often moved to other wetlands and

streams. This mobility may lessen effects on common mergansers in contrast to the common loon that has more affinity to natal wetlands and is incapable of overland travel. Recent models of Jeffries et al. (2003) suggest that improvement in habitat quality for common loons and common mergansers will occur, only if emissions of SO₂ are reduced below standards established under the 1991 Canada–US Air Quality Agreement. Double-crested cormorants used wetlands unequally, favoring beaver-created flowages, even with the dark-stained waters. These aforementioned species are ‘pursuit divers’, because they ‘peer’ to detect prey (Lindroth & Bergstrom, 1959) then dive in pursuit, and may benefit from greater water transparency resulting when humus precipitates in acidic water (Dickson, 1978). In contrast, belted kingfishers, ospreys, and the great blue heron, which forage in the littoral zone, exploit shallow water as ‘surface plungers’, and are not affected as much by changes in water transparency. Omnivore-1 foraging group (3 dabbling and 1 diving duck species) avoided glacial ponds; they foraged in shallow, densely vegetated wetlands and were readily attracted to habitat created by beaver (Beard, 1953; Knudsen, 1962; Ringelman and Longcore, 1982). Birds of Omnivore-2 group rarely used glacial ponds, but were uncommon even on beaver-created wetlands that they used almost exclusively. Of the Insectivore-1 group, hooded mergansers used beaver-created wetlands more, whereas common goldeneyes used glacial ponds predominantly and only in the Beddington area, where 3 of 4 ponds used were too acidic for fish. Although adults seem to prefer fishless ponds, the mean number of surviving ducklings in 7 common goldeneye broods was 0.86 per brood, consistent with low survival in western Maine (Gibbs, 1962). In Sweden, however, the number of fledged goldeneyes per lake was higher on fishless lakes than on those with fish (Eriksson, 1979). In Ontario, common goldeneye females led broods from nesting lakes with lower biomass of prey to brood-rearing lakes with higher biomass, although survival of broods was not related to prey biomass (Wayland & McNicol, 1994). Common snipes used marsh areas of beaver flowages, whereas spotted sandpipers frequented the margins of wetlands of both wetland types (Gibbs et al., 1991) but we have too few data to denote preferences.

Our findings regarding association of waterfowl broods with biological and physical characteristics of wetlands are similar to those of Staicer et al. (1994) for Nova Scotia. Although wetlands in the northeast are mostly oligotrophic or mesotrophic, duck broods used wetlands with the highest trophic status, reflected in higher levels of total phosphorus but low pH, which did not affect use by brood-rearing females. Seventy-seven percent of all broods for all years (Table 8) were raised on wetlands with $\text{pH} \leq 5.51$, which supports the comment of Staicer et al. (1994: 195) that, 'Moreover, total phosphorus was statistically more important than pH in predicting use of lakes by black ducks'. In our study the amount of total phosphorus predicted mean number of Insecta per wetland and mean brood density, which reinforces findings of Staicer et al. (1994). Our findings and that of Staicer et al. (1994), and Parker et al. (1992) in New Brunswick, however, are in contrast with DesGranges & Houde (1989) in Quebec who stated that black ducks avoid acidic lakes. Brood-rearing females seek wetlands with concealing vegetation (Ringelman & Longcore, 1982) and an abundance of aquatic macroinvertebrates (McNicol et al., 1987; McNicol & Wayland, 1992), which are essential for duckling growth (Reinecke, 1979; Hunter et al., 1986) (Table 10). Differences in measures (mean \pm SE) of fertility between Maine wetlands in a forested landscape [conductance ($\mu\text{S cm}^{-1}$) = 58 ± 11 , phosphorus ($\mu\text{g l}^{-1}$) = 39 ± 11] and in an agricultural landscape (conductance = 261 ± 15 , phosphorus = 64 ± 14) did not result in differences between black duck or mallard brood sizes (Longcore et al., 1998). On Lake J, a hypertrophic pond with high phosphorus (i.e., $23\,950 \mu\text{g l}^{-1}$), however, broods were larger than on wetlands in a forested landscape or other wetlands in an agricultural landscape and broods in Lake C (phosphorus = $170 \mu\text{g l}^{-1}$) were larger than on other wetlands in an agricultural landscape (Longcore et al., 1998).

Conclusions

Wetland trophic status related to water chemistry, especially the components 'eutrophication' and 'mineralization and buffering', in addition to

macrophyte diversity clearly affected macroinvertebrate abundance that influenced water bird use among wetlands. The effect of low pH was evident for several sensitive Orders and Families of invertebrates and the absence of fish may have affected invertebrate populations in some wetlands and benefited American goldeneyes and hooded mergansers. The shear size (117.1 ha) and diversity (6 of 6 vegetative life forms represented) of one wetland (Downing Bog), profoundly affected avian use (Brown & Dinsmore, 1986), wherein 59.8% of the pairs and 56.8% of all broods were recorded on this wetland. The importance of vegetative structure is evident (McCall et al., 1996) in that the highest densities of pairs or broods were recorded on beaver-created wetlands classified as Palustrine Forested Wetland, Palustrine Scrub-Shrub, and Palustrine Aquatic Bed even when wetland pH was low. Because acid rain continues to be a threat to aquatic ecosystems (Doka et al., 2003), these data of breeding bird status in habitats vulnerable to acidification in Maine may be useful in efforts to model regional effects (Jeffries et al., 2003), especially for the Atlantic Maritime region (McNicol, 1999). Biological recovery of wetlands is slower and not assured following chemical recovery of lakes after SO_2 emissions are reduced and recovery may vary spatially and temporally (McNicol, 2002). Current efforts to define biological recovery in aquatic systems are minimal, which poses a major challenge in understanding regional recovery from acid rain (Jeffries et al., 2003).

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Breeding waterbird wetland habitat availability and response to water-level management in Saint John River floodplain wetlands, New Brunswick

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Abstract

Wetland management by the Eastern Habitat Joint Venture (EHJV) has focused primarily on water level control to increase the amount of available brood-rearing habitat for waterfowl along the Saint John River floodplain in New Brunswick. Impounded wetlands make up approximately 13% of the Saint John River Floodplain complex. Study objectives included an evaluation of waterfowl brood, and wetland obligate bird use of impoundments and seasonally flooded wetlands within the Saint John River floodplain. Historical water level data and a GIS wetlands inventory were used to estimate the duration of flooding on seasonally flooded wetland habitats, and the distribution and relative amount of brood-rearing habitat throughout the breeding period by region. Aerial brood surveys and call response surveys were used to estimate the relative abundance of waterfowl broods and breeding wetland obligate birds respectively. The overall density of waterfowl broods was greater on impoundments than on seasonally flooded wetlands during both years of study but varied by site. Mean species richness of wetland obligate birds was significantly greater on impoundments than on seasonally flooded wetland habitat. Generally, use of seasonally flooded wetlands by wetland obligate birds during late summer declined while the use of impoundments increased. Current habitat management for waterfowl appears to be compatible with habitat requirements of wetland obligate birds by increasing the availability of interspersed open water and emergent vegetation throughout the breeding season. A watershed-based analysis of wetland habitat suggests future wetland management should focus on enhancing current impoundments within the Saint John River floodplain. Resources must be secured for maintenance and water level manipulation within existing managed wetlands rather than the construction of additional impoundments. Further evaluation of the distribution of wetland habitat types in the province is essential to identifying focus areas for waterbird conservation throughout NB.

Introduction

The lower Saint John River contains a variety of wetland habitats that are unique to Atlantic Canada and provide habitat for a high diversity of waterbird species. In addition, they comprise some of the most productive wetland habitats in New Brunswick and support large numbers of waterfowl. There are over 20,000 ha of wetlands

along the main river and its tributaries below Mactaquac Dam.

The lower Saint John River wetlands have become a focus of conservation efforts under the Eastern Habitat Joint Venture (EHJV) of the North American Waterfowl Management Plan (NAWMP) in New Brunswick. Currently, over 3200 ha have been secured through acquisition and 2000 ha through stewardship. An additional

4000 ha have been secured through Environment Canada's National Wildlife Area program at Portobello Creek including upland, riparian, open lake, river and wetland habitats. Other initiatives such as provincial parks, nature reserves, and private conservation agreements also contribute to maintaining wetlands in the region.

Since 1976, Ducks Unlimited has worked within the Saint John River floodplain to improve habitat for brood-rearing waterfowl. The primary mechanism has been to increase the amount of permanently flooded habitat (shallow and deep marsh) through impoundment. By 1990, 40 impoundments had been completed, totalling 1872 ha of wetlands. Currently, impounded wetlands and seasonally flooded emergent wetlands make up 13% and 50% of the Saint John River floodplain complex, respectively. While the focus of impoundments was initially for the creation of brood-rearing habitat for waterfowl, these wetlands also provide valuable habitat for other species that prefer stable water conditions. The benefits of impoundments for many wildlife species differ and are largely unknown in this region.

With multi-agency involvement in management of wetlands through the EHJV it is important to assess the value of existing techniques and develop a plan for future activities which ensures conservation of sensitive habitats together with maximum benefits to waterfowl and other wildlife. To date, wetland management has focused primarily on water level control through impoundment to increase the amount of available brood-rearing habitat for waterfowl and other wetland dependent species. Increased proportions of permanently flooded habitat (impoundments), however result in decreased proportions of seasonally flooded habitat. To ensure that critical habitat is not lost for species dependent on seasonally flooded wetlands, it is necessary to first determine species use and abundance in seasonally flooded wetlands to assist managers in evaluating the extent of various habitat types required to maintain viable populations of wetland wildlife species.

The study objectives were an evaluation of waterbird response to impoundment creation and an analysis of historical water levels and wetland habitat availability on the Saint John River floodplain. This included a comparison of species richness of and habitat use by waterfowl broods

and wetland obligate birds on seasonally flooded wetlands and impoundments, as well as an analysis of historical water levels and their influence on temporal changes in wetland habitat availability.

Materials and methods

Study area

The Saint John River is the largest river in the Maritimes, travelling 673 km before entering the Bay of Fundy at Saint John. The watershed of the Saint John River is 55,900 km², of which 51% is located in New Brunswick, 33% in Maine and 13% in Quebec (Department of the Environment, 1974). The landscape is primarily forested, but impacted largely by agriculture and hydro-electric power developments. The last 130 km of the river between Fredericton and the Bay of Fundy are tidal, flowing through the New Brunswick Lowlands and Caledonia Highlands topographical regions.

Annual precipitation varies from 900 mm in the headwaters to over 1400 mm in the Bay of Fundy region while snowmelt usually occurs in April and run-off occurs in late April or early May. Seasonal water levels change dramatically during the spring freshet period and can reach 6 m above annual minimum daily water levels (Environment Canada, 1988). Wetlands along the Saint John River floodplain below Fredericton total approximately 20,000 ha and make up 7% of the wetland base in New Brunswick (Fig. 1). The dominant wetland type within the region is emergent marsh of varying water regimes. Impoundments create stable shallow water levels throughout the brood-rearing period while seasonally flooded wetlands are typically dry by mid summer.

The concentrations of phosphorus, pH, and levels of alkalinity suggested greater fertility in floodplain wetlands than observed in inland wetlands of New Brunswick (Clay, 1988). Hanson et al. (1998) found water chemistry data on level ditched floodplain wetlands was similar to that of other Saint John River floodplain wetlands. Based on phosphorus and chlorophyll *a* concentrations, wetlands were classified as mesotrophic to eutrophic. The mean pH of water samples collected

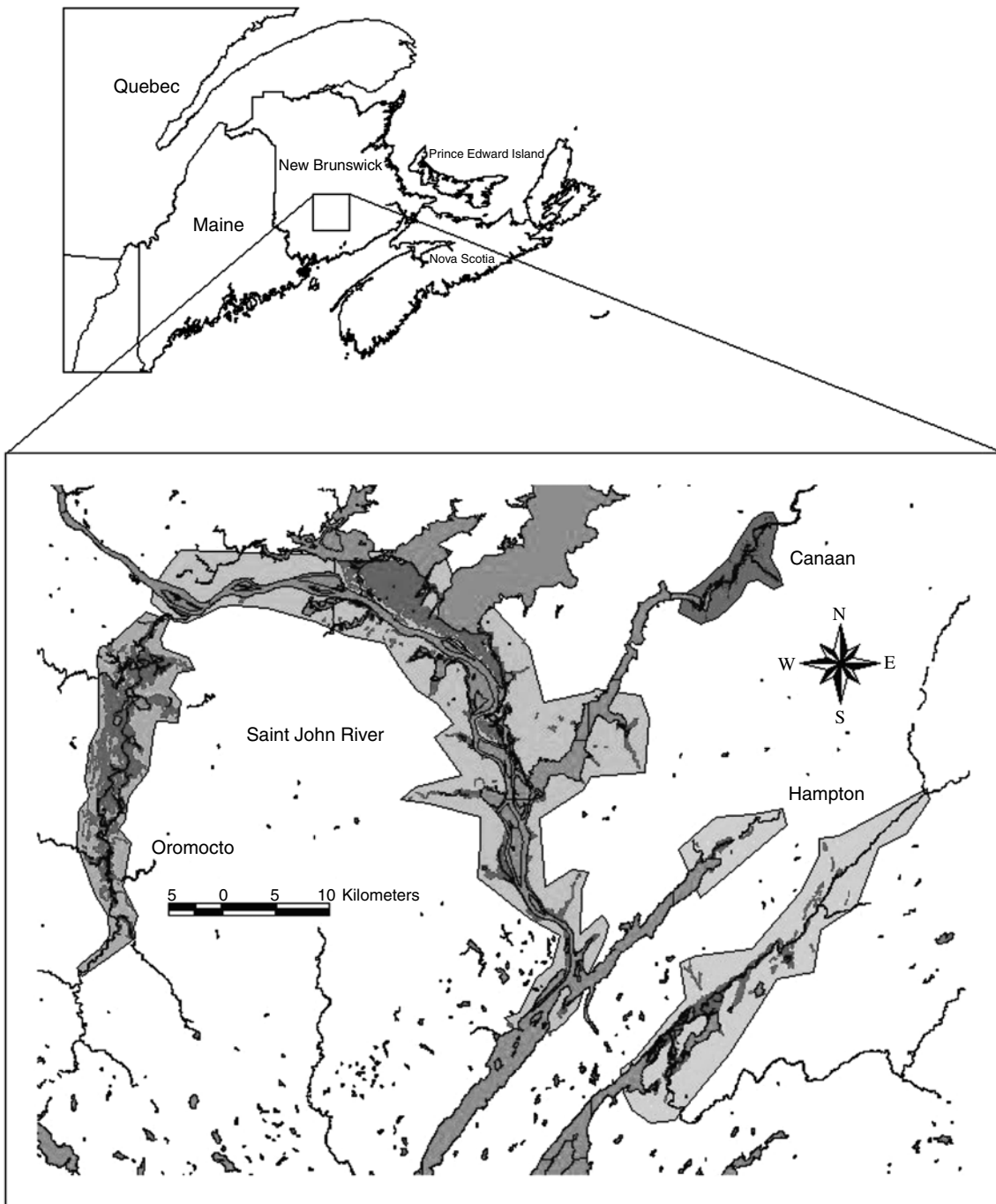


Figure 1. Location of wetlands by region (shaded areas) within the lower Saint John River floodplain, New Brunswick.

from three Saint John River floodplain wetland sites ranged from 6.4 to 6.8 (Hanson et al., 1998). Mean total phosphorus for all sites combined was 0.034, 0.035, and 0.051 mg/l in 1990, 1991 and

1992 respectively (Hanson et al., 1998). Boves (unpublished report) found pH levels ranging from 6.1 to 7.3 and total phosphorus ranging from 0.024–0.095 mg/l in managed floodplain wetlands.

Other studies have found similar pH levels within Saint John River floodplain wetlands ranging from 6.13 to 7.03 and organic phosphorus ranging from 0.052 to 0.0027 mg/l, also suggesting greater fertility than in inland wetlands (Nelson and Clay, unpublished report).

Research was conducted at five impoundments and five seasonally flooded wetlands varying in size from 15 to 59 ha. Seasonally flooded wetlands served as controls and were of similar size and vegetative composition as paired sites prior to impoundment creation. Sites were chosen systematically to represent five geographic areas within the Saint John River complex: Grand Lake Meadows/Portobello National Wildlife area, Oromocto River system, main stem of the Saint John River between Fredericton and Gagetown, main stem of the Saint John River below Gagetown, and Kennebecasis River.

Historical water levels and wetland classification

The temporal availability of brood-rearing habitat in seasonally flooded wetlands was evaluated by linking long term river level data to elevations from a sample of seasonally flooded wetlands. Elevations of seasonally flooded wetlands were surveyed during the freshet (21 April–14 May) in 1998–1999 and compared to current and long-term river levels to determine the availability of seasonally flooded wetland habitat from 15 May to 15 August. Historical river level data were available as mean daily elevations from 1966 to 1997. At each seasonally flooded wetland, on the day of the survey, a benchmark was set in a tree above the water level and the height of this mark above the marsh was recorded prior to and following the survey. The wetlands were traversed using a boat and water depths were taken at approximately 15 m intervals with transects 65 m apart. Changes in river elevation were used to determine changes in water levels within the seasonally flooded wetlands as the wetlands are adjacent the river and do not become isolated. Long-term river water elevation data was obtained for Jemseg and Oak Point gauging stations. River level data was used from the closest gauging station. When a site fell between the stations, mean river elevations were used. The river elevation during each survey period was used to estimate the

depth of water for the wetland. The extent of water depths at 15, 30 and 60 cm covering seasonally flooded wetlands were compared for each site from 15 May to 15 August. These water depths were chosen to determine the periods when the wetlands provided suitable brood-rearing habitat for waterfowl.

The digital wetland inventory of New Brunswick was based on photo interpretation of aerial photography at 1:12,500 scale. Total wetland area, the distribution of seasonally flooded wetland (SFW) and managed wetland (IMP) were determined from the provincial inventory. Analysis of the distribution and relative amount of brood-rearing habitat throughout the breeding period by region was completed by querying attributes of the wetland inventory representing emergent wetland and aquatic bed wetlands that maintained water throughout the growing season. Relative proportions of managed wetlands and the distribution of brood-rearing habitat were compared in four geographic regions of the lower Saint John River floodplain representing different ecoregions and dominant land use practices.

Waterfowl

Waterfowl brood use of floodplain wetlands and impoundments was estimated during 1997 and 1998. Aerial brood surveys were conducted during two periods; Survey 1 (29 June–8 July) and Survey 2 (26 July–31 July) each year. Surveys were conducted on impoundments ($n=5$) and seasonally flooded wetlands ($n=5$). Surveys were conducted from 0630 to 0900 h using a Bell Long Ranger helicopter at altitudes as low as 15 m, and at speeds ranging from 0 to 60 km/h with 3 observers. An observer in the front passenger seat navigated, recorded data and surveyed for broods. The age, species, and number of ducklings in observed broods were recorded (Gollop & Marshall, 1954). Two additional observers located in the rear of the aircraft assisted in brood detection. Complete coverage of each impoundment and seasonally flooded wetland was conducted.

Each survey period was tested separately by wetland habitat type. Species richness of and habitat use by waterfowl broods were compared between paired sites (i.e., seasonally flooded wetlands and impoundments) using Wilcoxon signed ranks tests.

Wetland obligate birds

The relative abundance of wetland obligate birds is often underestimated by point count surveys due to their secretive nature and infrequent vocalisations (Bystrak, 1981). Call responses can be elicited from wetland obligate birds by playing pre-recorded tapes of territorial birds (Glahn, 1974). Call-response surveys were conducted following methodology developed by Gibbs & Melvin (1993). Pre-recorded audio tapes were played in seasonally flooded wetlands ($n=5$), and impoundments ($n=5$). Surveys were completed during 3 h pre-sunset. Survey stations were established approximately 1 station/5 ha of wetland (Gibbs & Melvin, 1993). During periods of moderate to heavy precipitation, or wind conditions exceeding 30 km/h, surveys were discontinued. Each wetland was surveyed twice between 1 June and 22 July.

Observers played a series of calls composed of 30 s vocalisations of Sora (*Porzana carolina*), Pied-billed Grebe (*Podilymbus podiceps*), American Bittern (*Botaurus lentiginosus*) and Virginia Rail (*Rallus limicola*) followed by 30 s periods of silence for each species from the established survey stations. Each recording session was followed by a 5-min period of silence during which all aural and visual observations were recorded on point count data sheets. Portable cassette players were located 0.75 m above ground or water and able to produce a signal in excess of 80 dB at ≥ 1 m (Gibbs & Melvin, 1993).

Species richness of call responses between paired sites (i.e., seasonally flooded wetlands and impoundments) was tested using Wilcoxon signed ranks tests.

Significance levels were set at $p=0.10$, which increases the probability of Type I error (rejecting a true null hypothesis) and decreases the probability of a Type II error (accepting a false null hypothesis). A large alpha level was chosen to maximise our probability of detecting differences in use among wetland types. We felt it was more appropriate to decrease the probability of committing a Type II error as sample sizes were relatively low.

Results

Historical water levels and wetland classification

Historical water level data from the period of 1966–1997 revealed that by May 15, all of the seasonally flooded wetlands sampled had water depths > 60 cm. By June 1, water depths in most seasonally flooded wetlands ranged from 30–60 cm. On June 15, 40% of the seasonally flooded wetlands sampled had low water levels (i.e. most of the wetland had < 15 cm). From July 1 to August 15, all seasonally flooded wetlands sampled had low water levels (i.e., < 15 cm) (Table 1), some were probably completely dry. The variability in water levels at a given date was relatively low

Table 1. Percentage of area flooded (> 15 cm) on seasonally flooded wetlands during spring and summer months on the Saint John River floodplain, NB. Analyses conducted using geodetic river elevation averaged (on specific dates) from 1966–1997

Site (n^a)	Percentage of wetland flooded						
	May 15	June 1	June 15	July 1	July 15	Aug 1	Aug 15
Grand Lake Meadows (138)	100	100	9	0	0	0	0
Jemseg Flats (135)	100	100	89	26	8	1	1
Post Pond (161)	100	100	50	15	2	1	1
Scovil Point (133)	a100	100	4	0	0	0	0
Upper Musquash Is. (83)	100	100	42	10	2	0	0
Long Island Meadow (38)	100	100	13	0	0	0	0
Long Island Lake (39)	100	100	7	0	0	0	0
Johnson's Marsh (102)	100	100	20	7	1	1	1
Little River (76)	100	100	77	12	1	0	0
Evandale (50)	100	100	57	18	0	0	0

^aIndicates the number of water level measurements taken at each site.

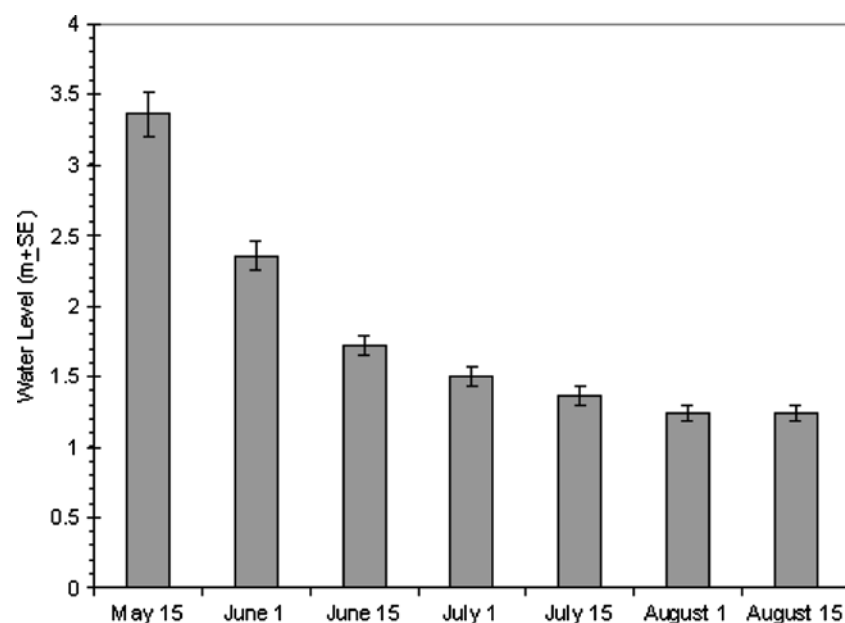


Figure 2. Mean (\pm SE) geodetic elevation (m) of water levels for specific dates from 1966 to 1997 at Jemseg gauging station, Saint John River, NB.

among years (1966–1997) (Fig. 2). No differences in the rate or timing of change in water levels were detected between the river and seasonally flooded wetlands. This suggests that no lag period exists for changing water levels in seasonally flooded wetlands following any changes in water levels of the river.

Overall, the total wetland area considered in this study was 14,267 ha. Seasonally flooded emergent wetland was the dominant wetland type and the proportion of seasonally flooded wetland converted to managed wetland was relatively low (15%). The distribution and extent of wetland habitat by type, the availability of brood-rearing

habitat, and the proportion of managed wetland all varied by region (Table 2). Managed wetland (IMP) made up 13.1% of the total wetland area and ranged from 5.4 to 17.1% of wetland area by region. The proportion of brood-rearing habitat ranged from 11.1 to 69.0% of wetland area by region.

Waterfowl

A total of 10 species of waterfowl broods were observed during each year. American Black Duck (*Anas rubripes*) was the most common species recorded during both surveys in 1997 and 1998.

Table 2. The distribution and extent of wetland habitat by type, the availability of brood-rearing habitat, and the proportion of managed wetland by region in the Saint John River Floodplain, 2003

Region	Wetland area (ha)	% Brood-rearing habitat ^a	SFW area (ha)	% SFW converted ^b	IMP area (ha) ^c
Oromocto	4062.3	11.1	3609.4	16.1	693.5 (17.1)
Main stem	7754.0	21.3	6102.7	13.9	985.5 (12.7)
Hampton	1945.7	69.0	603.1	21.1	161.5 (8.3)
Canaan	504.9	45.7	274.2	9.1	27.5 (5.4)
Total	14,266.9	25.8	10,589.4	15.0	1868.0 (13.1)

^aRepresents the proportion of wetland area providing brood-rearing habitat throughout the growing season.

^bRepresents the proportion of seasonally flooded wetland converted to managed (impounded) wetland by region.

^cParentheses indicate the proportion of wetland area that is currently managed (impounded) wetland by region.

Table 3. Total number of broods observed during survey 1 on impoundments (IMP), and seasonally flooded wetlands (SFW) on the Saint John River floodplain, NB, 29 June to 8 July, 1997 and 1998

Species	1997		1998	
	IMP (128 ha)	SFW (160 ha)	IMP (180 ha)	SFW (231 ha)
American Black Duck	23	26	46	1
Mallard	2	4	2	1
Wood Duck	4	0	3	0
Northern Pintail (<i>Anas acuta</i>)	0	1	0	1
Hooded Merganser (<i>Lophodytes cucullatus</i>)	3	1	0	0
Common Goldeneye	5	0	1	0
American Wigeon	0	4	6	2
Green-winged Teal	0	0	3	0
Blue-winged Teal	0	0	8	0
Ring-necked Duck (<i>Aythya collaris</i>)	0	0	4	0
Unknown	0	0	0	0
Total ^a	37 (0.29)	36 (0.23)	73 (0.41)	5 (0.02)

^aNumber of broods per ha.

During survey 1, American Wigeon (*Anas americana*), Mallard (*Anas platyrhynchos*), Blue-winged Teal (*Anas discors*), Wood Duck (*Aix sponsa*) and Common Goldeneye (*Bucephala clangula*) were the next most abundant species recorded in decreasing order of abundance (Table 3). Similarly for survey 2, American Wigeon, Wood Duck, Green-winged Teal (*Anas crecca*), Common Goldeneye, Mallard, and Blue-winged Teal were the most abundant

species observed following American Black Duck (Table 4).

In 1997, no difference in mean species richness of waterfowl broods was observed between seasonally flooded wetlands and impoundments during survey 1 ($df=1$, $S=3.5$, $p=0.50$) or survey 2 ($df=1$, $S=5.0$, $p=0.13$). Mean species richness during survey 1 was 3.0 (range 1–4) in impoundments and 2.0 (range 0–5) in seasonally flooded

Table 4. Total number of broods observed during survey 2 on impoundments (IMP), and seasonally flooded wetlands (SFW) on the Saint John River floodplain, NB, 26 July to 31 July, 1997 and 1998

Species	1997		1998	
	IMP (128 ha)	SFW (160 ha)	IMP (180 ha)	SFW (231 ha)
American Black Duck	31	7	24	8
Mallard	8	0	0	1
Wood Duck	10	1	7	0
Northern Pintail	1	0	1	0
Hooded Merganser	4	0	0	0
Common Goldeneye	8	0	7	1
American Wigeon	22	2	11	0
Green-winged Teal	9	0	8	1
Blue-winged Teal	6	0	2	0
Ring-necked Duck	0	0	0	0
Northern Shoveler (<i>Anas clypeata</i>)	0	0	0	1
Unknown	0	0	6	1
Total ^a	99 (0.77)	10 (0.06)	66 (0.37)	13 (0.05)

^aNumber of broods per ha.

wetlands. During survey 2, mean richness was 5.4 (range 0–8) in impoundments and 1.0 (range 0–3) in seasonally flooded wetlands. In 1998, mean species richness of waterfowl broods was higher in impoundments than in seasonally flooded wetlands during survey 1 ($df=1$, $S=7.5$, $p=0.06$) and survey 2 ($df=1$, $S=7.5$, $p=0.06$). During survey 1, mean species richness was 4.4 in impoundments (range 2–6) and 0.4 (range 0–2) in seasonally flooded wetlands. During survey 2, mean species richness was 5.2 in impoundments (range 2–7) and 1.6 (range 0–4) in seasonally flooded wetlands.

The total number of waterfowl broods observed was similar between years (Tables 3 and 4). However, the distribution of waterfowl broods between wetland habitats was not similar. There was a trend for higher densities on impoundments than on seasonally flooded wetlands.

In 1997, no significant difference was observed in total waterfowl brood densities on impoundments and seasonally flooded wetlands during survey 1 ($df=1$, $S=1.5$, $p=0.81$) or survey 2 ($df=1$, $S=5.0$, $p=0.13$). During survey 2, a shift from seasonally flooded wetlands to

impoundments occurred, as well as an increase in brood density on impoundments. This is likely in response to reduced water levels in seasonally flooded wetlands. In 1998, total waterfowl brood densities were higher on impoundments ($df=1$, $S=7.5$, $p=0.06$) than on seasonally flooded wetlands during survey 1. As well, total waterfowl brood densities were higher on impoundments ($df=1$, $S=7.5$, $p=0.06$) than on seasonally flooded wetlands during survey 2.

During survey 1, 18% of all broods combined were in the IA–IB category (Table 5), an age when they are extremely vulnerable to exposure to inclement weather and predation (Mauser et al., 1994). During survey 2, 13% of all broods combined were in the IA–IB age class category (Table 6). Brood backdating indicates that broods younger than age class IIA hatched on approximately 1 July.

Wetland obligate birds

Pre-recorded tapes elicited calls from four species of wetland obligate birds. A total of 91 responses

Table 5. Number of broods by species and age class for survey 1 conducted on Saint John River floodplain wetlands, NB, 29 June–8 July, 1997 and 1998

Species	Age class							Total
	IA	IB	IC	IIA	IIB	IIC	III	
American Black Duck	3	3	11	20	22	32	7	98
Green-winged teal	0	1	1	1	1	0	0	4
American Wigeon	4	6	1	1	0	0	0	12
Blue-winged Teal	3	2	3	1	0	0	0	9
Mallard	0	1	0	3	3	0	0	7
Wood Duck	1	1	2	1	2	0	0	7

Table 6. Number of broods by species and age class for survey 2 conducted on Saint John River floodplain wetlands, NB, 26 July–31 July, 1997 and 1998

Species	Age class							Total
	IA	IB	IC	IIA	IIB	IIC	III	
American Black Duck	0	4	6	11	17	21	20	79
Green-winged Teal	0	4	2	2	1	4	0	13
American Wigeon	0	7	11	12	4	4	0	38
Blue-winged Teal	2	3	1	0	1	4	0	11
Mallard	0	0	1	0	0	1	6	8
Wood Duck	0	2	4	3	3	5	2	19

were elicited during surveys from 98 plots between 1 June and 22 July, 1998. American Bittern, Pied-billed Grebe, Sora, and Virginia Rail were found in seasonally flooded wetlands and impoundments. The proportion of responses by American Bittern (17.6%) and Virginia Rail (15.4%) were second only to Soras which made up 54.9% of responses in seasonally flooded wetlands and impoundments overall (Table 7). Mean species richness was significantly higher ($df=1$, $Z=2.04$, $p=0.06$) on impoundments (2.2, range 2–3) than seasonally flooded wetlands (1.3, range 0–3). Response rates were similar between surveys (Table 8). Low response rates and subsequent low power of detection precluded analysis between habitat types by species for each survey period.

Discussion

Historical water levels and wetland classification

Results suggest that water levels in seasonally flooded wetlands typically change rapidly (i.e.

within a 15-day interval) in conjunction with the recession of the spring freshet and that most seasonally flooded wetlands are too deeply flooded to provide quality habitat for waterfowl broods before June 1 (i.e. > 60 cm water depth). By July 1, most of the areas within the seasonally flooded wetlands were < 15 cm, at which time some seasonally flooded wetlands are completely dry. After July 1, water levels in seasonally flooded wetlands decline considerably. Thus, by July 1, most seasonally flooded wetlands typically do not constitute brood-rearing habitat due to a lack of shallow water. However, seasonally and permanently flooded wetland habitats are not distributed evenly across the landscape.

Overall, brood-rearing habitat does not appear to be limited within the Saint John River floodplain. Approximately 25% of the total wetland area provides brood-rearing habitat throughout the growing season. Of this, 50.7% are impounded wetlands. Managed wetlands make up a large proportion of brood-rearing habitat while converting 15% of seasonally flooded wetland habitat. The proportion of brood-rearing habitat increases

Table 7. Relative abundance (% of total) of wetland obligate bird responses on impoundments (IMP), and seasonally flooded wetlands (SFW) on the Saint John River floodplain, NB, 1998

Species	SFW ^a (n = 42)	IMP ^a (n = 42)	Total ^a
American Bittern	9 (31)	7 (11.7)	17 (17.6)
Pied-billed Grebe	1 (3.4)	9 (15)	10 (11.0)
Sora	16 (55.2)	34 (56.7)	50 (54.9)
Virginia Rail	3 (10.3)	10 (16.7)	14 (15.4)
Total	29 (100)	60 (100)	91 (100)

^aPercentages of each species indicated in parentheses.

Table 8. Total bird species recorded (call-responses) and mean/ha on impoundments (IMP), and seasonally flooded wetlands (SFW) on the Saint John River floodplain, NB, 1998

Habitat	# (x/ha)					Total
	Area (ha)	American Bittern	Pied-billed Grebe	Sora	Virginia Rail	
Survey 1 ^a						
SFW	231	9 (0.04)	1 (0.004)	11 (0.05)	0 (0)	21 (0.09)
IMP	180	6 (0.03)	5 (0.03)	10 (0.05)	4 (0.02)	25 (0.13)
Survey 2 ^b						
SFW	231	0 (0)	0 (0)	5 (0.02)	3 (0.01)	8 (0.04)
IMP	180	1 (0.006)	4 (0.02)	24 (0.13)	6 (0.03)	35 (0.19)

^a 28 May–2 June. ^b 22 June–22 July.

dramatically during years with seasonal increases in precipitation or a late freshet that allows broods to use seasonally flooded wetlands later into the growing season. The distribution of brood-rearing habitat also varies dramatically by region and most wetland management appears to have occurred in appropriate regions where the availability of brood-rearing habitat is relatively low (Table 2).

Waterfowl

The date of peak flooding was earlier in 1998 than 1997, which resulted in seasonally flooded wetlands that were inundated for shorter periods than in 1997. Waterfowl brood densities were higher on impoundments during all periods when seasonally flooded wetlands were relatively dry and provided little open water.

Survey 1 (early July) coincided with the typical onset of low water conditions in seasonally flooded wetlands, and therefore brood habitat in seasonally flooded wetlands may be limited at this time. In general, most brood movements from seasonally flooded wetlands to impoundments, permanently flooded wetlands or river edge habitat probably occur between 15 June and 1 July. Research with radio-marked ducklings indicated that most duckling loss occurs within 10 days of hatch (i.e. 1A–1B) (Mauser et al., 1994). These young broods made up 18% of total broods observed during survey 1 and would likely have to move to other habitats at a time when they are most vulnerable.

Prior to 1 July, seasonally flooded wetlands probably provide adequate cover and foraging sites for brood-rearing waterfowl. On the Canadian Prairies, Swanson et al. (1974) found that during spring and early summer, temporary and seasonal wetlands provided abundant, readily available, high protein invertebrate foods. The positive relationship between high aquatic invertebrate abundance and waterfowl use of wetlands is well documented (Joyner, 1980; Murkin & Kadlec, 1986; Stacier et al., 1994). Swanson et al. (1974) also found that later in the summer as seasonal wetlands began to dry up, waterfowl feeding shifted to more permanent waters as insects began to emerge in semi-permanent ponds and lakes. During the same study it was also observed that this trend could be temporarily

reversed following heavy precipitation that refilled seasonal wetlands and stimulated invertebrate development. Generally, the value of intermittent types of wetlands to breeding waterfowl greatly increases during years with ample precipitation and decreases during years with lower than average wetland conditions (Kantrud & Stewart, 1977). Hickey (1984) studied impoundments along the Saint John River during high water conditions and observed broods entering and leaving impoundments during the course of a brood survey which suggests that wetland habitat conditions outside the impoundments were not limiting to brood-rearing waterfowl at that time. Clay (1988) also found that duck densities on floodplain projects showed considerable variability during years when high water conditions provided alternative habitat in the surrounding area. Other studies have reported avoidance of open wetland habitats by a number of waterfowl species suggesting that cover is an important brood habitat component (Patterson, 1976; Hepp & Hair, 1977; Ringelman & Longcore, 1982; Mauser et al., 1994; Monda & Ratti, 1988). Most impoundments have a heterogeneous interspersed of emergent vegetation cover and water. Murkin et al. (1982) and Kaminski & Prince (1981) found that emergent structure of a wetland may influence waterfowl use of an area. In addition, the abundance and biomass of aquatic invertebrates in impounded wetlands along the Saint John River is considerably more than in inland wetlands (Bowes, unpublished report) and level ditches (Hanson et al., 1998) in New Brunswick. Invertebrate food supplies that are important to broods are more abundant on productive wetlands (Krull, 1970; Reinecke & Owen, 1980), therefore making them attractive to brood-rearing waterfowl. Furthermore, impoundments may be most important to brood-rearing waterfowl during years when seasonally flooded wetlands are dry earlier than normal or when re-nesting is substantial. Impoundments that are strategically located where few natural permanently flooded wetlands occur provide stable habitat that will minimize brood movements and optimise cover and foraging opportunities for brood-rearing waterfowl.

Habitat use by waterfowl broods was highly variable among impoundments. Variables such as elevation, juxtaposition, vegetative composition

and availability of surrounding upland and wetland habitat probably influence the distribution and movement of waterfowl broods on floodplain wetlands. Staicer et al. (1994) found that a number of variables including invertebrates and macrophyte cover, affect the density and distribution of American Black Duck broods on freshwater lakes in Nova Scotia. Data is limited on brood movements and habitat use and therefore a number of variables must be carefully considered when evaluating the need and location of new impoundments created for brood-rearing waterfowl along the Saint John River floodplain.

Wetland obligate birds

During survey period 1, American Bitterns were heard in both seasonally flooded wetlands and impoundments. Only 2 responses of American Bitterns were heard during the second survey period. Gibbs & Melvin (1993) also reported decreasing trend in responses of American Bitterns from call-response surveys conducted from early May to mid-July. American Bitterns are the earliest nesters of the wetland obligate birds surveyed (Erskine, 1992). Its reclusive nature during the breeding season is reflected by its low frequency of confirmed atlas breeding reports in the region. Gauthier & Aubry (1996) also reported that American Bitterns actively seek out productive wetlands with large, well-vegetated margins of shallow water that are prolific in aquatic vegetation and wildlife such as fish and amphibians. Gibbs et al. (1991) found wetlands used by American Bitterns were dominated by emergent and aquatic bed vegetation with higher interspersions of open water and emergent vegetation and less open water than unused wetlands. Information from the study suggests that American Bitterns use seasonally flooded wetlands and impoundments equally.

Soras appeared to use seasonally flooded wetland and impoundment habitats similarly during the first survey period but appeared to be more abundant on impoundments during the second survey. Johnson & Dinsmore (1986) reported that practices used to encourage waterfowl use are compatible with habitat requirements of breeding Sora and Virginia Rails. Gibbs & Melvin (1993) stated shallow marshes with high interspersions of fine-leaved and robust emergents, flooded annuals,

and patches of open water constitute optimal Sora habitat. Gibbs et al. (1991) also found that Soras preferred emergent wetlands with intermediate cover-to-water ratios but a lower percentage of open water. Impoundments appear to be beneficial to Soras primarily during the late breeding season when it is likely that the majority of seasonally flooded wetlands are dry.

Pied-billed Grebes and Virginia Rails were recorded during both survey periods with Pied-billed Grebes occurring almost exclusively on impoundments. Virginia Rails were detected on impoundments during the first survey and on seasonally flooded wetlands and impoundments during the second survey. Erskine (1992) reported observations of these species were less numerous than that of American Bitterns and Soras in the Atlantic region. Virginia Rails prefer warm, freshwater marshes with dense emergent vegetation interspersed with open water or mud flats (Conway & Eddleman, 1994). Others have reported that Virginia Rails prefer littoral sites in a wetland dominated by robust emergents (Weller & Spatcher, 1965; Johnson & Dinsmore, 1986). Gibbs et al. (1991), in Maine, found Pied-billed Grebes used emergent wetlands with more open water; aquatic-bed, and ericaceous vegetation than unused wetlands. Nesting habitat of Grebes may be dependent on wetland size (Brown & Dinsmore, 1986) as they were not found on wetlands < 5 ha in size. Habitat use suggests that impoundments benefit Pied-billed Grebes and Virginia Rails through increased interspersions of open water and emergent vegetation. Other researchers have reported greatest avian species richness on wetlands approaching intermediate ratios (50:50) of open water to emergent vegetation (Weller & Spatcher, 1965; Gibbs et al., 1991).

Conclusion

Impoundments along the Saint John River floodplain provide stable water levels that benefit waterfowl broods and wetland obligate birds when seasonally flooded wetlands are dry. The creation of open water through impoundment creation and the subsequent increase in interspersions of open water to emergent vegetation benefits both waterfowl and wetland obligate birds in regions where

brood-rearing habitat is not abundant. Seasonally flooded wetland habitats are used early in the growing season by waterfowl and wetland obligate birds. However, seasonally flooded wetlands provide minimal brood-rearing habitat after 1 July and therefore most broods have to move from seasonally flooded wetlands to natural permanently flooded wetlands, impoundments or river edge habitat. Impoundments may be most important to brood-rearing waterfowl during years when the spring freshet is early, resulting in prolonged dry conditions in seasonally flooded wetlands or substantial brood movements of younger age classes when they are most vulnerable.

Generally, during late summer, use of seasonally flooded wetlands by wetland obligate birds declined while the use of impoundments increased. Species richness was significantly higher on impoundments than on seasonally flooded habitats. The information suggests that current habitat management for waterfowl, which involves increasing the extent of shallow and deep marsh habitat, is compatible with breeding habitat requirements of wetland obligate birds.

Overall density of waterfowl broods was greater on impoundments than seasonally flooded wetlands during both years of study. Brood density of most species was greater on impoundments especially during dry years. Habitat use by waterfowl broods was highly variable among impoundments. The distribution of brood-rearing habitat varies by region within the Saint John River floodplain. Overall, managed wetlands make up 13.1% of the wetland base, representing a large contribution (50.7%) of brood-rearing habitat in the Saint John River floodplain. Brood-rearing habitat does not appear to be limited within the Saint John River floodplain as it currently represents 25.8% of the wetland base considered in this study. An evaluation of the factors that may influence waterfowl use of impoundments in the region should be conducted prior to construction of additional impoundments. Impoundment creation should be strategically located within the floodplain in regions of low natural permanently flooded wetland availability. A watershed-based analysis of wetland habitat suggests future wetland management should focus on enhancing current impoundments within the Saint John River floodplain. Resources must be secured for main-

tenance and water level manipulation within existing managed wetlands rather than the construction of additional impoundments.

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Populations of ducks and trout of the River Laxá, Iceland, in relation to variation in food resources

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Key words: *Histrionicus histrionicus*, *Bucephala islandica*, *Salmo trutta*, density limitation, production of young, *Simulium vittatum*, long-term population monitoring

Abstract

We examined annual variation in production, recruitment and density of the three most abundant vertebrate species of the River Laxá at Lake Mývatn, Iceland: Barrow's goldeneye, *Bucephala islandica*, harlequin duck, *Histrionicus histrionicus*, and brown trout, *Salmo trutta*, in relation to food resources and other environmental variables. The study is largely based on correlations from long-term monitoring series in the period 1975–2002. Production of young in the harlequin duck was significantly correlated with food resources (the blackfly, *Simulium vittatum*) of the river, as was the recruitment of brown trout to the angling stock. In Barrow's goldeneye, which uses both the lake and the river, dispersion of adults in spring and young in August was influenced by the availability of aquatic insects in each habitat. The dispersion of Barrow's goldeneye tracks the availability of aquatic insects in each of these two main habitats. Introduced American mink, *Mustela vison*, may have affected spring numbers and dispersion of harlequin ducks, but the evidence was not conclusive. Numbers of both duck species and the trout (as CPUE) were relatively stable, although a sharp drop in numbers followed by slow recovery was observed in Barrow's goldeneye, and an increase was observed in harlequin ducks in the first year of study.

Introduction

Rivers are open, one way ecosystems. Their biotic communities and food webs are largely based on the influx of energy and nutrients from upstream in the catchment (Hynes, 1975; Vannote et al., 1980). It follows that bottom-up processes are likely to dominate in rivers and that top-down processes should be relatively unimportant. Also, river systems form longitudinal geomorphic-hydraulic continua that serve as templates upon which predictable patterns of biological organization can be discerned (Cummins et al., 1995), for instance when the food-web is narrowly based on a

spatially restricted source such as the outlet of a productive lake (see Wotton, 1979). Competition for resources which are continuously being renewed from upstream is likely to be most noticeable in the placement of individuals (or species) along a resource gradient (Allan, 1995).

In many Icelandic rivers, macroinvertebrate communities are characterized by chironomid larvae which feed on epilithic algae; lake-fed rivers, such as the Laxá, are often dominated by suspension-feeding simuliid (blackfly) larvae which reach exceptionally high densities at the river outlet (Gíslason et al., 1998). The River Laxá drains the shallow, eutrophic Lake Mývatn, a well-

known waterfowl site (Gardarsson & Einarsson, 1994, 2001). Monitoring studies centred on waterfowl and their environment have been carried out at Mývatn and the Laxá from 1975 on. Trout of the river have been monitored from 1973, and from 1977 aquatic insects of the upper River Laxá have also been monitored.

The aim of this study is to examine annual variation in indices of production, recruitment and density of the three most abundant vertebrate species of the Laxá, the Barrow's goldeneye, *Bucephala islandica* (Gmelin), harlequin duck, *Histrionicus histrionicus* (L.), and brown trout, *Salmo trutta* (L.), in relation to food resources and other environmental variables. The study is largely based on correlations from long-term monitoring series which are now approaching a length of 30 years. Strictly speaking, such observations should be followed up by experiments to demonstrate causal relationships. However, the value of an experiment is necessarily limited by scale in space and time. An experiment should be designed to address empirically relevant questions. We believe that such questions should have a solid observational foundation.

Study area and study species

The Laxá

The Laxá is a lake-fed river in the volcanic zone of North Iceland (Fig. 1). It flows over a bed of lava rock formed by a large eruption about 2300 years B.P. (Thórarinnsson, 1979). For detailed descriptions of the river see Rist (1979) and Gíslason (1994). Food webs are mainly based on drifting organic material from Lake Mývatn which has a drainage area of 1400 km², mostly without surface streams. At its outflow from the lake, the river has a flow of 33 m³ s⁻¹; flow increases to 55 m³ s⁻¹ at the river mouth, 61 km further north. The total drainage area is 2400 km². It is convenient to divide the Laxá (750 ha) into three sections, of which 151 ha are immediately below Lake Mývatn, LM; 223 ha in the Laxárdalur valley, LL; these two sections form the study area, the 'upper Laxá.' The third section, LA (376 ha) in the lowland valley Adaldalur, is separated from LL by waterfalls which form a barrier to fish movements.

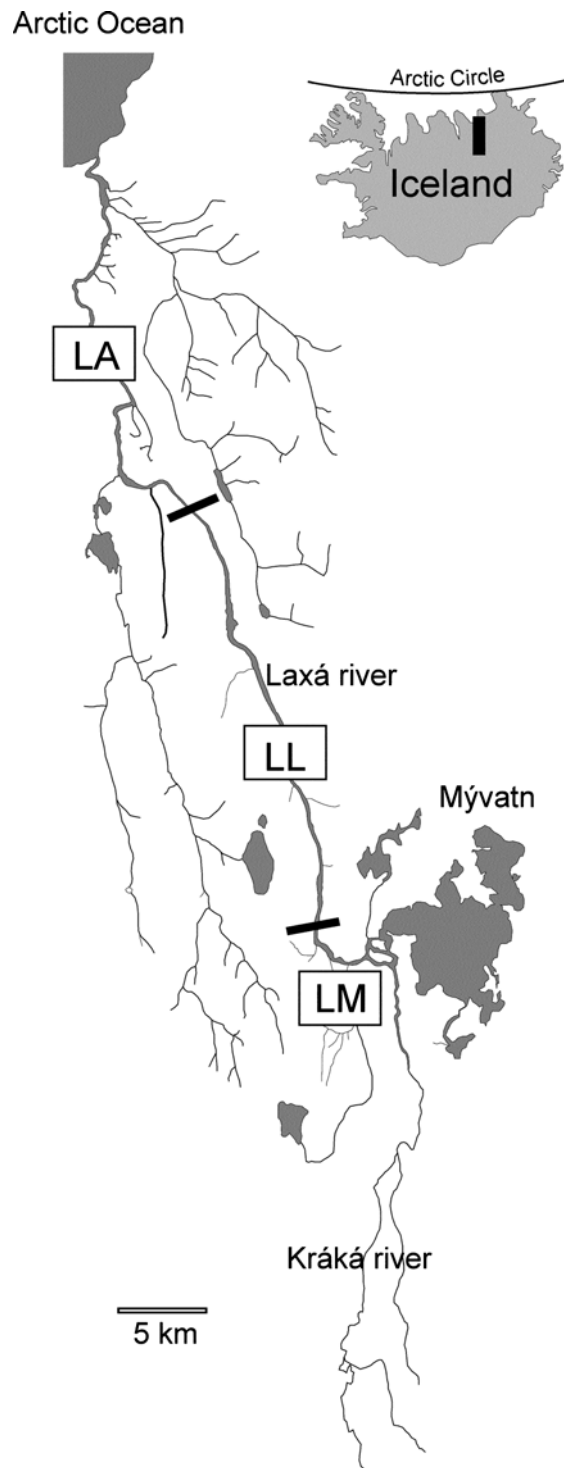


Figure 1. Map of the study area.

The benthic vegetation of the Laxá is mainly green algae (*Cladophora* spp.), mosses, *Fontinalis antipyretica* (Hedw.), and slender-leaf pondweed, *Potamogeton filiformis* (Pers.). Fine particulate organic matter originating from Lake Mývatn forms the base of the food-web of the most abundant invertebrate, the suspension-feeding larvae of the blackfly *Simulium vittatum* (Zett.) (Gíslason & Jóhannsson, 1991), which in turn serve as the primary prey of ducks and salmonid fishes of the river (Bengtson & Ulfstrand, 1971; Gudmundsson, 1971; Einarsson, 1988; Gíslason & Gardarsson, 1988; Steingrímsson & Gíslason, 2002). In 1977–1985, the mean production of *S. vittatum* was 178 g (ash free dry weight) $\text{m}^{-2} \text{year}^{-1}$ (range: 36–896) at 0.5 km from the lake outlet, but only 58 g $\text{m}^{-2} \text{year}^{-1}$ (range: 18–110) at 22 km downstream (Gíslason & Gardarsson, 1988). At the lake outlet, the blackfly population has two yearly cohorts, emerging in early June and in late July–early August, respectively, while some 20 km from the outlet only one cohort is produced with adults emerging in July (Gíslason, 1985; Gíslason & Jóhannsson, 1991). The gradient in blackfly production is related to downstream declines in nutritive value and quantity of fine particulate organic matter, which is being filtered by the decreasing densities of larvae away from the outlet (Gíslason, 1994).

The general landscape along the river is sparsely populated and mostly used for livestock farming. Since the mid-20th century, the pattern of human exploitation in the region has changed from subsistence farming; contemporary activities include tourism, hydroelectric and geothermal energy production, and production of diatomite from sediments in part of Lake Mývatn. Introduced American mink, *Mustela vison* (Schreber), arrived in this region in the 1950s. Most of the catchment is managed under a conservation law enacted in 1974 (Gardarsson & Einarsson, 2001).

The study species

The Laxá (literally the salmon river) supports a rich sports fishery centred on a land-locked population of brown trout in its upper part (LM and LL) and migratory Atlantic salmon, *Salmo salar* (L.), in the lower part (LA) (Gíslason, 1994; Gíslason et al., 2002). The brown trout is one

of only five species of freshwater fish native to Iceland, which forms the north-west limit of its natural distribution (see Elliott, 1994). In the upper Laxá, the brown trout is the dominant fish species, with an estimated stock size of 24,000 fish (>35 cm) in 1992–1994 (Gíslason, 1994; Gíslason et al., 2002). Throughout their life, the trout feed largely on blackfly larvae and pupae (Steingrímsson & Gíslason, 2002). The fishery is managed through the sale of permits; fly-fishing is the only method permitted. The angling season is limited to 90 days and the daily fishing period is 12 h. The minimum length of trout that anglers are allowed to retain is 35 cm. Annual exploitation of brown trout in the rod fishery is close to 10% of the stock >35 cm. Recruitment to the exploitable fishing stock takes 4–6 years from hatching and the average growth rate is 6.3 cm year^{-1} (Gíslason et al., 2002). The number of trout (>35 cm) caught on rod each year in the study area is positively correlated with blackfly production in the previous year, suggesting that the production of the Laxá trout is sensitive to fluctuations in blackfly availability (Gíslason, 1994; Gíslason et al., 2002).

A number of waterfowl use the river, especially the quieter parts. The most numerous species are the year-round resident Barrow's goldeneye, which uses both the river (in winter, LM is mostly and LL about 70% ice-free) and Lake Mývatn (about 10%, 4 km^2 , ice-free), and the harlequin duck which is restricted to the river for breeding, but otherwise spends much time on the sea coast.

The Barrow's goldeneye is a nearctic species with a widely separated small population in Iceland, its eastern boundary (Eadie et al., 2000). The Icelandic population totals about 2000 individuals; the breeding distribution is centred on the Mývatn–Laxá and it is restricted to freshwaters at all times of the year (Gardarsson, 1978). Within the Mývatn–Laxá system, the detailed dispersion of goldeneyes varies widely both seasonally and between years, and they seem to adjust their dispersion to current food availability (Einarsson, 1988; Einarsson & Gardarsson, 2003; Gardarsson et al., 2003). Outlet tributaries of the river and cold spring areas along the eastern bank of the lake form the core of reproductive activity (Gardarsson, 1978, 1979; Einarsson, 1990).

The harlequin duck is a northern holarctic species which breeds on rivers and streams in Iceland, Greenland and eastern North America, and western North America and Eastern Siberia; it winters on rocky coasts in the subarctic and boreal zones in the North Atlantic, east to Iceland, and in the North Pacific (Cramp & Simmons, 1977; Robertson & Goudie, 1999). In Iceland, the harlequin is a generally distributed breeder on rapid clear-water streams, from sea-level to 800 m a.s.l. Densities are generally low except at the lake outlets of streams where blackflies are abundant. Moulting harlequin ducks are found on the sea-coast and often stay close to cliffs or rocks. Harlequin ducks winter on exposed rocky coasts where in 1998–2001, the total population wintering in Iceland was estimated at 14,000, with 95% confidence limits 12,000–16,000 (Gardarsson, in press). Important ecological studies of this species on the Laxá were published by Bengtson & Ulfstrand (1971) and Bengtson (1972). Present knowledge on the status of the harlequin duck in Iceland is reviewed and updated by Gardarsson (in press).

Methods

Monitoring the ducks

The data on the waterbird populations are for the years 1975–2002. Counting methods are described by Gardarsson (1979) and Gardarsson & Einarsson (1994). For the diving ducks of the upper Laxá (area LM) and Lake Mývatn, we used single annual surveys in late May, when all breeding birds are presumed to have arrived, and in the first and second week of August when all young (mostly about 4 weeks old) and adults are counted. For the harlequin duck, we use the total young in area LM as a best index of production, for the Barrow's goldeneye we use total young in both the main brood rearing habitats, LM and Lake Mývatn. Few young were found on the lower stretches of the river and these were not surveyed regularly for young. Area LL was surveyed each spring from 1976 on, but in August only in 4 years.

Other monitoring

Aquatic insects, mainly Simuliidae (blackflies) and Chironomidae (midges), were monitored by

window traps operated in May through September each year, beginning in 1977 (Jónsson et al., 1986). The traps intercept flying insects, which drop into preservative and are collected at intervals of 7–12 days. For the upper Laxá, two trap sites were used: Trap DR, 2 km from Lake Mývatn, and trap HE, another 3 km downstream. Before counting and further identification, the catches were generally subsampled and separated into: Chironomidae (midges, later identified to species), Simuliidae (blackflies), and other insects. The blackfly, *S. vittatum*, is the most abundant benthic invertebrate of the Laxá and the main food of the ducks and trout. For monitoring midges and blackflies of the river, we used the geometric mean of the two traps and split the yearly catches into two periods, termed A and B, before and after about 15–20 July, corresponding to the two flight periods in the uppermost part of the river. Two annual indices were summed from these: $S_t = A_t + B_t$ and $S_t^* = B_{t-1} + A_t$; S_t is an estimate of current summer abundance and is used to compare with reproductive success of the ducks, S_t^* estimates abundance in the previous year and is used for comparison with population levels of goldeneyes and trout. In the river, fluctuations of insects were within one order of magnitude and the untransformed numbers were used for statistical comparisons. Because the Barrow's goldeneye divides its activities between the River Laxá and Lake Mývatn we also present data on the abundance of chironomids in the lake. Abundance fluctuations of chironomids at Lake Mývatn, which reached 3–4 orders of magnitude, were estimated from \log_{10} geometric means of the numbers caught in two traps, using yearly totals (Gardarsson & Einarsson, 2003).

Sport fisheries of the Laxá are closely regulated and the number of angling permits issued is recorded. Records of fish caught are submitted by the anglers to wardens and collected by the Institute of Freshwater Fisheries. In this study, the number of permits and the number of brown trout caught in the upper two sections of the river in 1973–2002 were examined and the catch per unit effort (rod day⁻¹) calculated.

From 1975 on, efforts were intensified to keep the Mývatn basin and the uppermost 20 km of Laxá free of mink. The hunting effort was similar throughout the study period, one person with

dogs, and there was no change in hunting strategy. Adults are mostly trapped in winter, in later years mainly at the western edge of the area (including the Laxá). Dens and their inhabitants are destroyed. Detailed records of mink, including numbers of full-grown animals caught and numbers of pups taken in dens, were kindly provided by Ingi Yngvason who is in charge of the mink eradication program.

Results

Insect abundance

The annual abundance of aquatic dipterans in the lake and the river traps tended to vary in an opposite fashion (Fig. 2). In the upper Laxá, fluctuations of blackflies in the upper Laxá never exceeded one order of magnitude (Fig. 2a). Blackfly abundance in the Laxá was especially high in 1984–1985, 1987–1989, 1998 and 2000; it was very low in 1978–1980, 1991, 1995 and 2002. Chironomid abundance in the Laxá traps was generally low and showed little annual variation (Fig. 2b). In Lake Mývatn, chironomid abundance varied cyclically, with differences of up to three orders of magnitude from year to year, as the dominant species, *Tanytarsus gracilentus* (Holmgren), went through its oscillations. Peak numbers occurred in 1978–1981, 1986–1987, 1991–1995 and 2000–2002. Very low chironomid numbers were found in 1983–1984, 1988–1989 and 1997–1998 (Fig. 2c).

Barrow's goldeneye

In spring 1976–2002, the mean total of Barrow's goldeneyes found on the upper Laxá and Lake Mývatn was 1384 ± 52 (SE). Total numbers were rather stable at about 1600 in 1975–1988; a sharp decline to about 1000 took place in 1988–1989, followed by a period of low numbers and a slow increase approaching the pre-1989 level around 2000 (Fig. 3b). During the summer wing moult, numbers in the Laxá–Mývatn study area were augmented in most years by moulting birds, suggesting that the total censused in spring was often around 90% of the total Icelandic population (Einarsson & Gardarsson, 2003). We found no

correlations between the total population and estimates of insect food or production of young.

The mean number of Barrow's goldeneye on the upper Laxá was 793 ± 58 , varying from 404 to 1347 (Fig. 3a) and on Lake Mývatn 591 ± 40 , range 179–1012 (Fig. 3b). The numbers of goldeneyes using the river and the lake, respectively, shifted noticeably and significantly between years, in direct response to the abundance of aquatic insects in each habitat (Fig. 5a and b; $r_P = 0.55$, $p < 0.01$, on the upper Laxá, $r_P = 0.77$, $p < 0.001$ on Lake Mývatn). Moulting males were also found in numbers reflecting the insect situation on Mývatn and LM (Einarsson & Gardarsson, 2003).

An average total of 465 ± 48 young were recorded annually in August, the number varying from 2 to 919. Of these 379 ± 46 (range 1–900) were on LM and 86 ± 19 (0–377) on Lake Mývatn. On LM, the numbers of young Barrow's goldeneyes were significantly correlated with numbers of blackflies, $r_P = 0.44$ ($p < 0.05$), using untransformed numbers but the power of the test was low. On Lake Mývatn, the log number of young Barrow's goldeneyes found was significantly correlated with log chironomids ($r_P = 0.62$, $p < 0.01$).

Harlequin duck

In 27 springs, 1976–2002, the mean number of harlequin ducks on the upper Laxá (Fig. 3c) was 435 ± 22 (SE) and the range was 199–608. Spring numbers showed an increasing trend during 1976–1991, (regression of log numbers on year: $r^2 = 0.66$, $p < 0.001$), and then levelled off to a mean of about 500 birds.

On LM, spring numbers averaged 320 ± 25 and increased significantly during the first 12 years (1975–1986) of the study period (regression of log numbers on years: $r^2 = 0.58$, $p < 0.01$). On LL, where the mean number in spring was 115 ± 7 , there was a decreasing though not significant trend in 1976–2002 (regression of log numbers on year, $r^2 = 0.13$, $p = 0.064$).

There were no significant correlations between catches of blackflies and the numbers of adult harlequins in spring on the upper Laxá as a whole or each of the sections LM and LL. Change in spring numbers was weakly correlated with numbers of young 2 years in advance ($r_P = 0.44$, $p < 0.05$).

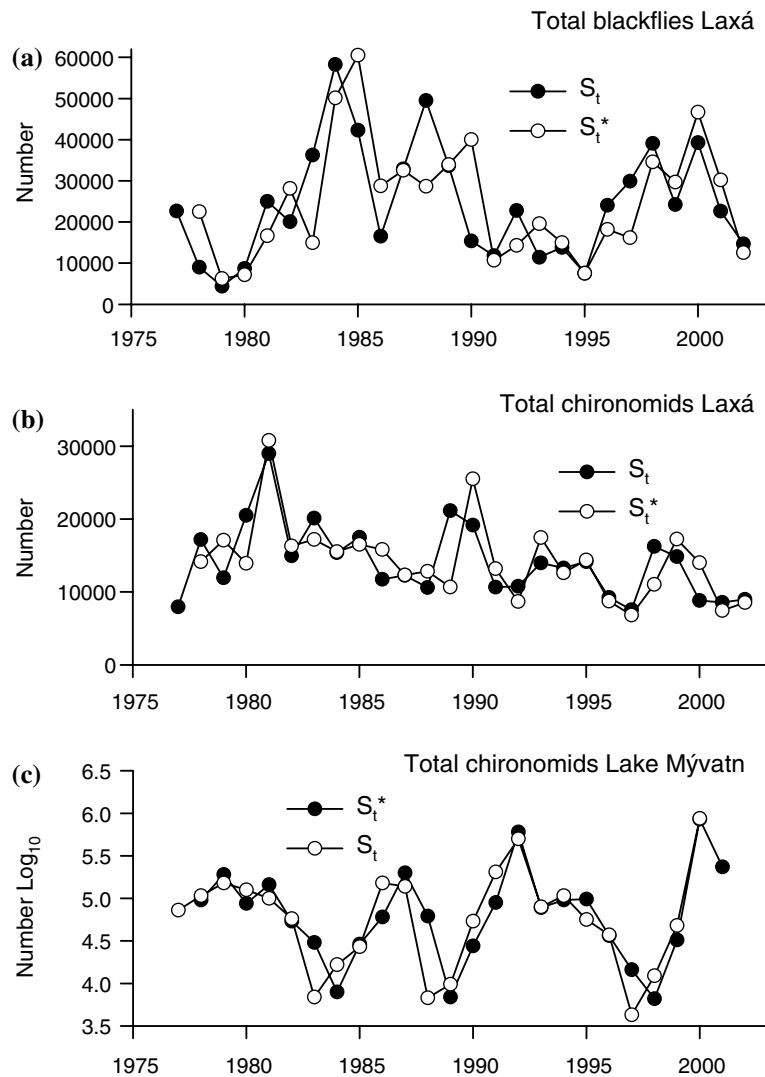


Figure 2. The abundance of aquatic insects (numbers trapped) at the River Laxá and Lake Mývatn: (a) blackflies on the upper Laxá, (b) chironomids on the upper Laxá, (c) log chironomids at Lake Mývatn. S_t , numbers trapped in current summer; S_t^* , numbers trapped in period from mid-July in preceding year to mid-July of current year.

Harlequin males leave the Laxá in late June to early July and moult on the sea. Each August, section LM was surveyed for females and broods (very few females and broods were found on LL). The number of females on LM in August was not obviously related to other variables estimated simultaneously, such as number of young or blackfly abundance (Gardarsson & Einarsson, in press). On average, only 18 ± 2 females (range 3–40) were accompanied by broods. We used the total number of young harlequin ducks found in section LM in August as the best estimate of

production (Fig. 3c). In 1975–2002, the number of young at LM averaged 74 ± 11 (range 3–235). This corresponds to a mean number of young per female of 0.49 ± 0.09 (range 0.02–1.76) if all females found in spring on the upper Laxá (LM and LL) are included; or 0.82 ± 0.17 (0.03–3.27), if only females on LM in spring are included.

The production of harlequin, as total young on LM, was closely correlated with blackfly abundance, S_t ; $r_p = 0.68$, $p < 0.001$ (Fig. 5c). The density of adults did not influence production of total young in 1975–2002 and a spell of cold weather in

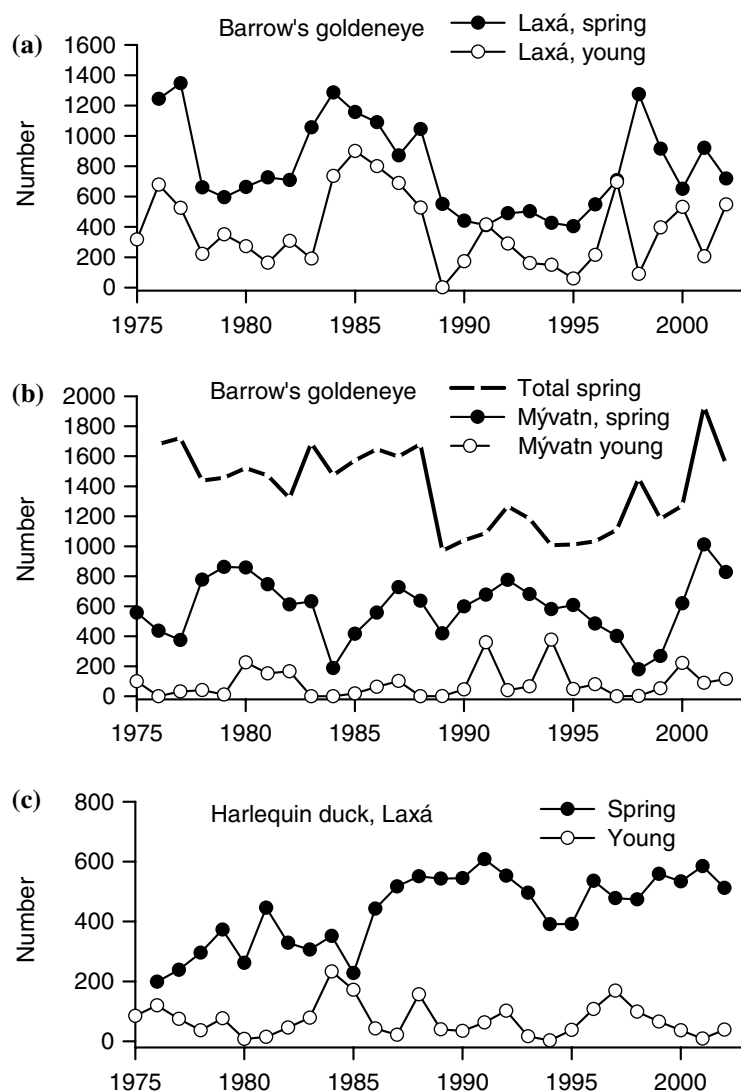


Figure 3. Spring numbers and numbers of ducklings in August: (a) Barrow's goldeneye on the upper Laxá, (b) Barrow's goldeneye total and Mývatn, (c) harlequin duck.

1992, which reduced production in several duck species at Mývatn (Gardarsson & Einarsson, 1994, 1997) did not affect the harlequin. When examined in a multiple linear regression, per capita production of harlequin (as arcsin number of young per adult) was significantly and positively associated with number of blackflies, S_t ($\beta = 0.618$, $R^2 = 0.36$, $p < 0.001$), but density (total number of adults) had a significant negative influence ($\beta = -0.448$, change in $R^2 = 0.20$, $p < 0.01$).

The distribution of harlequin ducks along the Laxá was significantly correlated with numbers of

mink caught. On LM we found a positive correlation of the number of adult mink caught ($p < 0.01$) with spring numbers of harlequin ducks ($r_p = 0.56$) and as arc-sine transformed proportion of the total number on the upper Laxá ($r_p = 0.58$). At the same time, mink numbers on LL were negatively correlated ($p < 0.05$) with spring numbers of harlequins ($r_p = -0.41$). However, only the overall annual trends of mink and harlequins were correlated, and the residuals were not, suggesting that perhaps these results reflected coincidence in time rather than a functional relationship.

Brown trout

The mean annual catch of brown trout in the upper Laxá in 30 years, 1973–2002, was 3211 ± 299 (SE), range 949 (in 1980) to 7550 (in 1998), this increase reflects the increasing number of permits issued (Fig. 4a), which averaged 1339 ± 119 . The mean catch per unit effort (CPUE) of brown trout was 2.35 ± 0.13 , range 1.16 (in 1991) to 4.18 (1973) and did not change significantly over time (Fig. 4b). CPUE was significantly ($t = 3.297$, $p < 0.01$, 56 d.f.) higher in the upper fishing section (2.58 ± 0.16) than in the lower section (1.93 ± 0.12). CPUE was significantly correlated with blackfly catches, as S_t^* , $r_P = 0.73$, $p < 0.001$, $n = 23$ (Fig. 5d).

American mink

Adult mink caught were mainly taken at the western borders of the basin and can be regarded as an index of influx from outside the study area. The mean number of adult animals caught each year

was 50 ± 4 , range 18–91 (Fig. 6) and the total showed a significant increasing trend ($r_P = 0.55$, $p < 0.01$). Numbers of adult mink showed a tendency to oscillate cyclically, with a periodicity of about 7 years. The cycle accords well with other parts of Iceland, where oscillations in numbers of mink have been shown to occur with a similar periodicity (Skirnisson, 1993). We found significant correlations of mink numbers with adult harlequins in spring but not with goldeneyes or trout. The numbers of young mink caught (Fig. 6) reflect the decreasing number of active dens in the area, and by 1990 mink had virtually ceased to breed in the area covered by intensive eradication efforts.

Discussion

Although long-term quantitative studies are an essential background to explanation in population ecology, they have many limitations and risks. For instance, it is difficult to choose reasonable and

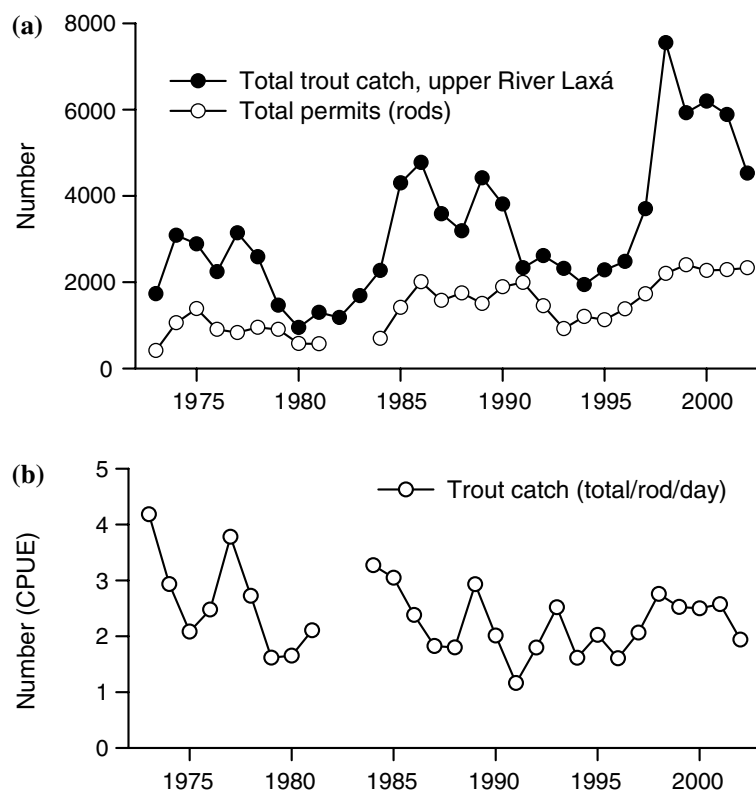


Figure 4. Brown trout caught in the upper Laxá in 1973–2002: (a) total catches and permits, (b) catch per unit effort (trout per rod per day).

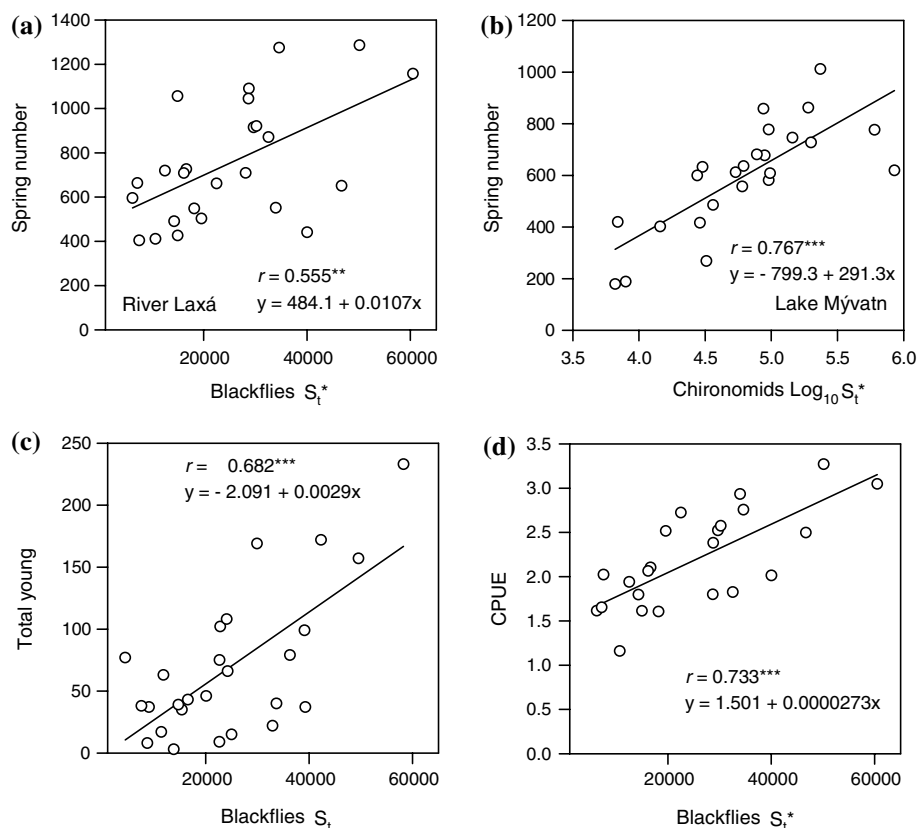


Figure 5. Scattergrams to show relationships between aquatic insects and vertebrate populations of the Laxá: (a) Barrow's goldeneye spring numbers on Laxá compared with recent numbers of blackflies, S_t^* ; (b) Barrow's goldeneye spring numbers on Mývatn as a function of recent chironomid numbers on the lake, S_t^* ; (c) total young harlequin ducks in August in relation to current numbers of blackflies, S_t ; (d) brown trout catch, CPUE, in relation to recent blackfly numbers, S_t^* .

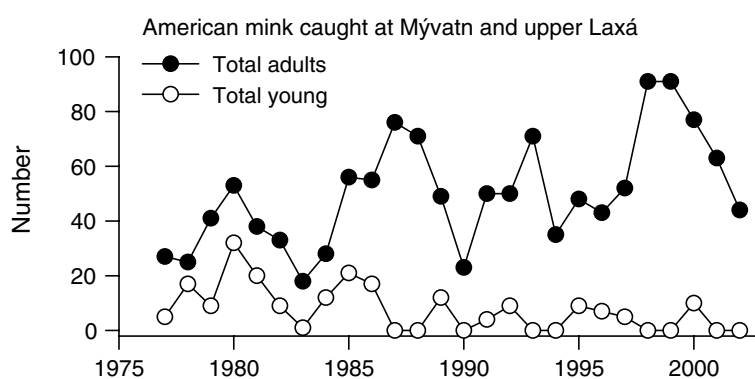


Figure 6. American mink, adults and young, caught at Mývatn and the upper Laxá in 1977–2002.

practical working hypotheses at the outset; the need to estimate many variables concurrently may overextend the economic resources available; and often important relationships only become

apparent after the event, making replication and sometimes remedial measures hard to apply.

Certain relationships have emerged from this study: the production of young in the harlequin

duck is limited by food resources of the river as is the recruitment of brown trout to the catchable stock. Production of the Barrow's goldeneye which uses two different habitats, the lake and the river, seems to be limited in a more complex manner by the availability of aquatic insects in these two habitats. Food limitation of the production of young goldeneyes on Lake Mývatn is rather obvious. On the river, the correlation was weak. The most likely reason for this was that young goldeneyes on the river originated partly from nests at the outlet and partly from nests at the lake. Thus the influence of food on LM may be obscured by local brood movements between the lake and the river (Einarsson, 1988). Normally, year to year variation in the total number of Barrow's goldeneyes, was not obviously related to food availability. The relatively stable high numbers in 1975–1988 and the subsequent return after a crash in 1988–1989 to former levels around 2000 suggest that the population is limited by carrying capacity. A food limit may well be reached in winter when most of the available habitat is frozen over.

The long-term stability of the total goldeneye population is clearly a consequence of this species being able to move between two habitats that typically alternate in production of useable food. At the same time, the population seems to be vulnerable to even short periods of poor feeding co-occurring in both habitats. In the long run, production of young in both the harlequin and Barrow's goldeneye on the Laxá is limited by food, and other environmental variables seem to be of far less importance. The density of adult harlequins on the Laxá was not directly tied to the local food situation, but the dispersion of the Barrow's goldeneye population, which was partitioned between the river and the lake was closely associated with food availability in each habitat.

In the first years of this study, an increase in the breeding population of harlequin duck on LM was underway and numbers on the Laxá as a whole showed an increasing trend. According to local information, numbers of breeding harlequin ducks declined markedly in the late 1950s, as American mink were beginning to invade the upper Laxá. Bengtson (1972) reported spring numbers of 39–55 female harlequins in the LM area in 1966–1970. In 1974, Fjeldsá (1975) counted 60 harlequins at LM,

corresponding to approximately 27 females and in 1975 we found similar numbers, 26 females and a total of 58 birds. In 1976–1980 the number of females on LM varied between 52 and 78, and the totals from 123 to 165 or about double the number in 1974–1975. The increase and change in distribution on the Laxá coincided significantly with the increasing trend in number of mink caught, suggesting that perhaps the successful eradication of American mink in LM (but not LL where harlequins decreased) may have contributed to increasing harlequin numbers on the LM. This line of explanation is supported by circumstantial evidence, but is contradicted by analysis of the residuals and may be a mere coincidence. American mink, escaping from fur farms, colonized much of Northern Europe in the past 60 years. A study of mink predation on breeding waterbirds in England showed that mink significantly affected both breeding densities and nesting success in two rallid species, European coot, *Fulica atra* (L.), and moorhen, *Gallinula chloropus* (L.). The predation impact of mink on these species was estimated as moderate to high, e.g., 30–50% of adult coots (Ferrerias & Macdonald, 1999). In the Finnish archipelago, removal of mink has been shown experimentally to increase breeding densities of velvet scoter, *Melanitta fusca* (L.), and tufted duck, *Aythya fuligula* (L.), as well as several other bird species (Nordström et al., 2002, 2003). In the 1980's, harlequin numbers on LM trebled. The increase coincided with increases of wintering harlequins on the north-east coast, 100 km away (Gardarsson, in press) and could have resulted from either ameliorated resource conditions or decreased hunting on the coast.

Although the per capita production of young was inversely density dependent, the large variation in spring numbers of harlequin ducks in LM did not affect the total reproductive output of the area, and the total number of young produced was limited by food each year.

While recruitment, and presumably stock size, in the brown trout is clearly related to food, there have been no studies in the Laxá on the role of food in limiting numbers of 0+ group trout (fry) produced. *A priori* such a limitation would seem likely, and it has been amply demonstrated by Elliott (1994). If numbers at the 0+ stage were likely to limit size of the stock available to anglers,

one would expect a significant positive relationship between the trout catch and blackfly abundance approximately 3 years in advance. This does not show up in the data, suggesting that stock size of trout may be limited by current food levels affecting each year class similarly and that the first year class is not particularly vulnerable to food limitation. Such a situation would be expected in a population where the composition of the diet of each year class remains the same (Steingrímsson & Gíslason, 2002).

Although the relatively stable shared resources of the Laxá system are obviously partitioned to a certain extent by three vertebrate species exploiting these resources in different ways, we did not find evidence indicating that interspecific competition was likely to limit production under existing conditions. Nor did we have evidence that such competition was non-existent, and for instance it seems very likely that harlequin ducks would be able to occupy more habitat and produce more young if there were no Barrow's goldeneyes on LM.

Conclusions

The river Laxá turns out to be less variable than its source, Lake Mývatn. In particular, blackfly numbers, reflecting the inflow of fine particulate organic matter, are far less variable than are those of chironomid midges of the lake. The supply of blackflies, especially the larvae, clearly limits the overall reproductive output in harlequin duck. Recruitment of brown trout into the angling catch is likewise limited by the blackfly resource. Reproductive output in the Barrow's goldeneye is influenced both by the blackflies of the river and the chironomid midges of the lake. The dispersion of the Barrow's goldeneye tracks the availability of aquatic insects in each of these two main habitats. The three species utilize the blackfly resource in a species-specific way, but we found no indication that competition between them affected numbers or production. An introduced mammalian predator, American mink, may have affected spring numbers and dispersion of harlequin duck but the evidence was not conclusive. A sharp drop in numbers followed by slow recovery was observed in the Barrow's goldeneye, but otherwise its numbers were stable for most of the period. The harlequin duck increased in the first

15 years of the study; after that numbers were stable. Although the total trout catch varied widely, the catch per unit effort was relatively stable during the study period.

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Influence of migrant tundra swans (*Cygnus columbianus*) and Canada geese (*Branta canadensis*) on aquatic vegetation at Long Point, Lake Erie, Ontario

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Abstract

Numerous studies have shown that large, herbivorous waterfowl can reduce quantity of aquatic plants during the breeding or wintering season, but relatively few document herbivory effects at staging areas. This study was done to determine if feeding activities of tundra swans (*Cygnus columbianus columbianus*) and Canada geese (*Branta canadensis*) had a measurable additive influence on the amount of aquatic plants, primarily muskgrass (*Chara vulgaris*), wild celery (*Vallisneria americana*), and sago pondweed (*Potamogeton pectinatus*), removed during the fall migration period at Long Point, Lake Erie, Ontario. Exclosure experiments done in fall 1998 and 1999 showed that, as compared to ducks and abiotic factors, these two large herbivorous waterfowl did not have any additional impact on above or below ground biomass of those aquatic plants. As expected, however, there were substantial seasonal reductions in above-ground and below-ground biomass of aquatic plants in wetlands that were heavily used by all waterfowl. We suggest that differences in large- and small-scale habitat use, feeding activity, and food preferences between tundra swans and other smaller waterfowl as well as compensatory herbivory contributed to our main finding that large waterfowl did not increase fall reductions of *Chara* spp, *V. Americana*, and *P. pectinatus* biomass.

Introduction

Submerged and emergent aquatic macrophytes provide important foods for many migratory waterfowl and several other species of aquatic herbivores (Thayer et al., 1984; Lodge et al., 1998; Knapton & Petrie, 1999). The relationship between waterfowl and their aquatic food resources is dynamic, resulting from seasonal changes in their feeding behaviour that ultimately is a response to herbivory and other biotic and abiotic factors

affecting the abundance and distribution of aquatic macrophytes (Lodge, 1991). Waterfowl congregate in and select areas with large concentrations of macrophytes, especially those that contain preferred forage species (Dirksen et al., 1991; Wicker & Endres, 1995; Mitchell & Wass, 1996; Nolet et al., 2001). Concentrations of waterfowl can cause large reductions in above- and below-ground biomass of their preferred forage species (Anderson & Low, 1976; Giroux & Bédard, 1987; Beekman et al., 1991; Evers et al., 1998; Idestam-Almqvist,

1998) and may even change species composition of some plant communities over longer periods of time (Jefferies et al., 1994; Kotanen & Jefferies, 1997). Abiotic factors, such as wave action and ice scour, and senescence also are major factors that contribute to biomass reduction in some aquatic macrophyte communities (Beekman et al., 1991; Crowder & Painter, 1991; Idestam-Almquist, 2000).

Recently, there has been concern about increasing populations of large herbivorous waterfowl and the influence these birds have on food resources in critical aquatic and terrestrial habitats (Conover & Kania, 1994; Ankney, 1996; Abraham & Jefferies, 1997; Petrie et al., 2002). There is a growing body of evidence showing that large numbers of geese can have pronounced and detrimental effects on the structure, quality, and quantity of habitat at breeding, staging, and wintering areas (Cargill & Jefferies, 1984; Bazely & Jefferies, 1986; Giroux & Bédard, 1987; Jefferies et al., 1994; Kotanen & Jefferies, 1997). These effects not only have population-level ramifications for species that are the main consumer of foods (Cooke et al., 1995; Abraham & Jefferies, 1997; Leafloor et al., 2000), but potentially also for other organisms that use the same habitats (Abraham & Jefferies, 1997). Purportedly, increasing populations of exotic mute swans, *Cygnus olor* (Gmelin), in eastern North America can have some negative impacts on submerged aquatic macrophytes (Reese, 1975; Petrie & Francis, 2003; but see Conover & Kania, 1994). Further, tundra swans, *Cygnus columbianus columbianus* (Ord), and Bewick's swans, *Cygnus columbianus bewickii* (Ord [Yarrell]), can substantially reduce densities of wild celery, *Vallisneria americana* (Michaux), and sago pondweed, *Potamogeton pectinatus* (L.), tubers at some of their major staging and wintering areas (Beekman et al., 1991; Nolet & Drent, 1998; Froelich & Lodge, 2000; Nolet et al., 2001).

Tundra swan populations in North America have increased since the early 1970s (Serie et al., 2002), causing concern that they may directly or indirectly influence aquatic plant and waterfowl communities at some of their staging areas (Petrie, 1998; Petrie et al., 2002). Thousands of these large, herbivorous waterfowl often congregate at traditional staging and wintering areas where they co-occur with large concentrations of many other

waterfowl species (Limpert & Earnst, 1994; Petrie et al., 2002). At fall staging areas, tundra swans spend much time feeding in aquatic habitats where they excavate and eat tubers and rhizomes of several different aquatic plants (Earnst, 1994; Limpert & Earnst, 1994; Badzinski, 2003). Tundra swans also consume above-ground parts of aquatic macrophytes and charophytes when available (Beekman et al., 1991; Earnst, 1994; Limpert & Earnst, 1994; Nolet et al., 2001). Some aquatic plant species consumed by tundra swans, including wild celery, sago pondweed, and muskgrass, *Chara* spp. (L.), also are preferred or common foods of many other staging waterfowl (Korschgen & Green, 1988; Korschgen et al., 1988; Kantrud, 1990; Rees & Bowler, 1991; Knapton & Petrie, 1999).

The wetland complex associated with Long Point, Lake Erie is a continentally important staging area for tundra swans and several other waterfowl species (Petrie, 1998) (Fig. 1). Considerable numbers of Canada geese also use these wetlands, but their numbers have decreased at Long Point, despite a large increase in the giant Canada goose population in southern Ontario, since the early 1970s (Petrie, 1998). Further, based on average peak numbers during fall aerial surveys flown from 1991 to 2002, tundra swans are much more abundant (~4 times: 6831 swans vs. 1714 geese) than Canada geese at Long Point, which also is reflected at much smaller spatial scales (Badzinski, 2003; this study). Tundra swan use has increased substantially at this staging area over the past 30 years (Petrie et al., 2002), mirroring this species' increase throughout North America (Serie et al., 2002). In light of their relatively recent population increase and the general lack of information concerning tundra swan staging ecology, it is important to determine the degree that staging tundra swans and other large herbivorous waterfowl affect seasonal abundance of aquatic plants and smaller waterfowl (Petrie, 1998; Petrie et al., 2002; Badzinski, 2003).

In this study, we designed an enclosure experiment to determine if large numbers of relatively large herbivorous waterfowl (primarily tundra swans) substantially reduce the availability of above- and below-ground vegetation beyond that resulting from activities of smaller aquatic consumers (mainly ducks) and abiotic factors during

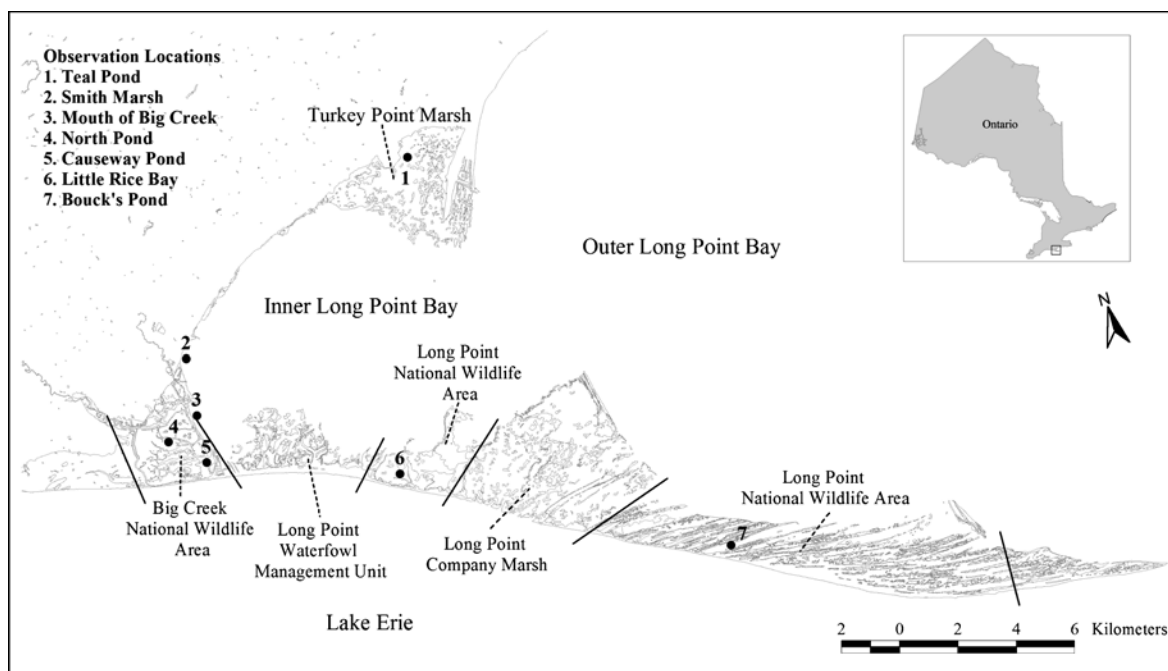


Figure 1. Map showing major wetland complexes and public, private, and government owned areas at Long Point, Lake Erie, Ontario. Locations where vegetation sampling and behavioural observations were conducted are shown as numbered points.

the fall staging season. More specifically, we sought to determine if activities of tundra swans (and Canada geese) exerted a measurable removal effect on total below-ground biomass and tuber mass and density of important waterfowl (duck) foods (i.e., wild celery, sago pondweed, and muskgrass) at locations that traditionally receive heavy fall-use by tundra swans and other waterfowl.

Study area

This study was conducted during fall 1998 and 1999 at Long Point, Ontario (80° 24' W, 42° 38' N) (Fig. 1). Long Point is a sand-spit extending 35 km east from the southern shore of Ontario into Lake Erie that has facilitated the formation of the Inner and Outer Long Point Bays and their associated freshwater marsh complexes (Petrie, 1998). The extensive wetlands where this study was conducted were classified as lacustrine, emergent and/or aquatic bed wetland habitats (Cowardin et al., 1979).

During 1998, three study locations were used: Bouck's Pond, North Pond, and Teal Pond,

whereas in 1999, four locations were used: Bouck's Pond, North Pond, Smith Marsh, and the Mouth of Big Creek (Fig. 1). Limnological characteristics of major wetland complexes associated with the inner and outer Long Point Bays have been summarized and discussed by Leach (1981) and Petrie (1998); in general, all locations containing enclosures were considered to be eutrophic and had maximum water depths ≤ 1.0 m.

Emergent plant species commonly found at nearly all of the study locations included cattails, *Typha latifolia* (L.) and *T. angustifolia*, (L.), common reed grass, *Phragmites australis* (Cavannes), hardstem bulrush, *Scirpus acutus* (Muhlenberg), softstem bulrush, *Scirpus validus* (Kuntze), pickerelweed, *Pontedaria cordata* (L.), wild rice, *Zizania palustris* (L.), and arrowheads, *Sagittaria latifolia* (Willdenow) and *S. rigida* (Pursh). Yellow water lily, *Nuphar variegatum* (Engelmann), and white water lily, *Nymphaea odorata* (Aiton), were common floating-leaved macrophytes. Common submerged macrophytes included bladderworts, *Utricularia* spp, Canada waterweed, *Elodea canadensis* (Michaux), coontail, *Ceratophyllum demersum* (L.), floating-leaved

pondweed, *Potamogeton natans* (L.), sago pondweed, slender pondweed, *Potamogeton pusillus* (L.), muskgrass, Richardson's pondweed, *Potamogeton richardsonii* (Rydberg), water-milfoils, *Myriophyllum* spp, water niads, *Najas* spp, and wild celery.

Methods

Exclosure design

Two types of structures, exclosures and reference (or control) plots, were placed in aquatic habitats to determine influence that large waterfowl have on aquatic vegetation (Fig. 2). Exclosures were square structures ($6 \times 6 \times 1.25 \text{ m}^3$) made by wiring modified

pieces of concrete reinforcing mesh (mesh dimensions: $15.3 \times 15.3 \text{ cm}^2$) to eight fence posts. Exclosures were designed to restrict only swans and Canada geese, but not ducks (and other small herbivores), from aquatic vegetation (Fig. 2). Once situated around a patch of vegetation, the bottoms of exclosures were pushed into the substrate so their height above the substrate-water interface was about 1.0 m. Tops of the exclosures were left uncovered so ducks could land inside of them, but the relatively small size of exclosures precluded larger waterfowl from doing so. Reference (or control) plots were $6 \times 6 \text{ m}^2$ plots demarcated by four corner posts extending approximately 1.0 m above the marsh bottom (Fig. 2). These plots represented plant community characteristics after exposure to all biotic and abiotic factors that could

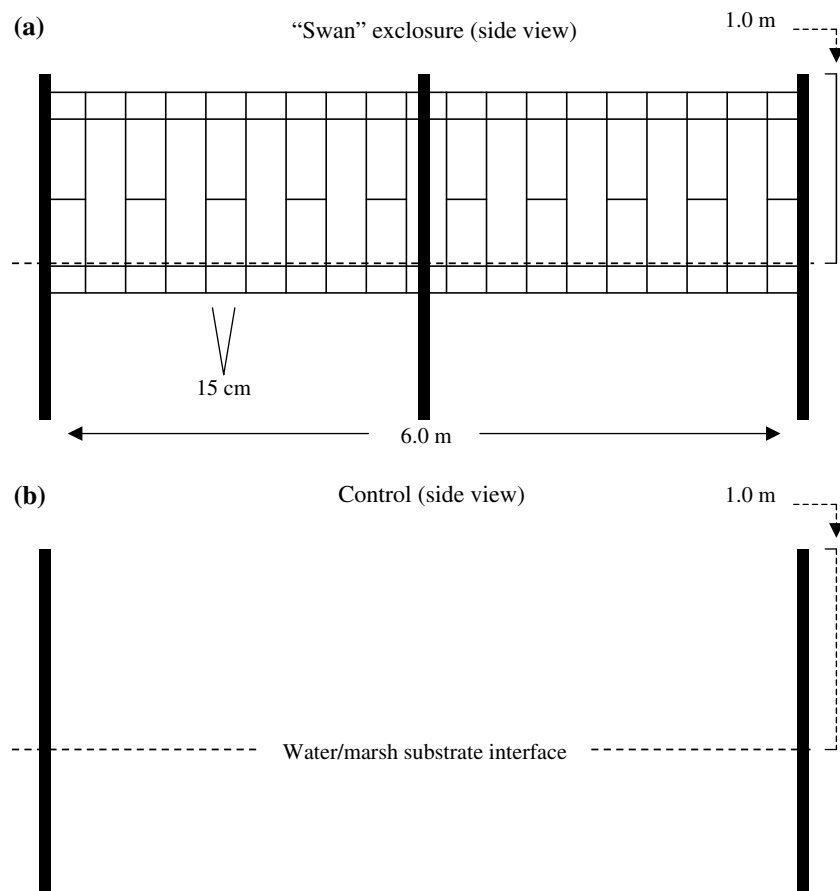


Figure 2. Design and dimensions of swan exclosures (a), and reference/control plots placed in wetlands during fall 1998 and 1999 at Long Point, Lake Erie, Ontario.

influence late season mass and seasonal change in aquatic plants. Most importantly, however, these plots were areas where large herbivores could freely access aquatic plants.

Exclosure placement

During late summer each year (18–25 September 1998 and 10–19 September 1999), three sets of experimental structures were placed in each of three (1998) or four (1999) geographically separate locations (see Fig. 1). Each experimental set consisted of one control and one “swan” exclosure. Several weeks before waterfowl arrival, locations of experimental sets were chosen and marked at each location. Structures at each location were placed in similar depths (0.3–0.9 m) of water at similar distances from shore or emergent vegetation. The range of water depths where exclosures were placed reduced the likelihood that they would become dry and unsuitable for waterfowl as water levels declined throughout the fall. Locations for each experimental set were chosen such that all had visually similar plant species composition and biomasses. Further, each set was situated in relatively dense, contiguous patches of *Chara* spp or *V. americana* and *P. pectinatus*, all of which are known to be very important foods for ducks at Long Point (Petrie, 1998). Structures within each set were grouped relatively close (range: 18–24 m) together, but much larger distances (range: 50–200 m) separated structures of different sets at the same locations. A few days prior to taking the early season sample, we randomly assigned treatments (control plot or “swan” exclosure) to each set of structures and then fastened the exclosure materials to the appropriate fence posts. Drought conditions forced us to change some study locations between years. If the same study location was used in consecutive years, structures within it were relocated so the destructive sampling during the previous year would not affect results the following season.

Aquatic vegetation sampling

Each year the fall was divided into early (27 September–8 October 1998 and 20 September–7 October 1999) and late (5–13 December 1998 and 3–10 December 1999) sampling periods. The early

period preceded arrival of large numbers of waterfowl, which usually occurs at Long Point during the first or second week of October. The late sampling period was late enough to allow for several weeks of waterfowl use, but early enough to reduce the chance that water at study locations would freeze. Comparison of early and late samples allowed us to determine the effect that large waterfowl (and other factors) had on the reduction of aquatic plants during fall.

To ensure that the vegetation samples were representative of their treatment, samples were taken ≥ 1.0 m from the edge of exclosures. This sampling area was further sub-divided into 2.0×2.0 m² quadrants, each of which was divided into 16 (0.25 m²) possible sampling locations. Potential sampling locations were sequentially assigned numbers. The actual sampling locations within each structure were chosen randomly by drawing numbers, without replacement, until two were assigned in each quadrant for each sampling period. A grid system using three ropes marked at 0.5 m increments was used to locate specific sampling locations in the field.

A small flat-bottomed boat was used to enter structures in order to take vegetation samples without destroying other potential sample locations. Once the appropriate sampling point was located, a metal sampling box ($0.5 \times 0.5 \times 0.75$ m³) was pushed into the marsh substrate and the water depth (± 1 cm) was recorded. Above-ground samples were obtained by clipping all plant stems within the sampling box at the substrate level. Samples were then sorted by species and placed into separate plastic bags labeled with date, sampling period, location, exclosure number, exclosure type, sampling coordinates, water depth, and plant species.

Below-ground samples were obtained by taking nine scoops of the marsh substrate with a perforated coffee can (total sample volume: 0.03 m³) at each of the eight sampling locations in an exclosure. Sampling in this way approximated the size and depth (~ 0.5 m) of feeding craters created by swans and ensured that all below-ground parts available to swans and ducks were collected (Beekman et al., 1991). These samples were passed through a fine mesh (2×2 mm²) sieve to separate the roots, rhizomes, and tubers from the marsh

substrate and were then sorted by species and part (roots, tubers, and rhizomes). Individual below-ground samples were placed into separate plastic bags and labeled as previously described for the above-ground samples.

At the end of the sampling day, all above- and below-ground samples were kept cool ($\sim 5^\circ\text{C}$) until they could be processed in the laboratory. Some large, heterogeneous samples were not processed in the field and were sorted, bagged, and labeled later in the laboratory.

Laboratory procedures

All species-specific above-ground vegetation samples were blotted dry with paper towels, and then weighed on a digital balance ($\pm 0.01\text{ g}$) to obtain the wet mass. Approximately 30 sub-samples of above-ground parts for each species from the 1998 vegetation sample were selected and then separately oven-dried at 80°C to constant mass ($\pm 0.01\text{ g}$); this was done so species-specific dry mass could be estimated from its wet mass via regression (Badzinski, 2003, p. 157, Appendix 2). All species-specific below-ground plant parts (roots, tubers, and rhizomes) were processed separately and oven-dried as previously described for above-ground samples.

Waterfowl use of enclosure locations

Several aerial surveys conducted by the Long Point Waterfowl and Wetlands Research Fund (1998: $N=10$ from 24 September to 10 December; 1999: $N=5$, 25 September–28 November) were used to estimate numbers of swans, Canada geese, dabbling ducks (*Anas* spp), and diving ducks (*Aythya* spp) in areas where enclosures were located. Surveys were done between 10:00 and 14:00 h EST by flying predetermined transects over Long Point's wetlands. Normally, two observers (S. Petrie and R. Ridout) would estimate waterfowl numbers on each transect without reference to individual ponds (Petrie, 1998). However, during fall 1998 and 1999, the survey protocol was modified so that waterfowl also were counted on individual "ponds" where enclosures were located.

Survey data were used to develop a seasonal index of waterfowl use (waterfowl use-days) at each

study location. Data were included in calculations only if they were collected after initial enclosure placement and before late-season sampling was done at each location. Because Inner Long Point Bay is an extensive, open water area that could not be reduced into discrete "ponds", waterfowl numbers were counted on transects flown over the Smith Marsh and mouth of Big Creek; those numbers were used in site-specific waterfowl use-day calculations. Numbers of waterfowl were converted to use-days by multiplying the average number of birds (by species or group) counted on two successive surveys by the number of days between those surveys; these individual survey pair values were then summed to provide total waterfowl use-days during fall (see Dennis et al., 1984).

Enclosure observations

Observers who were documenting diurnal and nocturnal activities of waterfowl for another study (Badzinski, 2003) monitored and recorded use of enclosures at Bouck's pond (1998 and 1999), North Pond (1999), and Smith Marsh (1999). A total of 302 observation-hours confirmed that: (1) other aquatic herbivores were present, but waterfowl were the most abundant consumers at each location, (2) ducks and tundra swans (to a lesser extent Canada geese) fed at these locations (see Badzinski, 2003, p. 89, Table 3.9), (3) ducks entered and fed in both control plots and enclosures, (4) tundra swans (rarely Canada geese) fed in reference plots, (5) large waterfowl species could not enter enclosures.

Response variable specification

Prior to data analysis, the individual vegetation samples (above-ground = 0.25 m^2 quadrats and below-ground = 0.03 m^3 scoop samples) in each enclosure were combined and averaged to provide one sample for above-ground, below-ground, and species-specific biomass estimates for each structure within each sampling period. Above-ground biomass is reported as g/m^2 and below-ground biomass is reported as g/m^3 .

Several different response variables were used in the analyses that follow. Above-ground biomass was the total dry mass of the plant parts for all species that were above the marsh substrate,

whereas below-ground biomass was the total dry mass of all subterranean plant parts of all species. The dry mass of *Chara* spp and above-ground and below-ground biomasses of wild celery and sago pondweed (combined) were also analyzed separately; combined tuber dry mass and tuber density of these species were also included in analyses. All of the preceding response variables were used to determine if plant biomass differed among treatments in the early and late sampling periods, but another set variables was used to determine if the treatments showed different relative changes from the early to late sampling periods. The following formula was used to calculate proportional change in biomass (Y) during fall:

$$\exp(\ln(a + \text{min}) - \ln(b + \text{min})) - 1 \quad (1)$$

where \exp = the natural logarithm raised to the power specified in the parentheses, \ln = the natural logarithm, a = late season sample mass, b = early season sample mass, and min = the minimum observed value for either a or b in the dataset for a response variable. The minimum value of the variable of interest in the dataset was added as a constant to both a and b because the natural logarithm of zero is undefined (Zar, 1996).

Statistical model selection and parameter estimation

We used an information-theoretic approach to evaluate statistical models and to provide estimates for effects of biological interest (Burnham & Anderson, 1998). This analytical method evaluates the strength of evidence favoring each statistical model specified in a candidate set of models and reduces bias in estimation of effect sizes and precision when model-averaging techniques are used (see Burnham & Anderson, 1998; Anderson et al., 2000). Akaike's Information Criterion with correction for small sample size (AIC_c) was used to select the best statistical model (i.e., the one with the lowest AIC_c or ΔAIC_c of zero) from a predetermined set of biologically meaningful candidate models. We used model averaging to incorporate model selection uncertainty into estimation of the treatment effect and its measure of precision (Burnham & Anderson, 1998). Model selection was done separately for analyses evaluating treat-

ment effects for: (1) early season plant biomass and tuber density (pre-waterfowl exposure), (2) late season plant biomass and tuber density (post-waterfowl exposure), and (3) relative (%) change in plant biomass or tuber density during fall (PROC MIXED; SAS Institute Inc., 1990).

Analyses using only early season data were done to determine if treatments or treatments within enclosure locations showed any differences in biomass or tuber density before exposure to waterfowl feeding activities. If differences were detected, we could then control for them by including early season biomass estimates as covariates in other analyses. To assess variation in initial plant biomass and tuber density estimates among treatments, three candidate models were developed that included effects and interactions of location (1998: North Pond, Bouck's Pond, & Teal Pond; 1999: North Pond, Bouck's Pond, Mouth of Big Creek, and Smith Marsh), enclosure set (1, 2, and 3) nested within location, and treatment (swan access [control plot] & no swan access [enclosure]) (see Table 4 for similar models). We included a model in the candidate set that lacked all treatment effects, {L, S(L)} (i.e., a candidate set "null" model), which assessed the strength of evidence for treatment effects in these data.

The amount of vegetation or density of below-ground plant parts remaining late in the fall was used as a response variable in evaluating if large herbivorous waterfowl removed more aquatic plants during fall than did other biotic and abiotic factors. Three candidate models, identical to those listed above, were specified to evaluate the strength of evidence for the prediction that control plots, as compared to enclosures, would have both reduced biomass and tuber densities during late fall (see Table 3). In this analysis, we have included an additional explanatory variable (P), early season (initial) plant biomass, to control for any effect that potential differences in early season biomass may possibly have on among enclosure differences observed later in the season. Again, one model lacking treatment effects was included to evaluate if treatment effects were substantially different between enclosure types.

We also evaluated the proportional change in aquatic vegetation during fall because it was another relative measure of the intensity of plant removal. If large waterfowl, as compared to other

biotic and abiotic factors, had an additive effect on removal of aquatic plants, then proportional seasonal changes in plant biomasses and tuber densities in control plots should be larger than those within exclosures. We developed three candidate models, one of which lacked treatment effects, to determine if seasonal removal intensity of plant biomass and tubers differed between treatments (see Table 4).

To aid in assessing the strength of evidence for each candidate model, relevant model selection information (R^2 [explained variation], K [number of parameters], N [sample size], ΔAIC_c , and $^W AIC_c$) were reported in tables. Model averaged least-squares means and $\pm 95\%$ confidence intervals ($\pm 95\%$ CI) for treatment effects were reported in all tables and text.

Results

Waterfowl and other herbivore use of exclosure locations

All study locations received much use by waterfowl during 1998 (range: 45,764–1,009,313 water-

fowl use-days) and 1999 (range: 57,393–924,623) (Table 1). During fall both years, Bouck's Pond had the highest number of waterfowl use-days, largely as a result of relatively greater use by diving ducks as compared to the other locations; this site also had the highest use by tundra swans each year. Ducks, especially dabbling ducks, showed much higher use of exclosure ponds than did larger herbivores; this pattern was evident at each location during both study seasons (Table 1). Further, a notable number and percentage of all waterfowl and duck use-days were recorded at each study location before swan arrival each year (Table 2).

Waterfowl exclosure and vegetation study

Early season plant biomass

For all six sets of analyses, there was no support ($^W AIC_c = 0.00$) that any estimate of initial above- and below-ground biomass or tuber density differed substantially between treatments within study locations (L×T) during fall; there also was virtually no support ($^W AIC_c = 0.01$ for all analyses) for an overall treatment effect in these data. Further, inspection of model averaged least

Table 1. Use of exclosure locations by waterfowl during fall 1998 and 1999 at Long Point, Ontario

Year and location (area)	Tundra swan		Canada geese		Large waterfowl ^a		<i>Anas</i> spp		<i>Aythya</i> spp		Total waterfowl	
	Use-days	#	Use-days	#	Use-days	#	Use-days	#	Use-days	#	Use-days	#
<i>1998</i>												
North pond (0.02 km ²)	2625	63	899	7	3577	70	42177	343	0	0	45764	412
	6		2		8		92		0			
Bouck's pond (0.25 km ²)	43523	813	435	4	44570	817	735305	7477	229438	1845	1009313	10138
	4		<1		4		73		23			
Teal pond (0.05 km ²)	2500	44	2156	15	4796	59	63970	513	0	0	68766	572
	4		3		7		93		0			
<i>1999</i>												
North pond (0.02 km ²)	28000	450	10390	74	3844	524	87985	700	0	0	126433	1224
	22		8		30		70		0			
Bouck's pond (0.25 km ²)	35315	667	9549	59	46462	726	557912	4473	320250	2870	924623	8069
	4		1		5		60		35			
Big creek mouth and Smith marsh (0.75 km ²)	5422	229	0	0	5837	229	1926	15	49630	1026	57393	1271
	10		0		11		3		86			

Species/group-specific and total number of use-days, average number of individuals counted (#), and the percentage of total waterfowl use-days (% shown below Use-days) are shown for each exclosure location.

^aLarge waterfowl = combined use-days and numbers of tundra swans, mute swans (*Cygnus olor*), and Canada geese; thus, percentages will not sum to 100%.

Table 2. Waterfowl use of enclosure locations before (Pre) and after (Post) tundra swan arrival during fall 1998 and 1999 at Long Point, Ontario

Year and location	Waterfowl use-days (% of use-days)									
	Canada geese		<i>Anas</i> spp		<i>Aythya</i> spp		Total duck		Total waterfowl	
	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
<i>1998</i>										
North pond	468	431	29070	13107	0	0	29070	13107	29538	13538
	52	48	69	31	0	0	69	31	69	31
Bouck's pond	60	375	144341	590964	8475	220963	152816	811927	152876	812302
	14	86	20	80	4	96	16	84	16	84
Teal pond	2156	0	40430	23540	0	0	40430	23540	32597	33529
	100	0	63	37	0	0	63	37	49	51
<i>1999</i>										
North pond	2900	7490	18633	69353	0	0	18633	69353	21533	76843
	28	72	21	79	0	0	21	79	22	78
Bouck's pond	3466	6083	50185	507728	0	320250	50185	827978	53650	834061
	36	64	9	91	0	100	6	94	6	94
Big creek mouth and Smith marsh	0	0	1044	882	0	49630	1044	50512	1044	50512
	0	0	54	46	0	100	2	98	2	98

Species/group-specific and total number of use-days and the percentage (% are shown below pre- and post-use-days) of use-days are shown for each enclosure location.

squares means and their 95% confidence intervals clearly showed no difference in any initial above-ground, below-ground, and tuber biomass estimate obtained from exclosures and reference plots (Figure 3). However, because there was some (albeit very weak) support of an overall treatment effect, we decided to include early season biomass estimates in models describing variation in late season biomass as covariates to control for any possible confounding effect.

Late season plant biomass

The best model describing variation in all estimates of late season above-ground (total, *Chara* spp, and combined *V. americana* and *P. pectinatus*), below-ground (total and combined *V. americana* and *P. pectinatus*) and tuber (combined *V. americana* and *P. pectinatus*) biomass overwhelmingly ($^W\text{AIC}_c$: 0.99–1.00) was one that contained only effects of study location, enclosure set nested within location, and early season biomass (i.e., the candidate set null model, {L, S(L), P}) (Table 3). The two other models, {L, S(L), P, T} and {L, S(L), P, T, L×T} both had extremely low model weights in the six sets of analyses ($^W\text{AIC}_c \leq 0.01$), which suggested there was virtually no support for any kind of

treatment effect. Thus, model averaged means showed that there were no real differences in the amount of remaining above-ground, below-ground, and tuber biomass in areas where large waterfowl had access to aquatic plants (control plots) as compared to where their access was restricted (exclosures) (Figure 3).

Proportional change in plant biomass

Model selection criterion indicated the candidate set null model, {L, S(L)}, was overwhelmingly ($^W\text{AIC}_c$: 0.93–0.99) the best model describing variation in each of the six measures of relative change in above- and below-ground biomass (Table 4). As such, there again was only very weak support ($^W\text{AIC}_c$: 0.01–0.07) for an overall treatment effect ({L, S(L), T}) and no support ($^W\text{AIC}_c = 0.00$) for an added effect of treatment dependent on study area ({L, S(L), T, L×T}) in these six sets of analyses (Table 4). Above-ground and below-ground biomass of all focal plant species (or species-groups) showed substantial reductions throughout fall, but there was no real difference in relative change between areas where large waterfowl could and could not access aquatic plants (Fig. 4). For example, in both controls and

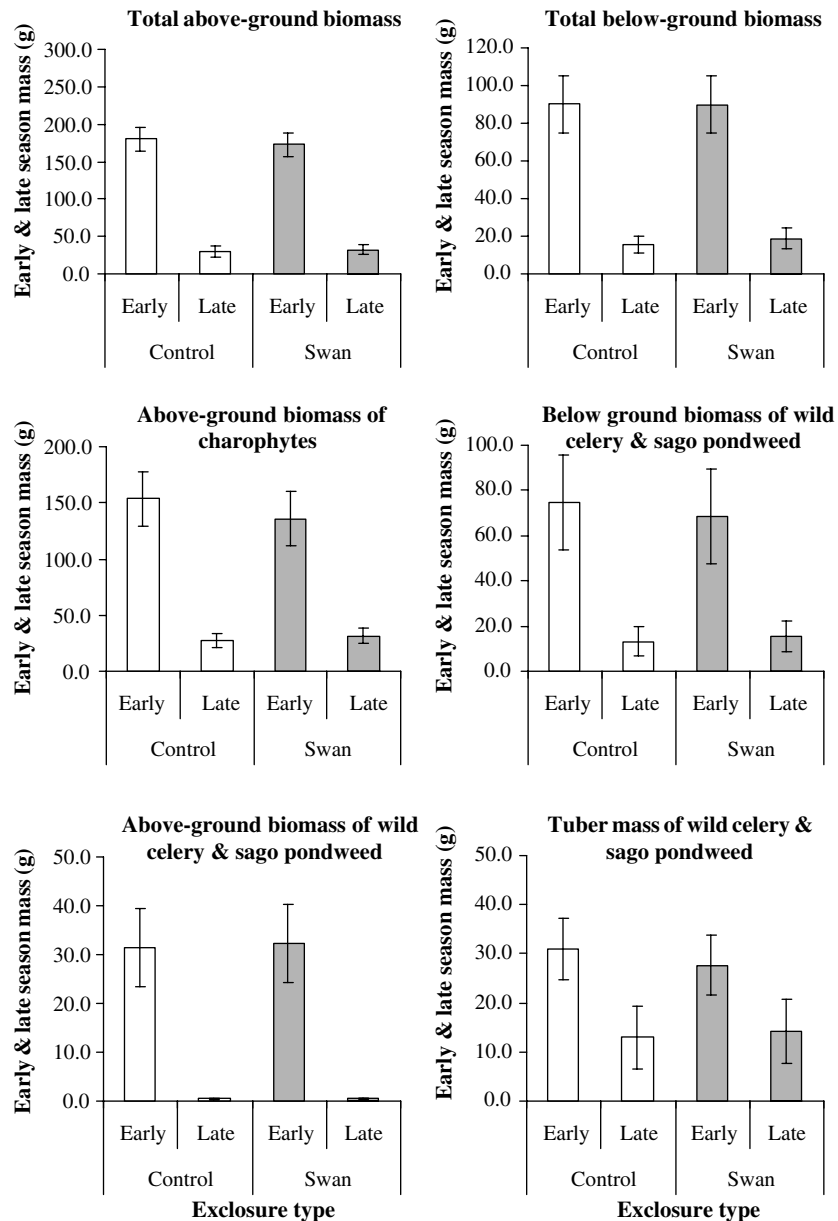


Figure 3. Early and late season estimates for the amount of dry above-ground (g m^{-2}), below-ground (g m^{-3}), and tuber (g m^{-3}) biomass present in reference/control plots (control) and swan enclosures (swan) during the 1998 and 1999 fall staging seasons at Long Point, Lake Erie, Ontario.

enclosures, total above- and below-ground biomass decreased by about $80 \pm 7\%$ during fall, whereas biomass of *Chara* spp declined by about $73 \pm 6\%$. Regardless of treatment, nearly all ($100 \pm 1\%$) above ground parts of both *V. Americana* and *P. pectinatus* were gone by early December each year, but below ground biomass of these species declined by $76 \pm 6\%$ throughout the

fall, whereas combined tuber mass of these two species declined by about $43 \pm 28\%$.

Discussion

The primary impetus for this study was concern that large numbers of large-bodied, herbivorous

Table 3. Model selection information for among enclosure variation in above- and below-ground biomass of aquatic plants after they were exposed to waterfowl during fall at Long Point, Ontario

Response variable (Y =) late season biomass	Model	<i>n</i>	<i>R</i> ²	<i>K</i>	AIC _c	ΔAIC _c	^W AIC _c
<i>Above-ground (g/m²)</i>							
Total above-ground	{L, S(L), P}	42	0.86	23	422.42	0.00	0.99
	{L, S(L), P, T}		0.86	24	432.97	10.55	0.01
	{L, S(L), P, T, L×T}		0.92	30	521.05	98.62	0.00
<i>Chara</i> spp	{L, S(L), P}	28	0.93	16	273.50	0.00	1.00
	{L, S(L), P, T}		0.94	17	284.90	11.40	0.00
	{L, S(L), P, T, L×T}		0.98	21	358.17	84.68	0.00
<i>Vallisneria americana</i> & <i>Potamogeton pectinatus</i>	{L, S(L), P}	38	0.47	21	-34.19	0.00	0.99
	{L, S(L), P, T}		0.50	22	-24.70	9.49	0.01
	{L, S(L), P, T, L×T}		0.54	28	97.75	131.94	0.00
<i>Below-ground (g/m³)</i>							
Total below-ground	{L, S(L), P}	38	0.78	21	493.92	0.00	1.00
	{L, S(L), P, T}		0.78	22	500.12	10.95	0.00
	{L, S(L), P, T, L×T}		0.87	28	596.39	116.25	0.00
<i>Vallisneria americana</i> and <i>Potamogeton pectinatus</i>	{L, S(L), P}	38	0.80	21	376.60	0.00	1.00
	{L, S(L), P, T}		0.80	22	387.80	11.20	0.00
	{L, S(L), P, T, L×T}		0.87	28	496.29	119.69	0.00
<i>Tubers (g/m³)</i>							
<i>Vallisneria americana</i> & <i>Potamogeton pectinatus</i>	{L, S(L), P}	38	0.80	21	373.24	0.00	1.00
	{L, S(L), P, T}		0.80	22	384.81	11.57	0.00
	{L, S(L), P, T, L×T}		0.87	28	493.27	120.02	0.00

Under Model, L=location (three in 1998 & four in 1999), S=enclosure set (1, 2, and 3), S(L)=enclosure sets nested within locations, P=early season (initial) biomass of Y in enclosures, T=enclosure treatment (swan and control), L×T=interaction among locations and treatments. Shown for each candidate model are: sample size (*n*), proportion of explained variation (*R*²), number of model parameters (*K*), Akaike Information Criterion corrected for small sample size (AIC_c), AIC_c difference (ΔAIC_c), and model weight (^WAIC_c).

waterfowl could substantially reduce the biomass of aquatic plants, and thus, directly or indirectly affect aquatic vegetation and waterfowl communities at Long Point (Petrie et al., 2002; Badzinski, 2003). Our results, however, showed that fall migrant tundra swans and Canada geese did not greatly add to the substantial seasonal reductions in total above- and below-ground biomass of aquatic vegetation, above-ground biomass of *Chara* spp, or the combined above-ground, below-ground, and tuber biomass of *V. Americana*, and *P. pectinatus*.

It was our original intent to provide data on the effect that large waterfowl may have on reducing food availability to smaller waterfowl that co-occur in time and space at a major staging area. However, within the temporal and spatial limitations of this study, it seems that diving and dabbling ducks may influence availability of some

aquatic plants, mainly *V. americana*, *P. pectinatus*, and *Chara* spp, and in turn may influence the behaviour and feeding activities of large waterfowl, especially tundra swans. There were several lines of supportive reasoning and circumstantial evidence. First, even though they are smaller, ducks were far more abundant than swans and geese. Secondly, ducks, especially dabbling ducks, begin to arrive at Long Point in sizable numbers during mid-September with peak numbers occurring in mid- to late October, whereas tundra swans generally begin to arrive late in October and reach their peak numbers during early- to mid-November (Long Point Waterfowl and Wetlands Research Fund, unpubl. data). Thus, by the time tundra swans and many Canada geese arrive, dabbling and diving ducks have been using (see Table 2) and feeding in aquatic habitats for a considerable amount of time and have already

Table 4. Model selection information for proportional changes in above- and below-ground biomass of aquatic plants among exclosures during fall at Long Point, Ontario

Response variable (Y =) Proportional change	Model	<i>n</i>	<i>R</i> ²	<i>K</i>	AIC _c	ΔAIC _c	^w AIC _c
<i>Above-ground (g/m²)</i>							
Total above-ground	{L, S(L)}	42	0.75	22	8.40	0.00	0.99
	{L, S(L), T}		0.75	23	18.44	10.04	0.01
	{L, S(L), T, L×T}		0.80	29	104.53	96.13	0.00
<i>Chara</i> spp	{L, S(L)}	28	0.77	15	2.29	0.00	0.99
	{L, S(L), T}		0.78	16	12.11	9.82	0.01
	{L, S(L), T, L×T}		0.90	20	68.74	66.45	0.00
<i>Vallisneria americana</i> & <i>Potamogeton pectinatus</i>	{L, S(L)}	38	0.47	20	-255.47	0.00	0.93
	{L, S(L), T}		0.54	21	-250.28	5.19	0.07
	{L, S(L), T, L×T}		0.65	27	-154.89	100.59	0.00
<i>Below-ground (g/m³)</i>							
Total below-ground	{L, S(L)}	38	0.84	20	274.71	0.00	0.99
	{L, S(L), T}		0.84	21	282.20	9.98	0.01
	{L, S(L), T, L×T}		0.89	27	364.85	101.86	0.00
<i>Vallisneria americana</i> and <i>Potamogeton pectinatus</i>	{L, S(L)}	38	0.44	20	79.98	0.00	0.99
	{L, S(L), T}		0.45	21	89.98	10.01	0.01
	{L, S(L), T, L×T}		0.53	27	189.43	109.46	0.00
<i>Tubers (g/m³)</i>							
<i>Vallisneria americana</i> & <i>Potamogeton pectinatus</i>	{L, S(L)}	38	0.72	20	128.81	0.00	0.99
	{L, S(L), T}		0.72	21	138.26	9.45	0.01
	{L, S(L), T, L×T}		0.76	27	238.23	109.42	0.00

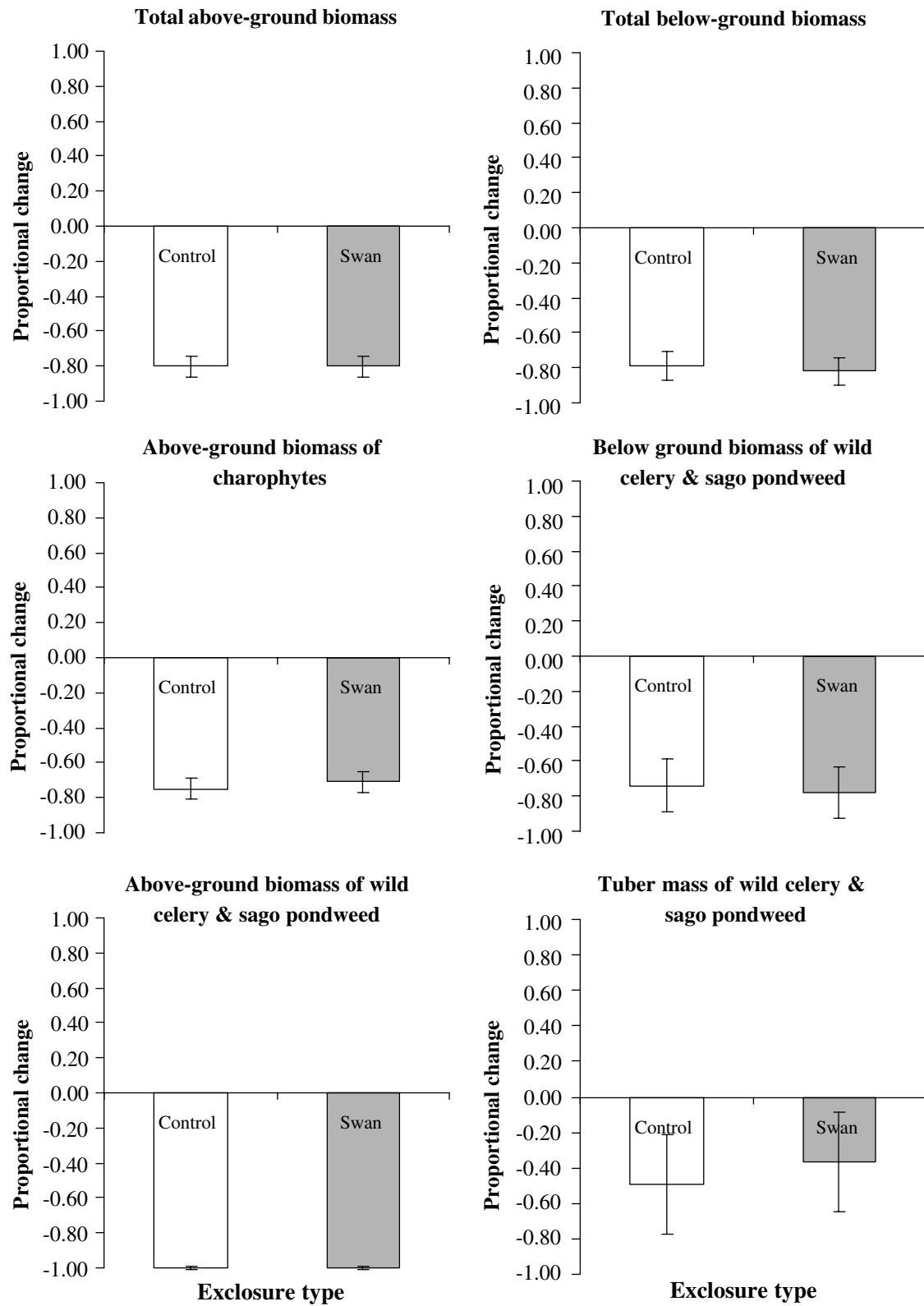
Under Model, L=location (three in 1998 and four in 1999), S=exclosure set (1, 2, and 3), S(L)=exclosure sets nested within locations, T=exclosure treatment (swan and control), L×T=interaction among locations and treatments. Shown for each candidate model are: sample size (*n*), proportion of explained variation (*R*²), number of model parameters (*K*), Akaike Information Criterion corrected for small sample size (AIC_c), AIC_c difference (ΔAIC_c), and model weight (^wAIC_c).

consumed much of the aquatic vegetation at study locations (S. Badzinski, pers. obs.). Further, tundra swans and Canada geese only spent from 3% to 10% of the day feeding at two study locations (Badzinski, 2003), Big Creek North Pond and Little Rice Bay, both of which had high duck densities and were used heavily by many species of waterfowl before swan arrival (see Table 2). Sampling immediately before swan arrival would allow determination of how much aquatic biomass ducks, early arriving geese, and other aquatic herbivores, remove and the potential these consumers have for influencing tundra swan feeding behaviour and energetics at staging areas.

Even though large waterfowl did not further reduce the amount of aquatic plants removed from wetlands throughout the fall, the substantial seasonal decline in aquatic plant availability and biomass warrants mention. Removal of aquatic

macrophytes by waterfowl and other small aquatic consumers, wave action, and senescence all can be important factors contributing to seasonal reductions in plant biomass (see reviews Lodge, 1991; Lodge et al., 1998). Clearly, because a true control (i.e., total herbivore exclusion) was not included in this study, biomass removal effects could not be partitioned unequivocally into those attributable to each of these factors and all likely contributed, in varying degrees, to the overall decline in plant availability during fall. Despite the presence of relatively small numbers of muskrat (*Ondatra zibethicus*, Linnaeus), fish, and turtles and the occurrence of wave action and senescence, both

Figure 4. Proportional change in dry above-ground, below-ground, and tuber biomass in reference/control plots (control) and swan exclosures (swan) throughout the 1998 and 1999 fall staging seasons at Long Point, Lake Erie, Ontario.



before and during the fall staging season, the combined effect of each of these factors on biomass of *Chara* spp and below-ground and tuber biomass of *V. americana* and *P. pectinatus* likely was less than that caused by the hundreds (sometimes thousands) of migrant waterfowl (primarily ducks) that fed in and used each of these study locations each day (Badzinski, 2003; see also Tables 1 and 2).

The main finding of this study, which was that large herbivores had no additional removal effect on aquatic vegetation, should not be interpreted as evidence that tundra swans and Canada geese had no effect at all on the seasonal biomass of aquatic plants at Long Point. In fact, both of these species used study locations and foraged in them to varying degrees. Canada geese, for example, used those locations primarily as diurnal roost sites between foraging bouts to agricultural fields, and thus spent less than 3% of their time feeding there (Badzinski, 2003); geese were, however, present and fed more in aquatic habitats earlier in the fall (S. Badzinski, pers. obs.). Tundra swans almost exclusively use aquatic habitats during fall (Petrie et al., 2002) where they spend 6–54% of their time feeding (Badzinski, 2003; S. Badzinski, unpubl. data). Further, individual tundra and Bewick's swans can eat 3–5 kg (wet mass) of tubers each day at staging areas (Limpert, 1974; Beekman et al., 1991). Thus, given that tundra swans were present at study locations in sizeable numbers and were feeding on aquatic plant rhizomes and tubers (Badzinski, 2003), it was notable that we did not detect an added effect of herbivory on *V. americana* and *P. Pectinatus* tubers (see Beekman et al., 1991; Limpert & Earnst, 1994; Froelich & Lodge, 2000).

There are several possible explanations regarding why a large waterfowl did not remove considerably more vegetation from unprotected areas during this study. One reason may be that tubers in both the control plots and swan enclosures were depleted to a threshold level beyond which it became unprofitable for waterfowl to continue foraging on them (Tome, 1988; Beekman et al., 1991; Lovvorn, 1994). Such a lower feeding threshold (7.2 ± 3.4 g tuber dry-mass m^{-2}) was detected for Bewick's swans feeding on *P. pectinatus* tubers during fall in the Netherlands (Beekman et al., 1991). Our estimates of combined tuber mass (control plot: 13.3 ± 6.6 g dry-mass m^{-2} and

enclosure: 15.4 ± 6.7 g dry-mass m^{-2}) were close to the lower threshold values reported by Beekman et al. (1991), showing that tuber densities at our study locations were very low by the end of the fall staging period. Low aquatic food availability also may partly explain why tundra swans (and Canada geese) increase their use of agricultural fields during late fall and spring at Long Point (Petrie et al., 2002) and the considerable time spent feeding on crops during those periods (S. Badzinski & S. Petrie, unpubl. data).

The similarity in late season tuber densities between "enclosure" types also suggested that even if tundra swans and Canada geese did contribute to some of the removal of tubers from control plots, other waterfowl likely removed tubers to an identical, low density in areas where swans could not forage, i.e., removal by ducks compensated for the lack of "large waterfowl" herbivory. Many other herbivory studies have been done at locations where only one species or ecological group of consumers (e.g., geese) was present and biomass removal effects could be reliably attributed to one specific consumer (or group) (e.g., Bazely & Jeffries, 1986; Giroux & Bédard, 1987; Beekman et al., 1991; Conover & Kania, 1994; Mitchell & Wass, 1996). However, the potential for compensatory herbivory in aquatic habitats at Long Point, where many different species and types of consumers and removal agents were present, was very high. Thus, it was not entirely unexpected that we did not detect an additive effect due to removal of aquatic vegetation attributable solely to large waterfowl during this short-term study.

Differences in food preferences between ducks and larger waterfowl, particularly tundra swans, are another possible explanation why a "large waterfowl" herbivory effect was not detected. For example, observations and collections of foraging tundra swans showed that some of the same plants that are important duck foods, specifically *V. americana* and *P. pectinatus* tubers, were eaten by swans (Badzinski, 2003, Appendix 1). However, tundra swans also spent much time feeding in shallow water in areas dominated by emergent or floating leaved aquatic plants where they excavated and consumed the relatively large tubers (and rhizomes) of *Sagittaria latifolia*, *Sagittaria rigida*, *Nuphar variegatum*, and likely *Scirpus* spp (S. Badzinski, pers. obs., see also Limpert, 1974;

Limpert & Earnst, 1994). This was notable because smaller waterfowl at Long Point commonly consumed *Chara* spp (*Anas* and *Aythya* spp), seeds of various aquatic plants (primarily *Anas* spp), and the relatively small tubers of *V. americana* and *P. pectinatus* (primarily *Aythya* spp) (Petrie, 1998; Knapton & Petrie, 1999). Near the end of fall, however, tundra swans began to feed much more in deeper water, where large *V. americana* and *P. pectinatus* beds were located and where thousands of diving ducks had been feeding earlier (S. Badzinski, pers. obs.). This seasonal change in foraging behaviour suggests that swans had depleted other more energetically profitable and preferred foods (see also Beekman et al., 1991; Nolet & Drent, 1998). Thus, the impact that large numbers of tundra swans (and other large waterfowl) have on *V. americana* and *P. pectinatus* tuber banks may be more important during winter or during spring migration, especially at staging or wintering areas that have extensive shallow wetlands that are dominated by these plants and/or have limited availability of large tuber-producing plants (Froelich & Lodge, 2000). Wetlands such as these are present in some of the large, private hunting clubs at Long Point, so results from our study locations may not be entirely representative what is occurring throughout this large staging area. Further reductions of the tuber bank during spring in these types of wetlands could decrease primary plant production later during the growing season, which may in turn have future, longer-term consequences for plant, thus waterfowl, abundance or distribution (Anderson & Low, 1976; Tubbs & Tubbs, 1983; Idestam-Almquist, 1998; Lodge et al., 1998).

Longer-term impacts of waterfowl herbivory on the aquatic plant community remain to be determined at Long Point, but its evaluation is necessary to understand better plant-herbivore dynamics at staging areas used by tundra swans and other waterfowl. Given the importance of *Sagittaria* spp, *Nuphar* spp, and *Scirpus* spp as foods for staging tundra swans, the short-term and longer-term effects that swan herbivory have on the seasonal abundance and distribution of these plants should be determined. Future studies also should try to assess how much different consumer

groups overlap in use of specific aquatic forage plants and how herbivores affect relative abundances, compositions, and distributions of these plant species in the short-term (i.e., fall and spring staging or winter periods) and over the longer term (i.e., over several years of exposure). The relative contribution of each group of herbivores and other removal agents could be investigated by designing a more complex enclosure experiment, which also might allow more subtle indirect effects, such as compensatory herbivory, to be detected (e.g., see Evers et al., 1998; Hamilton, 2000). Broader scale and longer-term studies of aquatic plant abundance and distributions could be combined with similar investigations of waterfowl at staging areas. Doing so would greatly increase our understanding of waterfowl-plant interactions/associations and provide the framework necessary for improved monitoring of aquatic macrophyte and waterfowl populations at important waterfowl staging and wintering areas.

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Part III
Loons – Population Trends, Behaviour, Habitat Use
and Ecotoxicology

Factors influencing productivity of common loons (*Gavia immer*) breeding on circumneutral lakes in Nova Scotia, Canada

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Abstract

Common loons (*Gavia immer*) are top predators that are sensitive to biotic and abiotic conditions associated with their breeding lakes, so factors such as lake chemistry and human activity or disturbance are thought to influence their seasonal and long-term reproductive success. We used two indices of loon productivity to evaluate (1) temporal patterns and (2) relationships with physical and chemical lake characteristics and human activities. Data collected from 1991 to 2000 by volunteers of the Canadian Lakes Loon Survey (CLLS) in Nova Scotia showed that loon productivity, as indexed by both the proportion of resident pairs that produced at least one large young (P_{s1}) and the proportion of successful pairs that produced two large young (P_{s2}), did not vary substantially from year to year and showed no linear trend from 1991 to 2000. Average estimates (1991–2000) for P_{s1} and P_{s2} were 0.49 ± 0.02 and 0.43 ± 0.03 , respectively, and the mean number of chicks per residential pair over that time was 0.75 ± 0.04 . We found that human disturbance and shoreline development did not influence loon productivity during the pre-fledging stage on lakes surveyed by CLLS volunteers. Proportion of resident pairs rearing at least one large young was independent of dissolved organic carbon (DOC) concentrations of breeding lakes, but there was a positive relationship between the proportion of successful pairs rearing two large young and DOC. Both indices of loon productivity tended to be negatively correlated with lake pH. These results were not consistent with other findings that loon productivity generally declines with lake acidity, but likely reflect the preponderance of circumneutral (pH 6.5–7.0) lakes surveyed by the CLLS volunteers in Nova Scotia.

Introduction

Common loons, *Gavia immer* (Brünnich) (hereafter loons), are often top predators in freshwater environments where they breed. Because of this, factors that influence this species' reproductive success have been studied in attempt to use loons as a bioindicator of lake health (Strong, 1990; Wayland & McNicol, 1990; McNicol et al., 1995). As such, many studies have identified a variety of biotic and abiotic factors that influence loon survival and

reproductive success (see review by McIntyre & Barr, 1997), including predation (McIntyre, 1975, 1988a; Sutcliffe, 1980; Titus & VanDruff, 1981; Yonge, 1981; Belant & Anderson, 1991), weather (McIntyre & Barr, 1997), water-level fluctuations (Vermeer, 1973; Fair, 1979; Sutcliffe, 1980; Barr, 1986; McIntyre, 1988b; Belant & Anderson, 1991), anthropogenic influences (Vermeer, 1973; Sawyer, 1979; Robertson & Flood, 1980), and limnological parameters (Alvo et al., 1988; Wayland & McNicol, 1990; McNicol et al., 1995).

Breeding loons and humans often come into contact because both are attracted to the same lakes during summer. Construction of homes, boat docks, and retaining walls on lakes where loons prefer to nest can cause nesting habitat destruction and increased disturbance, both of which can reduce pair densities and chick production (Tate & Tate, 1970; Vermeer, 1973; McIntyre, 1975, 1988a). Typically, there is a positive correlation between intensity of shoreline development and recreational use and human disturbance rates of lakes (Heimberger et al., 1983). Human disturbance and watercraft use on lakes may lower nest attentiveness of adults and thus increase nest predation (Robertson & Flood, 1980; Titus & VanDruff, 1981; Heimberger et al., 1983; Ruggles, 1994). During the pre fledging period, human activities can reduce feeding opportunities of chicks (and adults) and increase the possibility of loon/boat collisions or abandonment of young (McIntyre, 1988a; McIntyre & Barr, 1997; but see Titus & VanDruff, 1981; Belant & Anderson, 1991; Caron & Robinson, 1994; Ruggles, 1994), all of which may ultimately reduce loon productivity on lakes.

It has been known for decades that deposition of acid precipitation can lower pH in lakes and may result in reduced abundance and diversity of fish and other prey favoured by loons (Dillon et al., 1984; Schindler, 1988), which in turn can lower loon reproductive performance and chick survival (Alvo et al., 1988; Wayland & McNicol, 1990; McNicol et al., 1995; but see Parker, 1988). Acidification also tends to increase bioavailability of methyl-mercury in aquatic environments (Spry & Wiener, 1991; Wiener et al., 2002), and mercury concentrations in fish often are elevated in acidic lakes (Schuehammer & Blancher, 1994; Schuehammer & Graham, 1999; Carter et al., 2001). In turn, bioaccumulation of mercury by loons and other piscivorous birds may impair their behaviour, survival, or reproductive success (Burgess et al., 1998b; Meyer et al., 1995, 1998; Nocera & Taylor, 1998; Wiener et al., 2002).

Organic carbon concentrations (Dissolved Organic Carbon (DOC) and Total Organic Carbon (TOC)) in lakes can influence bioavailability of methyl-mercury, but their role in doing so is not entirely understood (Carter et al., 2001; Rencz et al., 2003). Large organic carbon concentrations in the water-column can facilitate mercury trans-

port within watersheds (Mierle, 1990; O'Driscoll & Evans, 2000) and enhance bacterial production of methyl-mercury (Hecky et al., 1991; Miskimmin et al., 1992). Yet under some conditions DOC may act to reduce bioavailability of mercury to fish (Driscoll et al., 1995; Choi et al., 1998; Scheuhammer et al., 1998; Rencz et al., 2003), and thus top-level predators such as loons. Thus, investigating correlations between loon productivity and DOC concentrations within breeding lakes is interesting given the complex associations among DOC, methyl-mercury, and loon productivity (Burgess et al., 1998a, b).

The purpose of our study was to first describe temporal patterns of loon productivity from 1991 to 2000 using data collected by volunteers of the Canadian Lakes Loon Survey (CLLS) in Nova Scotia. Second, we evaluated the influence that chemical attributes of lakes (pH and DOC) and human activity (shoreline development and disturbance indices) had on loon productivity. We hypothesized that loon productivity would be (1) positively correlated with lake pH (i.e., higher on lakes that were less acidic) and (2) lower on lakes that had higher disturbance regimes and more highly developed shorelines. Given the complex associations among DOC, pH, methyl-mercury, and loon productivity, we had no clear expectation as to how DOC may affect loon productivity.

Methods

Reproductive performance

The CLLS is a long-term monitoring program that strives to maintain survey coverage of loon breeding lakes by the same volunteers for several consecutive years (see McNicol et al., 1995). Data included in this paper were collected on loon breeding lakes in Nova Scotia, Canada, from 1991 to 2000. Prior to their inaugural survey season, participants of the CLLS selected a lake (or sometimes part of very large lakes) at which they would survey and observe adult and young loons throughout the breeding season. From early June through mid-September volunteers recorded numbers of resident pairs (displaying breeding behaviour and/or territoriality; nesting period) and downy/small (<2/3 adult body length;

hatching period) young and large ($\geq 2/3$ adult body length; pre fledging period) young. Volunteers were required to survey lakes (or their section of large lakes) at least three times during the breeding season (nesting [early June–mid-July], hatching [early–late July], and pre fledging [mid-August–mid-September] periods) in an attempt to obtain the best estimate of maximum numbers of resident pairs and young on their survey areas; most volunteers, however, collected data more frequently (e.g., weekly, biweekly, etc.) than the minimum requirements. If no pairs or young were present on lakes, volunteers also reported that information each year the lake was surveyed. Data meeting eligibility and quality requirements were used to derive two indices of loon productivity:

$$P_{s1} = N_{s1}/N_{pr} \text{ and } P_{s2} = N_{s2}/N_{s1},$$

where P_{s1} is the proportion of resident pairs that reared at least one large young to pre-fledging age and P_{s2} is the proportion of successful pairs that produced at least two large young. N_{s1} and N_{s2} are the number of pairs observed with at least one large young and two large young, respectively, and N_{pr} is the total number of resident pairs on a lake. To better compare our productivity estimates to those of other studies, we also calculated annual and 10-year (1991–2000) averages for the number of large young per resident pair (McIntyre, 1988a; McIntyre & Barr, 1997).

Human disturbance & shoreline development

Each year, volunteers estimated the percentage of shoreline on lakes that was developed (e.g., cottages, houses, marinas). Lakes were assigned to one of five categories that each represented a 20% increase (i.e., 0–20%, 21–40%, 41–60%, 61–80%, 81–100%) in shoreline impacted by human development. Each month throughout the breeding season, volunteers assigned levels (1–8) of human activity and watercraft disturbance to lakes as follows: (1) no people, no boats; (2) people but no boats; (3) occasional use of boats/canoes without motors; (4) frequent use of boats/canoes without motors; (5) occasional use of boats with motors; (6) frequent use of boats with motors; (7) occasional water skiing and/or boat racing, and (8) frequent water skiing and/or boat racing.

Although there was little variation in activity indices among summer months (CLLS, unpubl. data), we used the highest disturbance category recorded annually at each lake for analyses. For analyses, the original eight categories were combined into three broader ones, where categories 1–3, 4–6, and 7–8 became indices of low, moderate, and high disturbance, respectively.

Chemical and physical characteristics of lakes

Personnel of the Canadian Wildlife Service of Environment Canada collected the majority of the limnological data in this study (N. Burgess, pers. comm.). For some lakes, however, volunteers collected water samples using an established protocol; those samples were sent to an environmental water chemistry laboratory in Dorset, Ontario for determination of limnological values. In our analyses, mean pH and DOC values were used as explanatory variables in linear logistic regression models because (1) data for these chemical variables were not measured or available on an annual basis for each lake, (2) most lakes only had one pH or DOC measurement taken during the 1991–2000 study period, and (3) lake-specific pH showed little annual variation in Nova Scotia in general over the period of study (Clair et al., 2002). Lake surface areas (hectares) were obtained from the Gazetteer of Canada (Natural Resources Canada, 1997) and were log-transformed (\log_e) to normalize error distributions of those data.

Data available for statistical analyses

Loon productivity data (young per resident pairs) were available for 223 (497 annual volunteer reports) lakes in Nova Scotia, but that number varied from year to year depending on volunteer participation. In total, there were 59 (247 reports) and 47 (126 reports) lakes where pH and lake area and where DOC and lake area were available for analyses for P_{s1} and P_{s2} , respectively. There were 111 (321 reports) and 81 (167 reports) lakes where human disturbance/watercraft activity index and lake surface area data were available for analyses for P_{s1} and P_{s2} , respectively. In addition, there were 114 (322 reports) and 81 (162 reports) lakes where shoreline development index and lake sur-

face area data were available for analyses for P_{s1} and P_{s2} , respectively.

Statistical analyses

Proportions reflecting breeding successes or failures of loons on lakes (i.e., P_{s1} and P_{s2}) approximated a binomial distribution and were treated as events/trials in all analyses. Generalized Linear Models (PROC GENMOD; SAS Institute Inc., 2001), which assumed a binomial error distribution and a linear logistic response probability distribution (i.e., logit link function: $\log[\text{mean}/(1-\text{mean})]$), were used to evaluate effects of pH (continuous), DOC (continuous), human activity/watercraft disturbance (categorical index), and shoreline development (categorical index), while controlling for year (categorical) and lake area (continuous), on each of the two indices of loon productivity (P_{s1} and P_{s2}). Lakes were treated as repeated clusters (n) in analyses to account for within-lake correlations in productivity (because pairs often return to the same lake each year to breed (McIntyre & Barr, 1997)) by using Generalized Estimating Equations (GEE). Evaluation of degrees of freedom and deviance indicated overdispersion in both P_{s1} and P_{s2} (Collett, 1991), so we used the DSCALE option in PROC GENMOD (SAS Institute Inc., 2001) to account for overdispersion. Standardized residuals were plotted against continuous variables of interest to evaluate fit of linear logistic models (Collett, 1991); doing so showed that all models specified adequately fit these data. Only main effects models were evaluated and statistical significance ($p \leq 0.05$) of those effects were assessed using score statistics from Type III GEE analyses. Temporal trends (year: continuous variable) and annual variation (year: class variable) in (1) numbers of resident pairs that raised at least one large young to pre fledging age and (2) numbers of successful pairs that reared two large young to pre fledging age were examined using Generalized Linear Models (PROC GENMOD; SAS Institute Inc., 2001) that assumed a Poisson error distribution and where lakes were treated as repeated clusters. As stated above, overdispersion was accounted for and statistical effects were deemed significant at $p \leq 0.05$. Unless otherwise stated, means and parameter estimates are reported to ± 1 SE.

Results

Temporal variation in adult loon productivity

Linear logistic regression analysis using the entire CLLS Nova Scotia data set (i.e., not constrained to include only lakes with matching pH, DOC, and lake area data) consisting of 283 lakes for P_{s1} and 180 lakes for P_{s2} showed that the proportion of resident pairs that reared at least one large young to pre fledging age and proportion of successful pairs that reared two large young to pre fledging age was stable (year linear effect, $p > 0.10$ for P_{s1} and P_{s2}) through time and did not vary annually (year class effect, $p > 0.10$ for P_{s1} and P_{s2}) (Fig. 1a, b). Over the 10-year period, the average proportion of resident pairs that reared at least one large young was 0.49 ± 0.02 and proportion of pairs that reared two large young was 0.43 ± 0.03 (Fig. 1a, b). Given these estimates, about 28% of resident pairs raised one large young and 21% of resident pairs, on average, raised at least two large young to pre fledging age. There were, on average, 0.75 ± 0.04 chicks per resident pair (Fig. 1c); annual average estimates ranged from a low of 0.50 ± 0.13 chicks per resident pair in 1997 to a high of 1.19 ± 0.17 chicks per resident pair in 1998 (Fig. 1c).

Lake physical and chemical parameters

The majority (78%) of lakes in this study were between 20 and 400 ha in size (Fig. 2c). Further, most lakes surveyed (70%) were circumneutral for pH (6.5–7.5) and few lakes (<10%) had pH of ≤ 5.5 (Fig. 2a). The range and distribution of pH values for CLLS lakes were identical to those reported by Clair et al. (2002) for a larger sub-sample of Nova Scotia lakes, except that the range of values reported by Clair et al. (2002) included more lakes with pH < 5.0. In our sample of Nova Scotia lakes, there was a negative correlation between pH and DOC (Fig. 3). Because of this inter-correlation, we performed four separate statistical analyses to investigate the possible influence that each of these chemical parameters had on each measure of loon productivity. On the subset of lakes where both pH and lake area data were available, both measures of productivity (i.e., P_{s1} and P_{s2}) varied by year, but neither was

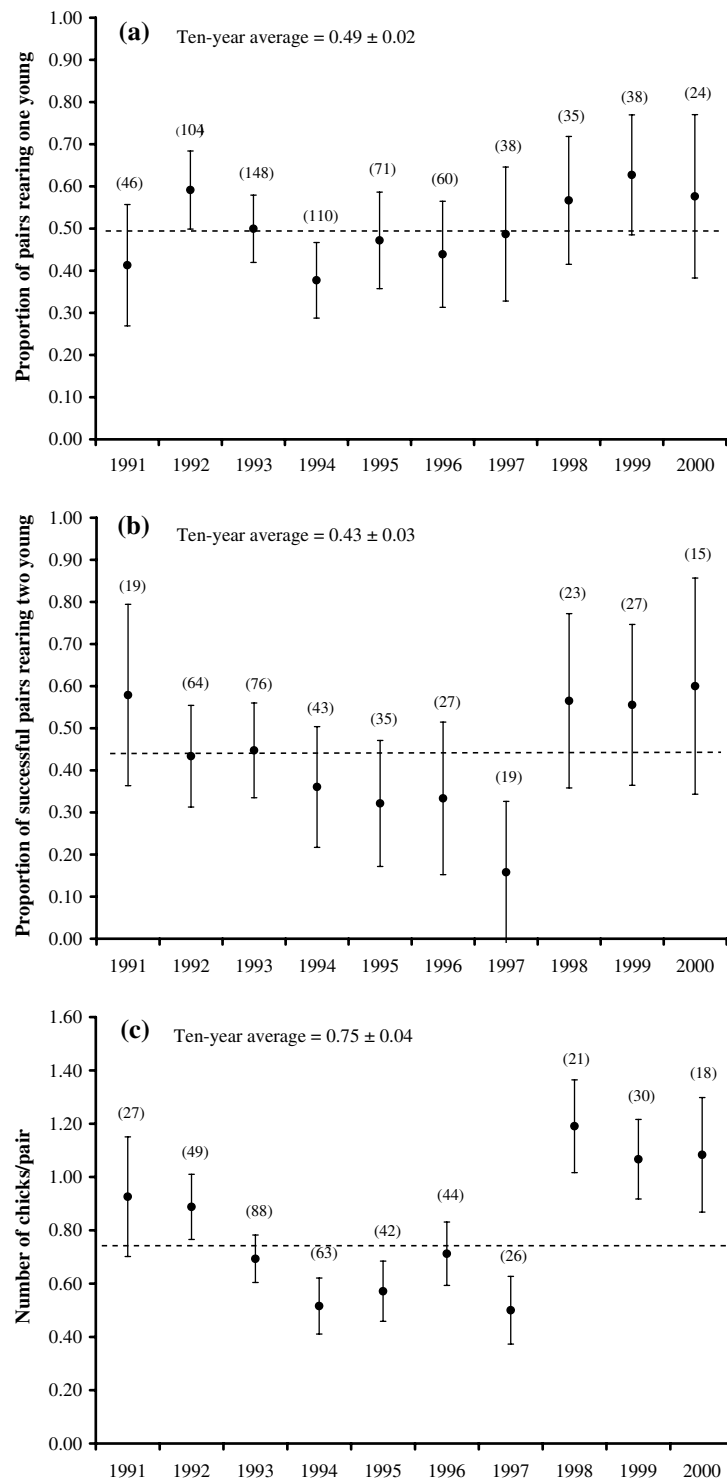


Figure 1. Temporal patterns in proportion of (a) resident pairs of common loons (*Gavia immer*) that raised at least one large chick to pre fledging age, (b) successful resident pairs that raised two large chicks to pre fledging age, and (c) number of chicks per resident pair on lakes. Sample sizes are shown in parentheses above bars and 95% confidence intervals. The dashed lines represent 10-year average values.

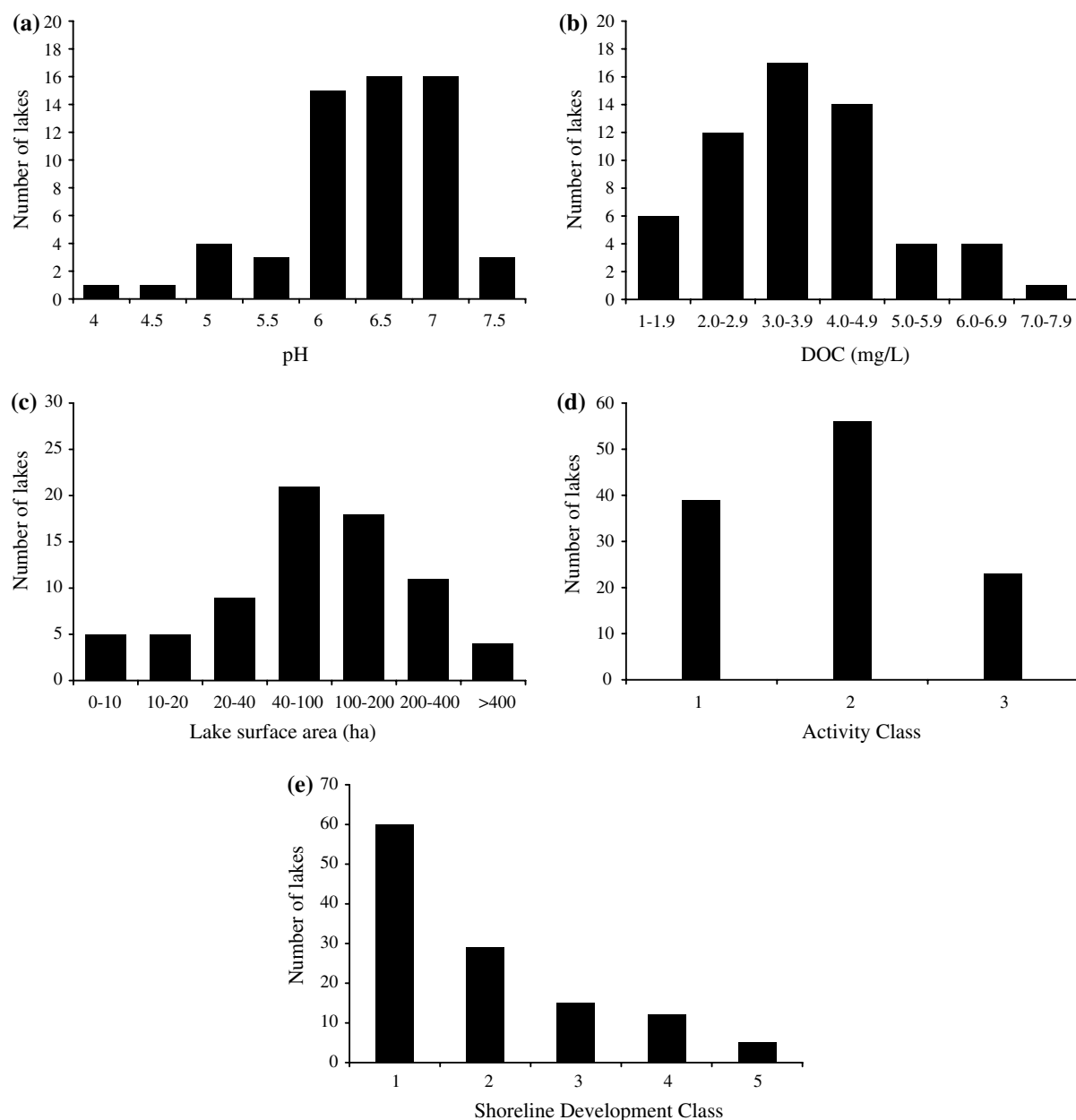


Figure 2. Frequency distributions for (a) lake acidity (pH), (b) dissolved organic carbon (DOC) concentration (mg/L), (c) lake surface area, (d) over-water human activity classes, and (e) relative shoreline development classes of lakes surveyed by the Canadian Lakes Loon Survey during 1991–2000 in Nova Scotia, Canada.

strongly correlated with lake area (Table 1). The probabilities of resident pairs rearing at least one large young, and successful pairs rearing two large young, tended to be lower on lakes of higher pH (Table 1).

DOC concentrations on CLLS lakes ranged from 1.6–7.9 mg/l (Fig. 2b). DOC concentrations

of CLLS lakes had a similar, but truncated, frequency distribution as compared to that shown for a larger sample of lakes in Nova Scotia (see Clair et al., 2002). For lakes where both DOC and lake area data were available, both measures of loon productivity tended not to vary by year or lake area (Table 1). When controlling for year and

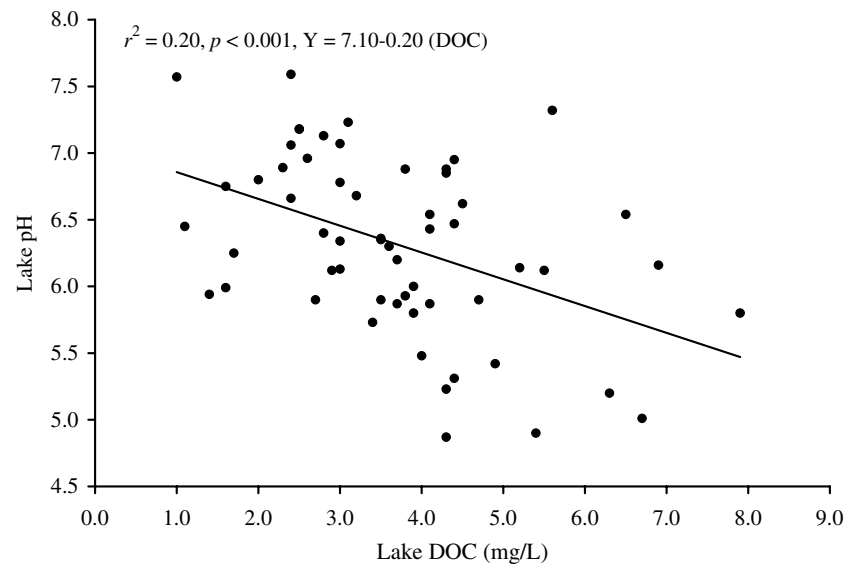


Figure 3. The relationship between lake acidity (pH) and dissolved organic carbon (DOC) data collected from 59 lakes surveyed by the Canadian Lakes Loon Survey in Nova Scotia from 1991 to 2000.

Table 1. Relationships between lake chemical and physical parameters and two indices of common loon (*Gavia immer*) productivity (P_{s1} and P_{s2}) on lakes during 1991–2000 in Nova Scotia, Canada

Response variable ^a	Explanatory variables	$\beta \pm SE^b$	<i>n</i>	<i>df</i>	χ^2	<i>p</i> ^c
P_{s1}	Year	–	59	9	19.11	0.02
	Lake area (ln)	-0.10 ± 0.21		1	0.20	0.66
	pH	-0.59 ± 0.21		1	4.87	0.03
P_{s2}	Year	–	47	9	15.89	0.08
	Lake area (ln)	$+0.19 \pm 0.18$		1	1.04	0.31
	pH	-0.37 ± 0.26		1	2.18	0.14
P_{s1}	Year	–	41	9	12.95	0.16
	Lake area (ln)	-0.01 ± 0.25		1	0.00	0.97
	DOC	$+0.36 \pm 0.26$		1	1.69	0.19
P_{s2}	Year	–	30	8	14.12	0.08
	Lake area (ln)	$+0.33 \pm 0.23$		1	1.47	0.23
	DOC	$+0.89 \pm 0.34$		1	4.70	0.03

^a P_{s1} = proportion of resident pairs rearing at least one large young; P_{s2} = proportion of successful pairs rearing two large young.

^bParameter estimates from Generalized Estimating Equations (GEE) shown as logit-transformed values. Year effects are not presented, as they were included only to account for annual variation.

^cBased on score statistics from Type III GEE analysis.

lake-area, we found the probability of resident pairs raising at least one large young was independent of DOC concentrations of lakes (Table 1). However, the probability that successful pairs reared two large young was positively correlated with DOC concentrations (Table 1).

Human activity/disturbance and shoreline development

The majority of CLLS lakes where chick success was monitored tended to have low to moderate levels of water-based human activity (as indexed

by water-based disturbance/boating) and relatively little shoreline development (0–20%) (Fig. 2d, e). Given this, our analyses showed that human activity on lakes had no measurable/detectable impact on either measure of loon productivity (Table 2). Two separate analyses where pH and DOC were included as additional explanatory variables also showed that probability of resident pairs rearing at least one young did not differ among lakes with differing activity classes (sample sizes were too low to evaluate effects on P_{s2}). Further, after accounting for both year and lake area, we found that probability of resident pairs rearing at least one large young and successful pairs rearing two large young did not differ among the five classes of shoreline development (Table 2). Again, we entered pH and DOC separately into models (which also included year and lake area) and found no measurable difference in the probability of resident pairs rearing at least one large young on lakes with different levels of shoreline development.

Discussion

Productivity was relatively high for adult loons breeding on lakes surveyed by the CLLS in Nova

Scotia from 1991–2000. For example, we found that about 49% of pairs were accompanied by at least one large young during late August and 43% of those pairs were able to raise two large young to pre fledging age. McIntyre (1994) has suggested that 0.50 chicks/territorial pair is needed to maintain common loon populations, which has been more recently supported by a value of 0.48 chicks/territorial pair derived from a loon population model developed by Evers (2004). Our 10-year (1991–2000) average estimate of 0.75 chicks/resident pair was consistent with loon populations being relatively stable on lakes surveyed by the CLLS. The range of annual productivity estimates we report for Nova Scotia lakes (0.50–1.19 chicks/resident pair) also were well within the range of values (0.07–1.40) reported in several other loon studies conducted in eastern North America (see McIntyre, 1988a; Clay & Clay, 1997; McIntyre & Barr, 1997), but were much higher than the 0.33 and 0.29 chicks per resident pair reported for several lakes in Kejimikujik National Park in Nova Scotia (see Kerekes et al., 1993, 1995). Estimates of chicks per residential pair are dependent on our volunteer's ability to detect all resident pairs and those with large young on lakes. If the detection of resident pairs is lower than that of pairs with large young,

Table 2. Relationships between human activity and shoreline development and two indices of common loon (*Gavia immer*) productivity (P_{s1} and P_{s2}) on lakes during 1991–2000 in Nova Scotia, Canada

Response variable ^a	Explanatory variables	$\beta \pm SE^b$	<i>n</i>	<i>df</i>	χ^2	<i>p</i> ^c
P_{s1}	Year	–	111	9	19.20	0.02
	Lake area (ln)	+0.04 ± 0.11		1	0.12	0.73
	Activity index	–		2	3.31	0.19
P_{s2}	Year	–	81	9	17.15	0.05
	Lake area (ln)	+0.1 ± 0.15		1	0.67	0.41
	Activity index	–		2	0.81	0.67
P_{s1}	Year	–	114	9	18.71	0.03
	Lake area (ln)	+0.14 ± 0.13		1	1.30	0.25
	Development	–		4	6.12	0.19
P_{s2}	Year	–	81	9	16.76	0.05
	Lake area (ln)	+0.08 ± 0.15		1	0.23	0.63
	Development	–		4	4.00	0.41

^a P_{s1} = proportion of resident pairs rearing at least one large young; P_{s2} = proportion of successful pairs rearing two large young.

^bParameter estimates from Generalized Estimating Equations (GEE) shown as logit-transformed values; year effects are not shown, as they were included only to account for annual variation.

^cBased on score statistics from Type III GEE analysis.

our productivity estimates would be biased high. This may occur at some of the very large lakes that volunteers surveyed in Nova Scotia and could be one reason why our productivity estimates were higher than those of other more intensive studies.

The lack of agreement between our productivity values and those reported by Kerekes et al. (1993, 1995) for lakes in Kejimikujik National Park may be due to the broader geographic representation of the CLLS. Monitoring productivity over a larger area naturally includes lakes with a much wider range of abiotic and biotic attributes that can influence loon productivity (Barr, 1986; McNicol et al., 1995; Scheuhammer et al., 1998; McNicol, 2002). The majority of the lakes in this study were circumneutral (see Fig. 2a), compared to the more acidic lakes in the Kejimikujik Park, which may partly explain our higher productivity estimates. Productivity estimates from each of these two subsets of Nova Scotia lakes (CLLS and Kejimikujik lakes) at least collectively show how variable loon productivity is within the province.

Despite some documented negative effects on loons associated with human induced disturbance/habitat alteration (McIntyre & Barr, 1997), our results showed no meaningful patterns in loon productivity attributable to intensity of human water-based disturbance or shoreline development (see also McIntyre, 1975; Titus & VanDruff, 1981; Caron & Robinson, 1994). It is possible that loons on CLLS lakes in Nova Scotia have habituated to human activities and habitat modifications or simply avoid areas on lakes that humans frequent (McIntyre, 1988a; Caron & Robinson, 1994). Our study did encompass a sizeable number of lakes that were surveyed over a relatively long period of time, but relatively few of them had "high" levels of disturbance and many had relatively undeveloped shorelines, which could have reduced our ability to detect differences in productivity among lakes with different activity and shoreline development indices. It is also possible that measures of human activity recorded by volunteers (e.g., documenting boat traffic in general on lakes) might not adequately quantify levels of disturbance (or capture important one-time events) close to nests during incubation and early brood rearing, two

periods that are critical in determining loon productivity (McIntyre, 1988a). Human disturbance likely has the greatest effect on loon productivity before young hatch from eggs (Robertson & Flood, 1980; Heimberger et al., 1983), but the CLLS currently does not intensively monitor fate of loon nests, only of hatched young.

Loons on some lakes may be at risk from human induced disturbance or habitat loss (Vermeer, 1973; Ream, 1976), but effects of environmental contaminants, including lake acidification and the associated uptake and bioaccumulation of methyl-mercury extend much farther into loon's breeding range (McIntyre, 1988a; McIntyre & Barr, 1997). Loon pairs typically return to the same lakes to breed each year and require large quantities of prey to feed their young (Barr, 1996; McIntyre & Barr, 1997), so reductions or changes in the forage base due to lake acidification can affect loon productivity (Alvo et al., 1988; Wayland & McNicol, 1990; McNicol et al., 1995).

In regional studies of loons in Ontario, productivity was lower on acidic lakes ($\text{pH} < 6.5$) as compared to lakes that were circumneutral ($\text{pH} 6.5\text{--}7.5$) or more alkaline ($\text{pH} > 7.5$) (Alvo et al., 1988; Wayland & McNicol, 1990; McNicol et al., 1995). Within our subset of Nova Scotia lakes, however, productivity of loons breeding on the more acidic lakes was not reduced as compared to those breeding on less acidic lakes (see also Parker, 1988). In fact, resident pairs had a higher probability of rearing at least one large young to age of fledging on lakes with relatively low pH; there also was a tendency for higher probability of success for rearing two large young on lakes of lower acidity. It must be noted that the majority of lakes surveyed by the CLLS volunteers in Nova Scotia were not highly acidic (e.g., $<10\%$ had $\text{pH} < 5.5$, mean $\text{pH} = 6.2$, see Fig. 2a) and tended to be ones that were accessible, popular for fishing or boating, and had permanent or seasonal residences. Such lakes also tend to have relatively clear water, near neutral pH, and likely healthy fish populations. Further, our findings regarding lake pH and loon productivity also may reflect (1) the relatively small number of lakes where loon productivity and pH were monitored; (2) our inability to control for other correlated or confounding variables that affect productivity (e.g., fish abundance, loon

predation rates, other lake chemistry variables, etc.); and (3) other potential weaknesses/biases of volunteer surveys (e.g., non-random sampling, sampling frequency, and ability to detect pairs and young, etc.) (McNicol et al., 1995). Thus, productivity patterns captured by CLLS are most representative of loons breeding on “recreational” lakes and are not necessarily representative of loon productivity, or its relation to environmental factors, over the entire range of these parameters for all lakes in Nova Scotia (e.g., lakes in Kejimikujik National Park).

Mercury content in lakes throughout Nova Scotia and other northeastern provinces and states are among the highest recorded in North America (Burgess et al., 1998a, b; Evers et al., 1998). Loon chicks exposed to relatively high levels of mercury may develop anomalous behavioural patterns that reduce time available for foraging, which ultimately affects fledging success (Nocera & Taylor, 1998). Relatively high concentrations of DOC, especially on acidic lakes, can reduce availability of mercury to fish, and thus to loons, by binding with mercury on a molecular level (Driscoll et al., 1995; Choi et al., 1998; Rencz et al., 2003). The increased productivity (i.e., two fledged chicks) we observed for loons on lakes with relatively high DOC was at least consistent with the possibility that DOC reduced the incorporation of mercury into these food webs and thus reduced maladaptive behaviour in chicks and enhanced their survival.

In summary, lakes in Nova Scotia monitored by the CLLS generally had relatively high loon productivity and no reductions attributable to human activities, or increased acidity of breeding lakes. Our results, however, should not be interpreted to mean lake acidification (and its facilitative effect on mercury uptake) does not currently threaten loons in Nova Scotia because some lakes in this province have some of the lowest surface water pH values measured in North America (Kerekes et al., 1982). Several of the areas that contain some of the more acidic lakes in Nova Scotia are also of concern for mercury contamination (Evers et al., 1998) and show little recovery from effects of reduced sulphur dioxide deposition (Clair et al., 2002). Monitoring loon productivity, abundance, and distribution and its relation to pH, DOC, and other important limnological

factors should continue as part of longer-term, loon/lake monitoring programs aimed at evaluating recovery of acidified lakes. Efforts need to be made to encourage volunteers to consistently survey lakes annually and include more lakes in the lower pH range throughout the province, possibly by employing a stratification strategy for sampling. Doing so will improve long-term monitoring of loon productivity and provide a more sensitive biomonitoring tool for lakes in Nova Scotia and other regions of Canada.

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A landscape-scale model of yellow-billed loon (*Gavia adamsii*) habitat preferences in northern Alaska

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Abstract

We modeled yellow-billed loon (*Gavia adamsii*) habitat preferences in a 23,500 km² area of northern Alaska using intensive aerial surveys and landscape-scale habitat descriptors. Of the 757 lakes censused, yellow-billed loons occupied 15% and Pacific loons (*G. pacifica*) 42%. Lake area, depth, proportion of shoreline in aquatic vegetation, shoreline complexity, hydrological connectivity (stream present within 100 m or absent), and an area–connectivity interaction were positive, significant predictors of yellow-billed loon presence in a multivariate logistic regression model, but distance to nearest river or Beaufort Sea coast were not. Predicted yellow-billed loon presence was 13 and 4.7 times more likely on deep and medium lakes, respectively, than on shallow lakes that freeze to the bottom. On small lakes (<60 ha), predicted yellow-billed loon presence was 4.8–1.7 times more likely on lakes with hydrological connectivity than without, but connectivity was not important at most lake sizes (65–750 ha). Yellow-billed loon broods depend on fish available in the brood-rearing lake, and we suggest that a dependable supply of fish is more likely in larger lakes, those deep enough to have open water under winter ice, and those near streams. Highly convoluted shorelines and those with aquatic vegetation provide loon nesting and brood-rearing sites, as well as fish habitat. Pacific loon absence was a significant, positive predictor when added to the habitat model, indicating that yellow-billed loons were four times more likely on lakes without Pacific loons.

Introduction

Characteristics of lakes used by loons have been described at several sites, but little has been done to describe habitat preferences across large geographic areas. On the Colville River Delta in northern Alaska, yellow-billed loons, *Gavia adamsii* (Gray), typically rear broods on lakes >13.4 ha that have fish, avoid lakes with fluctuating water levels and high turbidity, and nest on low-lying shorelines (North & Ryan, 1989). At more southerly latitudes, lakes used by the closely related common loon, *G. immer* (Brünnich),

compared to unused lakes, were typically larger, deeper, clearer, more oligotrophic, had higher proportion of low-relief shoreline (i.e., <25 cm in height), more fish, more shoreline emergent vegetation, and were more often hydrologically connected by streams (Blair, 1992; Ruggles, 1994). While local studies provide detailed insights into habitat selection, landscape studies provide inferences to vast areas and may elucidate processes obscured at the local scale (Johnson, 1980; Morris, 1987). Yellow-billed loon habitat relationships are well suited to landscape-scale analyses because this species is readily sighted during aerial surveys, and

large lakes, which are the spatial units of ecological relevance to yellow-billed loons, are easily discernable in satellite imagery.

It is becoming increasingly important to understand yellow-billed loon habitat preferences across northern Alaska as oil and gas development proceeds in the National Petroleum Reserve – Alaska (NPR-A) (BLM, 1998a, 2004) where approximately 91% of Alaska's yellow-billed loons reside (Earnst et al., 2005). Yellow-billed loons are patchily distributed and rare in northern Alaska (~3300 individuals) and world-wide (~16,000 individuals) (Earnst, 2004; Earnst et al., 2005), and are a Bird of Conservation Concern to the United States Fish and Wildlife Service (USFWS, 2002). In this study, we examined yellow-billed loon habitat preferences at the landscape scale with a combination of intensive aerial surveys across a large area and existing Geographical Information Systems (GIS) databases of seven habitat parameters thought to be important to loons (e.g., North & Ryan, 1989; Blair, 1992; Ruggles, 1994). Specifically, we used logistic regression to model yellow-billed loon presence in relation to lake size, lake depth, proportion of the shoreline in emergent vegetation, shoreline complexity, hydrological connectivity, distance to river, and distance to the Beaufort Sea coastline.

Study area

The study area was the 23,500 km² between the Colville River and Meade River, from the Beaufort Sea coast to approximately 100 km inland (~70 degrees latitude) on the west-central North Slope of Alaska (Fig. 1). Approximately 69% of the yellow-billed loon sightings on systematic USFWS surveys flown across the species' entire range in northern Alaska during 1992–2003 occurred in the study area (surveys described in Mallek et al., 2004).

Surface water dominates the landscape – 27% of the study area's surface is water and an additional 20% is aquatic or flooded vegetation (based on USDI, 1995). Approximately 83% of the 22,885 lakes within the study area are shallow (<1.6 m); 16% are of medium depth (1.6–4 m) and 2% are deep (>4 m) (based on Mellor, 1987). Shallow lakes are defined as those that typically freeze to the bottom during winters on the North Slope (Mellor, 1987; Jeffries et al., 1996), and thus do not support over-wintering populations of fish. Published studies of lake limnology and fish presence in northern Alaska are lacking, but winter kill (and thus lake depth) may be the most important factor determining fish presence in arctic lakes. In addition, some lakes that might not otherwise

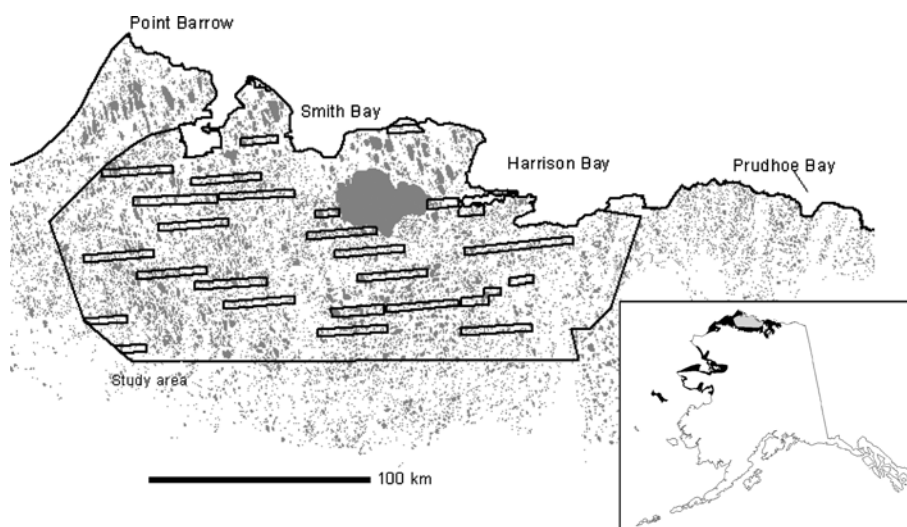


Figure 1. Location of the plots and study area in northern Alaska (lakes are gray). Inset map shows the range of the yellow-billed loon (black) and the study area (gray).

support over-wintering fish are flooded by nearby rivers or connected to other lakes by small streams. Ninespine sticklebacks, *Pungitius pungitius* (Civier), and least ciscos, *Coregonus sardinella* (Valenciennes), are thought to be the primary food of yellow-billed loon adults and chicks on brood-rearing lakes at one field site on the North Slope, the Colville River Delta (Earnst, 2004). Alaska blackfish, *Dallia pectoralis* (Bean), and fourhorn sculpin, *Myoxocephalus quadricornis* (Berg), isopods, and amphipods are also available in breeding lakes and probably utilized to some extent (North, 1994).

Most lakes on the North Slope are freshwater thaw lakes oriented perpendicular to the prevailing northeast winds (Carson & Hussey, 1962), but basins near floodplains reflect shaping by historic and active river channels. Semi-saline lakes are present near the Arctic Ocean, especially in river deltas, where basins may be periodically inundated by autumn storm surges and spring flooding. In addition to lakes, fields of small (typically <1 ha) polygonal ponds, formed by the seasonal thawing and freezing of the upper permafrost layer, are common.

Methods

Aerial surveys

Twenty-one plots, each 32×3.2 km, were placed approximately systematically throughout the area (Fig. 1). The first six plots, surveyed in 1998, were placed in the center of the south-central, north-eastern and northwestern thirds of the study area; the remaining 15 plots, surveyed in 1999–2000, were distributed at equal intervals along systematically placed east–west transects used in ongoing USFWS surveys.

Prior to surveys, we identified each lake that had its centroid (i.e., geometric center) within the plot boundary and was greater than 10 ha in size, as portrayed on standard 1:63,360 topographic quadrangles. The size threshold was set just below the smallest known brood-rearing lake (13 ha) on the Colville River Delta (North & Ryan, 1989). We censused all lakes within each plot exceeding the 10 ha threshold. During surveys, a pilot-observer and passenger-observer circled the shoreline

of each designated lake and plotted locations of yellow-billed loon and Pacific loon pairs, singles, flocks, and nests. Surveys were flown at 65 m altitude in a Cessna 206 fixed-wing aircraft and were conducted during late June to August, a period which encompassed late incubation (nine plots) to mid-brood-rearing (12 plots).

Habitat parameters

The landscape-scale parameters investigated were (a) lake area; (b) maximum lake depth, classified as shallow (<1.6 m), medium (1.6–4 m), or deep (>4.0 m); (c) proportion of the shoreline in aquatic vegetation; (d) an index of shoreline complexity; (e) hydrological connectivity, classified as connected if the lake's perimeter was within 100 m of a stream; (f) distance from the lake's centroid to a river and (g) distance from the lake's centroid to the coast of the Beaufort Sea.

Lake area, perimeter, and location of rivers and streams were obtained from digital line graphics of USGS topographic quadrangles. Rivers were defined as those coded 605 and 606 (left and right banks) and streams as those coded 412. Inconsistencies in lake area between paper-copy topographic maps (used to select lakes) and digital line graphics (used for analyses) resulted in the analysis including 107 lakes <10 ha. A few of those inconsistencies arose because lake area was approximated during lake selection. However, most inconsistencies arose because a wetland appeared as one large lake on the paper map, but on the digital map appeared as multiple smaller lakes with varying degrees of hydrological connectivity to one another. We chose to retain all lakes in the original analysis to avoid any potential bias associated with a post hoc change to our sampling design, and because we had no a priori basis for choosing either the paper or digital map as most closely matching “actual” lake size or loon use. As a post hoc analysis, we removed all lakes <10 ha and re-evaluated the final model.

Maximum lake depth categories were taken from Mellor (1987) who used side-looking airborne radar which has different reflectance from lakes that are frozen entirely to the bottom (<1.6 m), those with some open water beneath ice (1.6–4.0 m), and those with substantial water beneath ice (>4 m). Recent evidence suggests that

maximum over-winter ice depth is 2.2 m rather than 1.6 m (Jeffries et al., 1996). In this study, shallow lakes are defined as those freezing entirely to the bottom (as determined by airborne radar), regardless of exact depth.

Proportion of the shoreline in aquatic vegetation was defined as the proportion of a 100 m buffer around the lake comprised of cover types coded as aquatic or flooded vegetation. This category was obtained by pooling the four USDI (1995) categories having >25% water: aquatic *Carex aquatilis* (Wahalenb.) (50–80% water), aquatic *Arctophila fulva* (Trin.) (50–80% water), flooded low-center polygons (25–50% water), and flooded non-patterned ground (25–50% water).

The index to shoreline complexity was calculated as the ratio of the lake's perimeter (in km) to the perimeter of a circle of equal area (in km²). This provided a unitless index with a minimum of 1, which is equivalent to the shoreline complexity of a circle.

Statistical analyses

Multiple logistic regression is often used in habitat modeling when presence/absence is known with some certainty (see reviews in Millspaugh & Marzluff, 2001; Manly et al., 2002), as is true with our method of intensive lake-circling. Because we used two-stage sampling, rather than choosing lakes at random, lakes within plots are not statistically independent. Thus, we used the GLIMMIX macro in SAS, with a logit link, to apply a generalized linear mixed-effects model. This method treats the plot as a random effect and accounts for the covariance between lakes within a plot (Littell et al., 1996). We used the default covariance structure of GLIMMIX, which models a constant, but non-zero, covariance between lakes. Model deviance, which is defined as the difference between quasi-likelihood for the saturated model and quasi-likelihood under the fitted model, is used to assess goodness-of-fit and compare models. Another goodness-of-fit indicator is the overdispersion scale, which approximates 1.0 if the assumed binomial distribution fits that of the data. The difference between the deviance of two models is distributed as a χ^2 statistic with degrees-of-freedom equal to the difference in the degrees-of-freedom of the two models, with statistical

non-significance implying the models explain the data equally well.

Model selection followed Hosmer & Lemeshow (2000). Each potential predictor variable was first examined for normality, a linear relationship to yellow-billed loon presence, and strength as a univariate predictor of loon presence in a generalized mixed-effects model. Only predictors significant at $p < 0.25$ were considered further. The most appropriate multivariate model was selected by including all potential main effects in a full model, removing predictors with non-significant coefficients ($p > 0.05$) one at a time, and then comparing the deviance of the reduced model to that of the previous model. These steps were discontinued when all predictors had significant coefficients. Each one-way interaction term was then added to the model, and retained if its coefficient was significant and if the resulting model significantly reduced the deviance compared to the main effects model.

We used odds ratio to examine the magnitude of the effect of a predictor variable, at fixed values of other variables, on the probability of seeing a yellow-billed loon. The odds ratio represents the change in odds of seeing a loon for a unit change in the predictor variable. The odds ratio of a predictor is calculated as $e^{(b \cdot \text{unit change})}$, where b is the parameter's coefficient in the multivariate model, and the test of whether $b > 0$ is equivalent to testing whether the confidence interval of the odds ratio crosses 1.0.

Results

Of the 757 lakes surveyed, 115 (15%) were occupied by yellow-billed loons (211 total individuals) and 321 (42%) were occupied by Pacific Loons (935 total individuals). Of the 115 lakes occupied by yellow-billed loons, 22% were shared with Pacific loons.

Lake size ranged from 1.1 to 1933 ha in the sample of lakes surveyed, but 54% were <35 ha and 92% were <200 ha. We used the natural log of lake area (hereafter lnarea) in analyses to make the distribution more normal and improve linearity with yellow-billed loon presence. Most lake depths were shallow (40%) or medium (52%), only 8% were deep. Streams occurred within 100 m of

39% of the lakes. Mean shoreline complexity was $1.43 (\pm 0.02 \text{ SE})$, which can be interpreted as 43% more complex than a circle, and mean proportion of shoreline in aquatic vegetation was $0.43 (\pm 0.007 \text{ SE})$.

The proportion of lakes with yellow-billed loons present increased with increasing lake size, depth, proportion of shoreline in aquatic vegetation, shoreline complexity, and connectivity

(Figs. 2, 3, and 4). Each of these parameters was a positive, significant predictor of yellow-billed loon presence in the final multivariate model (Tables 1 and 2). Distance to river was not a useful univariate predictor ($b = -0.007 \pm 0.03$, $p = 0.83$) and was not considered further. Distance to coast was a negative, univariate predictor ($b = -0.01 \pm 0.008$, $p = 0.06$), but was not significant in a multivariate model ($b = -0.008 \pm 0.008$, $p = 0.34$, Model 2). Of

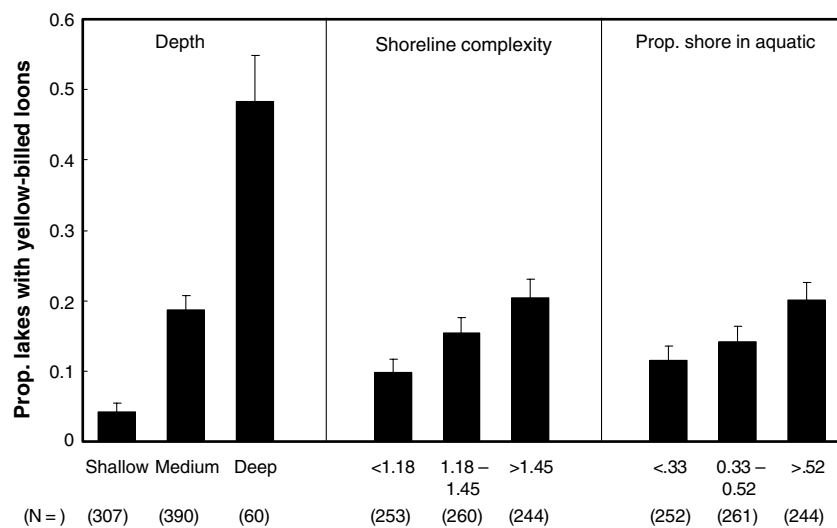


Figure 2. Proportion of lakes with yellow-billed loons present by depth, shoreline complexity, and proportion of shoreline in aquatic vegetation. Shoreline complexity and aquatic vegetation were modeled as continuous variables but are shown as categories for ease of presentation. Each of the three categories comprises approximately one-third of the 757 surveyed lakes.

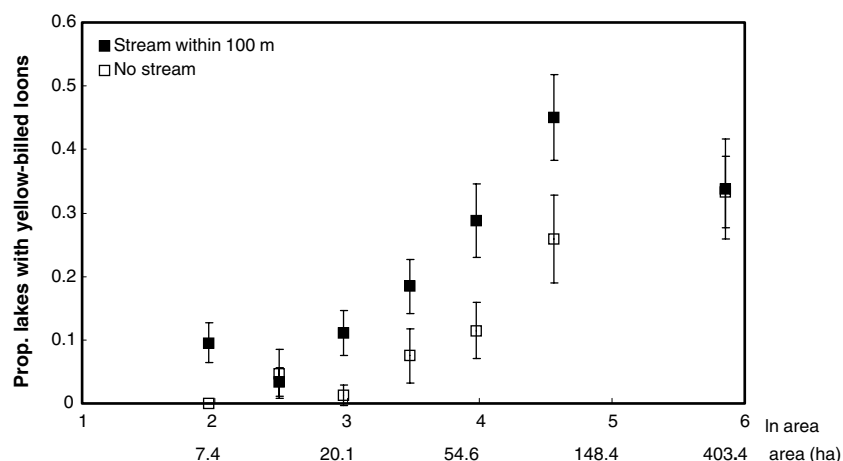


Figure 3. Proportion ($\pm 1 \text{ SE}$) of yellow-billed loons by lake area for lakes with streams within 100 m and those without. Lake area was modeled as a continuous variable but shown in categories for ease of presentation, with data plotted at the category mean. Number of lakes with and without streams, respectively, for the six lake area categories were ≤ 10 ha (86, 21), 10–15 ha (65, 30), 15.1–25 ha (78, 45), 25.1–40 ha (80, 38), 40.1–70 ha (61, 52), 70.1–130 ha (54, 40), and >130 ha (36, 71).

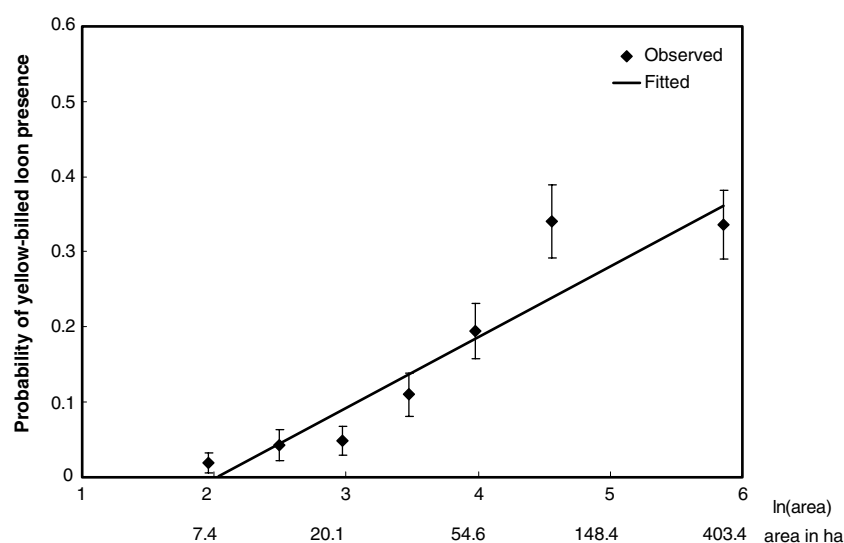


Figure 4. Observed and fitted values for probability of yellow-billed loon presence by lake size categories. Fitted values are calculated from the regression equation using the lake-specific characteristics and averaged within lake size categories. Lake area categories are described in Figure 3 legend.

Table 1. Comparison of the initial main effects model (Model 1) to models with distance to coast and the connectivity*area interaction

Model ^a	Deviance	Deviance difference	Df difference	<i>p</i>
(1) LnArea + Depth + ShComp + PrAq + Con	475.3	–	–	–
(2) LnArea + Depth + ShComp + PrAq + Con + DisCst	474.2	1.1	1	0.59
(3) LnArea + Depth + ShComp + PrAq + Con + Con*LnArea	469.6	5.7	1	0.015

The deviance difference is distributed as a χ^2 statistic with degrees-of-freedom (df) equal to the difference between models in degrees-of-freedom (in this case, always 1). Of all possible one-way interactions (not shown), only the addition of the connectivity–area interaction reduced the deviance significantly, thus Model 3 is the final model.^aAbbreviations used: natural logarithm of lake area (LnArea); shoreline complexity (ShComp); proportion of shoreline in aquatic vegetation (PrAq); and hydrological connectivity (Con).

Table 2. Logistic regression coefficients, using plot as a random variable in a mixed-effects model, of habitat parameters predicting yellow-billed loon presence on 757 lakes in northern Alaska

Parameter	Coefficient (<i>b</i>)	SE	<i>p</i> -value
Lake area	1.01	0.21	<0.0001
Depth 3 (deep vs. shallow)	2.58	0.50	<0.0001
Depth 2 (med. vs. shallow)	1.54	0.37	<0.0001
Prop. shore in aquatic veg.	3.23	0.85	0.0001
Shoreline complexity	0.58	0.27	0.034
Connectivity	3.52	1.07	0.001
Connectivity * LnArea	–0.73	0.25	0.003

Positive coefficients indicate a positive relationship with yellow-billed loon presence. See Table 3 for further interpretation.

the one-way interaction terms, only the lnarea* connectivity interaction was a significant predictor (Table 2) and reduced model deviance significantly (Table 1). Thus, the final model contained

five main effects and one interaction term. The final model did not exhibit significant lack-of-fit ($\chi^2_1 = 0.63$, $p = 0.86$) and the estimated overdispersion ($\hat{c} = 1.14$) was near 1. Observed and

fitted probabilities of yellow-billed loon presence are plotted against lake area in Figure 4, where fitted values are obtained for each lake in the sample by inserting the lake's characteristics into the regression equation.

Lake depth, area, and connectivity had the largest effect on yellow-billed loon presence as indicated by their large odds ratios (Table 3). Yellow-billed loon presence was 13.2 and 4.7 times more likely on deep and medium lakes, respectively, than on shallow lakes, and 2.8 times more likely on deep lakes than medium lakes. The negative $\ln\text{area} \times \text{connectivity}$ interaction indicated that connectivity was more important at small lake sizes than at large sizes, and this was apparent in the sample data (Fig. 3). On small lakes (<60 ha), predicted yellow-billed loon presence on lakes with connectivity was 4.8–1.7 times more likely than on unconnected lakes (Table 3). Over most lake sizes (65–750 ha), stream presence did not significantly affect the predicted probability of loon presence

Table 3. Odds ratios of habitat parameters predicting yellow-billed loon presence on 757 lakes in northern Alaska

Parameter	Unit change	Odds	95% confidence limits	
			Upper	Lower
Area	10 ha	10.3*	3.9	27.0
Depth	Deep vs. shallow	13.2*	4.9	35.5
	Med. vs. shallow	4.7*	2.3	9.7
	Deep vs. med.	2.8*	1.4	5.8
Prop. shore in aqu. veg.	0.20	1.9*	1.4	2.7
Shoreline complexity	0.20	1.1*	1.0	1.2
Connectivity +	At 15 ha	4.8*	2.0	11.5
Connectivity-x-area	At 60 ha	1.7*	1.05	2.9
	At 65 ha	1.64	0.99	2.7
	At 750 ha	0.28	0.08	1.001
	At 800 ha	0.27*	0.07	0.99

The odds ratio for a given unit change in parameter equals $e^{(b \times \text{unit change})}$, where b is the parameter's coefficient in the multivariate model, and the test of whether $b > 0$ is equivalent to testing whether the confidence interval of the odds ratio crosses 1.0. Because of the connectivity–area interaction, odds ratios for connectivity are only interpretable in relation to a given lake area. The * indicates odds ratios significantly different from 1.

(i.e., the odds ratio did not differ from 1). On very large lakes (>800 ha), predicted yellow-billed loon presence was less likely on connected than unconnected lakes, but this should be interpreted with caution since only eight of the sampled lakes were >800 ha. On lakes without streams, yellow-billed loon presence was 10 times more likely for each 10 ha increase in lake size.

Predicted yellow-billed loon presence was only 1.9 and 1.1 times greater, respectively, for each 0.20 increase in proportion of shoreline in aquatic vegetation or 0.20 increase in shoreline complexity (an 0.20 change from the median in each of these variables was approximately equivalent to the first and third quartiles) (Table 2).

Inconsistencies between paper-copy maps used to select lakes and digital maps used for analyses resulted in the analysis including 107 lakes <10 ha (see Methods). To examine the effect of these small lakes, we removed all lakes <10 ha and re-evaluated the final model chosen above ($\ln\text{area} + \text{depth} + \text{shoreline complexity} + \text{proportion aquatic} + \text{connectivity} + \ln\text{area} \times \text{connectivity}$). Results were similar with all coefficients remaining significant at $p < 0.05$.

Pacific loon absence was a significant predictor of yellow-billed loon presence, whether used alone or added in combination with habitat variables in the final model ($b = 1.39 \pm 0.29$, $p < 0.0001$). When Pacific loon absence was added to the multivariate model, coefficients of habitat parameters remained significant, and the odds ratio indicated that yellow-billed loons were four times more likely when Pacific loons were absent.

Discussion

Yellow-billed loons feed chicks fish from the brood-rearing lake; adults do not bring fish in from elsewhere (North, 1994). Thus, fish availability is a critical factor in choice of a breeding territory. Many of the significant landscape-scale predictors in our model can be interpreted as indicating the probability of fish presence. For example, lake area and depth largely dictate the volume of ice-free water available to overwintering fish. The predicted probability of yellow-billed loon presence increased with lake size and was 13 and 4.7 times greater on deep and medium

lakes than on shallow lakes that freeze to the bottom during winter. Likewise, at small lake sizes, yellow-billed loon presence was more likely on lakes with streams nearby than those without. We interpret stream presence as a measure of hydrological connectivity to rivers and other lakes. Such connectivity may facilitate the re-supply of fish to lakes that do not support over-wintering or otherwise self-sustaining populations, but be less important for large lakes that are more conducive to self-sustaining fish populations. Lake depth, size, and hydrological connectivity also are related to the presence of common loons (Blair, 1992; Ruggles, 1994), a closely related species that also feeds chicks solely on fish from the brood-rearing waterbody (McIntyre & Barr, 1997).

Shorelines with aquatic vegetation, as defined by the Landsat imagery used here, probably include those with patches of emergent vegetation suitable for foraging, those with wet or shallowly flooded land suitable for nesting, and those having a fine-scale (relative to 30-m pixel) interspersion of land and water such as might be produced by nearshore islands or narrow peninsulas. This broad interpretation is necessary because it is difficult to interpret satellite signatures at the land-water interface, and emergent vegetation often grows in narrow patches that are missed at this resolution. Thus, we simply interpret shorelines with aquatic vegetation as being generally low-lying and more suitable for foraging or nesting than other shorelines. Common loon pairs also were more likely on lakes with low-lying shoreline (<25 cm in height) and emergent vegetation as determined from ground-based measurements (Ruggles, 1994).

The shoreline complexity index was calculated from hydrological maps and is thus indicative of embayments at the scale of several hectares. Lakes with complex shorelines typically had large bays or shapes suggestive of multiple waterbodies that had merged into one. Yellow-billed loons use bays and other protected shorelines for nesting and brood-rearing (North, 1994; see also McIntyre, 1983). Complex shorelines also provide visual isolation between potential nesting or brood-rearing sites, and thus promote lake use by multiple pairs, including the sharing of lakes by Pacific loons and yellow-billed loons.

Distance to river and distance to coast were not significant predictors of yellow-billed loon presence in this study. The negative, univariate relationship between yellow-billed loon presence and distance to coast did not persist in multivariate models, and may indicate that lakes near the coast were less suitable in other measures, such as depth or connectivity. Distance to river was expected to be important because (a) rivers are used by adults for foraging, (b) lakes near rivers may be more likely to have fish because of historic or periodic flooding, (c) rivers facilitate early spring occupation of nearby territorial lakes (North, 1994), and (d) several yellow-billed loon concentration areas are near major rivers such as the Meade, Ikpik-puk, Chip, and Colville (see map in Earnst et al., 2005). In preliminary analyses of aerial surveys on the North Slope, McIntyre (1991) found that yellow-billed loon presence was significantly related to distance to river in some areas but not others. Our analysis of distance to rivers and coast was largely limited by the number of plots in our study, and the lack of variation in distance to coast or river among lakes within a plot. A recently completed aerial survey using the lake-circling method over a larger sample of lakes (>1000 lakes in 61 plots) throughout the species' range on the North Slope will allow refinement of the model presented here.

The inverse relationship between Pacific loon presence and yellow-billed loon presence may arise from opposite habitat preferences, from some degree of resource competition and competitive exclusion, or both. Presumably fish availability is less critical to the Pacific loon which is able to rear young on a combination of invertebrates and fish brought in from elsewhere when necessary (Bergman & Derksen, 1977). The larger yellow-billed loon is usually behaviorally dominant and able to expel Pacific loons from its territory, sometimes with intense fighting (pers. obs.). On the other hand, Pacific loon pairs on established territories are able to exclude single yellow-billed loons (North, 1994). We suspect that the presence of Pacific loons, especially multiple pairs, may reduce lake suitability and affect yellow-billed loon habitat selection and distribution among lakes. This inter-specific interaction is worthy of further investigation.

In our study, and others of bird–habitat relationships at the landscape scale, model performance is limited by the detail of data available for large areas (e.g., Karl et al., 2000). For example, more precise measures of the free-water volume available to over-wintering fish would be valuable and perhaps feasible with synthetic aperture radar methodology (Kozlenko & Jeffries, 2000). Similarly, higher resolution land cover data might more precisely identify emergent vegetation, low-lying shorelines, protected bays, islands and peninsulas, and hydrologically connected lakes with stable as opposed to fluctuating water levels (the latter being unfavorable for loons; North & Ryan, 1989). Much could be learned from a landscape-scale fish–habitat relationship model, produced by combining GIS-based lake characteristics with ground-based sampling of pH, water clarity, nutrient availability, and fish abundance.

Management implications

The small population size of yellow-billed loons in northern Alaska and world-wide (Earnst, 2004; Earnst et al., 2005), and their specific habitat requirements, has raised concern about oil and gas development in the NPR-A (e.g., Schoen & Senner, 2002). Results of this study, and other ongoing surveys, could be used to predict yellow-billed loon presence on specific lakes, or to identify regions of particular importance to yellow-billed loons, and thus guide development accordingly.

A specific example of the use of our data involves the definition of deep lakes. In an attempt to protect over-wintering fish habitat (which would simultaneously protect yellow-billed loon habitat), special stipulations were developed to minimize impacts to “deep” lakes (defined as >2 m) in the NPR-A (BLM, 1998a, 1998b). In a more recent planning document, the definition of “deep” lake has been changed to >4 m (BLM, 2004, 2005). In our study, yellow-billed loons preferred both lakes 2–4 m and those >4 m over shallow lakes (corresponding to our medium and deep categories, respectively), but because the latter are quite rare on the North Slope, 64% of yellow-billed loon sightings were on lakes 2–4 m and only 27% were on lakes >4 m. This suggests that many more yellow-billed loons could

potentially benefit from the original definition of “deep” lakes as those >2 m.

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Testing hypotheses of social gatherings of common loons (*Gavia immer*)

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Abstract

Three hypotheses are tested to explain the function of common loon social gatherings: Cooperative Foraging, Familiarity, and Reconnaissance. From 1993 to 1999, I studied social gatherings through behavioral observations in Michigan, Wisconsin and Maine. There was no or little evidence for the Cooperative Foraging Hypothesis. Partial or indirect evidence for the Familiarity Hypothesis included the following: (1) Social gatherings lasted both longer and occurred more frequently later in the breeding season (2) Approximately 25% of all the social gatherings observed occurred on neutral territories, and (3) Social gatherings consisted of the same individuals on consecutive days. Predictions from the Reconnaissance Hypothesis were also supported in that a large proportion of individuals participating in social gatherings were non-breeders and that the number of social gatherings observed were not equally distributed across loon territories, but instead increased on territories that had recently undergone a divorce. No one hypothesis was adequate to explain social gatherings and more observations on uniquely marked individuals are needed to further substantiate these initial findings.

Introduction

Common loons, *Gavia immer*, are highly aggressive following their return to their breeding territories in late April through early June (depending on latitude) and attack both conspecifics and most other waterbirds. However, by mid-July many populations begin to join in short-term aggregations of three to 15 individuals (occasionally more). This social behavior is in stark contrast to the previous highly territorial and aggressive behavior exhibited one or two months prior. These aggregations have been called social gatherings (McIntyre, 1988) and although they appear to play an important role in the life history of loons there remains much speculation about their function. Previous researchers have suggested that they may form for the benefit of cooperative foraging (Cooperative Foraging Hypothesis: Rand, 1948; Olson, 1951; Nero, 1963, 1974), may function to

reinforce cooperation among adults prior to migration (Familiarity Hypothesis: McIntyre, 1988), or may be composed of individuals searching for new or unoccupied territories (Reconnaissance Hypothesis: Piper et al., 1997). These hypotheses may not necessarily be mutually exclusive. The primary difficulty facing researchers addressing this question is that the relationship of participants in social gatherings is unknown (McIntyre & Barr, 1997). Loons are monomorphic, and although males are on average 28% heavier than females (Evers, 2001, 2004), this size difference is detectable only under certain conditions. Unless an entire population is banded, it is difficult to know the sex, breeding status, and relationships among the individuals in the social gatherings in order to differentiate and test the proposed hypotheses.

There is some confusion in the literature regarding the term “social gathering.” According

to McIntyre (1988), social gatherings have distinct "ritualized and stereotyped" components (e.g., circle swimming and jerk-diving, line swimming, facing away, bill dipping, etc.) and occur later in the breeding season (e.g., beginning in mid-July). Loons do flock in late spring and late summer/early fall and these aggregations are often confused with social gatherings, but they lack distinct ritualized and stereotyped behaviors. Also, encounters between residents and territorial intruders during late spring/early summer typically display ritualized components, but these encounters are mostly intrusions of a single individual and should not be classified as a social gathering.

The objectives of the study were to study social gatherings and evaluate the three hypotheses proposed for their occurrence. Specific predictions made from each hypothesis were tested. Predictions derived from the Cooperative Foraging Hypothesis include the following: (1) Loons should spend a significant proportion of time underwater during social gatherings; (2) Loons should be diving synchronously if they are foraging, as seen in Double-crested Cormorants; (3) Loons should be facing the same direction when in groups; (4) Loons should periodically surface with prey; and (5) When loons surface after diving, they should be spatially distributed as they were when they dove. The following predictions were derived from the Familiarity Hypothesis: (1) Loons should exhibit low levels of aggression when in social groups; (2) Social gatherings should occur more frequently later in the breeding season; (3) Social gatherings should be longer later in the breeding season; (4) Social gatherings should occur at neutral sites; and (5) Social gatherings should consist of the same individuals on consecutive days. Predictions from the Reconnaissance Hypothesis include that a large proportion of individuals participating in social gatherings should be non-breeders and that social gatherings should not be randomly distributed across loon territories, but occur more frequently on territories that may not be as vigorously defended (e.g., recently undergone a divorce) or are more productive (e.g., presence of chicks). This study is unique in that the majority of individuals in two breeding populations were uniquely marked and studied for several years.

Study site

Loons were studied (1993, 1994, 1997–1999) at Seney National Wildlife Refuge (Seney NWR), Michigan and Turtle Flambeau Flowage (TFF), Wisconsin (1995–1997). Videotaping of loon social gatherings occurred at TFF in 1996 and 1997 and also at Aziscohos Lake, Maine, 1998.

Seney NWR (45° N, 86° W) is located in the eastern Upper Peninsula of Michigan. It contains 21 artificially controlled, shallow pools, generally 1 m deep, but up to 3 m deep along the dikes. The refuge is divided into 3 management units, but the majority of established loon pairs reside in Unit 1 (50–60%). I restricted the investigation of loon social gatherings to Unit 1 pools because loon territories were highly aggregated and easily accessible, unlike loon territories in Units 2 and 3, which were spaced considerably further apart. The size (ha) of the pools in Unit 1 are: A=104.8, B=98.4, C=122.3, D=79.8, E=198.4, and G=81.8. Lake alkalinity, pH and clarity (Secchi disc) were measured for each pool in June. Total alkalinity varied most, but was low overall (29.9–54.8 mg/l), pH was slightly basic (7.7–8.7) and water clarity was high (1.8–2.0 m). Banding of juveniles began in 1987 and adults in 1989 (Evers, 1993). Banding has been conducted annually since 1989 by BioDiversity Research Institute (Evers, pers. com.), with a minimum of 80% of the adult population marked during any one year. Between seven and 11 nesting pairs of loons have been present each of the summers from 1989–1999 (Evers et al., 2000).

Turtle Flambeau Flowage (TFF) (46° N, 90° W) is a large impoundment (5978 ha) created in 1926 in northern Wisconsin. The average depth is 3 m, with a maximum depth of 16 m. Less than 5% of the shoreline is developed with cabins/resorts. It has over 150 islands and irregular shorelines. The breeding loon population (22–24 nesting pairs) was monitored since 1985 with some associated banding efforts in 1987 (Belant, 1989). Annual banding of this population began in 1992 (Evers et al., 2000) with approximately 55–65% of the adult population being marked at any one time (Paruk, 1999a). Dominant recreation use includes fishing and camping. Lake alkalinity, pH and clarity (Secchi disc) were measured from four locations in June. Alkalinity was low (avg. = 28.2 mg/l),

pH was slightly basic 7.5 and water clarity was high, 1.9m.

Aziscohos Lake, Maine (45° N, 71° W) is a large impoundment (2506 ha) created in 1911 with <1% of the shoreline developed. It has an average depth of 9.9 m and a maximum depth of 19.2 m. The breeding loon population consists of 18 nesting pairs. Annual banding of adults and juveniles began in 1994, and 83% of the adult population is banded (D. Evers, pers. com.).

Methods

The capture and banding procedure has been reported previously (Evers, 1993, 2001). All adults were fitted with a single U.S. Fish and Wildlife Service band and one to three UV-resistant colored plastic bands (Hermes, Inc., New York) on their legs in unique combinations. Identification of color-marked individuals was determined through close (10×50 binoculars) and remote (20–60× spotting scope) observations. Band colors are most easily determined during frequent foot waggling and preening behaviors.

Each loon territory was surveyed during the breeding season at least once every three-four days to evaluate the status of each breeding pair. Data recorded include the following: egg first laid, egg first hatched, number of young that hatched, number of chicks that fledged (as observed 6–8 weeks after hatching). Thus, breeding status information was known at a high resolution and allowed for testing the various predictions made by the Familiarity and Reconnaissance Hypotheses.

Predictions derived from the Cooperative Foraging Hypothesis were tested and analyzed by videotaping (Sony Camcorder image stabilizer, 60×) social gatherings from the time they were first detected until the last individual left. Eleven hours and 50 min of videotape were logged from thirty-one social gatherings either from shore or boat in 1996–1997 at TFF and in 1998 at Aziscohos Lake, Maine. To determine distances from the videotape between individual loons the length of an adult loon was used, or one loon unit (LU, a loon 5 body lengths from a conspecific = 5LU's).

Social gathering surveys

Social gathering surveys were restricted to early morning and late afternoon as these are the times they most frequently take place (McIntyre, 1988; Paruk, 1999a). At Seney NWR, surveys were conducted by car once or twice a day and 5–6 times per week from 15 July to 20 August (1993–94, 1997), from 30 July to 20 August (1998) and Aug 1 to Aug 15 (1999). All areas of each pool were observable from either one or two locations so the likelihood of missing a social gathering was low. At TFF, surveys were conducted by boat from 15 July to 15 August in 1996 and 1997. The routes afforded excellent views of multiple loon territories ($n=11$) and neutral sites or non-territories ($n=8$) that covered greater than half of the TFF. Inclement weather and concomitant increased wave action occasionally limited surveys to once a day (22%) or 4 times a week (28%) in 1996. If a social gathering was observed, the observer stayed until the participants flew off the lake. Individuals were identified as they left with the use of a spotting scope or binoculars. It took 2.0–3.0 h to complete a survey. The following data were collected each year for every social gathering: date, time of day, number of loons involved, and duration. A brief description of each social gathering was also recorded.

Data analysis

Duration of social gatherings was not normally distributed and could not be normalized using standard transformations. Thus, a nonparametric Spearman rank correlation coefficient (r_s) was used to assess the relationship between duration of the gathering with day in the breeding season. The number of loons at a gathering was normally distributed and this was correlated with days in the breeding season using Pearson's correlation coefficient (r). Surveys of daily social gatherings at TFF and Seney NWR were normalized using square root transformations and compared using a Proportion's Test. Both the Chi-square and G test were used for contingency table analysis. If the former was used, a continuity correction was incorporated (Zar, 1984). A Fisher's Exact Test was employed when N was <30. All statistical tests were two-tailed with an acceptance of a Type 1 error 0.05.

Results

In total, 320 social gatherings were observed at Seney NWR ($n=137$) and TFF ($n=183$) over their respective study periods. Social gatherings were most common during the first three hours after sunrise ($n=201$, 62.3%, 0600–0900 h) and late in the afternoon ($n=100$, 31.2%, 1700–2000 h). Both males and females were present at every social gathering (94%), although not always in equal abundance. At Seney NWR, more banded females than banded males were observed at social gatherings (66%–34%, respectively) (G test: $G_1=6.87$, $p<0.05$) (Table 1). Moreover, females were roughly twice as likely as males to intrude on another loon's territory (41–21 intrusions respectively) (G test: $G_1=6.05$, $p<0.05$) (Table 1).

Cooperative foraging hypothesis

Loons spent 81% of their time above water during a social gathering ($n=31$) and above water time was positively correlated with group size ($r_s=0.64$, $p<0.05$). Most dives (74.5%, $n=65$) were of relatively short duration (<30 s), and resurfacing individuals did not face the same direction (82% of the time). In most cases (86%, $n=27$), if one individual dove, the whole group did. Loons that did not dive were typically >5 LU's away. Individuals or pairs resurfacing a considerable distance from each other would regroup 56.2% of the time and continue ritualized and stereotypical behaviors. At no time did an individual bring fish or any other prey item to the surface.

Familiarity hypothesis

Duration of the social gathering was positively correlated with day of breeding season (simple

regression, $r_s=0.56$, $p<0.05$). More loons participated in social gatherings later in the year (Spearman's $r=0.41$, $p<0.05$). There were significantly more social gatherings observed in established pairs' territories ($n=16$) versus non-breeding territories ($n=10$) (proportions test $Z=3.31$, $p<0.05$). The same individuals were observed repeatedly at social gatherings on consecutive or multiple days. For example, the same five birds (all banded) were observed at TFF each morning between 0610 and 0630 for three consecutive days (July 23–25, 1995). This group consisted of a female from the central territory (successful nester) and two pairs (both males and females) from adjacent territories (unsuccessful nesters). The male from the central territory remained with the two chicks each morning. There was a minimum of six cases when individual birds could be recognized as revisiting and interacting with the same individuals on consecutive days. Aggression levels were positively correlated with the amount of time spent peering ($r_s=0.36$, $p<0.05$).

Reconnaissance hypothesis

There were significantly more unbanded ($n=194$, 55%) than banded birds ($n=156$, 45%) involved in social gatherings ($\chi^2=12.35$, 1 df., $p<0.05$) at Seney NWR (Table 1). Most territorial loons at Seney NWR were banded (80–90% annually) thus the unbanded loons participating in social gatherings were presumably coming from outside the refuge. Because nearly half of the population at TFF was unbanded, the ratios of banded and unbanded loons were not included in the analyses.

July social gatherings consisted more of unsuccessful nesters (69.0%) than successful nesters (31.0%) ($\chi^2=6.3$, 1 df., $p<0.01$) among breeding

Table 1. Total number of social gatherings at Seney NWR, Michigan 1997–1999

Year	Total # loons	# Banded	# Un-banded	Unknown*	Banded Males	Banded Females	Male Intrusions	Female Intrusions
1997	193	81	98	14	35	37	5	20
1998	58	21	33	4	6	10	1	3
1999	125	54	63	8	17	26	15	18
Total	376	156	194	26	58	73	21	41

*6.9% of the total number of loons could not be identified.

birds. This difference did not exist during August social gatherings ($\chi^2 = 1.34$, 1 df., NS). The number of successful nesters in August social gatherings increased from 31% to 48%. Earlier in the breeding season (1–21 July), loons were more likely to arrive at social gatherings individually rather than in pairs, ($\chi^2 = 5.344$, 1 df., $p < 0.05$); however, after 21 July, loons were just as likely to arrive in pairs or as individuals ($\chi^2 = 2.987$, 1 df., NS).

Social gatherings were not randomly distributed across loon territories at Seney NWR ($\chi^2 = 1.85$, 4 df., $p < 0.05$, Table 2) and TFF ($\chi^2 = 6.23$, 7 df., $p < 0.05$, Table 3). During 35 territory-years of late summer observations at Seney NWR, territories that had experienced a recent divorce (within same-summer or previous summer) had the highest percentage of social gatherings.

Four of five territorial loon pairs divorced between 1993 and 1999. In 1994, no established pairs divorced, but 45% of all the social gatherings took place on G pool, where a divorce occurred the previous year. Similarly, in 1997, 42% of social gatherings took place on B pool, a pool that had experienced a divorce in 1996.

Thus, the proportion of all social gatherings observed on B pool remained high the year following a divorce (the exception being E pool in 1998). A similar pattern emerged at TFF, where territories experiencing divorce within season and one year after the event had disproportionately more social gatherings than territories that did not undergo divorce. For example, in 1996, 67% of the gatherings occurred at just 4 locations (out of a possible 19, Table 2). One location was a neutral territory, Crow, ($n = 36$, 29%), the other was an established territorial pair (Merkle) that had undergone a divorce that season ($n = 19$, 15%). Other loon territories that did not experience a divorce averaged ~ 1 social gathering/territory. Similarly, in 1997, a territory that experienced a divorce, South Horseshoe, saw a dramatic rise in social gatherings from $< 1\%$ to 12%.

There was no significant difference between the number of social gatherings on territories with chicks ($n =$ varied annually from 7 to 11) or without chicks ($n =$ varied annually from 5 to 9) (G test: $G1 = 1.56$, NS).

Table 2. Total number of social gatherings recorded (%) at Seney NWR, Michigan 1993–94 and 1997–99 (% given only for those > 10)

Year	Pools							Total
	A	B*	C	D	E	F	G	
1993	1	3	3	4	3	0	13 (49)	27
1994	2	4	5	5	4	0	16 (45)	36
1997	3	15 (42)	0	3	13 (33)	0	5	39
1998	1	6 (50)	2	0	2	1	0	12
1999	0	1	6 (22)	14 (60)	0	0	2	23
Total								137

Bold = pair broke up early in the year.

*B pool pair broke up in 1996.

Table 3. Summary of social gathering participation at 11 territories and 8 neutral sites at Turtle Flambeau Flowage, Wisconsin, 1996–1997

Year	Crow*	Merkle**	S. Horse-shoe***	Trude-C	Trude-W	Trude-E	Others	Total
1996	36, 29%	19, 15%	2, $< 1\%$	16, 13%	13, 10%	1, $< 1\%$	38, 30%	125
1997	14, 24%	6, 10%	7, 12%	8, 14%	4, 7%	0, 0%	16, 28%	58
Total								183

*Crow was a neutral site.

** Merkle experienced a pair break up in 1996.

***S. Horseshoe experienced a pair break up in 1997.

Discussion

Foraging hypothesis

There is no any evidence that the function of social gatherings is for individual members to benefit from flock feeding. Loons spent the majority (81%) of the time during a social gathering interacting with one another on the surface of the water. Although loons primarily swallow their prey whole underwater, they often bring large fish to the surface to swallow (Barr, 1996; McIntyre and Barr, 1997; Paruk pers. obs.). At no time during a social gathering did a loon surface with a prey item. When the group dove, 42% of the time they surfaced at a greater distance apart from each other than when they dove. Moreover, they were not facing in the same direction as is typical of species that flock feed. For example, Bartholomew (1942) observed large foraging groups of Double-crested Cormorants, *Phalacrocorax auritus* (Lesson) and movements of individuals were highly synchronized with individuals diving and surfacing in unison. Also, most of the Cormorant's flock's time was spent underwater and flock members surfaced with prey frequently. Without observing underwater behavior of loons, it is difficult to ascertain what each loon is doing, but such coordinated patterns in movements were not observed in common loon social gatherings during July and August at Seney NWR, TFF or Aziscohos Lake. Synchronized foraging, or flock feeding, does exist in common loons, but this behavior has only been observed during late summer/fall flocking (Olson, 1951; Nero, 1963; McIntyre and Barr, 1997; Vlietstra, 2000; Paruk pers. obs.). Thus, social gatherings do not serve individuals for any possible benefits associated with cooperative foraging.

Familiarity hypothesis

This hypothesis predicts that loons should frequently engage in group foraging during post-reproductive aggregations, they should exhibit lower levels of aggression and should serve to foster familiarity and cooperation among loons (McIntyre, 1988). Social gatherings then would facilitate reduced levels of aggression among conspecifics which may be important during migration when many individuals migrate in small groups

and stage at lakes where feeding flocks occur (McIntyre and Barr, 1983). Conspecific foraging, especially in areas with schooling fish, or where food availability is unknown, may be more successful than solitary individuals (McIntyre, 1988; Vlietstra, 2000). Similarly, groups of wintering loons may have higher survival than solitary ones if rafting loons have lower depredation rates than solitary ones (McIntyre, 1978; Daub, 1989; L. Vlietstra, pers. comm.). The highest mortality rates of loons occur during migration and winter (McIntyre and Barr, 1997; Piper et al., 2000; Evers, 2001; 2004).

This hypothesis proved difficult to test directly and will remain elusive for future researchers until uniquely marked individuals can be (1) followed during the time of social gatherings and (2) subsequently followed to measure survivability and reproductive success. From my observations, some initial speculations can be made. First, some social gatherings consisted of the same individuals on consecutive days suggesting the potential for familiarity (and cooperation) among group members exists. Second, 22% of all the gatherings recorded were observed at neutral locations, or non-breeding territories, where it would seem the only real purpose such a location offers is to allow for familiarity with other loons. Third, the duration of gatherings increased more during August than July (31 min to 19 min), the number of individuals participating in them also increased similarly (4.1 individuals/July vs. 6.8 individuals/August) and gatherings appeared less aggressive over time. The above suggests individual birds are more comfortable with each other possibly due to familiarity with neighboring conspecifics.

Lastly, some social gatherings occurred each year in neutral locations (primarily on large lakes >1000 ha) (Olson, 1951; Nero, 1963; McIntyre, 1988; Paruk, 1999a) where it would appear there is little information to be gained by residents and/or nonbreeders with regard to territorial openings and habitat quality. Thus, it remains possible that this fact alone may serve as indirect evidence for the Familiarity Hypothesis. On average, first-year breeding age in loons is seven years (Evers, 2004) and since most loons are philopatric and return to breeding areas at age three, there is a time period of several years when they interact with resident loons during social gatherings.

Reconnaissance hypothesis

The Reconnaissance Hypothesis maintains that social gatherings represent efforts by non-breeders to locate future territories (Piper et al., 1997). The following data supports the Reconnaissance Hypothesis: (1) 55% of the loons involved in social gatherings at Seney NWR were unbanded and most likely non-breeders since the great majority of all of the adults on the refuge in any one year were banded (80–90%); (2) I observed three cases in mid-late July where unbanded individuals interacted aggressively with a territorial pair member resulting in usurpation of one member of the established pair and (3) social gatherings increased over 200% on territories that had experienced a divorce during the breeding season.

Several banded pairs outside of the refuge had never been observed on the refuge. This suggests that the unbanded birds are probably nonbreeders. I observed many large gatherings on both Lake Superior and Lake Michigan, situated just north and south of the refuge, respectively, during the breeding season. Given an average flight speed of 160 km/hr an exploratory flight from either Great Lake to Seney NWR would take about 30 min. Croskery (1988) observed many nonbreeding loons in western Ontario remained in flocks on large lakes where arrivals and departures were frequent throughout the breeding season. Thus, it is likely that nonbreeders are using large lakes to feed as bases, but then make forays inland to potential breeding lakes. Previous studies have found that unsuccessful territorial pairs, nonbreeding pairs and unpaired adults are prevalent on breeding grounds and may comprise up to 46% of an entire summer loon population (Taylor and Vogel, 1999).

A more reliable support of the Reconnaissance Hypothesis would be to show that individuals participating in social gatherings return the following year and challenge for that territory. This happened three times during the study period. Piper et al. (1997, 2000) and Paruk (1999b) documented similar usurpations and given that divorce rates in common loons has recently been shown to be between 15 and 20%, (Evers, 2001), this allows for the distinct possibility that social gatherings are a way of nonbreeders to assess territory availability, territorial quality and possibly mate

stability. Consequently, it would be more appropriate to broaden the Reconnaissance Hypothesis (Piper et al., 1997) to include some aspect of information transfer. In many birds, nonbreeders are likely to acquire territories they visited more frequently during the post-breeding period (Reed & Oring, 1992; Zack & Stutchbury, 1992; Piper et al., 2000).

One or two territories always had more social gatherings each year. An intriguing aspect of this shifting visitation is the associated status of the resident loons upon the most visited site. At Seney NWR, all pools which had 10 or more social gatherings were not only occupied by a breeding pair, but were also territories where there was a divorce within the previous months. For example, D pool, which had been held by the same pair since 1993, and which had seen little late summer visitation in recent seasons, underwent two changes in 1999 with the death of the resident male in spring and the displacement of his successor following nest failure. During August, with the resident female now paired to her third male (unbanded) of the season, D pool became the nexus of social gatherings. Interestingly in 1998, a year where no birds divorced, the number of social gatherings was the lowest recorded. This pattern was also seen at TFF, where two pairs that experienced divorce had significantly more social gatherings. Overall, this pattern suggests that loon social gatherings are not simply individuals aimlessly wandering between or among lakes in a shotgun approach, but instead appear to be non-random and directed to territories that have unstable or recently formed pair bonds.

The Reconnaissance Hypothesis further proposes that nonbreeding loons will visit territories that produce chicks more often than those that do not as an indication of habitat quality (Piper et al., 1997). Of the five heavily visited pools mentioned above, three pairs had bred successfully during the season, but overall the pattern did not hold. Social gatherings occurred on territories without chicks just as frequently as they did on territories that produced chicks. Piper et al. (2000), however, had a larger sample size and found more social gatherings on lakes with young than without.

One final consideration is that it may not be the nonbreeders who are choosing which territory to visit, but rather the resident pair that determines

how many social gatherings are allowed or permitted to take place in the territory. For example, the E pool pair had been together since 1989 and very few social gatherings were observed there during all those years. Then in 1997, the nest failed and the female appeared to lose interest in the resident male and was observed with two other males during the rest of the summer. Moreover, E pool was one of the sites where most of the social gatherings occurred that year. It appeared that the E female was leading and orchestrating the gatherings. How do loons choose mates? Is the territory more important or the mate? Piper et al. (2000) concluded that usurpation is common in loons as a means of acquiring a territory and that it is the territory that loons are competing for, not necessarily mates. Although my data support this notion, several observations, such as the ones on E and B pool, suggest in some situations, it may be the individual rather than the pair that may control the number of social gatherings on a territory.

Conclusions

The temporal and spatial patterns of social gatherings in loons has no doubt been shaped by selection such that they occur at specific times, both daily and seasonally, and often at specific places, both within and outside of established territories. This important aspect of loon life history has important implications for conservation.

Social gatherings occur primarily in the morning and late afternoon/early evening. Lake water tends to be calmest in the early morning thus allowing the best opportunity for loons to find aggregates of conspecifics. Late afternoon gatherings were not as consistent or as numerous as early morning ones. When lake water was turbulent and winds were strong (>20 km), social gatherings rarely occurred. A set time and a set place would allow for predictable visits by both breeders and nonbreeders. These aggregations, or social gatherings, occur in animals of all kinds and allows for communication and public information to take place (Wagner & Danchin, 2003). Such information sharing would include such things as developing social skills for cooperation and flock foraging (copying), territory availability, habitat

quality, territorial pair stability, potential neighbors and rivals, and intra-sexual assessment. Both the Familiarity and Reconnaissance Hypotheses are possible explanations for social gatherings in common loons. More intense monitoring of individually marked loons will be necessary to further substantiate these initial findings.

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Feeding behavior and modeled energetic intake of common loon (*Gavia immer*) adults and chicks on small lakes with and without fish

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Abstract

We examined the behavior of common loons, *Gavia immer* (Brünnich), breeding on small, shallow lakes in central Alberta, Canada that were naturally fishless or contained only small-bodied fishes (minnow lake). For both lake types, adults spent >90% of their time on the nesting lake and >50% of their time foraging. Adult loons on fishless lakes dove more frequently, but dives were of shorter duration than loons on lakes with fish. On two intensively studied fishless lakes, adults fed chicks macroinvertebrates, particularly leeches, whereas on a focal minnow lake, fish made up >70% of prey items delivered by adults. Chicks >36 days of age on a minnow lake spent >50% of their time foraging, whereas older chicks on fishless lakes were highly dependent on food provisioning by adults. Models based on observed foraging patterns indicated that prey size was a better predictor of success in meeting energetic requirements than was feeding behavior (e.g., dive rate, dive success). For most models, estimated energetic intake was higher for loons on minnow lakes than on fishless lakes. Our behavioral observations and model results are consistent with surveys in central Alberta that indicate that breeding Common Loons frequently establish territories on small lakes, but that chicks hatched on lakes completely lacking fish rarely fledge and only if sufficient large invertebrates such as leeches are available.

Introduction

Many studies have examined whether breeding success of aquatic birds is directly related to abundance of preferred food. The results have been divergent, with strong evidence that reductions in preferred food results in poor reproductive output in some cases (Barrett et al., 1987; Baird, 1990), and no evidence of a relationship in others (Martin, 1989; Uttley et al., 1994). Some of this divergence may be explained by the extent to which a species is able to compensate behaviorally to changes in food supply (e.g., Bukacinska et al., 1996; Weimerskirch et al., 1997). For example,

various bird species adjust dive rates (Monaghan et al., 1994), chick provisioning rates (Hamer et al., 1999), time budgets (Burger & Piatt, 1990) and diet (Crawford & Dyer, 1995) when prey abundance changes.

The common loon, *Gavia immer* (Brünnich), is a highly territorial, foot-propelled diver that is typically thought to have specialized dietary requirements. Although loons may eat invertebrates and vegetation, the main component of the diet is characteristically fish (McIntyre & Barr, 1997), with both large- and small-bodied fish species consumed by adult loons during the breeding season (Barr, 1996). Because common loons are

primarily piscivores that rarely carry food to their nesting lakes from other lakes (McIntyre, 1988; but see Parker, 1985) and only hatch one to two chicks per season, populations may be sensitive to changes in the prey base in lakes on which they breed.

In eastern North America, large, oligotrophic lakes are the characteristic breeding habitat for common loons (McIntyre & Barr, 1997). In many of these lakes, acidification has reduced or eliminated the fish populations that loons use as prey. Studies have linked concomitant declines in loon occupancy and productivity with reductions in fish populations (e.g., Alvo et al., 1988; McNicol et al., 1995). Such linkages may be confounded, as acidification can also be associated with other factors such as increases in mercury accumulation in biota (Meyer et al., 1998; Scheuhammer & Graham, 1999), a neurotoxin that may cause reproductive and behavioral impairment in loons (e.g., Barr, 1986; Nocera & Taylor, 1998). Thus, if and how prey base influences loon behavior and ultimately fledging success remains unclear.

Lakes in boreal Alberta are productive (total phosphorus 10–500 $\mu\text{g l}^{-1}$) and vary greatly in size, depth, and prey base (Robinson & Tonn, 1989; Mitchell & Prepas, 1990). They have not experienced the cultural acidification of lakes in the East and mercury concentrations in loons from Alberta are also comparatively low (Scheuhammer et al., 2001). Loons in boreal Alberta nest on large (≥ 40 ha), deep (≥ 5 m) lakes that contain large-bodied fish such as northern pike, *Esox lucius* (L.), white sucker, *Catostomus commersoni* (Mitchell), and yellow perch, *Perca flavescens* (Lacépède), (Gingras & Paszkowski, 1999), similar to loon habitat in eastern Canada (e.g., Kerekes, 1990; McNicol et al., 1995). However, they are also regularly found nesting on small, shallow lakes with only small-bodied fish such as fathead minnow, *Pimephales promelas* (Rafinesque), and brook stickleback, *Culaea inconstans* (Kirtland), and occasionally on small lakes that are naturally fishless (Gingras & Paszkowski, 1999). Basic behavior of common loons on the latter two kinds of lakes is of interest because small, shallow lakes are not commonly thought of as breeding habitat. These lakes also present the opportunity to contrast loon foraging behavior on lakes with differing prey bases (i.e., small-bodied fish vs. inverte-

brates), thus providing insight into the relation between foraging flexibility and breeding success.

Here, we document the behavior of common loons breeding on the “atypical” habitat of small, shallow lakes and compare the behavior of loons on small lakes with and without fish. On both lakes with and without fish, we examined if adults fed primarily from nesting lakes, the amount of time adults spent foraging, the nature of adult foraging patterns (e.g., dive rate, duration and success), prey fed to chicks, and how feeding patterns changed with age of young. Finally, we created simple empirical models to evaluate the ability of adult loons to meet their own energetic requirements and that of growing chicks on small lakes with and without fish.

Methods

Study sites

Research was centered in Athabasca County, approximately 150 km north of Edmonton, Alberta, Canada. We conducted intensive behavioral observations of territorial common loon pairs on a total of 10 small lakes during the summers of 1994 (5 lakes) and 1995 (five new lakes, three from 1994; Table 1). Four of the lakes were fishless and six contained brook stickleback and/or fathead minnow, hereafter referred to as minnow lakes (Table 1). The number of fishless and minnow lakes studied reflects the relative abundance of each lake type with loon pairs present in the landscape. Not all territorial pairs on study lakes hatched eggs, thus detailed foraging data on chicks was limited to three focal lakes in both years: Beaver Pond (minnow lake), Tempo Lake and Joseph Lake (both fishless).

Shorelines of the 10 study lakes were undeveloped and recreational activity was absent (see Gingras & Paszkowski 1999 for habitat descriptions). However, in late June/early July 1994 trees were logged within 200 m of two fishless lakes. Each lake had only one pair of territorial loons and was small enough that the entire surface could be observed from a single location. Previous (Robinson & Tonn, 1989) and concurrent (Paszkowski & Tonn, 2000) studies characterized the morphometry, water chemistry, and fish

Table 1. Location (latitude and longitude) and physical (area, maximum depth) and chemical characteristics (pH, TP = total phosphorus, Cond. = Conductivity) of fishless lakes and minnow lakes studied in central Alberta, Canada

Lake	Location	Area (ha)	Max. Depth (m)	TP ($\mu\text{g/l}$)	pH	Cond. $\mu\text{S cm}^{-1}$	Year studied	No. chicks	Fish assemblage
Tempo	54°37' N 113°19' W	9.4	2.5	108.1	7.2	230	1994; 1995	1 & 1	Fishless
Joseph	54°37' N 113°12' W	12.1	1.5	13.5	7.8	220	1994; 1995	2 & 1	Fishless
Shumaker	54°38' N 113°18' W	20.0	6.8	36.0	8.2	289	1995	2*	Fishless
Little Buck	54°39' N 112°30' W	51.6	1.1	181.0	9.7	181	1995	0	Fishless
Beaver	54°38' N 113°35' W	2.7	4.3	26.2	7.3	241	1994; 1995	2 & 1	FTMN
Bobier	54°33' N 113°10' W	25.2	1.1	86.3	6.4	339	1994	0	BRST
Tawatinaw	54°21' N 113°28' W	47.4	4.3	46.4	8.2	319	1994	0	BRST
Mystic	54°23' N 113°21' W	14.3	2.2	42.7	7.2	110	1995	0	FTMN; BRST
Cloudberry	54°44' N 113°40' W	25.3	1.5	80.0	9.1	80	1995	0	FTMN; BRST
Two Island	54°26' N 113°13' W	57.8	1.00	96.0	9.1	160	1995	0	BRST

Behavioral data were collected on two adult Common Loons and their chick(s) on each of the study lakes (number of chicks observed indicated during one or two breeding seasons). FTMN, fathead minnow; BRST, brook stickleback.*2 chicks were present but behavioral data were not collected.

assemblages of the lakes. Most of the study lakes were shallow and alkaline, with meso- to hypereutrophic phosphorus levels (Table 1). Fishless and minnow lakes did not differ in any of the measured morphometric or chemical characteristics (Table 1; Two sample *t*-tests, all $p > 0.53$).

Behavior

Observations began when loons arrived in early May and continued until birds left in late August or early September. Similar to methods employed by Alvo & Berrill (1992), Evers (1994) and Nocera & Burgess (2002), we performed continuous observations (Martin & Bateson, 1993) using a 45 \times spotting scope or 8 \times 36 binoculars from a canoe or from vantage points on shore. Blinds were not used as they commonly distract loons more than a visible human observer (McIntyre, 1988). Two observers were present and each focused on one bird during an observation period. Distance between observers and loons ranged from approximately 10–300 m. Lakes were visited at least once each week during which at least 1 h of observations was made on each member of the loon family present. Observation sessions were normally conducted between 09:00 and 17:00 MDST, with additional recordings made in early morning (05:30–09:00) and late evening (19:00–23:00) at least once each month. Observations on

each lake were staggered during the core 8 h sampling period to randomize observations among lakes.

During each observation period, the frequency and duration of all foraging related behaviors were recorded. Adult foraging behaviors consisted of peering (loon's head submerged underwater, body at surface), diving (loon's head and body completely submerged), and chick provisioning (adult delivers prey to chick). Loons dive for purposes other than feeding (grooming, courtship, territory defense), but foraging dives typically followed peering and occur in bouts. Chick behavior associated with feeding consisted of peering, foraging dives, and "provisioning episodes" (chick waits on the water's surface to accept prey from adult), and begging (chick pecks at adult's bill or neck).

To determine if loons fed primarily on their small nesting lakes, we calculated the total amount of time spent on a lake by each pair member during each of our visits. Time budgets and foraging patterns were characterized for each hour-long observation period for an adult loon as: (1) percentage of time spent foraging; (2) dive rate, i.e., number of dives per minute during foraging bouts; (3) mean foraging dive duration; and (4) percentage of successful dives, i.e., dives that resulted in an adult delivering food to a chick. For chicks, in addition to items 1–3, we also calculated begging rate and provisioning rate.

We identified prey items fed to chicks and classified them as vegetation, invertebrate, fish, or unidentified. Invertebrates were further classed as amphipods, insects, leeches, and small, unidentified invertebrates. The length of each prey was estimated as a proportion of the length of the adult loon's bill. These estimates were converted to actual lengths by multiplying the proportional length of prey by an adult bill length of 78.5 mm (Storer, 1987; specimens from University of Alberta Zoology Museum). We calculated percentage of fish, vegetation, and invertebrates fed to chicks for all observations on a lake combined. As adult loons usually consume food underwater (Barr, 1996), prey identification was limited to chick provisioning observations.

Statistical analyses

Analyses of behavioral data for adult loons were done separately for 1994 and 1995. This was appropriate because adults were not observed on all lakes in both years and, given that the loons were not marked, we did not know if the birds from 1994 were the same individuals as in 1995. For both adults and chicks, each 1 h observation period for an individual bird was treated as an independent behavioral sample if separated from other observations by ≥ 1 h. Foraging parameters of adult loons were calculated over the whole summer after preliminary analyses indicated they did not change as chicks aged. Values for behavioral measures were not normally distributed, thus non-parametric statistical tests (Mann–Whitney *U*-test, Two-Sample Kolmogorov–Smirnov test, or Kruskal–Wallis One-way Analysis of Variance) were used for comparisons of patterns between minnow and fishless lakes.

Typical of loon productivity on small lakes in the region (see Gingras & Paszkowski, 1999) few chicks were hatched ($n=8$) and fledged ($n=4$) on our study lakes. Because of the small number of chicks, statistical tests comparing feeding behavior of chicks on fishless and minnow lakes were not performed. However, we present means \pm SD of the chick behavioral data because such detailed observations are rare. We examined ontogenetic changes by comparing the behavior on an individual chick at ≤ 35 days old with its behavior after 36 days of age. This demarcation reflects the

fact that a “bottleneck” for survival occurs around 35 days of age (Parker, 1988; Gingras & Paszkowski, 1999). Frequent visits to the study lakes allowed us to determine exact hatch dates and thus chick age. In total, we collected data on eight younger (≤ 35 days old; 3 chicks from 1 minnow lake, and 5 chicks from 2 fishless lakes) and five older chicks (36+ days old; 3 chicks from 1 minnow lake, and 2 chicks from 2 fishless lakes). Across the three focal lakes, the oldest chick for which data was collected was 67 days at Beaver Pond, 65 days at Tempo Lake, and 48 days at Joseph Lake. Chicks are considered to be capable of fledging at 77 days (Barr, 1996).

Energetic models

We created simple models to estimate energy intake of adult and chick loons on fishless and minnow lakes. We used observed patterns of foraging and prey capture in the models, and compared our field-based estimates of energy intake to values for captive loons reported by Barr (1996). Our foraging parameters were calculated from birds actively engaged in foraging bouts and thus do not incorporate long periods of inactivity (e.g., incubation).

The basic model for adult loons is as follows:

$$E_h = \sum_{i=1}^N D_r D_s p_{(i)} e_{(i)} m_{(i)}$$

where E_h is the net energy gain ($J h^{-1}$), D_r is foraging dives h^{-1} , D_s is % successful dives h^{-1} , $p_{(i)}$ is % prey item i in diet, $e_{(i)}$ is energy content ($J mg^{-1}$ dry mass) of prey item i and $m_{(i)}$ is dry mass (mg) of prey item i .

We manipulated dive rate, dive success, and diet composition to create a variety of model scenarios. For dive rate, we created models for each lake type using the average or the maximum dive rate observed for 14 adult loons on six minnow lakes (75 and 144 dives h^{-1} , respectively) and 12 adult loons from four fishless lakes (96 and 206 dives h^{-1} , respectively); data were combined 1994 and 1995 values (see Fig. 1 for sample sizes). Adult loons consume their prey under water, thus we had no direct measure of the success rate of dives by foraging adults. Therefore, we used the percentage of observed dives resulting in food delivery to

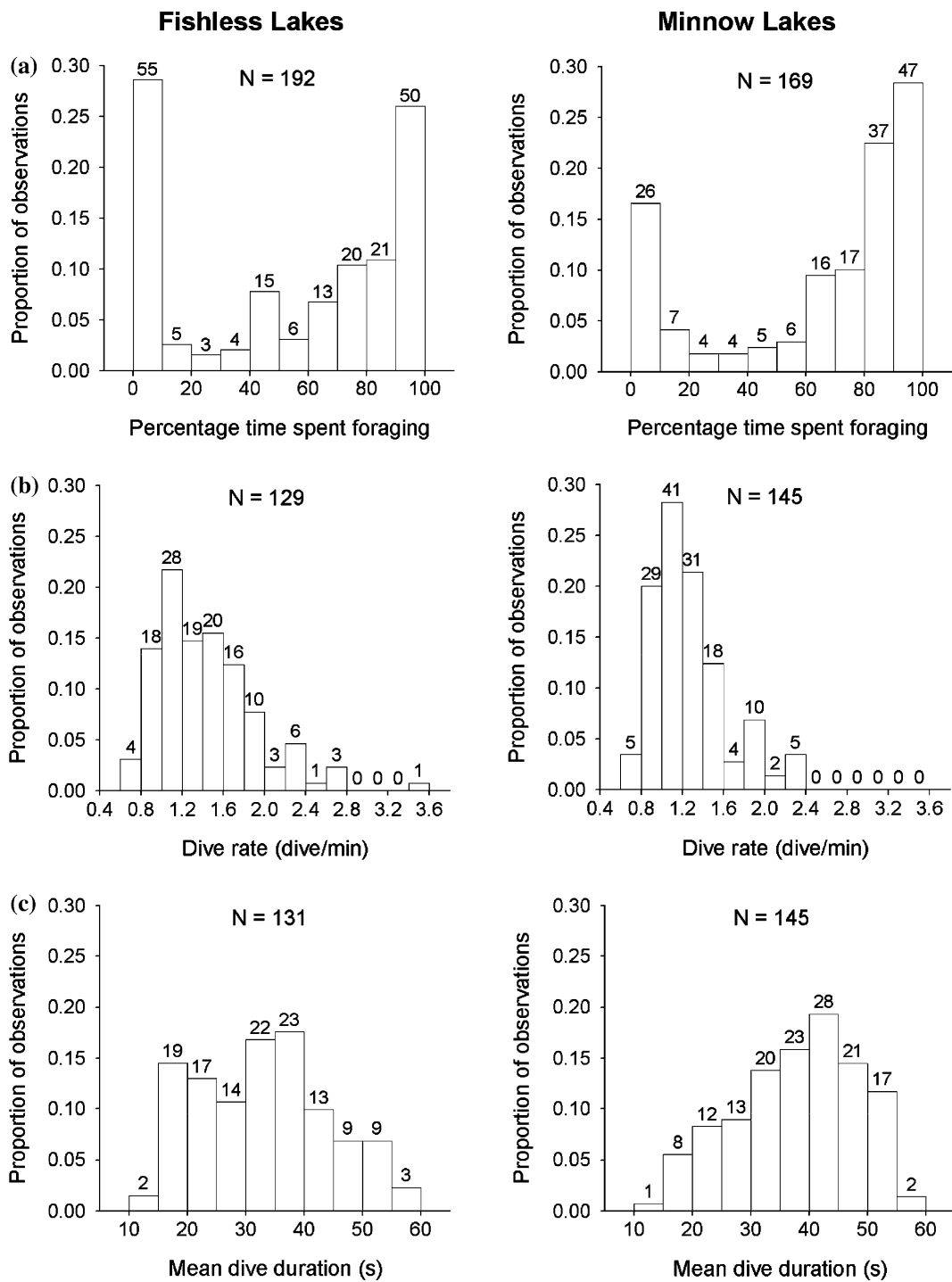


Figure 1. Distributions of foraging parameters for adult Common Loons on four fishless lakes and six minnow lakes: (a) % time spent foraging, (b) dive rate (dive min^{-1}), (c) dive duration (s). Data are combined 1994 and 1995 values. Numbers of 1 h observation periods are on top of bars. N = total number of 1 h observation periods.

Table 2. Observed average and/or maximum values (p = % of prey types in diet; m = mg dry mass prey) used in hourly energetic intake models for adult, young chick (age 1–35 days), and older chick (age 36+ days) Common Loons on minnow and fishless lakes

Parameter	Value type	Prey type	Minnow lake		Fishless lakes	
<i>Adult models</i>						
P	Observed average	Fish	82		NA	
		Amphipods	1		9	
		Insects	6		27	
		Leeches	11		64	
m	Observed average	Fish	18.0 (19.5)		NA	
		Amphipods	2.4 (7.9)		2.3 (7.7)	
		Insects	4.2 (22.6)		3.9 (20.4)	
		Leeches	33.0 (42.0)		33.0 (42.0)	
m	Observed maximum	Fish	1406.6 (78.5)		NA	
		Amphipods	2.4 (7.9)		14.3 (15.7)	
		Insects	8.6 (31.4)		33.3 (58.9)	
		Leeches	240.0 (95.0)		240.0 (95.0)	
<i>Chick models</i>						
			Minnow	Fishless	Minnow	Fishless
			Age 1–35	Age 1–35	Age 36+	Age 36+
P	Observed average	Fish	78	NA	89	NA
		Amphipods	1	12	0	3
		Insects	9	26	4	28
		Leeches	12	62	11	69
m	Observed average	Fish	13.0 (17.6)	NA	23.8 (21.3)	NA
		Amphipods	2.4 (7.9)	2.3 (7.7)	NA	2.4 (7.9)
		Insects	4.0 (22.1)	2.3 (17.1)	4.6 (23.6)	3.6 (20.9)
		Leeches	33.0 (42.0)	33.0 (42.0)	33.0 (42.0)	33.0 (42.0)
m	Observed maximum	Fish	1406.6 (79.0)	NA	1406.6 (78.5)	NA
		Amphipods	2.4 (7.9)	14.3 (15.7)	NA	2.4 (7.9)
		Insects	8.6 (31.4)	33.3 (58.9)	8.9 (31.9)	13.9 (39.3)
		Leeches	240.0 (95.0)	240.0 (95.0)	240.0 (95.0)	240.0 (95.0)

Average and maximum estimated prey lengths (mm) used in calculations of dry mass are in parenthesis. Lengths of leeches are based on direct measurements of 99 *N. obscura*. NA = not applicable.

chicks as a substitute for adult success rate. Specifically, we combined observations for all chicks and years ($N=42$ 1-h observation periods) and used average and maximum percentage values for minnow (59 and 98%, respectively) and fishless lakes (60 and 85%, respectively) in models. We also created hypothetical models in which every dive was successful.

The percentage of prey items in the diet was based on chick provisioning patterns on minnow and fishless lakes, using the total percentage of delivered prey that was comprised of fish, leeches, odonate larvae, and amphipods (Table 2). Because adult loons might, when foraging for themselves, focus on large, abundant prey, we also created

hypothetical models where fathead minnow was the sole prey eaten in minnow lakes and the leech, *Nepheleopsis obscura* (Verrill) (the most common species of leech in the study lakes) was the sole prey in fishless lakes. Finally, we generated models that used either the average or maximum length of prey to estimate dry mass for prey organisms (except for leeches, see below) observed in minnow and fishless lakes.

Energetic values ($e_{(i)}$) of invertebrate prey were obtained from previous studies (expressed as $J\ mg^{-1}$ dry mass: amphipods = 16.95, odonate larvae = 21.41, Cummins & Wuycheck, 1971; leeches = 22.36, Driver, 1981). We directly measured the energy content of fathead minnows

($25.04 \pm 0.5 \text{ J mg}^{-1}$ dry mass based on 10 adults). To generate realistic models, we used observed lengths of prey based on comparisons with adult loon bill length described earlier. We then converted length (mm) to dry mass (mg) using regression models for *Gammarus* (mass = $0.0119 \times \text{length}^{2.57}$, $r^2 = 0.86$, F. Wilhelm, unpublished data), odonate larvae (mass = $0.005 \times \text{length}^{2.16}$, $r^2 = 0.86$, Mittelbach, 1981), and fathead minnows (wet mass = $0.0069 \times \text{total length}^{3.13}$, $r^2 = 0.97$, assuming 76% water content by mass, W. Tonn, unpublished data; Table 2). The size of leeches captured by loons was difficult to estimate because leeches contract when handled. Thus, we weighed 99 *N. obscura* collected from the study lakes (preserved in 90% ethanol) and converted wet mass to dry mass (see Wrona, 1982; Table 2).

We used all possible combinations of values for our model's parameters to generate 24 models estimating hourly energetic intake for adult loons for both lake types. We compared these values to Barr's (1996) estimate that an adult Common Loon requires 960 g of fish per day during the breeding season, or 5800 kJ day^{-1} based on our measurements of the average energy content and water content of fathead minnows (see also McIntyre & Barr, 1997). Direct observations and the average hours of daylight at our study site during summer indicate that loons could forage for up to 16 h day^{-1} . Thus, to meet daily energy needs, adult loons must take in 363 kJ h^{-1} during daylight hours. We present only those models that produced values $\geq 95\%$ of this hourly rate for one or both lake types.

For younger chicks (1–35 days) that rely heavily on parents for food, we created energetic models that excluded foraging efforts by young chicks. Models for older chicks (≥ 36 days) included dives performed by the chicks in addition to parental feeding.

The models for loon chicks are described as:

$$E_h = \sum_{i=1}^N D_r D_s p_{(i)} e_{(i)} m_{(i)}$$

Younger chicks

$$E_h = \sum_{i=1}^N (D_r D_s p_{(i)} e_{(i)} m_{(i)}) + (P_r p_{(i)} e_{(i)} m_{(i)})$$

Older chicks

Parameters are the same as for the adult model with the addition of $P_r = \text{Provisioning rate h}^{-1}$.

As for adults, we constructed a variety of models for chicks based on our own observations on minnow and fishless lakes with appropriate values for younger vs. older chicks (four models for younger chicks on each lake type and eight models for older chicks). Models incorporated average or maximum provisioning rates and assumed that one prey was eaten per provisioning episode. For older chicks, models included average or maximum observed dive rates and assumed 32% of foraging dives were successful. This value is in the midpoint of the range reported by Barr (1996) where the success rate of a chick was 14% at 6 weeks and 51% at 9 weeks. We assumed that composition and size of prey captured by older chicks were similar to that provided by adults, and thus used the observed average and maximum dry mass of prey delivered to chicks in the models.

We compared our calculated hourly energy intake values to that of Barr (1996) who found that Common Loon chicks eat 53 kg of food in 15 weeks. A young chick (1–35 days) consumes roughly half the amount of food as an older chick. Thus, at 5 weeks a chick has eaten 10.6 kg of fish (1790 kJ day^{-1} or 112 kJ h^{-1} , based on the average energy and water content of fathead minnows and a 16 h daily activity period). From week 5–15, a healthy chick requires 42.4 kg of fish (3590 kJ day^{-1} or 224 kJ h^{-1} ; similar to 3330 kJ day^{-1} reported by Fournier et al. 2002). We only present models that produced values 95% of this hourly rate for one or both lake types.

Results

Lake use by loons

During our visits to the study lakes (544 h in 1994, 511 h in 1995), adult loons were almost continually present on their territorial lakes May–September. The percentage of time loons were present on their territorial lakes was similar for minnow and fishless lakes in 1994 (Mann–Whitney *U*-test, $U = 14$, $p = 0.65$; minnow = $94.2 \pm 9.3\%$, fishless = $96.0 \pm 4.5\%$, $n = 10$ individuals), and 1995 ($U = 32$, $P = 1.00$; minnow = $91.3 \pm 12.3\%$,

fishless = $93.1 \pm 7.4\%$; $n = 16$). In both years, prenesting and nesting loons were always present on the lakes and it was not until after chicks hatched that adult loons began to leave the lakes (Gingras, 1997). At least one adult was present on the lake when chicks were young; only late in the season, when chicks were almost adult size and able to forage for themselves (≥ 8 weeks old), did both adults leave the lake simultaneously. We observed adult loons flying into or out of lakes on several occasions, but on none of those occasions were they carrying food.

Adult feeding patterns

Adult loons on both lake types engaged in foraging more than any other activity, but loons concentrated on foraging more strongly on minnow lakes than on fishless lakes (Fig. 1a). Distributions of the time spent foraging differed significantly between the lake types in 1995 (Two-Sample Kolmogorov–Smirnov tests, $p = 0.01$; minnow = $64.5 \pm 33.4\%$; fishless = $50.7 \pm 33.9\%$), but not in 1994 ($p = 0.31$; minnow = 62.9 ± 38.2 , fishless = $56.4 \pm 38.9\%$). Non-foraging activities of the adult loons, combined across years and lakes, included nesting and incubation (14% of time), floating (11%), preening (8%), sleeping (4%), territorial behavior (3%), and reproductive behavior (1%).

Loons on fishless and minnow lakes exhibited similar ranges of dive rates and dive durations, but birds on minnow lakes dove less frequently than birds on fishless lakes (Fig. 1b; Kolmogorov–Smirnov tests: 1994, $p = 0.03$; minnow = 1.28 ± 0.43 dives min^{-1} , fishless = 1.47 ± 0.53 ; 1995, $p = 0.02$; minnow = 1.25 ± 0.33 dives min^{-1} , fishless = 1.40 ± 0.43) and spent more time under water per

dive (Fig. 1c; Kolmogorov–Smirnov tests: 1994, $p = 0.06$; minnow = 38 ± 12 s, fishless = 32 ± 11 ; 1995, $p = 0.01$; minnow = 37 ± 10 s, fishless = 33 ± 11).

During our 2-year study, we observed 4510 foraging dives by adult common loons tending chicks and over half of these resulted in delivery of food to chicks (minnow = $59.1 \pm 19.0\%$, fishless = $60.3 \pm 14.3\%$). The percentage of successful dives per observation period did not differ among the three focal lakes in either year (Kruskal–Wallis Tests: 1994, $H = 0.22$, $p = 0.96$; $n = 21$ observation periods; 1995, $H = 1.69$, $p = 0.43$, $n = 21$).

Chick feeding patterns

Common loon chicks spent much of their time foraging or being fed. Chicks on fishless lakes spent a greater percentage of time being fed (Joseph Lake, $65.6 \pm 35.5\%$, $n = 7$ observation periods; Tempo Lake, $45.7 \pm 36\%$, $n = 7$) than chicks on the minnow lake ($17.9 \pm 31.1\%$, $n = 21$). Provisioning rates of adults on the fishless lakes (Joseph Lake, 0.77 ± 0.63 times min^{-1} , $n = 7$; Tempo Lake, 1.02 ± 0.75 times min^{-1} , $n = 11$) tended to be higher than adults on Beaver Pond (0.36 ± 0.42 times min^{-1} , $n = 37$) and begging rates of chicks tended to be lower on the fishless lakes (Joseph Lake, 0.20 ± 0.22 times min^{-1} , $n = 7$; Tempo Lake, 0.13 ± 0.15 times min^{-1} , $n = 11$) than on Beaver Pond (0.30 ± 0.45 times min^{-1} , $n = 36$).

On the minnow lake, the percentage of time a chick spent foraging for itself increased with age whereas provisioning rates declined (Table 3). Older chicks on the minnow lake dove more frequently and made longer dives than younger chicks (Table 3). In contrast, provisioning rates

Table 3. Feeding patterns of young (1–35 days old) and older (36+ days old) Common Loon chicks on one lake containing minnows (Beaver), and two fishless lakes (Joseph and Tempo). Values are mean \pm SD (# of observations)

	Provisioning rate (deliveries min^{-1})	Begging rate (beggings min^{-1})	% Time spent foraging (by chicks)	Dive rate (dives min^{-1})	Dive duration (s dive^{-1})
Beaver, 1–35	0.58 ± 0.47 (11)	0.16 ± 0.32 (11)	8.8 ± 22.1 (8)	0.43 ± 1.01 (8)	7 ± 6 (6)
Beaver, 36+	0.28 ± 0.37 (26)	0.35 ± 0.49 (25)	50.5 ± 10.0 (13)	0.54 ± 0.47 (13)	25 ± 6 (11)
Joseph, 1–35	0.72 ± 0.30 (3)	0.04 ± 0.01 (3)	7.0 ± 12.2 (3)	0.28 ± 0.48 (3)	7 (1)
Joseph, 36+	0.81 ± 0.57 (4)	0.32 ± 0.23 (4)	13.6 ± 11.8 (4)	0.23 ± 0.18 (4)	8 ± 1 (3)
Tempo, 1–35	1.02 ± 0.92 (6)	0.08 ± 0.09 (6)	8.8 ± 12.4 (4)	0.05 ± 0.07 (4)	18 ± 3 (2)
Tempo, 36+	1.01 ± 1.50 (5)	0.20 ± 0.18 (5)	1.0 ± 1.8 (3)	0.02 ± 0.04 (3)	18 (1)

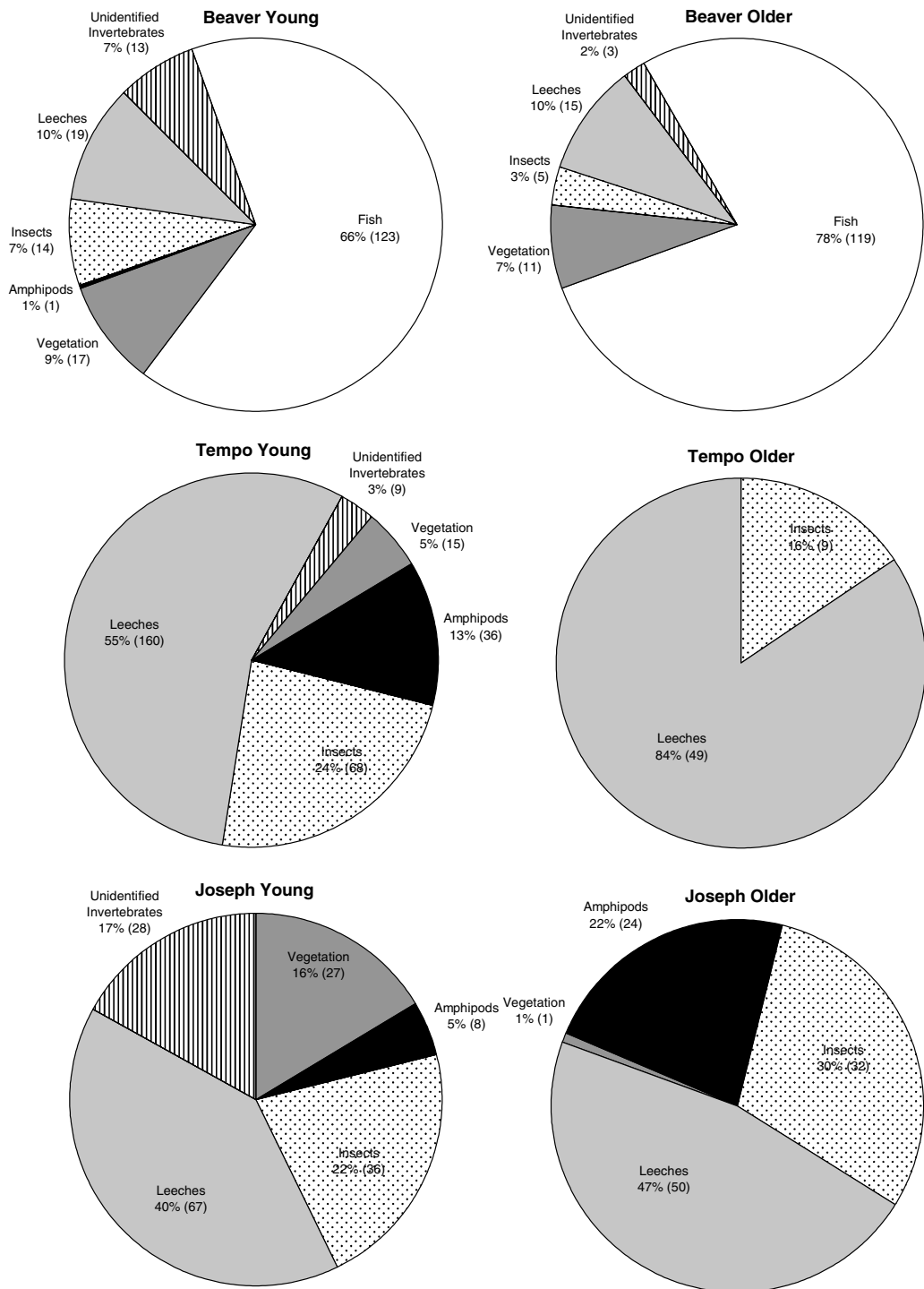


Figure 2. Percentage and number (in parentheses) of prey items fed to Common Loon chicks 1–35 days old (Young) and 36+ days old (Older) on a minnow lake (Beaver Pond) and two fishless lakes (Tempo Pond and Joseph Lake).

remained relatively high and dive rates low on the two fishless lakes (Table 3). Begging rates of chicks on all lakes initially increased with age (Table 3). On the minnow lake, begging rates peaked when chicks were 40–45 days old then declined. The begging rate of the single chick observed to fledging on a fishless lake (Tempo) remained high; the chick begged and was fed by its parents when last observed at 65 days of age.

Prey

The majority of items fed to chicks on Beaver Pond were fish, although both younger and older chicks were also fed invertebrates and vegetation (Fig. 2). Leeches were the most common invertebrates fed to chicks on all lakes, but made up a larger proportion of invertebrate food on the fishless lakes. Leeches and amphipods were more common, and small, unidentified invertebrates less common, in chick diets on Tempo Lake compared to Joseph Lake (Fig. 2).

On each of the three lakes, the prey fed to chicks changed with age, but the change was less marked on Beaver Pond where the contribution of fish simply increased for older chicks while leeches

remained constant (Fig. 2). On both fishless lakes, vegetation virtually disappeared from the diet of older chicks, whereas the proportion of leeches increased (Fig. 2).

Models

The first pair of models (Table 4, model 1), based completely on average observed values for behavioral measures and prey, indicate that adult loons should not be able to meet maintenance energetic requirements on either lake type. For this pair of models, predicted energetic intake on fishless lakes is actually higher than on minnow lakes because the average-sized leech we collected from the lakes was heavier (33 mg, dry weight) than the average-size minnow (18 mg, dry weight) we observed fed to chicks. None of the models for minnow lakes or fishless lakes that included prey of average mass predicted sufficient intake to meet energetic requirements of adult loons, even if diving rates were maximized and success was assumed to be 100%. On the other hand, if adult loons ate only the largest prey items fed to chicks, adults on both lake types could meet their needs under a variety of foraging scenarios involving both mixed

Table 4. Estimated hourly energetic intake for adult Common Loons on minnow and fishless lakes generated by models that used a mixture of values for the variables D_r = foraging dives h^{-1} , D_s = % successful dives h^{-1} , p = proportion of different prey types in diet, and m = mg dry mass of prey

Model number	Variables				Estimated intake	
	D_r	D_s	p	m	Minnow $kJ h^{-1}$	Fishless $kJ h^{-1}$
(1)	Observed average	Observed average	Observed	Observed average	(20.3)	(28.5)
(2)	Observed average	Observed average	Observed	Observed maximum	1300	(210)
(3)	Observed average	Observed average	1 prey type†	Observed maximum	1560	(309)
(4)	Observed average	Observed maximum	Observed	Observed maximum	2160	(298)
(5)	Observed average	100%	Observed	Observed maximum	2210	350
(6)	Observed average	Observed maximum	1 prey type†	Observed maximum	2590	437
(7)	Observed average	100%	1 prey type†	Observed maximum	2640	515
(8)	Observed maximum	Observed average	Observed	Observed maximum	2500	450
(9)	Observed maximum	Observed average	1 prey type†	Observed maximum	2990	663
(10)	Observed maximum	Observed maximum	Observed	Observed maximum	4150	639
(11)	Observed maximum	100%	Observed	Observed maximum	4240	752
(12)	Observed maximum	Observed maximum	1 prey type†	Observed maximum	4970	940
(13)	Observed maximum	100%	1 prey type†	Observed maximum	5070	1110

The pair of models (number 1) based strictly on observed values are presented, plus all models with results $\geq 95\%$ of the required energetic intake value of $363 kJ h^{-1}$ (Barr, 1996) for one or both lake types. Estimates in parentheses indicate that required intake values were not met. † Assumes only leeches (fishless lakes) or fish (minnow lakes) in diet.

Table 5. Estimated hourly energetic intake for young (age 1–35 days) and older (age 36+ days) Common Loon chicks on minnow and fishless lakes generated by models that used a mixture of values for the variables P_r = # prey received via paternal provisioning h^{-1} , D_r = # foraging dives h^{-1} , D_s = % successful dives h^{-1} , p = proportion of different prey types in diet, and m = mg dry mass of prey

Model number	Variables					Estimated intake	
	P_r	D_r	D_s	p	m	Minnow kJ h^{-1}	Fishless kJ h^{-1}
<i>Age 1–35</i>							
(1)	Observed average	Not applicable	Not applicable	Observed	Observed average	(12.2)	(23)
(2)	Observed average	Not applicable	Not applicable	Observed	Observed maximum	985	170
(3)	Observed maximum	Not applicable	Not applicable	Observed	Observed maximum	2080	534
<i>Age 36+</i>							
(4)	Observed average	Observed average	Observed average	Observed	Observed average	(15.5)	(23.9)
(5)	Observed average	Observed average	Observed average	Observed	Observed maximum	801	(170)
(6)	Observed average	Observed maximum	Observed average	Observed	Observed maximum	1430	223
(7)	Observed maximum	Observed average	Observed average	Observed	Observed maximum	2360	348
(8)	Observed maximum	Observed maximum	Observed average	Observed	Observed maximum	3010	401

The two pairs of models (numbers 1 and 4) based strictly on observed values are presented, plus all models with results $\geq 95\%$ of the required energetic intake values of 112 kJ h^{-1} (chicks 1–35 days old) and 224 kJ h^{-1} (chicks 36+ days old; Barr, 1996) for one or both lake types. Estimates in parentheses indicate that required intake values were not met.

diets and single prey types (Table 4, models 5–13). For all models where energy-intake rates met maintenance levels, rates were higher on minnow lakes than fishless lakes.

Comparable to adult models, daily energetic requirements of young and older chicks on both lake types could not be met when models used prey of average size (Table 5, models 1 and 4). This held even when provisioning rates were maximized. However, the energetic demands of young and older chicks on both lake types could be met if adults fed them, and chicks themselves captured, the largest individuals across prey categories (Table 5, numbers 3, 6–8). Again, for models where energy-intake rates met maintenance levels, rates were higher on minnow lakes than fishless lakes.

Discussion

Our study showed that the behavior of common loons differed between small lakes with and without fish in central Alberta, and between Alberta lakes and elsewhere. Unlike red-throated loons, *Gavia stellata* (Pontoppidan), (e.g., Reimchen & Douglas, 1984) and common loons in other localities (e.g., New York, Christoff, 1979; Wisconsin and Michigan, Piper et al., 1997), both members of common loon pairs foraged almost

exclusively on territorial lakes. Loons with and without chicks, resident on lakes since early May, periodically left their lakes for short periods of time at the end of July. Except for cases of abandonment, at least one adult was present with chicks ≤ 2 months old. Short-term departures from territorial lakes by common loons with and without chicks late in the breeding season has also been documented by Piper et al. (1997) and termed “post-reproductive wandering”. They suggested that wandering loons might be investigating future breeding sites, avoiding depletion of food in nesting lakes, or congregating for group foraging.

Consistent with other studies of common loon behavior (see review by Nocera & Taylor, 2000), adults on our study lakes allocated much of their time to foraging. This concentration on foraging occurred whether birds were feeding primarily on small fish or invertebrates. Cairns (1987) proposed that the amount of time that aquatic birds spend foraging is influenced by prey abundance but constrained by the need for other behaviors. Many studies (e.g., Burger & Piatt, 1990; Hamer et al., 1993) have reported increases in the percentage of time birds spend foraging as the abundance of preferred prey declines. Our comparisons of loons on lakes with and without fish indicate that adults on fishless lakes either could not adjust time budgets to procure more food for themselves and

chicks (i.e., foraging effort was already maximized) or an increase was not necessary (i.e., energetic demands were routinely met from an invertebrate prey base). The poor survivorship of loon chicks on fishless lakes (Gingras & Paszkowski, 1999) makes the latter explanation unlikely.

Unlike Nocera & Burgess (2002), who found no relation between common loon dive duration or dive pause (interval between dives) and fish biomass on lakes in Nova Scotia and New Brunswick, we found that adult loons on minnow lakes dove less frequently and spent more time underwater per dive than loons foraging solely for invertebrates. Dive rates are negatively related to dive durations (Ydenberg & Forbes, 1988) but may also be influenced by prey attributes. Compared to fish, large invertebrates are easy to find, pursue and consume, and thus loons on fishless lakes may spend less time underwater per dive than loons foraging for fish. Loons on minnow lakes may also spend more time underwater exploiting prey aggregations in the form of fish schools. Alternatively, invertebrates such as leeches contain somewhat less energy on a unit basis (22.4 J mg^{-1} dry mass, Driver, 1981) than fishes (25.0 J mg^{-1} , for fathead minnow), and are typically smaller. Therefore, loons eating invertebrates may require a larger number of prey per unit foraging time, and consequently dive more frequently than loons eating fishes.

Our data on chick behavior were based on a small sample size, which may limit broad conclusions. Nonetheless, we observed that, as for adults, the behavior of common loon chicks fed invertebrates differed from that of chicks fed primarily fish. Generally, loon chicks on the two fishless lakes spent more time accepting food from their parents and less time foraging for themselves than on the minnow lake. Chicks on the minnow lake developed in an expected manner, i.e., they became less dependent on adults for food and foraged for themselves more frequently as they grew (e.g., Alvo & Berrill, 1992). In contrast, adult provisioning with invertebrates continued to be the primary source of food even for older chicks on fishless lakes. That chicks on fishless lakes showed no compensatory behaviors, such as increased begging or diving, is surprising given that four of the five died before they were 7 weeks old. Loon chicks appear to be capable of such adjustments,

as Parker (1988) reported continuous begging by loon chicks on a fishless acidified lake but not on similar lakes with fish. Perhaps, on our fishless lakes where provisioning rates were high, the chicks would have expended more energy by diving and begging than could be gained by these behaviors. Unlike on the minnow lake, provisioning rates did not decline as chicks aged on fishless lakes, again suggesting that adult foraging efforts were at a maximum on fishless lakes. Similar observations have been reported by Weimerskirch et al. (1997; black-browed albatrosses, *Diomedea melanophris* (Temminck)) and Hamer et al. (1999; manx shearwater, *Puffinus puffinus* (Brünnich)) who found that parents reduce provisioning rates when chicks are well fed but will not or cannot increase provisioning rates when chicks are underfed.

Adult loons in our study fed chicks a variety of food items even when fish were available. In other geographic regions invertebrates and vegetation are also major components of the diet of loon chicks, particularly when young (e.g., Alvo et al., 1988; Parker, 1988; Alvo & Berrill, 1992). We found leeches to be a large part of a chick's diet, especially on fishless lakes. Compared to other invertebrates, leeches have high caloric values and grow quite large, and thus offer an important alternative prey source to fish. Comparing the two fishless lakes, leeches and amphipods made up a larger proportion of the chick's diet on Tempo Lake than on Joseph Lake where aquatic insects were more important items. Sweep-net samples in 1994 and 1995 collected more leeches and amphipods in Tempo Lake than in Joseph Lake, thus diet composition seemed to reflect availability.

In our models, prey size of both fish and invertebrates was the parameter most sensitive to manipulation and determined whether loons met their energetic needs or not. Surprisingly, when combinations of observed foraging patterns, prey composition and prey sizes were used in the model, adult loons and chicks were never predicted to meet their energetic requirements on either type of lake. This pattern held even if dive and provisioning rates were maximized, and prey were limited to the most energetically rewarding leeches and fish.

That adult loons almost never left nesting lakes during the first month of the breeding season indicates they must have been meeting energetic

requirements and foraging on prey of adequate size. Thus, our visual estimates (comparing food caught to bill length) may have systematically underestimated prey size. Indeed, when maximum observed prey size was used in models, energetic requirements were met for both adults and chicks. Further, the actual diets of adult loons likely differ somewhat from the surrogate measure we used (i.e., food fed to chicks). The ability of adults to eat larger prey than chicks, capture and swallow several prey during a single dive, as well as consume the occasional very large prey, may all contribute to our models underestimating energy intake for adults. The average estimated length of fish fed to chicks was less than 2 cm and likely represents young-of-the-year minnows. When the model is used to back-calculate prey size, it shows that on minnow lakes, loons would be able to meet their energetic needs of 363 kJ h^{-1} by eating fish weighing 397 mg (dry mass) or larger if loons dove at an average rate, with an average rate of success. This is about the size of a small adult fathead minnow in this region (W. M. Tonn, University of Alberta, unpublished data) and falls between our observed average (18 mg dry mass) and maximum (1407 mg dry mass) prey sizes for minnows. Obtaining more accurate measures of the size of prey seems to be key to improving future estimates of energetic intake.

For most of the models based on adult and/or chick behavior, energetic intake was higher on minnow lakes than on fishless lakes. Energetic needs would have been met on minnow lakes but not on fishless lakes in four out of 18 model scenarios (22%). Thus, despite some behavioral adjustments by adults and young, survival of chicks to fledging on small lakes offering only invertebrate prey appears more tenuous than on small lakes containing fish. Our regional surveys indicate that chicks hatched on minnow lakes generally survive to fledging, however, nine of 10 chicks hatched on fishless lakes failed to fledge in 1993–1995 (Gingras & Paskowski, 1999). In two cases, adults on fishless lakes abruptly abandoned chicks 3–4 weeks old (Gingras, 1997). Abandonment could have reflected deteriorating foraging conditions; invertebrates are still abundant in midsummer, but water levels drop in these shallow lakes and submerged macrophyte beds become extremely dense. By abandoning or neglecting chicks, adult loons are behaving comparably to

other long-lived species of birds (e.g., arctic skuas, *Stercorarius parasiticus* (L.), Phillips et al., 1996) that under poor food conditions shunt the costs of reproduction to current chicks rather than jeopardize future reproduction.

Our study indicates that common loons are more flexible in their foraging patterns and reproductive habitats than commonly thought. In central Alberta, they regularly use small lakes for breeding, including lakes without fish. Indeed, nearly every lake in the study area was occupied by common loons. Although our energetic models and foraging observations indicate that productive small lakes can offer adequate feeding conditions to support adult loons for months, and these adults can fledge young (Gingras & Paszkowski, 1999), breeding success on these lakes is clearly lower than on larger, deeper lakes in the region that have larger fish populations and more diverse fish assemblages (Gingras & Paszkowski, 1999). It is possible that small lakes are habitat primarily for “marginalized” younger pairs, and appear to play an important, but under appreciated role in the ecology of common loons in the western boreal forest of North America.

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Assessment of mercury exposure and potential effects on common loons (*Gavia immer*) in Québec

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Abstract

Results from recent studies report increases in mercury in the environment and increased bioaccumulation in aquatic food webs. The Canadian Wildlife Service (CWS) and the Canadian National Park Service initiated this study to determine whether common loons (*Gavia immer*) are exposed to sufficiently high mercury concentrations in prey fish to impair their reproduction and survival. Monitoring of loon reproduction, measurement of lake physicochemistry, and fish sampling for mercury analysis were conducted in various regions in Québec, Canada, during summers from 1997 to 2002. Reproductive success was assessed and loons were captured at night and banded. Blood and feathers were collected to measure mercury. Mean blood and feather Hg concentrations in males (2.6 µg/g w.w and 17.6 µg/g d.w.) and females (1.8 µg/g w.w and 8.9 µg/g d.w.) were within the normal range of samples from north-eastern North America. However, one third (33%) of the loons sampled had mercury levels in blood or feathers exceeding the high risk levels for health and reproduction. Loons from western Québec showed significantly lower Hg levels than those from eastern Québec, both in blood and feathers. This study will help to determine the potential effects of mercury on the Québec and North-American loon population and provide information to assist in decisions on pollution abatement policies.

Introduction

Many recent studies report increases in mercury (Hg) from anthropogenic sources in the environment and increased bioaccumulation in aquatic food webs (Fitzgerald et al., 1998; Scheuhammer & Graham, 1999). Analysis of sediment cores from lakebeds indicates that current rates of Hg deposition are greater than pre-industrial levels (Lucotte et al., 1995; Kamman & Engstrom, 2002). Studies comparing fish Hg concentrations with rates of atmospheric deposition have found that these sources account for much of the Hg loading into aquatic ecosystems (Fitzgerald, 1995; Lucotte et al., 1995; Rudd, 1995). Levels of

mercury in fish in many regions of eastern North America are high enough to affect reproductive success and health of piscivorous birds like the common loon *Gavia immer* (Brunnich) and mammals. Elevated methylmercury (MeHg) levels have been demonstrated to affect the behavior, reproduction, and survival of wildlife (Eisler, 1987; Thompson, 1996; Wiener & Spry, 1996), are related to neurological, immunological, and genetic toxicosis (Wolfe & Norman, 1998), and disrupt the biochemical functions with cortisol (Friedmann et al., 1996) in fish and cholinesterase in quail (Dieter, 1974). Organisms at the top of the aquatic food chain can be affected by higher mobilization of metals caused by acidity and their

accumulation in fish, in addition to being affected by ecological changes resulting from acidification (Scheuhammer, 1991; Wiener & Spry, 1996). Although sulfate depositions have been declining markedly since 1990, current deposition levels are still above the critical load in sensitive regions of eastern Canada and southwestern Québec (Jeffries et al., 2003). The common loon is a useful indicator of mercury in the environment (Meyer et al., 1995; Burgess et al., 1998a, b; Evers et al., 1998; Evers et al., 2003) and of recovery of aquatic food chain from acidification because of its longevity, fidelity to breeding territory on freshwater lakes, obligate piscivorous diet and ease of observation (McNicol, 2002). Although mercury exposure in loons has been reported from various regions across North America (Meyer et al., 1995; Burgess et al., 1998a, b; Meyer et al., 1998; Scheuhammer et al., 1998; Evers et al., 1998), no study has focused on regions of high acid deposition in Québec.

This paper presents the results of a study initiated in 1997 to document Hg contamination in loons in regions of high acid deposition in Québec and determine whether they are exposed to Hg concentrations in prey fish sufficiently high to impair their reproduction and survival. We present Hg concentrations in loon blood, feathers and eggs as well as in prey fish. We examine the relationships between Hg contamination, lake pH and characteristics, and loon productivity.

Methods

Sample collection

From 1997 to 2002, common loons were surveyed and sampled on 24 lakes from various regions in Québec: Outaouais, La Mauricie and the Laurentides. Sites were selected on the basis of available information on productivity and included La Mauricie National Park (LMNP), three wildlife provincial reserves, Portneuf, Mastigouche and St. Maurice Reserves, Mont-Tremblant Park and lakes outside the parks (Fig. 1). Most lakes were situated on the Precambrian shield and remote from point source Hg emissions. Loons were captured from canoes and small motorboats using

the night lighting capture technique developed by BioDiversity Research Institute (Evers, 2001). A million-candlepower spotlight, tape recordings and mimicked vocalizations of loon calls attracted family groups to the boat. Individual loons were caught with a large landing net, restrained, and brought to shore. Both second secondary flight feathers were removed from adult birds by cutting at the calamus (below the base of the feather vane). Blood samples were taken from the medial metatarsal vein with 20–25 gauge butterfly needles fitted with multiple sample Luer Adapter into 7 cc Vacutainers[®] containing powdered sodium heparin (green top), 5 cc Vacutainers[®] containing calcium EDTA (purple top), and 5 cc Vacutainers[®] containing no additive (red top). All loons were uniquely marked with an aluminum USFWS band and 1–3 colored leg bands glued with an acetone-based adhesive. Finally, each individual was weighed prior to being released unharmed in its respective territory. Each family was monitored to ensure that adults and juveniles regrouped after capture. Unhatched eggs from failed nesting attempts were also collected opportunistically. Detailed productivity information on breeding loons was available for lakes in LMNP since 1987 as well as for lakes from the Canadian Lakes Loon Survey (McNicol et al., 1995). On other lakes, productivity data were collected as much as possible through the study period.

Small fish of various species representative of loon prey (10–20 cm; Barr, 1996), were collected from the lakes using minnow traps, nets or angling with worms. Fish were sacrificed with a blow on the head, stored in whirl-paks, placed on ice and frozen within 48 h of collection. Fish were later thawed, measured (total length), weighed and homogenized in composite samples of 3–5 whole fish of like species for Hg analysis.

Detailed lake physicochemical data were available from LMNP and a few others. On other lakes, an integrated water sample (generally 1–5 m depth) was collected in the middle of the lake with a van Dorn sampler. pH was measured in the field with a portable Oakton pH-meter and secchi depth was also taken. In addition to those sampling efforts, data on loon productivity and physicochemistry were collected and small fish were sampled on an additional set of lakes to

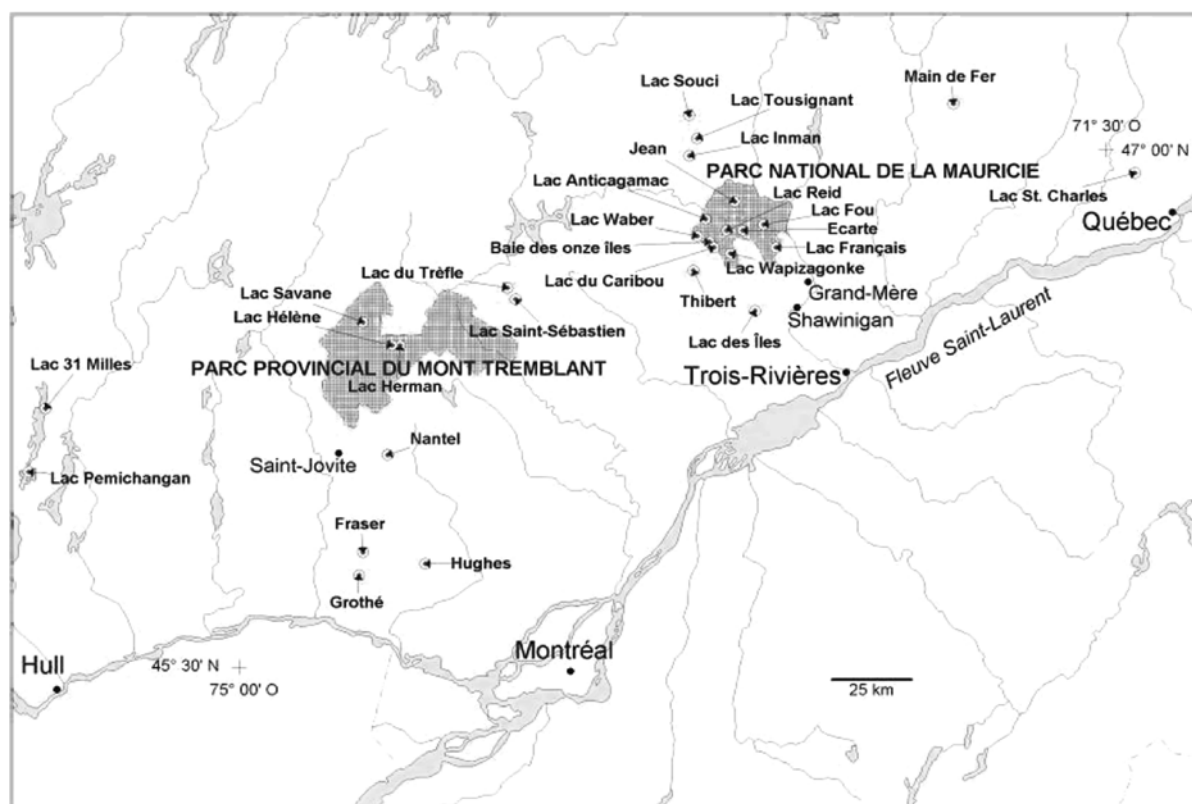


Figure 1. Common loon study sites and lakes sampled in Québec, 1997–2002. Location of major cities also shown.

increase sample size, in order to further document factors responsible for variation in loon productivity.

Sample analysis

One feather from each adult and a blood sample from each individual loon were analyzed for total Hg concentrations at the National Wildlife Research Centre (NWRC, Ottawa, Canada) of the Canadian Wildlife Service, following the standard procedure described in the Laboratory Services Manual under MET-CHEM-AA-03D and MET-CHEM-AA-03E (Neugebauer et al., 2000). The NWRC also analyzed all fish and egg samples. Feathers were cut (calamus discarded) and washed in Triton X, acetone and deionized water, dried in a clean air station, digested overnight and diluted to volume. An aliquot of the sample was then taken and analyzed for total Hg by cold-vapor atomic absorption spectrometry (3030-AAS,

Perkin-Elmer). A 100 mg aliquot of each homogenized whole blood sample was digested with 2 ml conc. HNO_3 overnight, diluted to volume with ultra pure water, and analyzed by cold-vapor atomic absorption spectrometry. Eggs and fish samples were freeze-dried, digested and analyzed. After 2001, total mercury in the blood, fish and egg samples was determined without acid digestion on the AMA-254 (Advanced Mercury Analyzer, ALTEC, Czech Republic) which employs direct combustion of sample in an oxygenated decomposition furnace, and feather samples were acid digested and analyzed on the AMA-254. Quality assurance results on reference materials and interlab check samples from the CFIA (Canadian Food Inspection Agency) gave confidence that the instrument gives accurate readings comparable to CVT-AAS. The accuracy was determined by concurrent analysis of standard reference materials (SRM DOLT-2 and DORM-2, National Research Council of Canada, Ottawa, Canada), procedural

blanks and random duplicate samples. All recoveries of Hg from reference materials were within the certified range. The mean (\pm SE) recovery of 26 SRM analyses was 97.5 ± 8.4 with a range of 80–116%. Both methods' detection limits were 1.0 ng/g. A few chick blood samples as well as samples from the Outaouais region were analyzed at the Animal Health Diagnostic Laboratory at Michigan State University in 1997 and the University of Pennsylvania in 1998, 1999 and 2001 following comparable protocols.

Statistical analysis

Normal distribution of data was tested prior to other analyses and was found to be abnormal for most variables. Mean Hg levels in blood and feathers were compared between adults, chicks, sex, lake and regions using the non-parametric Kruskal–Wallis test. Mercury levels of adults captured twice were averaged. For lake and region comparisons, Hg levels of males, females and chicks were averaged by lake. Non-parametric Spearman rank correlations were calculated among variables. Loon and fish Hg concentrations were log-transformed to calculate linear regressions. All statistics were calculated using JMP™ Software (SAS Institute, 1999).

Results

Lake morphometry and physicochemistry

Lakes surveyed had a surface area varying from 0.1 to 49.7 km² and a drainage area between 1.3 and 165 km² (Table 1). Mean pH was 6.30 for the 24 lakes where loons were sampled and 6.74 for all the lakes monitored. pH was higher in the western region of Outaouais, probably because of catchment geology.

Mercury in loon blood, feathers and eggs

Between 1997 and 2001, 85 loons were sampled on 24 lakes. Of those, 58 were adults (34 males four of which were recaptures and 24 females) and 27 chicks. Blood and feather Hg concentrations for adults and chicks are presented in Table 2. Adult males had significantly higher feather Hg

concentrations than females ($p < 0.001$). Chicks had significantly lower blood Hg concentrations than males ($p < 0.0001$) and females ($p < 0.0001$). A significant difference also appears among regions: loons from western Québec (Outaouais region: lakes Pemichangan and Trente-et-un-Milles) show lower Hg levels than those from eastern Québec, both in blood (males: $p < 0.001$; females: $p < 0.001$) and in feathers (males: $p < 0.01$; females: $p < 0.04$). This difference was not related to difference of size, since males and females from both regions were not different in size ($p = 0.32$). Mean mercury concentrations in 10 eggs collected from 9 lakes in the eastern region was 0.74 $\mu\text{g/g}$ w.w. (range 0.42–1.55 $\mu\text{g/g}$ w.w.).

At Lac des Iles, in La Mauricie region, adult and juvenile blood Hg concentrations were double those at other sites in Québec. The only chick for which Hg was measured in feathers came from that lake and showed a high level for a chick despite its large weight (blood: 1.80 $\mu\text{g/g}$; feather: 26.68 $\mu\text{g/g}$). One male from Lac Caribou, captured twice, had a feather Hg concentration more than two times higher than any other loon in this study (54.9 and 83.04 $\mu\text{g/g}$, mean 68.97 $\mu\text{g/g}$).

Feather Hg levels were positively related to blood Hg levels in both males (Spearman $r = 0.77$, $p < 0.0001$) and females ($Sr = 0.73$, $p < 0.001$). Male blood Hg levels were positively related to female blood Hg levels ($Sr = 0.83$, $p < 0.001$), however, male feather Hg levels were not related to female feather Hg levels. Egg Hg levels showed a significant relation with female blood Hg ($Sr = 0.81$, $p = 0.05$), while chick Hg levels were marginally related to female blood Hg levels ($Sr = 0.58$, $p = 0.06$).

Loon productivity

Productivity information on breeding loons in LMNP has been collected for 16 years. Productivity information has also been collected for many other lakes in Québec by volunteers in the Canadian Lakes Loon Survey, a program administered by Bird Studies Canada (McNicol et al., 1995). CWS also monitored a number of other lakes. The mean productivity (number of chicks fledged per territorial pair per year) in Québec for the past 6 years (1997–2002, minimum 3 years of data per lake needed to use the data) is 0.57 ± 0.38 ($n = 76$

Table 1. Morphometry and physicochemistry data for lakes sampled and monitored in Québec

	Lake sampled ($n=24$)					Lake monitored ($n=77$)				
	n	Mean	SD	Min	Max	n	Mean	SD	Min	Max
Lake area (km ²)	24	3.9	9.8	0.1	49.7	76	2.3	6.1	0.1	49.7
Drainage area (km ²)	11	36	48	1	166	28	18	33	1	166
Altitude (m)	24	311	106	152	511	76	320	137	151	804
Maximum depth (m)	20	32	17	6	88	41	30	18	5	88
pH	23	6.30	0.67	4.59	8.28	76	6.73	0.87	4.59	8.84
Alkalinity (mg/L)	11	3.7	5.2	-0.9	20.1	30	2.8	3.4	-0.9	20.1
Secchi depth (m)	23	5.0	1.5	2.3	7.6	72	4.8	1.5	1.3	8.0
DOC (mg/L)	11	3.8	1.1	2.5	6.7	30	4.5	1.4	2.5	8.2

territories, range 0–1.67). The mean productivity for the 24 lakes where loons were sampled was 0.68 ± 0.35 (range 0–1.5). No relationship was observed between loon productivity and associated loon Hg levels for the territories sampled in Québec.

Mercury in fish

Mean Hg concentrations in prey size fish (10–20 cm) from the 24 lakes where loons were sampled was 0.15 ± 0.06 $\mu\text{g/g}$ w.w. (range 0.06–0.32). Mean Hg levels in prey size fish from all the lakes where small fish were sampled was 0.14 ± 0.07 $\mu\text{g/g}$ w.w. (range 0.03–0.34, $n=56$). Most common fish species collected were Yellow Perch, *Perca flavescens* (Mitchill), Creek Chub, *Semotilus atromacul-*

atus (Mitchill), Pumpkinseed, *Lepomis gibbosus* (L.), and Brook Trout, *Salvelinus fontinalis* (Mitchill). Yellow perch was the target species and was used wherever possible, but was obtained in only 6 of the 24 lakes. Fish from Lake Pemichangan, in Outaouais, where loon Hg levels were lower, had Hg levels in the lower portion of the range but comparable to other lakes from eastern Québec (18.5 cm yellow perch: 0.10 $\mu\text{g/g}$ w.w.; 12.9 cm pumpkinseed: 0.05 $\mu\text{g/g}$ w.w.). There was a significant positive relationship between Hg levels in fish and Hg levels in male, female and chick blood (Fig. 2) as well as in female feathers, but not between Hg levels in fish and loon productivity (Table 3).

Relationships with lake parameters

Within the 24 lakes where loons were sampled, pH show significant negative relationships were detected between pH and Hg levels in male blood (Fig. 3a) and feathers (Table 3). No significant relationship was detected between Hg levels in fish and loon productivity at these lakes. Lake area, perimeter, altitude and dissolved organic carbon (DOC) all show significant relationships with loon Hg levels (Table 3). Hg levels tend to decrease with increasing lake area and perimeter, and increase with increasing altitude and DOC. Adding the additional lakes allowed the detection of other relationships. With 77 lakes, we find that loon productivity tends to increase with lake drainage area ($S_r=0.47$, $p<0.01$) and pH ($S_r=0.30$, $p<0.01$), and fish Hg tend to increase with DOC ($S_r=0.48$, $p<0.01$) and decreasing pH ($S_r=-0.43$, $p<0.001$; Fig. 3b).

Table 2. Mean (standard deviation and range) weight and blood and feather mercury concentrations for adult common loons and chicks in Québec

	N	Weight (g)	Blood Hg ($\mu\text{g/g}$ w.w.)	Feather Hg ($\mu\text{g/g}$ d.w.)
Males	34	4735 (671) 2650–5750	2.55 (2.19) 0.32–11.19	17.59 (14.88) 5.00–83.04
West	10		0.69 (0.29)	9.86 (3.37)
East	24		3.32 (2.18)	20.81 (16.63)
Females	24	3804 (424) 3250–4700	1.77 (1.94) 0.17–8.29	8.87 (4.06) 3.30–20.86
West	8		0.51 (0.23)	6.21 (2.34)
East	16		2.40 (2.12)	10.04 (4.16)
Chicks	27	1779 (810) 400–3700	0.35 (0.37) < 0.0125–1.80	26.68 ($n=1$)
West	1		0.01	–
East	26		0.36 (0.37)	26.68 ($n=1$)

Table 3. Spearman correlations ($p < 0.05$) between loon mercury concentrations and other variables ($n = 24$ lakes)

	Fish Hg	Male blood Hg	Male feather Hg	Female blood Hg	Female feather Hg	Chick blood Hg
Fish Hg		0.45		0.79**	0.74*	0.73*
Lake area	-0.39			-0.49	-0.51	-0.64*
Perimeter					-0.49	-0.56
Altitude		0.43				
DOC				0.75		
pH		-0.78**	-0.65*			

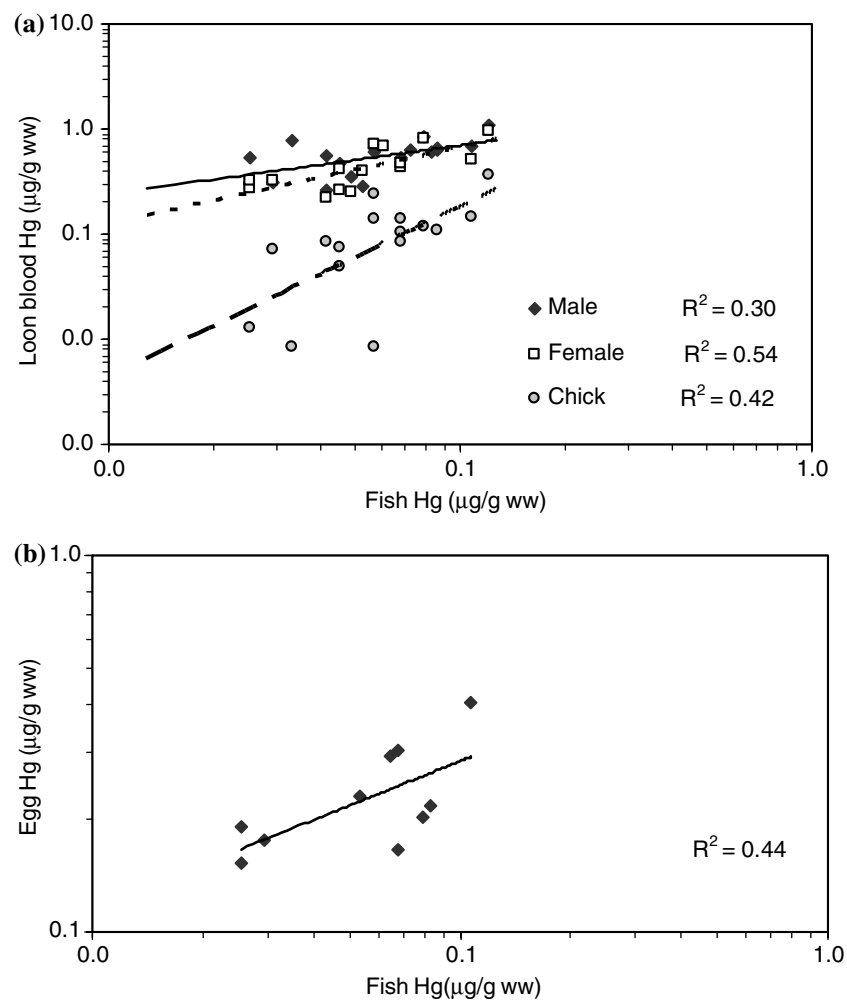
* $p < 0.01$.** $p < 0.001$.

Figure 2. Fish mercury concentrations in relation to: (a) loon blood mercury concentrations (males, females and chicks); (b) loon egg mercury concentrations.

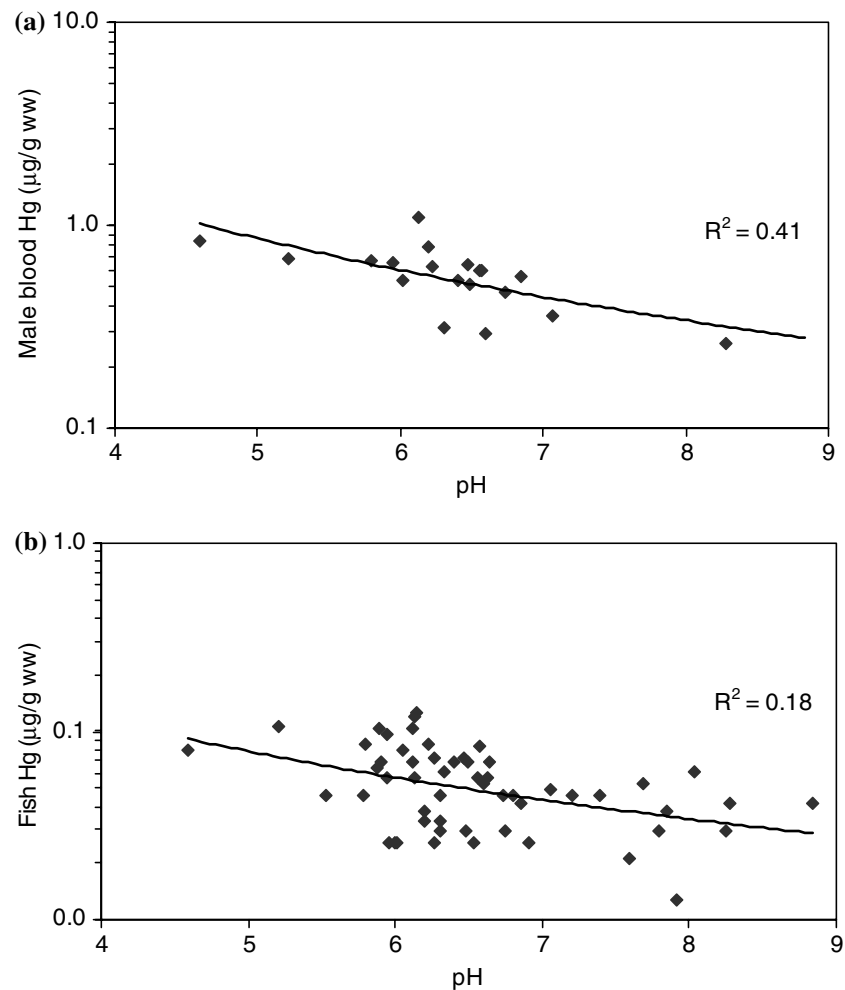


Figure 3. Lake water pH in relation to: (a) male loon blood mercury concentrations; (b) fish mercury concentrations.

Risk evaluation

Previous studies by the authors and their collaborators as well as literature were used to develop risk categories for three matrices (Evers et al., 2002, 2003; Table 4). Low risk indicates background levels. Moderate risk comprises loons from territories with elevated MeHg availability but levels most likely do not impact individuals. Loons in the high risk category are exposed to toxic levels of Hg that have potential effects on the organism. The extra high category comprises Hg levels with known impacts on loons and other birds. Mean concentrations in Québec loons are moderate and within the normal range of North-east samples, however, 33% of individuals (26% of

adults and 48% of chicks) exceeded the threshold level for high risk in blood and, 17% (15% of adults and 22% of chicks) exceeded the threshold for extra high risk in blood. Loons from eastern Québec appear to be second after Nova Scotia's loons in terms of risk from the negative effects of Hg exposure in North America (Fig. 4).

Discussion

Adult male loons typically have higher Hg levels than females in both blood and feathers (Evers et al., 1998). The differences in Hg concentrations between sexes could be attributed to different prey selection by the two sexes. Male common loons are

Table 4. Risk categories for methylmercury availability in the Common Loon

Matrix	Low	Moderate	High	Extra high	Reference
Eggs ($\mu\text{g/g}$ w.w.)	0–0.6	0.6–1.3	1.3–2.0	>2.0	Barr, 1986; Evers et al., 2002
Blood-adult ($\mu\text{g/g}$ w.w.)	0–1.0	1.0–3.0	3.0–4.0	>4.0	BRI ^a
Blood-juvenile ($\mu\text{g/g}$ w.w.)	0–0.1	0.1–0.3	0.3–0.4	>0.4	Meyer et al., 1998
Feather ($\mu\text{g/g}$ d.w.)	0–9.0	9.0–20.0	20.0–35.0	>35.0	BRI ^a , Thompson, 1998

^aBRI: Biodiversity Research Institute.

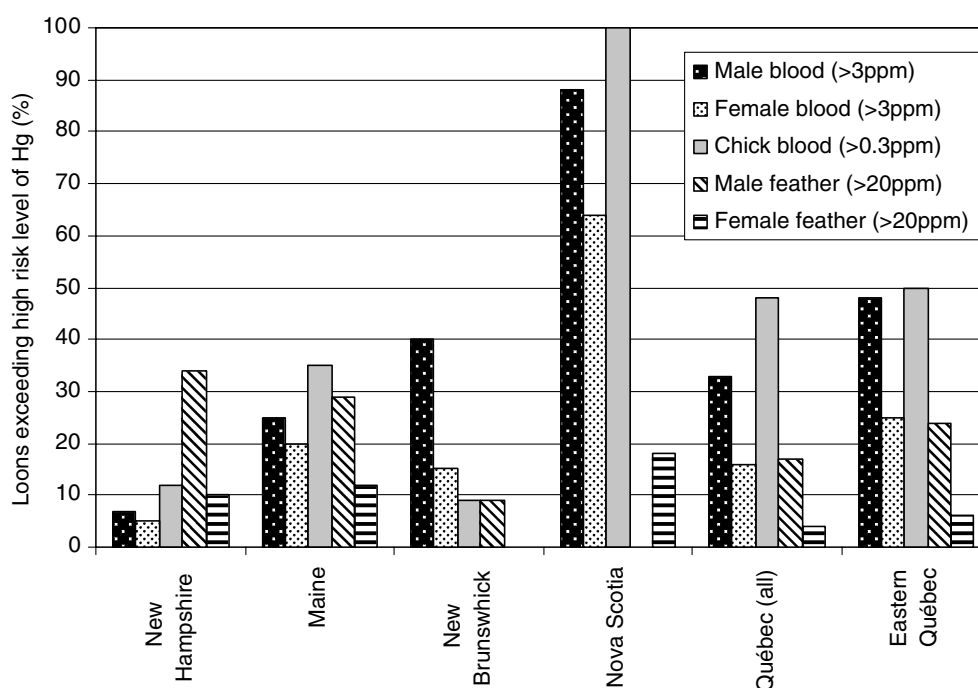


Figure 4. Common loons exceeding high-risk level of mercury in blood and feathers across North America.

bigger than the females and therefore may select and consume bigger fish with higher Hg concentrations. In addition, females can depurate some of their Hg burden in eggs.

On average, blood and feather Hg concentrations in loons from Québec are comparable to the mean of the Northeast but are elevated in comparison with control sites in the Northwestern United States and Alaska (Evers et al., 1998). Hg concentrations in loons from western Québec are low and similar to Alaska concentrations, while those from eastern Québec are higher than in other northeast areas except Nova Scotia. Many factors may be playing a role in this difference among the two regions. Only two very large lakes with many

loon territories were sampled for loons in the western region. Those lakes have a basic pH (8.28), probably because of a different catchment geology. Those factors may well explain the lower bio-magnification of Hg in the food chain of those two lakes.

Adult whole blood and feather Hg concentrations across North America show a highly significant positive relationship ($F=55.4$, $p<0.001$), however, the correlation coefficient is weak ($r^2=0.20$; Evers et al. 1998). The significance of the blood–feather relationship increases from west to east with increasing Hg concentration.

Blood represents a good indicator of recent dietary Hg uptake while feathers are recognized as

a major excretory pathway for Hg (Evers et al., 1998). Nearly all Hg in the blood is MeHg bound to erythrocytes and because the half-life of MeHg in avian blood is 2–3 months (Scheuhammer, 1988), it is one of the better matrices for determining exposure on a breeding lake. Wolfe & Norman (1998) showed a significant correlation between blood and brain Hg. Feather Hg, which is sequestered in the winter during a full remigial molt, is directly related to breeding ground Hg ingestion at sites with high Hg concentrations in the prey. Loons breeding on lakes with low Hg levels do not bioaccumulate high amounts of Hg and therefore do not have extra Hg to excrete into their feathers.

Blood Hg concentration in juveniles is an excellent indicator of local Hg availability, since loon chicks are fed exclusively from the natal territory. The chicks large enough to sample had high blood Hg burdens for their age compared with those presented in Evers et al. (1998) for North America (mean 0.16 $\mu\text{g/g}$, range 0.03–0.78 $\mu\text{g/g}$). However, other piscivorous species also had similar or higher levels. Great Blue Heron chicks, *Ardea herodias* (L.), from the St. Lawrence River had mean blood and feather Hg concentrations of 0.66 and 5.21 $\mu\text{g/g}$ (Champoux et al., 2002). Mean blood and feather Hg concentrations in Osprey chicks, *Pandion haliaetus* (L.), from hydroelectric reservoirs were 1.94 and 37.35 $\mu\text{g/g}$ (DesGranges et al., 1998).

Adult loons from Lac des Iles had extremely high blood Hg levels but moderate feather concentrations, suggesting that the breeding adults were relatively young birds, and had not had time to bioaccumulate Hg. The high Hg levels in birds from Lac des Iles could be explained in part by the fact these birds were among the heaviest loons captured and hence may consume larger fish with higher Hg levels. One 16 cm Yellow Perch from this lake had a Hg concentration of 0.32 $\mu\text{g/g}$. Lac des Iles is a relatively small lake (0.6 km²), moderately acidic (pH=6.1) and with a moderate secchi depth (4.1 m), factors that may contribute to some biomagnification of Hg but do not explain completely the high levels observed.

Egg Hg levels are comparable to those from New England (Evers et al., 2003) and Canada (Scheuhammer et al., 2001). The significant positive relationship between female blood Hg and egg

Hg reflects the depuration route of MeHg from females to eggs (Evers et al., 2003). Although these authors found that egg Hg concentrations reflect prey Hg from the lake, this relation was not significant for our small dataset ($n=10$, $Sr=0.58$, $p=0.08$). One other factor that may explain this weak relation is that although eggs and females came from the same lake, they were not necessarily from the same territory or sampled the same year.

Productivity information on breeding loons in Québec has been collected for the past several years. In northern Saskatchewan, stable populations produce 0.535 fledged young/pair/year (McIntyre & Barr, 1997). The 25-year mean loon productivity for New Hampshire is 0.52 ± 0.09 birds/territorial pair/year (K. Taylor, pers. com.). For comparison, the number of fledged chicks/territorial pair/year in Kejimikujik National Park, Nova Scotia was 0.28, the lowest productivity among sites currently included in the North American Loon Biomonitoring Program (Kerekes & Masse, 2000). The blood mercury levels in Kejimikujik Park were significantly greater than those in all other study areas. In the Maritimes, the maximum productivity of loons with low blood mercury (<2.5 $\mu\text{g/g}$) was 1.0 fledged young per territorial pair, while loons with high blood mercury (>6.0 $\mu\text{g/g}$) produced only 0.2 fledged young per pair (Burgess et al., 1998b). These authors observed a pattern between productivity and loon blood Hg similar to that observed in Québec: although it was clear that loons with high Hg levels always had poor reproductive success, the correlation was not significant. In this study, Hg appeared to limit the nesting rate of territorial pairs and their hatching success (Burgess et al., 1998b). Many factors may affect chick survival and no apparent relationship was observed between productivity and associated Hg levels for the territories sampled in Québec. Meyer et al. (1998) found that four to 8 week old loons with blood Hg levels of 0.30 $\mu\text{g/g}$ or higher were associated with territories where fewer chicks hatched or survived to 8 weeks of age.

Barr (1986) found reproductive impairment in loons (e.g., reduced egg laying and territorial fidelity) feeding on fish with 0.30 $\mu\text{g/g}$ Hg and no reproduction in loons feeding on fish with 0.40 $\mu\text{g/g}$ or more. Evers et al. (2002) present evidence to suggest that the threshold prey Hg concentration is closer to 0.15 $\mu\text{g/g}$ w.w. Although forage fish with Hg concentrations higher than

0.3 $\mu\text{g/g}$ have been found in many areas (Evers et al., 1998; Burgess & Hobson, 2004), we only found three samples with this level and mean lake fish Hg levels were below 0.3 $\mu\text{g/g}$. A total of 24 lakes out of 56 (43%) have fish Hg levels over 0.15 $\mu\text{g/g}$. The different trophic levels occupied by the various species of fish that we were able to sample in our lakes explain the weakness of some of the relationships observed. Yellow perch is considered the preferred prey of loons (Barr, 1996) and is known to accumulate Hg, however, it could not be sampled on all lakes. Other common species like the brook trout generally have lower Hg levels at loon prey size, although bigger specimen can accumulate higher levels. Fish community structure and benthic invertebrate populations may also influence Hg bioaccumulation (Wong et al., 1997).

Threshold blood Hg levels of effects in adults are relatively unknown. Evers et al. (2002) have categorized adult loon blood Hg levels based on qualitative observations of effects in the wild and associations with highly contaminated lakes. Adult loons with blood Hg levels of 2–3 $\mu\text{g/g}$ are considered at moderate risk and those over 3 $\mu\text{g/g}$ are at high risk to effects from Hg contamination. Fourteen (10 males and 4 females) of the 54 adult loons sampled (26%) and 13 (48%) of the 27 chicks sampled in Québec were in the high-risk category. All loons captured on Lac des Iles were at extra high risk to Hg contamination.

Feather Hg threshold levels vary according to feather type and bird species. Few species other than seabirds and raptors typically have feather Hg concentrations greater than 15 $\mu\text{g/g}$ (Burger, 1993). Eisler (1987) considered 5 $\mu\text{g/g}$ while Heinz (1979) suggested 9 $\mu\text{g/g}$ Hg as a LOAEL for feathers. Scheuhammer (1991) and Thompson (1996) consider a higher risk threshold of 20 $\mu\text{g/g}$ and the co-authors have observed abnormal behavior in loons with feather Hg above 30 $\mu\text{g/g}$ (Evers and Lane, pers. com.). Of the 30 adult male birds sampled 5, or 17%, exceeded 20 $\mu\text{g/g}$ in Québec. The high feather Hg level in the male from Lac Caribou is the highest known feather Hg of any loon tested in North America. Only one female loon exceeded the 20 $\mu\text{g/g}$ threshold. One juvenile loon captured on Lac des Iles had a feather concentration of 26.7 $\mu\text{g/g}$, the highest concentration ever recorded in a hatch year loon. Four of the ten eggs collected in

Québec (40%) were in the moderate class and one (10%) in the high class.

Lakes that pose a high risk to loons are those with high fish Hg concentrations, which is influenced, among others, by low pH, high dissolved organic carbon and large watersheds (Scheuhammer & Blancher, 1994; Evers et al., 1998; Meyer et al., 1998; Scheuhammer et al., 1998). Meyer et al. (1998) found a negative linear relationship between log of chick and adult blood Hg and pH. Addition of acid-neutralizing capacity and lake area improved the relationship for chicks but not for adults. Meyer et al. (1998) also found a negative linear relationship between chick blood Hg and productivity. In a controlled study, Kenow et al. (2003) observed a lake-source effect, chicks from low pH lakes showed a lower growth rate than chicks from neutral pH lakes. Authors attributed this finding to in ovo exposure to MeHg. Our data also confirm the importance of fish Hg, pH, lake area and DOC, however, other environmental and ecological processes like fish and invertebrate populations also need to be considered.

Conclusion

Mean blood and feather Hg concentrations in loons from Québec are comparable to those from other locations in Northeast North America but are elevated in comparison with control sites in the North-western United States and Alaska. However, 26% of the adult loons and 48% of juvenile loons exceeded the threshold level for high risk in blood. Loons from eastern Québec appear to be second after those from Nova Scotia in terms of risk to the negative effects of Hg exposure in North America. High Hg levels were linked to high lake acidity. Further research and monitoring are needed to clarify the relative importance of environmental and ecological processes in Hg transfer and adequately protect loons and aquatic ecosystems.

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Bioaccumulation of mercury in yellow perch (*Perca flavescens*) and common loons (*Gavia immer*) in relation to lake chemistry in Atlantic Canada

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Abstract

Mercury biomagnifies in aquatic foodwebs in freshwater lakes, and common loons (*Gavia immer*) breeding in eastern Canada can be exposed to reproductively toxic concentrations of mercury in their fish prey. We assessed the bioaccumulation and biomagnification of mercury in juvenile and adult common loons, and their preferred prey: yellow perch (*Perca flavescens*) in Kejimikujik National Park (KNP), Nova Scotia by measuring mercury levels and stable isotope ratios in tissues. Total mercury levels and stable-carbon ($\delta^{13}\text{C}$) and nitrogen isotope ratios ($\delta^{15}\text{N}$) were determined in composite whole-fish samples from lakes in KNP and blood samples from juvenile and adult loons captured on lakes in KNP and southern New Brunswick. Geometric mean mercury concentrations were 0.15 and 0.38 $\mu\text{g/g}$ (wet wt.) in small (9-cm fork length) and large (17-cm fork length) yellow perch, and were 0.43 and 2.7 $\mu\text{g/g}$ (wet wt.) in blood of juvenile and adult common loons, respectively. Mercury concentrations in perch and loons were positively associated with body mass and $\delta^{15}\text{N}$ values. Juvenile loons and large yellow perch had similar mercury levels and $\delta^{15}\text{N}$ values, indicating similar trophic status despite their 22-fold difference in body mass. Mercury concentrations were higher in yellow perch and common loons in acidic lakes. Our findings highlight the importance of both chemical and ecological factors in understanding mercury biomagnification in lakes and associated risks to fish-eating wildlife.

Introduction

Elevated mercury (Hg) concentrations are often found in common loons, *Gavia immer* (Brünnich), their eggs, and young in Atlantic Canada (Burgess et al., 1998a, in press; Daoust et al., 1998; Evers et al., 1998; Scheuhammer et al., 2001). High Hg levels in common loons are associated with reduced reproductive success (Barr, 1986; Burgess et al., 1998b; Meyer et al., 1998), smaller egg size (Evers et al., 2003), and altered behaviour (Nocera & Taylor, 1998; Olsen et al., 2000). Recent concerns about possible population-level effects of aquatic Hg contamination on common loons are focused on northeastern North America

(Scheuhammer & Blancher, 1994; Evers et al., 2003), where exposure of breeding loons to Hg is greatest (Burgess et al., 1998a, in press; Evers et al., 1998, 2003, in press; Scheuhammer et al., 2001; Champoux et al., this volume).

Common loons are exposed to Hg through their diet (Fournier et al., 2002), which consists mainly of small fish (i.e., < 20 cm in length) and aquatic invertebrates (Barr, 1996). Mercury levels in freshwater fish in Atlantic Canada are correlated with lake acidity and dissolved organic carbon concentrations (Peterson et al., 1990; Carter et al., 2001; Rencz et al., 2003; Drysdale et al., in press). Loons in Atlantic Canada frequently nest on low-pH, low-alkalinity, oligotrophic lakes (Kerekes, 1990;

Burgess et al., 1998a; Hope, this volume); such lakes tend to have elevated fish Hg levels (Wiener et al., 2003). This is the case for yellow perch, *Perca flavescens* (Mitchill), which is the preferred prey of common loons (Barr, 1996). In a study of oligotrophic lakes in Kejimikujik National Park (KNP) in Nova Scotia, Carter et al. (2001) found that Hg concentrations in whole yellow perch (5–20 cm, fork length) ranged from 0.05 to 0.77 $\mu\text{g/g}$ (wet wt.). Mercury concentrations in the perch were strongly correlated with fish length, weight and age. Mean perch Hg levels were negatively correlated with lake pH and alkalinity, and positively correlated with lakewater concentrations of total and methylmercury, total and dissolved organic carbon, aluminum, and iron (Carter et al., 2001; Rencz et al., 2003; Drysdale et al., in press).

The influence of lake acidity on the bioaccumulation of Hg in yellow perch is well documented across northeastern North America (Driscoll et al., 1994, Greenfield et al., 2001; Kamman et al., 2004, in press). Similarly, Hg levels in common loons are related to lake acidity and Hg concentrations in prey fish (Meyer et al., 1995, 1998; Burgess et al., 1998a; Scheuhammer et al., 1998; Champoux et al., this volume), but little investigation has focused on the trophic patterns of loons in relation to their accumulation of Hg.

Measurements of stable-nitrogen and carbon isotopes in aquatic animals can provide valuable insights into trophic relationships with contaminant bioaccumulation and biomagnification (Kidd et al., 1995; Dominguez et al., 2003). Within aquatic systems, stable-nitrogen isotope ratios ($\delta^{15}\text{N}$) provide information on the relative trophic level of consumers (e.g., Cabana & Rasmussen, 1994). Comparisons of trophic levels of the same organism across systems using $\delta^{15}\text{N}$ values is possible if these systems have similar baseline foodweb $\delta^{15}\text{N}$ values. If they differ, organism $\delta^{15}\text{N}$ values can be compared only after correcting for such baseline differences typically by using an organism common to all systems such as a sessile filter feeder (Cabana & Rasmussen 1996, Vander Zanden & Rasmussen 1999). Stable-carbon isotope ratios ($\delta^{13}\text{C}$) can distinguish between different food sources in aquatic ecosystems (Fry & Sherr, 1984) by differentiating between inshore or benthically linked foodwebs and offshore or more pelagically linked foodwebs (France 1995).

Our objectives were to: (i) investigate the bioaccumulation and biomagnification of Hg in yellow perch – common loon foodchains in Atlantic Canadian lakes using stable-carbon and nitrogen isotopes and (ii) assess the associations between fish and loon Hg concentrations, stable isotope ratios and lakewater chemistry parameters. We anticipated a positive correlation between loon and perch $\delta^{15}\text{N}$ values, their body masses, and their Hg concentrations, reflecting patterns of Hg bioaccumulation seen elsewhere.

Materials and methods

Yellow perch were collected from 14 lakes in KNP, Nova Scotia (lake names, locations, and sample sizes are provided in supplementary material)¹, using minnow traps, nets, and angling in July and August 1996 and 1997. For this study, we targeted two size classes of yellow perch for analysis. Both size classes are typically consumed by common loons (Barr, 1996). The smaller size class (ca. 9 cm, fork length) was representative of non-piscivorous perch and the larger size class (ca. 17 cm, fork length) was representative of piscivorous perch (Scott & Crossman, 1973: 759; Clady, 1974). Up to three fish from each size class were collected from each lake. Fish mass was measured on an electronic balance (± 0.1 g). Fish were individually wrapped in plastic wrap and placed on ice. They were frozen within 24 h and shipped to the Environment Canada laboratory, Moncton, New Brunswick for processing and Hg analysis.

Composite samples of whole-body homogenate from 1–3 yellow perch of similar length from each lake were analysed for total Hg by cold-vapour atomic-absorption spectrometry (CVAAS), following Environment Canada (1982). Briefly, organomercury compounds in the fish samples were oxidized to inorganic mercury by sulphuric acid, dichromate, and UV photooxidation. The mercuric ions were then reduced with stannous sulfate (10% w/v) in hydroxylamine sulphate–sodium chloride solution (12% w/v) to elemental Hg. Total Hg content was then measured using

¹ Electronic supplementary material is available for this article at <http://dx.doi.org/10.1007/s10750-006-0065-8> and accessible for authorised users.

CVAAS (Thermo Separation Products, Mercury Monitor 1255). Quality assurance procedures included analyses of method blanks, sample replicates, spiked tissues, and dogfish muscle (DORM-1) standard reference material (SRM). Recoveries of Hg in SRM were 88–101% ($n=6$), and mean recovery (± 1 SE) of spiked tissues was $90 \pm 4\%$ ($n=33$). Mercury concentrations are expressed as $\mu\text{g/g}$ on a wet weight (wet wt.) basis. Further details on the fish sampling and Hg analysis are provided by Carter et al. (2001) and Drysdale et al. (in press).

Adult and juvenile common loons were captured opportunistically using a night-lighting technique (Evers, 1992) in August, 1995, 1996 and 1997 on ten lakes in KNP, Nova Scotia, and on four lakes in eastern Charlotte County and on one lake in Fundy National Park, New Brunswick (lake names, locations, and sample sizes are provided in supplementary material). Body mass was measured using a spring scale ($\pm 1\%$). Blood samples were collected from adult and juvenile (1–4 weeks of age) common loons, as previously described in Evers et al. (1998) and Burgess et al. (in press). Total Hg was measured in whole loon blood by CVAAS (Perkin-Elmer 3030B) at the National Wildlife Research Centre, Hull, Quebec, following the methods of Scheuhammer & Bond (1991) and Scheuhammer et al. (1998). Quality assurance procedures included analyses of procedural blanks, sample replicates, dogfish muscle and liver SRM (DOLT-2 and DORM-2), and spiked samples of freeze-dried animal blood (A-13 IAEA SRM). Recoveries of Hg from SRM ranged from 94–106% ($n=7$). Analytical spike recoveries were 90–102% ($n=4$).

Subsamples of homogenate from composite samples of whole yellow perch and samples of common loon blood were also analysed for stable-carbon and nitrogen isotopes. Only loon blood samples collected in 1997 were analysed for stable isotopes (lake names and sample sizes are provided in supplementary material). Dried tissue samples were loaded into tin cups and combusted at 1200°C in a Robo Prep elemental analyzer (Europa Ltd., Crewe, England) interfaced with a Europa 20:20 continuous-flow isotope-ratio mass spectrometer (Hobson et al., 1999). Two standards (egg albumin) were measured in sequence for every five unknowns. Analytical error is estimated to be

$\pm 0.3\text{‰}$ for $\delta^{15}\text{N}$ and $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ analyses. Stable isotope ratios in tissue samples are reported in delta notation as parts per thousand (‰) according to the following: $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (‰) = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is the corresponding ratio $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$. R_{standard} for ^{15}N and ^{13}C are atmospheric N_2 (AIR) and the PDB standard, respectively.

Lakewater samples were collected in May and October in 1995–1997 from 19 lakes. Analyses of water chemistry parameters, including total mercury, are described by Vaidya et al. (2000).

Mercury concentrations and body masses were \log_{10} -transformed prior to statistical analysis to meet assumptions of normality. Differences in parameters between small perch, large perch, and juvenile and adult loons were identified by one-way analysis of variance followed by Tukey's paired comparisons. We did not collect filter-feeding organisms common to all lakes and so we were unable to normalize organism (loon or perch) $\delta^{15}\text{N}$ values in the manner recommended by Cabana & Rasmussen (1996). In addition, small yellow perch could not be used for this purpose since the number of lakes with complete small perch, large perch, and loon samples were relatively low. Instead, we compared raw $\delta^{15}\text{N}$ values vs. Hg levels in perch and loons across all lakes. This approach would encompass variability due to any differences in baseline foodweb $\delta^{15}\text{N}$ values, and so would produce weaker relationships than those actually occurring between these variables, had they been normalized. Pearson correlations were calculated among mean perch and loon Hg concentrations and selected lake chemistry parameters. Analysis of covariance (ANCOVA) was used to test for differences in mean $\delta^{15}\text{N}$ values in perch and loon tissues, including lake pH as a covariate. Statistical analyses were conducted using SYSTAT 10 for Windows (SPSS Inc., Chicago, IL).

Results

Composite samples of small (mean fork length 8.8 cm, mean age 3.4 years) and/or large yellow perch (mean fork length 17.5 cm, mean age 7.5 years) were obtained from 14 KNP lakes. Blood samples were obtained from 14 juvenile loons and 23 adult loons (samples from 5 juveniles

Table 1. Geometric mean (lower standard deviation, upper standard deviation) mercury concentrations ($\mu\text{g/g}$, wet wt.) and stable-nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$, ‰) isotope ratios in whole yellow perch and common loon blood, and body mass (g) of yellow perch and common loons in Atlantic Canada

	Small perch ¹	Large perch ²	Juvenile loons	Adult loons
<i>N</i>	11	11	5	13
Mercury conc. ($\mu\text{g/g}$, wet wt.)	0.15 ^A (0.09, 0.23)	0.38 ^B (0.23, 0.62)	0.43 ^B (0.18, 1.01)	2.7 ^C (1.5, 5.1)
$\delta^{15}\text{N}$ (‰) ³	8.0 ^A (7.0, 8.9)	8.8 ^{AB} (7.8, 9.9)	9.0 ^{AB} (8.6, 9.3)	9.6 ^B (8.7, 10.5)
$\delta^{13}\text{C}$ (‰) ³	-28.5 ^A (-30.2, -26.9)	-26.7 ^B (-28.1, -25.4)	-26.6 ^{AB} (-28.2, -25.1)	-27.14 ^{AB} (-28.6, -25.7)
Body mass (g)	7.7 ^A (7.0, 8.4)	65 ^B (59, 70)	1440 ^C (860, 2420)	4890 ^D (4280, 5590)

Row means not sharing the same letter are significantly different ($p < 0.05$). ¹Composite samples of whole yellow perch, mean fork length 8.8 cm. ²Composite samples of whole yellow perch, mean fork length 17.5 cm. ³Arithmetic means.

and 13 adults were analysed for stable isotopes). Geometric mean Hg concentrations in large yellow perch and juvenile loon blood were similar (Table 1), and these were more than double those in small yellow perch and almost seven times less than those in adult loon blood. Similarly, $\delta^{15}\text{N}$ values were similar in large yellow perch and juvenile loons but were significantly greater in adult loons than in small perch. In contrast, $\delta^{13}\text{C}$ values were significantly greater in large yellow perch than in small perch, while $\delta^{13}\text{C}$ values in loon blood were not different from either group of fish. Body masses were significantly different between the four groups of animals (Table 1).

Total Hg concentrations in whole yellow perch and common loon blood were strongly related to body mass ($R^2 = 0.73$, $p < 0.0001$; Fig. 1). Similarly, Hg concentrations in perch and loons were related to their $\delta^{15}\text{N}$ values ($R^2 = 0.22$, $p = 0.002$; Fig. 2).

In 19 study lakes, mean pH was 5.3 (range: 4.2–6.5) and mean concentration of total organic

carbon was 9.4 mg/l (range: 2.2–27.9). Mean concentration of total Hg in unfiltered lakewater in 17 lakes was 4.0 ng/l (range: 1.0–9.6). Correlation analysis identified significant positive associations between total Hg concentrations in small yellow perch and adult loons, large perch and juvenile loons, and between adult and juvenile loons (Table 2). Negative correlations were found between lake pH and total organic carbon in lakewater, and between pH and total mercury concentrations in lakewater and juvenile and adult loons. Mercury levels in adult loons and lakewater were positively associated with total organic carbon concentrations in lakewater (Table 2).

Stable nitrogen isotope ratios in yellow perch and common loons were positively associated with lake pH (Fig. 3a & b, respectively). There were no significant differences among the slopes of $\delta^{15}\text{N}$ vs. lake pH for small perch, large perch, and juvenile and adult loons ($p > 0.6$). ANCOVA results indicated that, adjusted for lake pH, mean $\delta^{15}\text{N}$ values

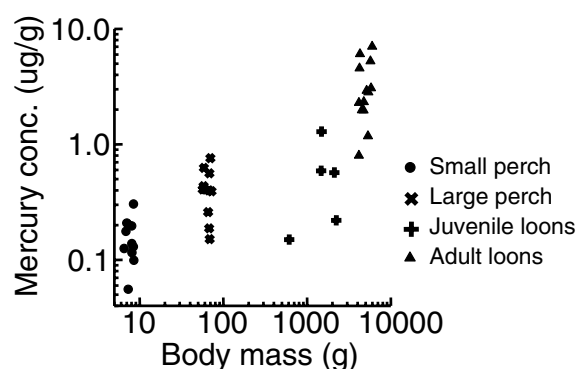


Figure 1. Total mercury concentrations ($\mu\text{g/g}$, wet wt.) in whole yellow perch and common loon blood in relation to perch and loon body mass (g).

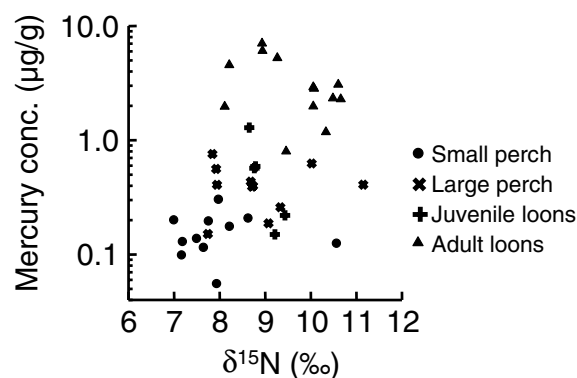


Figure 2. Total mercury concentrations ($\mu\text{g/g}$, wet wt.) in relation to stable-nitrogen isotope ratios ($\delta^{15}\text{N}$, ‰) in whole yellow perch and common loon blood.

Table 2. Correlation matrix of total mercury concentrations in whole yellow perch, common loon blood ($\mu\text{g/g}$, wet wt.), and lakewater (ng/l), lake pH, and total organic carbon concentrations (mg/l)

	Small perch Hg	Large perch Hg	Juvenile loon Hg	Adult loon Hg	Lakewater Hg	Lake pH
<i>n</i> (number of lakes)	13	14	10	13	17	19
Large perch Hg	0.55					
Juvenile loon Hg	0.30	0.77				
Adult loon Hg	0.86	0.67	0.86			
Lakewater Hg	0.43	0.42	0.54	0.58		
Lake pH	-0.36	-0.34	-0.69	-0.76	-0.81	
Total organic carbon (<i>n</i> = 19)	0.43	0.29	0.43	0.57	0.95	-0.79

Correlation coefficients in bold are significant ($p < 0.05$).

for small perch (8.1‰) were significantly less than those for both large perch (9.1‰) and adult loons (9.2‰) ($p < 0.05$).

Discussion

Mercury biomagnified in the yellow perch – common loon foodchains in Atlantic Canadian lakes. The greater mercury concentrations in older perch and loons also confirm the bioaccumulation of Hg in both species. Since Hg in fish is typically greater than 90% methyl Hg (Bloom, 1992; Scheuhammer et al., 1998; Drysdale et al., in press), biomagnification and bioaccumulation are expected in these aquatic foodwebs (Wiener et al., 2003).

We acknowledge that our ability to interpret the stable-nitrogen isotope data is weakened by our inability to normalize the data to baseline for each lake, as recommended by Cabana & Rasmussen (1996). Nevertheless, the Hg and $\delta^{15}\text{N}$ data indicate that juvenile loons and large yellow perch forage at a similar trophic level, between that of small perch and adult loons. While they occupied a similar trophic level, the body masses of juvenile loons and large yellow perch differed by 22 times. The positive correlations between Hg concentrations and both body mass and $\delta^{15}\text{N}$ values are typical of foodwebs in freshwater lakes (Cabana et al., 1994; Kidd et al., 1995). Some of the variation observed in the relationship between Hg concentrations and $\delta^{15}\text{N}$ values (Fig. 2) may result from among-lake differences in baseline, which we did not measure. This may explain the apparent lack of association between $\delta^{15}\text{N}$ and Hg values within perch size classes and loon age classes.

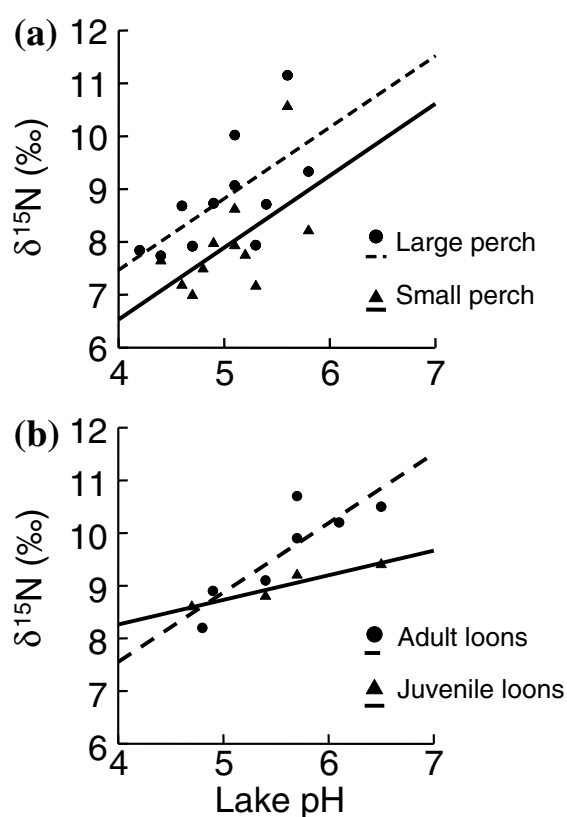


Figure 3. Stable-nitrogen isotope ratios ($\delta^{15}\text{N}$, ‰) in small and large yellow perch (a) and juvenile and adult common loons (b) in relation to lake pH.

The stable-carbon isotope results indicate that small yellow perch had lower $\delta^{13}\text{C}$ values than larger perch. This suggests that foraging of smaller perch was more pelagic and less benthic than larger perch (Hecky & Hesslein, 1995). Yellow perch less than 15 cm tend to feed more on zooplankton,

while larger perch feed increasingly on small fish and benthic macroinvertebrates (Clady, 1974). The overlapping $\delta^{13}\text{C}$ values of both juvenile and adult loons suggest they fed on both small and large perch.

The correlations found between mercury concentrations in yellow perch and common loons are not surprising since yellow perch are the preferred prey of loons (Barr, 1996). Similar associations between mercury concentrations in common loon blood and prey fish tissue are found in Ontario and Quebec (Scheuhammer et al., 1998; Champoux et al., this volume). The correlation we found between blood mercury concentrations in adult loons and their chicks is confirmed by other studies (Scheuhammer et al., 1998; Fevold et al., 2003).

The association between lake pH and $\delta^{15}\text{N}$ values in both yellow perch and common loons is striking. This may confirm the general trend towards lower species diversity of phyto- and zooplankton, and shorter planktonic food-chain length, in acidic lakes (Seigfried, 1988; Keller & Gunn, 1995; Locke, 1996). However, because we could not unequivocally determine that lake foodweb $\delta^{15}\text{N}$ values did not vary across lakes, it is not possible to make inferences about relative food-chain length. An alternative explanation is that baseline $\delta^{15}\text{N}$ values were correlated with lake pH through some biogeochemical process, and food-chain lengths were similar across lakes. In spite of possible shorter aquatic food chains, acidic lakes in this study area have higher Hg levels in yellow perch and common loons (Table 2; Burgess et al., 1998a; Drysdale et al., in press). This indicates that the effects of low pH on factors that increase fish mercury levels, such as increased Hg methylation (Winfrey & Rudd, 1990), decreased lake productivity (Larsson et al., 1992), and decreased perch growth rates (Carter et al., 2001), appear to over-ride any counteracting effect of reduced food-chain length. Recent findings of mercury bloom dilution by Chen et al. (2000) and Pickhardt et al. (2002) emphasize how decreases in planktonic biomass can concentrate available methylmercury and lead to increases in mercury levels further up aquatic food webs, which could occur in low-pH lakes.

Our findings illustrate the utility of combining chemical and ecological data to better understand

bioaccumulation and biomagnification of Hg in freshwater ecosystems and the associated risks to fish-eating wildlife. They also highlight the interplay between aquatic mercury contamination and lake acidification. Aquatic ecosystems and their wildlife face the cumulative impacts of atmospheric deposition of both Hg and acidic precipitation in Atlantic Canada (Jeffries, 1997; NESCAUM et al., 1998). Continued research and monitoring are essential to guide policy initiatives to better protect the health of lakes in this sensitive region (FPTMEE, 1998).

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Part IV
Shorebirds – Habitat Use, Limnology and Trophic Dynamics

Shorebirds, snails, and the amphipod (*Corophium volutator*) in the upper Bay of Fundy: top–down vs. bottom–up factors, and the influence of compensatory interactions on mudflat ecology

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Abstract

During their annual mid- to late-summer southward migration, Semipalmated Sandpipers (*Calidris pusilla*) feed intensively on the amphipod *Corophium volutator* on intertidal mudflats in the Bay of Fundy. *Corophium*, in turn, feed on diatoms and bacteria. Using a series of bird exclosures and fertilizer addition, we examined top–down and bottom–up effects, and investigated the presence of a trophic cascade in the mudflat community during the period when birds are abundant. Although both top–down and bottom–up forces were present in this system, neither transmitted beyond a single trophic link. Predation by shorebirds, which may be less size-selective than previously thought, reduced *Corophium* abundance in control plots by approximately 80% relative to exclosures, but most other species were unaffected. Shorebird predation did not result in an increase in diatom abundance, as predicted under the trophic cascade hypothesis. Fertilizer increased diatom abundance, but had no effect on *Corophium* abundance or bird predation, and little effect on other mudflat invertebrates. The only indirect effect observed was on mud snails (*Ilyanassa obsoleta*), which, by rapidly responding to changes in diatom abundance, compensated for both bird exclusion and fertilizer addition, and prevented the trophic cascade. This population response by snails, possibly stemming from competition with *Corophium*, probably contributed to the stability of the community. Our results provide an example of short-term compensation in a simple intertidal community, and highlight the importance of considering direct and indirect effects in community ecological studies. We conclude that while compensatory interactions that block trophic cascades may be more common in more complex ecosystems, they are not restricted to them.

Introduction

Community ecologists have long been interested in how predation and primary production influence community structure. Top–down and bottom–up influences on communities (*sensu* McQueen et al., 1986, 1989) have been well studied in marine systems. Top–down effects (e.g., Paine, 1966, 1994, 1980; Posey et al., 1995; Wootton, 1995) have

historically been given more attention in intertidal communities. However, examples of the influence of bottom–up factors, either alone or in combination with top–down effects, do exist (e.g., Bosman et al., 1986; Duggins et al., 1989; Menge et al., 1997, 1999; Nielsen, 2001). It is now recognized that the two types of effects are rarely independent and often difficult to separate (Pace et al., 1999), and that communities are often influenced

by a combination of the two (Hunter & Price, 1992; Menge, 1992; Power, 1992; Posey et al., 1995; Menge et al., 1997, 1999; Hagerthey et al., 2002).

Related to the idea of top-down and bottom-up community control is the notion of the trophic cascade. This term refers to reciprocal predator-prey effects that have a detectable impact (e.g., a change in biomass, number, or some other measure of abundance) across more than one link in a food chain (a species-level cascade) or web (a community-wide cascade) (Pace et al., 1999; Persson, 1999; Polis, 1999). A classic example of a trophic cascade is provided by sea otters, urchins, and kelp in Alaska (Estes & Palmisano, 1974; Estes & Duggins, 1995). By feeding on urchins, sea otters facilitate persistence of extensive kelp beds that would otherwise be destroyed by urchin herbivory.

The importance of trophic cascades and the frequency with which they are found in nature has been debated for years. Cascades are well documented in marine systems (e.g., Estes & Palmisano, 1974; Estes et al., 1978; Wootton, 1995; Lindberg et al., 1998; Silliman & Bertness, 2002), but Strong (1992) and Polis & Strong (1996) argued that true trophic cascades are confined to simple communities in which a few species can have a great influence on the rest of the system (see Pace et al., 1999, for an alternative view). In more complex communities, but sometimes simple ones as well (see Hamilton, 2000), compensatory interactions among predators may block transmission of indirect effects across trophic levels (e.g., Navarrete & Menge, 1996; Pace et al., 1998, 1999).

Migrating shorebirds, 95% of which are Semipalmated Sandpipers, *Calidris pusilla* (L.), (Hicklin, 1987), feed extensively on mudflats in the intertidal zone of the upper Bay of Fundy, Canada, primarily from mid-July to late August each year, though a few persist into September. The birds feed predominantly on the amphipod *Corophium volutator* (Pallas) (Hicklin & Smith, 1984), the most abundant macroinvertebrate in the system. *C. volutator* (hereafter *Corophium*) are primarily deposit feeders, and benthic diatoms make up a large part of their diet (Gerdol & Hughes, 1994a).

The mudflat ecosystem has many of the conditions necessary for a trophic cascade. It contains a simple community (i.e., has low species richness), so the probability of compensatory interactions is

reduced (Strong, 1992; Pace et al., 1999). Sandpipers feed intensively and almost exclusively on *Corophium* where it is most abundant (Hicklin & Smith, 1984), enhancing the potential for strong top-down effects (Wootton, 1997). The vast majority of the primary production is in the form of highly edible diatoms (Trites, 2002), so substantial herbivory is also possible (Polis & Strong, 1996).

Using bird exclosures and fertilizer, we investigated the relative importance of top-down and bottom-up effects, and whether shorebird predation generated a trophic cascade on a Bay of Fundy mudflat. Assuming community dynamics as described in models developed by Hairston et al. (1960), Fretwell (1977), and Oksanen et al. (1981), if a top-down cascade is present here, exclusion of predators should lead to an increase in *Corophium* abundance and a reduction in chlorophyll *a* concentration (a good index of diatom abundance in this system, I. Kaczmarska, personal communication). If a community-wide cascade occurs, effects should be observed on species outside the targeted food chain. If bottom-up factors act together with top-down effects, fertilizer addition should lead to no change in chlorophyll *a* and an increase in *Corophium* when birds are absent. When birds are present, chlorophyll *a* should increase, *Corophium* should decline, and bird predation should increase in fertilized plots. An increase in chlorophyll *a* and no other change would represent a bottom-up effect that did not transmit up the food chain. Finally, if the entire system is food-limited and consumers have no effects on trophic levels below them, fertilizer should lead to increases in all trophic levels.

Results from previous exclosure experiments investigating interactions of shorebirds and *Corophium* both in our study area (Wilson, 1989) and in Europe (Raffaelli & Milne, 1987) indicated no substantial community-wide effects of shorebird predation. However, neither study considered the role of bottom-up effects in the system, nor the interaction of top-down and bottom-up processes. Our study explicitly addresses these questions, while at the same time considering the issue of compensatory interactions in a community much simpler than that envisioned by Strong (1992) or Polis & Strong (1996).

The question of how this intertidal mudflat community is structured, and whether or not a

trophic cascade exists, is also important in an applied context. Benthic diatoms, a major primary producer on the mudflat (Schwinghamer et al., 1983; Underwood & Paterson, 1993), secrete a mucopolysaccharide that helps to bind the sediment together (Grant et al., 1986). If a simple 3-level trophic cascade is operating on the mudflat, as has been suggested by Daborn et al. (1993), shorebirds, by eating *Corophium* and, consequently, reducing the consumption of diatoms, may indirectly enhance sediment cohesion and thus contribute to the stability of the mudflat. If that is the case, care should be taken to avoid activities that may disrupt feeding by shorebirds. Similarly, shorebird biologists are interested in factors that determine feeding locations for these birds in the upper Bay of Fundy, an area that has been designated by the Western Hemispheric Shorebird Reserve Network as one of nine sites of critical importance in North America (Shepherd & Boates, 1999). A clear understanding of these factors is not possible without first clarifying the relationship between shorebirds and the rest of the mudflat community. The paper concludes with a brief discussion of how results of this research improve our ability to answer these applied questions.

Methods

Study area

The experiment was carried out on an intertidal mudflat at Avonport, Nova Scotia, Canada (45° 9' N, 64° 23' W), between 10 July and 22 August, 1999. This area is part of the Minas Basin, an extension of the upper Bay of Fundy, in which tidal amplitude varies from 11 to 17 m during neap and spring tides, respectively. The intertidal zone at Avonport extends roughly 1 km from shore. This particular mudflat was chosen because previous enclosure work has been done there (Wilson, 1989) and its relatively short length compared to some other mudflats in the area (e.g., Starr's Point) made transport of enclosure materials possible, and facilitated frequent monitoring of the site. Our study area covered approximately 1.9 ha (320 m × 60 m), and was located 480 m from shore in an area that was exposed for 5.5 h during each twice-daily tidal cycle. Total nitrogen (both avail-

able and unavailable) in the sediment (measured in 2000) is approximately 0.12% (range 0.09–0.14%), and carbon:nitrogen ratios are very low (mean 6.8, range 6.5–7.1), suggesting mineralization and rapid decomposition.

The invertebrate community associated with the mudflat is relatively species-poor, and is dominated by *Corophium*. The common mud snail, *Ilyanassa obsoleta* (Say), and several polychaete taxa (*Heteromastus filiformis* Claparede, *Nephtys* spp., *Eteone* spp., Spionidae) are also common. The *Corophium* population in this area has two annual generations (Peer et al., 1986; Matthews et al., 1992). Overwintering individuals reach adulthood and reproduce in spring. Their offspring mature and reproduce in mid-summer, producing the following spring's adults. This study covered the periods of maturation and reproduction in of the summer cohort, and juvenile growth in the following generation.

Experimental design

Within the study area, 20 experimental plots, each consisting of an enclosure (that prevented birds from feeding) and a paired control (where birds fed freely), were set up on 10 July 1999. Based on preliminary data collected in June 1999, these replicates provided approximately 90% power to detect a 30% difference among mean *Corophium* densities. Although the exact position of each plot was chosen randomly, plots were spread 25–30 m apart across the study area in two rows parallel to the shore line (Fig. 1). Enclosures and controls in each plot were laid out side by side, also parallel to shore. This experimental set-up ensured a uniform substrate throughout the study area and that all plots, and enclosures and controls within each plot, experienced approximately the same tidal regime. The shallowest plots were exposed to air for only about 4 min longer than the deepest plots during each tidal cycle.

Enclosures measured 1.8 m × 1.2 m and consisted of four "rebar" corner posts (protruding approximately 30 cm from the sediment) connected by three rounds of monofilament fishing line at 10 cm intervals starting 5 cm above the sediment, and multicoloured flagging tape tied around the posts and to the fishing line. Controls,

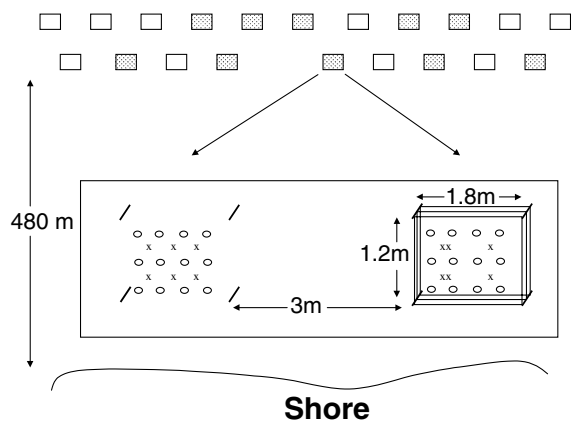


Figure 1. Representation of the experimental area (not to scale). Filled boxes are fertilized plots and open boxes unfertilized plots. The lower portion of the figure shows a single fertilized plot, with the enclosure on the right and control on the left. Corner posts of enclosures are 30 cm high. The circles inside the enclosure and control represent locations where fertilizer was placed, and "x"'s indicate the six predetermined sampling locations. Six equivalent sampling locations were used in unfertilized plots.

also 1.8×1.2 m, were marked by four bamboo posts and positioned 3 m from enclosures (Fig. 1). Enclosures successfully excluded the majority of shorebirds because the flagging tape made enclosures highly visible and discouraged birds from entering them (see Results). It is unlikely that other potential predators were either attracted to or prevented from entering enclosures. Enclosures provided no shelter, and certainly could not exclude either bottom-dwelling flat fish or pelagic species, so there is little chance that results were confounded by differential fish predation in enclosures and controls.

Enclosure work, especially when done in soft-bottom systems, is frequently associated with problems such as sediment disturbances around sides and reduction in water flow (Hulberg & Oliver, 1980). Partial cages that simulate effects of caging on the substrate but do not exclude the animals in question are often used to quantify these confounding effects (e.g., Virnstein, 1977). However, in our case enclosures had no covers or solid sides, so water flow was not impeded. Further, because the only part of enclosures in contact with the sediment was corner posts, which were also present in controls, physical effects on the substrate should be identical for both treat-

ments. Therefore, partial cages, which can run the risk of confounding results further if animals are partially deterred by them (Marsh, 1986a, b), were neither necessary nor appropriate for this study. There was also potential for unanticipated effects on intertidal fauna resulting from trampling of the surrounding area during enclosure set-up and monitoring. Although this trampling was similar for enclosures and controls, we assessed this possibility in 2000 by simulating effects of trampling, and collecting samples in July and August from trampled and undisturbed areas. Results indicated no effect of trampling on *Corophium* or mud snail abundance, or chlorophyll *a* concentration (Hamilton unpublished data). Therefore, we are confident that physical disturbance around enclosures did not influence our results.

After plots were set up, we randomly selected half of them to fertilize in an effort to stimulate primary production (Fig. 1). Plots were fertilized by placing 12 14-g fertilizer stakes (11% ammoniacal nitrogen, 5% phosphoric acid, and 7% soluble potash) horizontally approximately 2 cm under the sediment in enclosures and controls. This formula was chosen because diatoms are known to grow well under nitrogen-enriched conditions (Fisher & Cowdell, 1982). To ensure even fertilizer application within plots, stakes were positioned 40 cm apart in a grid pattern (Fig. 1). This grid generated six points in each enclosure and control that were equidistant (28 cm) from all fertilizer stakes (Fig. 1).

Sample collection and processing

Samples were collected from enclosures and controls three times during the experiment – immediately after plots were set up (12–13 July, hereafter mid-July), three weeks later (2–3 August, hereafter early August), and again 3 weeks after that (21–22 August, hereafter late August). The beginning and end of the experiment corresponded with the arrival and departure of the majority of shorebirds at Avonport. During each sampling period, sediment cores to assess chlorophyll *a* concentration and invertebrate abundances and species composition were collected. Locations within plots from which cores were drawn were randomly chosen from the six points equidistant from fertilizer stakes. In unfertilized plots, six

equivalent sampling points were designated. Individual sampling points were never used more than once. None of these points were near corner posts to ensure that sediment erosion around the posts did not affect results.

Two replicate invertebrate sample cores were collected from each enclosure and control during each sampling period using a plexiglass tube (6.8 cm diameter) pushed into the sediment to the bottom of the aerobic layer (4–10 cm), below which macroinvertebrates are mostly absent. Sediment was rinsed through a 0.5-mm sieve, which retains most *Corophium* longer than 2 mm and approximately 10% of smaller individuals (Crewe et al., 2001). All invertebrates were preserved in 95% ethanol, and at a later date animals were sorted and identified – amphipods and gastropods to species, and polychaetes to family or genus, following Appy et al. (1980) and Pollock (1998). *Corophium* were measured and sorted into 2-mm size classes. Gastropods were measured and shells separated from tissue. All invertebrates were counted, dried to constant mass (80 °C for 24 h), and weighed. Numbers and dry tissue biomasses were used as measures of invertebrate abundance in subsequent analyses.

Using a 10 cc syringe cut off at the end, we collected two sediment samples for analysis of chlorophyll *a* from areas adjacent to each invertebrate sample, for a total of four cores from each enclosure and each control during each sampling period. The top 2–3 mm of sediment was removed from the syringe, stored in a scintillation vial, and frozen. Two to 3 days after collection, samples were removed from the freezer and 5 ml of 90% acetone was added to each vial to extract chlorophyll. Samples were refrigerated for approximately 22 h, then brought to room temperature (2–3 h) in a dark environment. The acetone was then pipetted off and centrifuged for 10 min at 2500 rpm to remove suspended sediment. To determine chlorophyll *a* content, absorbencies were read on a spectrophotometer (LKB Biochrom Ultrospec II) at 630, 647, 664, and 750 nm wavelengths. We then added two drops of 10% hydrochloric acid, waited 90s for chlorophyll to degrade, and re-read absorbencies at 664 and 750 nm. The acid procedure made it possible to separate intact chlorophyll from phaeophytin.

Chlorophyll *a* concentration (mg/m^2) was calculated following Eaton et al. (1995).

Shorebirds feeding in the study area were observed and counted a minimum of three times weekly. However, because birds moved frequently while feeding and were difficult to monitor consistently within the small study plots, bird tracks and droppings (McCurdy et al., 1997) were also monitored in enclosures and controls throughout the experiment. Droppings were counted and the percentage of each enclosure and control that was covered with footprints was estimated at least three times weekly using a quadrat marked off in uniform divisions. Details of this method and a figure illustrating its use are provided in Hamilton et al. (2003). Observations were made at least 2 h after the sites had been exposed to allow ample time for birds to feed in the area. To supplement these data, on seven occasions between 2 and 19 August, two to four study plots were randomly chosen and monitored intensively for 30-min intervals. Numbers of birds entering and leaving enclosures and controls were noted.

A few snails were noted in the experimental area in mid-July, and their densities increased by August, so during the early and late August sampling periods we counted mud snails, which are visible either on the surface or as bumps just under the surface, in enclosures and controls. This was necessary because the core samples were too small to accurately estimate abundance of the snails. Counts were carried out at approximately the same tide level during each sampling period, minimizing the potential for differential effects of tide level on snail behaviour.

Additional sediment samples were collected from half of the plots (five fertilized and five unfertilized), from positions equidistant from fertilizer stakes, during each sampling period to assess the effect of fertilizer on nitrogen in the sediment. These were frozen and later analysed for nitrogen (ammonium) content using the Kjeldahl distillation method for nitrogen determination. Samples collected for this purpose from the middle sampling period were discarded because they were improperly collected. Analysis of ammoniacal nitrogen was chosen over total nitrogen because the goal was to identify differences among the plots caused by addition of ammonia-based fertilizer.

Statistical analyses

All analyses were carried out using SAS version 6.12 (SAS Institute Inc., Cary, NC). Before analyses, data were checked visually for violation of the assumption of normality and using Bartlett's test to assess homogeneity of variance. If violations were detected, we used Taylor's Power Law (Elliot, 1977) to determine (a) if variances and means were linked, and (b) if so, the appropriate transformation to remove this linkage. In most cases, transformations indicated by this method successfully eliminated violations of assumptions. The few that remained were minor. Because the statistical methods used (univariate and multivariate analysis of variance, analysis of covariance, and regression) are robust in such situations (Winer et al., 1991), parametric methods were used for all data. When repeated measures ANOVA (RM-ANOVA) was employed, we also tested for sphericity using Mauchly's Criterion (Potvin et al., 1990). When this assumption was not met, tests of significance for within subjects effects employed either the Huyn-Feldt correction, or were carried out in multivariate mode (von Ende, 1993). Significance of all tests was evaluated at $\alpha=0.05$. The nature of interactions with $p \leq 0.1$ was also investigated as a conservative measure to ensure that main effects were not inappropriately interpreted in the presence of an interaction.

RM-ANOVA was used to analyse chlorophyll data, *Corophium* densities, and snail counts. *Corophium* data were analysed for both number and biomass, and numbers were considered separately for size categories 0–2.9, 3–4.9, and 5–10 mm when overall results were significant. Within-subjects factors were the three sampling periods; predation (exclosure vs. control), fertilizer (fertilized vs. unfertilized plots), and plot (a random variable) constituted among-subjects factors. All factors except plot were fixed. Appropriate error terms associated with each factor are listed in Table 1. When interactions were detected or suspected, reduced models were run separately for each level of one of the interacting variables to facilitate their interpretation (see Keppel, 1982). The reduced models involved only pre-planned comparisons and did not include repeated use of the same data, so α -level correc-

Table 1. Error terms associated with each factor tested in RM-ANOVA and MANOVA models used in the paper

Factor	Error term
Fertilizer	Plot (Fertilizer)
Predation	Predation \times Plot (Fertilizer)
Predation \times Fertilizer	Predation \times Plot (Fertilizer)
Date	Date \times Plot (Fertilizer)
Date \times Fertilizer	Date \times Plot (Fertilizer)
Date \times Predation	Date \times Predation \times Plot (Fertilizer)
Date \times Fertilizer \times Predation	Date \times Predation \times Plot(Fertilizer)

A term in parentheses indicates that the term to the left of it is nested within it, e.g., plot(fertilizer) means plot nested within fertilizer level. Date refers to sampling period. Plot is a random factor; all others are fixed.

tions for *a posteriori* testing were not necessary. However, when main effects were detected and *a posteriori* comparisons among means were required, Tukey's HSD test (Zar, 1999) was used to correct for multiple comparisons.

A split-plot MANOVA was used to examine the relationship among the five most common taxa (*Corophium* and the polychaetes *Heteromastus*, *Eteone*, *Nephtys*, and Spionidae). This model was identical to the RM-ANOVA described above (the split-plot design is equivalent to univariate repeated measures analysis), but with the five species included simultaneously as dependent variables. We evaluated significance of results using Pillai's trace, the most robust and conservative of available multivariate tests (Tabachnick & Fidell, 1996; Scheiner, 1993). Standardized canonical variates generated by the model were used to examine relationships among the species. The magnitude and sign of the loadings for each species indicate their relative importance in the overall result. High absolute values indicate a large contribution to the result, and differences in sign indicate that species abundances vary inversely with each other. Significant interactions were handled as described above. When helpful in interpreting results, RM-ANOVAs (as described above) were also performed on individual species that contributed most to significant multivariate results.

The relationship between *Corophium* and mud snail abundances in each exclosure and control for early and late August sampling periods was exam-

ined using ANCOVA and regression. The analysis was conducted for total number of *Corophium*, and for amphipods 0–2.9, 3–4.9 and >5 mm long. To determine whether the relationship differed among sampling periods, we set number of *Corophium* as the dependent variable, sampling period as the classification variable, and number of mud snails as the covariate. An interaction between sampling period and snail number indicated that the relationship between the species varied with sampling period. When this occurred, data were analysed separately for each period. Within sampling periods, additional ANCOVAs were used to determine whether the relationship between species was influenced by fertilizer application. As before, homogeneity of slopes was assessed using the interaction term. In the absence of an interaction, the effect of fertilizer was assessed by comparing intercepts. If intercepts differed, separate regressions were run for fertilized and unfertilized plots. If both slopes and intercepts were consistent across fertilizer levels, we performed a single regression, pooling fertilized and unfertilized plots (Zar, 1999).

Bird droppings and footprints in exclosures and controls, and in fertilized and unfertilized plots for each survey day averaged across replicate plots (to handle the large number of zeros), were compared using a randomized block ANOVA (univariate repeated measures analysis), in which each date was considered a block, on appropriately transformed data. Ammonium concentration in sediment was compared during the first and last sampling periods using a doubly randomized block ANOVA in which adjacent fertilized and unfertilized plots were paired (to control the substantial environmental heterogeneity – see Fig. 2).

Results

Bird abundance and effectiveness of experimental manipulations

Shorebirds first arrived on the mudflat on 20 July, 10 days after exclosures were set up. Tracks were present in the plots from 22 July to 20 August. Exclosures, although not completely effective, kept out the majority of birds. During the period when shorebirds were present in the study area, substantially more control than exclosure substrate

was covered by tracks (22.5% vs. 4.7%, ANOVA $df=1,19$, $F=66.2$, $p<0.0001$). Similarly, there were more droppings in controls than exclosures (1.6 vs. 0.23 per plot, ANOVA $df=1,17$, $F=22.6$, $p=0.0002$). This translates into exclusion of roughly 80% of birds, which is a conservative estimate because it was impossible to exceed 100% cover in controls, and in some cases we observed birds in exclosures become temporarily trapped and run around, creating many footprints but not feeding. Focused observations on individual plots during the second half of the experiment yielded a total of 69 birds sighted in control areas and only one in exclosures, so we are confident that bird predation inside exclosures was minimal.

Birds used the plots more heavily during the second half of the experiment (between early and late August) than in the first half (between mid-July and early August). In controls, tracks covered an average of 11% of the area of plots per day in the first interval and 29% during the second interval. No statistical comparisons of these numbers were possible because birds were present for only part of the first interval and observations were not started until they arrived, so the average during that time had to be adjusted to reflect the entire period.

Fertilizer application led to an increase in ammonium concentration in sediment (Fig. 2, fertilizer effect $df=1,4$, $F=8.67$, $p=0.042$), indicating that the method of adding nutrients to sediment was successful. The fertilizer pulse was largest during the first sampling period, with a 26% increase in ammonium 2 days after fertilizer application (117.3 ppm in fertilized plots vs. 92.9 ppm in unfertilized plots). The elevation in nitrogen declined to 15% (90.2 ppm vs. 78.5 ppm) by the final sampling period, but the overall effect of fertilizer was statistically consistent throughout the study (fertilizer \times sampling period interaction $df=1,4$, $F=2.4$, $p=0.20$), and ammonium levels did not decline from beginning to end of the study (sampling period effect $df=1,4$, $F=3.0$, $p=0.16$). Addition of fertilizer did not influence bird activity in plots (ANOVA $df=1,19$, $F=2.7$, $p=0.12$). During the period when birds were present, fertilized control plots had an average of 22.2% of the substrate covered by tracks, compared with 20.6% coverage for unfertilized control plots.

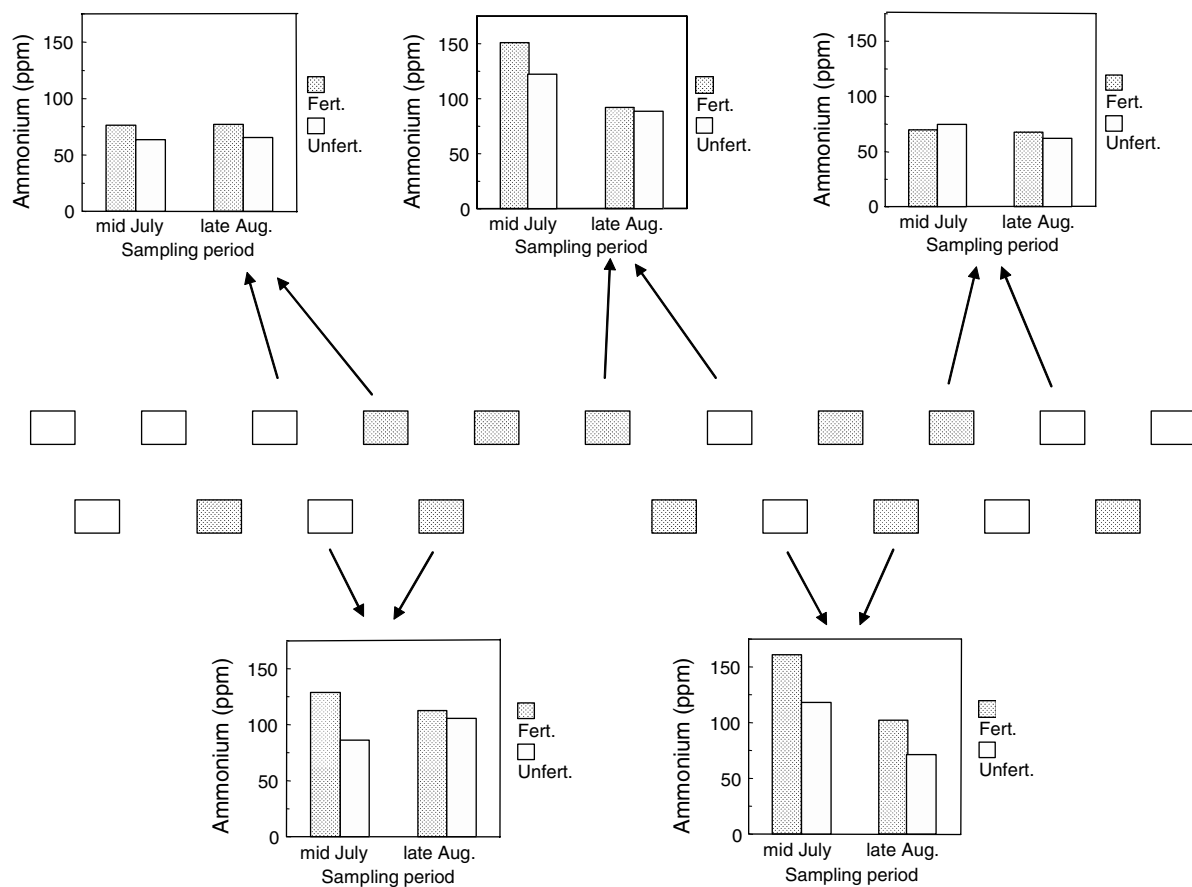


Figure 2. Ammonium concentrations for fertilized and unfertilized plots during mid-July and late August sampling periods. Each individual graph represents a pair of plots. Differences among the pairs demonstrate the spatial heterogeneity present in the system. Results of statistical tests are provided in the text.

*Effects of predation and fertilizer on *Corophium* abundance*

Avian predation significantly reduced *Corophium* densities, in terms of both biomass and number, in controls relative to exclosures by late August; no effects were detected earlier (Table 2: date \times predation interaction and predation main effect; Fig. 3a and b). Fertilizer had no effect on *Corophium*, and effects of birds on their prey were consistent in fertilized and unfertilized plots (Table 2: predation \times fertilizer interaction; Fig. 3).

Although the similar effects of shorebird predation on *Corophium* number and biomass suggest that the birds were not size-selective predators, to further assess this we analysed *Corophium* number from late August separately for three different

size classes. In all cases, birds significantly reduced *Corophium* densities in controls relative to exclosures (df = 1, 18; < 3 mm, $F = 7.63$, $p = 0.013$; 3–4.9 mm, $F = 9.77$, $p = 0.006$; ≥ 5 mm, $F = 4.76$, $p = 0.043$). As before, fertilizer had no effect on *Corophium*, and did not influence the effect of predators (p -values ranging from 0.25 to 0.73).

Effect of fertilizer and predation on the macroinvertebrate community

The effect of fertilizer on the relative abundances of the five most common invertebrate taxa varied with sampling period (Table 3: date \times fertilizer interaction). Fertilizer had no effect in mid-July and late August. The effect approached significance in early August, with *Heteromastus*

Table 2. Results of RM-ANOVAs of *Corophium* number and biomass based on effects of fertilizer, predation, and sampling period (date)

Date	Factor	df	Number		Biomass	
			<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
All	Fertilizer	1,18	0.04	0.85	0.03	0.86
All	Predation	1,18	1.28	0.27	0.74	0.4
All	Predation × Fertilizer	1,18	0.24	0.62	0.02	0.88
All	Date	2,36	8.72	0.008	19.05	<0.0001
All	Date × Fertilizer	2,36	1.06	0.36	0.86	0.43
All	Date × Predation	2,36	5.83	0.006	4.93	0.01
All	Date × Fertilizer × Predation	2,36	0.02	0.98	0.04	0.96
Mid July	Fertilizer	1,18	0.84	0.37	1.06	0.32
Mid July	Predation	1,18	0.21	0.65	0.01	0.92
Mid July	Predation × Fertilizer	1,18	0.19	0.67	0.05	0.82
Early Aug.	Fertilizer	1,18	0.23	0.63	<0.01	0.99
Early Aug.	Predation	1,18	0.34	0.57	0.41	0.53
Early Aug.	Predation × Fertilizer	1,18	0.17	0.68	0.03	0.86
Late Aug.	Fertilizer	1,18	0.79	0.39	0.76	0.39
Late Aug.	Predation	1,18	9.98	0.005	10.05	0.005
Late Aug.	Predation × Fertilizer	1,18	0.09	0.76	0.01	0.94

Error terms associated with each test are provided in Table 1. Bold values indicate significant results that are interpretable (i.e., not part of a higher order interaction).

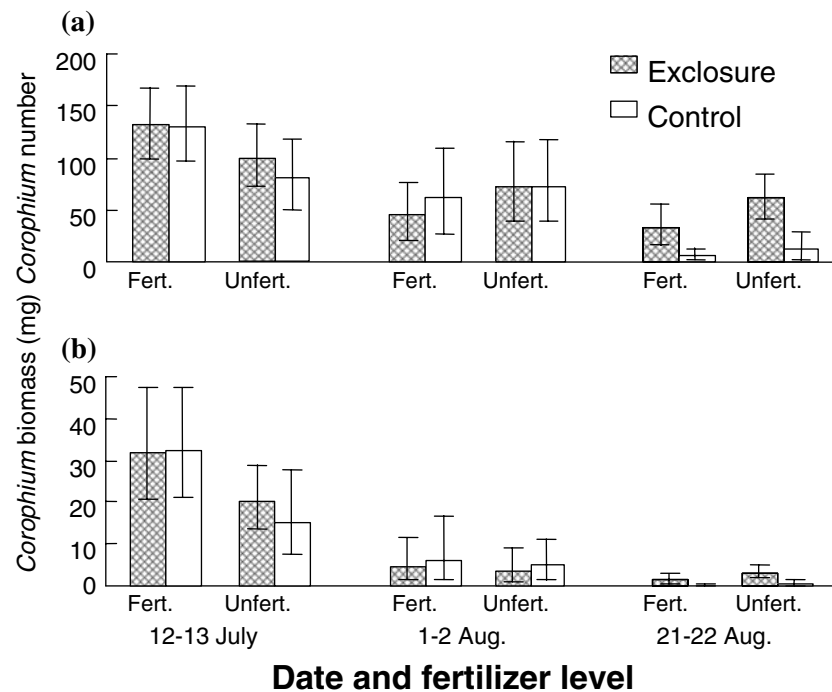


Figure 3. *Corophium* (a) number and (b) biomass in exclosures and controls of fertilized and unfertilized plots during each sampling period. Values are back-transformed means from statistical tests. Error bars are ± 1 SE. Results of statistical comparisons are provided in Table 2.

and *Eteone* contributing most to the result (Table 3: coefficients of standardized canonical variates). *Heteromastus* increased in abundance in fertilized relative to unfertilized plots (ANOVA $df = 1, 18$, $F = 4.5$, $p = 0.049$). There was an opposite, but non-significant trend for *Eteone* (ANOVA $df = 1, 18$, $F = 2.1$, $p = 0.17$), with more polychaetes in unfertilized plots. Predation also varied with date (Table 3: date \times predation interaction), with an effect on the relative abundances of the different species only in late August. Based on loadings of standardized canonical variates, *Corophium* was the only species driving this result (Table 3), suggesting that bird predation had no direct or indirect effect on any of the polychaetes in the community.

Effect of fertilizer and predation on primary production

The effect of fertilizer on chlorophyll *a* in the sediment varied with sampling period (Table 4: date \times fertilizer interaction). At the beginning of

the experiment (mid-July), neither predation nor fertilizer influenced chlorophyll abundance. In early August, there was again no predation effect, but there was significantly more chlorophyll *a* in fertilized than unfertilized sediment (Table 4, Fig. 4). The effect of fertilizer disappeared by late August (Table 4), but was replaced by a predation effect; there was more chlorophyll *a* in enclosures than in controls by that time (Table 4, Fig. 4).

Effects of fertilizer and predation on mud snails and their interaction with Corophium

Mud snails were rare in the plots during mid-July, but by early August were very abundant. Fertilizer affected snails differently in each sampling period (Table 5: date \times fertilizer interaction). During early August, there were more snails in fertilized than unfertilized plots (Table 5, Fig. 5), and there was a trend toward more snails in controls than in enclosures, particularly in unfertilized plots (Table 5, Fig. 5). By late August, the fertilizer effect had disappeared, but the predation effect

Table 3. Results of MANOVA of biomass of the five most common invertebrate species (or species groups) in samples, based on effects of fertilizer, predation, and sampling period (date)

Date	Factor	df	F	p	Canonical loadings ^a				
					<i>Coro.</i>	<i>Eteone</i>	<i>Heter.</i>	<i>Neph.</i>	<i>Spio.</i>
All	Fertilizer	5,14	0.95	0.47					
All	Predation	5,14	3.57	0.03					
All	Fert. \times Pred.	5,13	0.42	0.83					
All	Date	10,66	6.86	<0.0001					
All	Date \times Fert.	10,66	1.91	0.06					
All	Date \times Pred.	10,66	1.84	0.07					
All	Date \times Fert. \times Pred	10,66	0.83	0.60					
Mid July	Fertilizer	5,14	0.81	0.56					
Mid July	Predation	5,14	0.72	0.62					
Mid July	Fert. \times Pred.	5,14	1.27	0.33					
Early Aug.	Fertilizer	5,14	2.53	0.08	0.27	-1.00	0.84	-0.21	0.01
Early Aug.	Predation	5,14	1.58	0.23					
Early Aug.	Fert. \times Pred.	5,14	0.15	0.98					
Late Aug.	Fertilizer	5,14	1.94	0.15					
Late Aug.	Predation	5,14	3.00	0.05	1.14	0.40	0.33	-0.08	0.48
Late Aug.	Fert. \times Pred.	5,14	0.93	0.49					

Coefficients are loadings of standardized canonical variates and are provided to aid interpretation of significant main effects (see Methods). Bold values are as in Table 2 and italicized values indicate trends that approached significance and were discussed in Results, or interactions that were investigated further. Error terms are provided in Table 1.

^aNote: Coro. = *Corophium*, Heter. = *Heteromastus*, Neph. = *Nephtys*, and Spio. = *Spionidae*.

Table 4. Results of RM-ANOVAs of Chlorophyll *a* concentration (mg/m²) based on effects of fertilizer, predation and sampling period (date)

Date	Factor	df	<i>F</i>	<i>p</i>
All	Fertilizer	1,18	5.29	0.03
All	Predation	1,18	3.42	0.08
All	Predation × Fertilizer	1,18	0.53	0.47
All	Date	2,36	37.68	<0.0001
All	Date × Fertilizer	2,36	6.48	0.004
All	Date × Predation	2,36	0.94	0.40
All	Date × Fertilizer × Predation	2,36	0.57	0.57
Mid July	Fertilizer	1,18	1.08	0.31
Mid July	Predation	1,18	0.97	0.34
Mid July	Predation × Fertilizer	1,18	1.53	0.23
Early August	Fertilizer	1,18	26.67	<0.0001
Early August	Predation	1,18	0.36	0.62
Early August	Predation × Fertilizer	1,18	0.04	0.85
Late August	Fertilizer	1,18	0.74	0.40
Late August	Predation	1,18	10.54	0.005
Late August	Predation × Fertilizer	1,18	0.01	0.96

Appropriate error terms associated with each test are provided in Table 1, and bold values are as in Table 2.

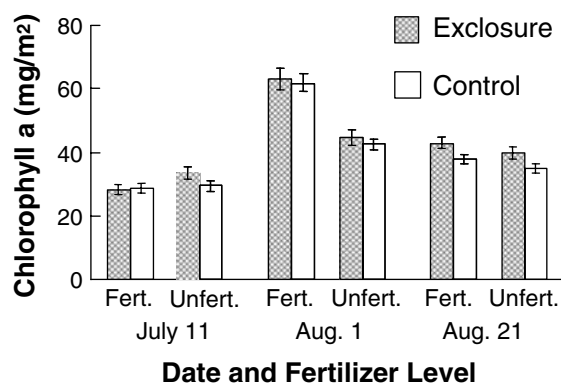


Figure 4. Chlorophyll *a* concentrations in exclusions and controls of fertilized and unfertilized plots during each sampling period. Values are back-transformed means from statistical tests. Error bars are ± 1 SE. Results of statistical comparisons are provided in Table 4.

became well established (Table 5), with more snails in controls than in exclusions (Fig. 5).

The relationship between snails and *Corophium* varied with sampling period (ANCOVA snail

Table 5. Results of RM-ANOVAs of mud snail abundance (counts) based on effects of fertilizer, predation, and sampling period (date)

Date	Effect	df	<i>F</i>	<i>p</i>
All	Fertilizer	1,18	0.26	0.62
All	Predation	1,18	8.21	0.01
All	Predation × Fertilizer	1,18	3.00	0.10
All	Date	1,18	15.57	<0.0001
All	Date × Fertilizer	1,18	4.37	0.05
All	Date × Predation	1,18	0.22	0.64
All	Date × Fertilizer × Predation	1,18	0.13	0.73
Early August	Fertilizer	1,18	4.33	0.05
Early August	Predation	1,18	3.53	0.08
Early August	Predation × Fertilizer	1,18	2.31	0.15
Late August	Fertilizer	1,18	1.03	0.32
Late August	Predation	1,18	7.02	0.02
Late August	Predation × Fertilizer	1,18	1.41	0.25

Appropriate error terms associated with each test are provided in Table 1 and bold and italicized values are as in Table 3.

abundance × sampling period $df=1,76$, $F=13.0$, $p=0.0006$). In early August, there was a highly significant negative relationship between the two ($df=1,38$, $F=31.0$, $p<0.0001$, $r^2=0.45$, Fig. 6a), whereas in late August, they were uncorrelated ($df=1,38$, $F=0.89$, $p=0.35$, Fig. 6b).

Corophium and snails may compete for diatoms, and the relationship between the two species could depend on body size. Therefore, this relationship was also analysed for the three different *Corophium* size classes from the early August sampling period. Fertilizer did not affect the relationship between 0 and 2.9-mm *Corophium* and snails; again *Corophium* abundance declined as snails became more common ($df=1,38$, $F=24.7$, $p<0.0001$, $r^2=0.39$, Fig. 7a). For 3 to 4.9-mm *Corophium*, amphipod and snail numbers were also negatively correlated (Fig. 7b, $df=1,19$; fertilized plots: $F=26.1$, $p<0.0001$, $r^2=0.59$; unfertilized plots: $F=9.58$, $p=0.0063$, $r^2=0.35$). Slopes of the lines relating *Corophium* and snails in fertilized and unfertilized plots were consistent (i.e., no snail × fertilizer interaction), but the intercepts differed; there were more *Corophium* present in fertilized than unfertilized plots for a given number of snails (ANCOVA fertilizer effect, $df=1,37$, $F=4.42$, $p=0.042$). A similar relationship existed

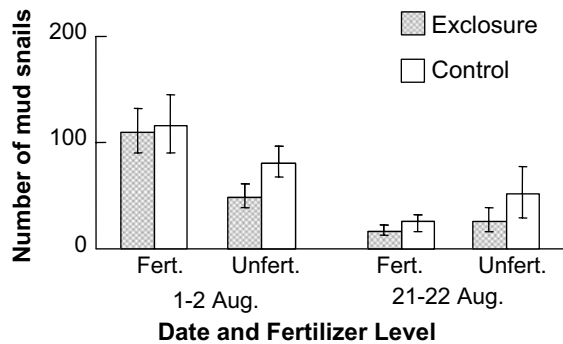


Figure 5. Numbers of mud snails in exclosures and controls of fertilized and unfertilized plots during early and late August. Values are back-transformed means from statistical tests. Error bars are ± 1 SE. Results of statistical comparisons are provided in Table 5.

for 5–10-mm *Corophium* (Fig. 7c, $df = 1, 19$; fertilized plots: $F = 29.1$, $p < 0.0001$, $r^2 = 0.62$; unfertilized plots: $F = 10.47$, $p = 0.0046$, $r^2 = 0.37$). In this case the separation of intercepts was even greater (ANCOVA fertilizer effect, $df = 1, 37$, $F = 17.1$, $p = 0.0002$), suggesting that the effect of fertilizer increased with increasing amphipod size.

Discussion

Effects of predation by shorebirds on Corophium

Shorebirds, primarily Semipalmated Sandpipers (Hicklin, 1987), feeding on the mudflat at Avonport, NS, reduced *Corophium* densities by approximately 80% in control plots relative to exclosures by the end of the experiment. This is a conservative estimate of the effects of these birds, because exclosures, while reasonably effective, did not keep out all individuals. No effects were noted mid-way through the study because there were relatively few birds present on the mudflat in July, but after abundance increased in August shorebirds clearly exerted a top-down effect in this ecosystem (Fig. 8). Effects were significant for all size classes of amphipods, suggesting that birds at this location may not have been size-selective predators. These findings contrast with results of other studies from both the Bay of Fundy and Europe, where shorebird predation had either no significant effect on *Corophium* numbers (Raffaelli & Milne, 1987), or resulted in more *Corophium*

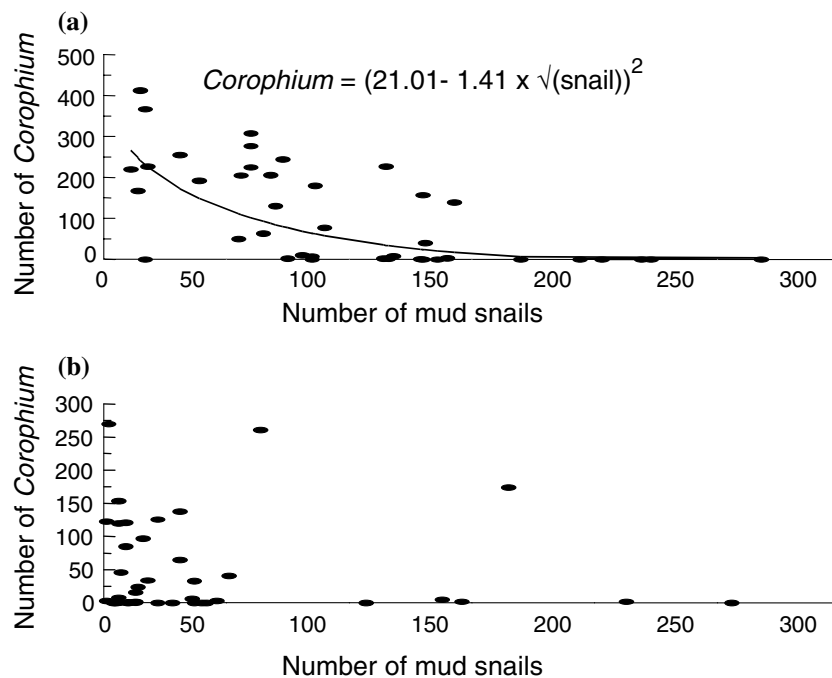


Figure 6. Plot of number of *Corophium* found in samples vs. number of mud snails counted in exclosures and controls for (a) early August and (b) late August. The regression equation relating the two species is provided for early August, but the two are unrelated in late August. Statistics associated with regressions are provided in the text.

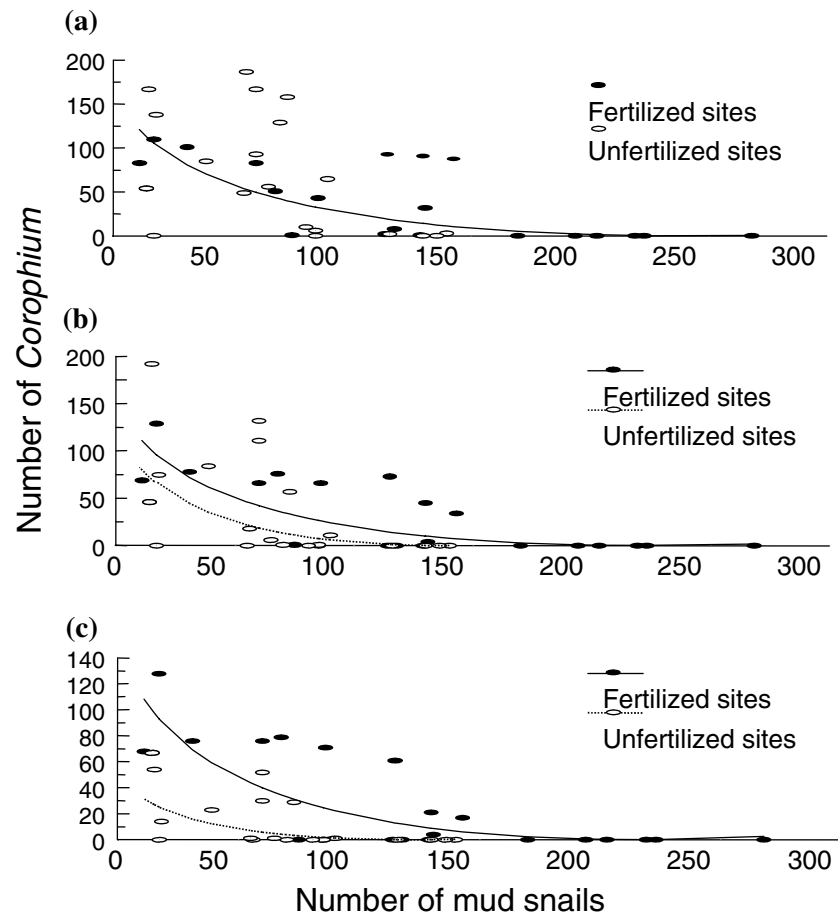


Figure 7. Plot of numbers of *Corophium* (a) 0–2.9, (b) 3–4.9, and (c) 5–10 mm long found in early August vs. number of mud snails counted in enclosures and controls. Regression lines for 3–4.9 and 5–10 mm *Corophium* were significantly different for fertilized and unfertilized plots (see text). Regression equations are as follows: 0–2.9 mm: *Corophium* number = $(13.98 - 0.895 \times (\sqrt{\text{snail number}}))^2$; 3–4.9 mm fertilized: *Corophium* number = $(13.55 - 0.91 \times (\sqrt{\text{snail number}}))^2$; 3–4.9 mm unfertilized: *Corophium* number = $(12.69 - 1.08 \times (\sqrt{\text{snail number}}))^2$; 5–10 mm fertilized: *Corophium* number = $(13.46 - 0.92 \times (\sqrt{\text{snail number}}))^2$; 5–10 mm unfertilized: *Corophium* number = $(7.99 - 0.72 \times (\sqrt{\text{snail number}}))^2$. Statistics associated with regressions are provided in the text.

(Wilson, 1989). However, in both of those cases, researchers concluded that predators were size-selective, preferentially feeding on the larger amphipods. Such feeding behaviour, coupled with intraspecific competition between adult and juvenile *Corophium* (Raffaelli & Milne, 1987; Wilson, 1989; Limia & Raffaelli, 1997), may have generated the patterns they observed.

The size-selective nature of predation by shorebirds has been well documented (e.g., Peer et al., 1986), and it may help to maintain discrete generations in *Corophium* (Matthews et al., 1992). Boates (1980) found that birds needed to consume

Corophium >4 mm long to avoid negative energy budgets. Further, there is some evidence across mudflats that birds feed preferentially in areas where large *Corophium* are found (Hamilton et al., 2003), implying selectivity at least at the patch level. Therefore, it is surprising that selectivity was not detected in our study. The 0.5-mm sieve lost about 90% of the smallest (<2-mm) *Corophium* (Crewe et al., 2001), so it is possible that birds avoided these very small prey and we failed to detect it. However, even assuming that is the case, based on observed differences between enclosures and controls for medium and small *Corophium*,

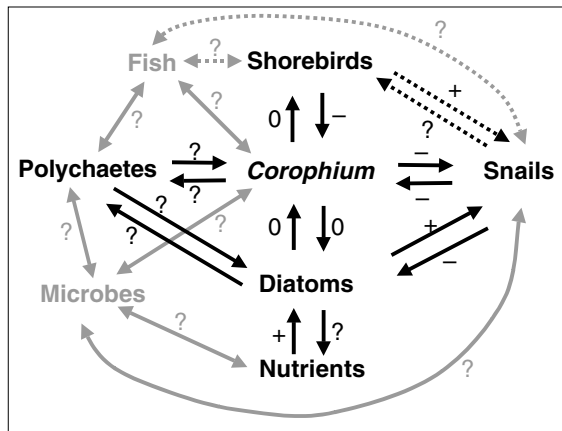


Figure 8. Schematic diagram of trophic interactions within the Avonport, NS, mudflat. Arrows indicate direction of interactions, i.e., effects of one group on another. Signs indicate the type of effect, i.e., + indicates a positive effect, - a negative effect, and 0 no observed effect. Question marks indicate that effects are undetermined. Solid lines represent direct effects and dashed lines indirect effects. Black text and lines represent taxa and interactions that were studied in this experiment. Grey text and bidirectional lines indicate taxa and interactions that were not considered, but which are hypothesized to be reasonable based on published information about those taxa. Note that although interactions between polychaetes and *Corophium*, and polychaetes and diatoms were considered and found to be minimal, they are represented with question marks because results of other studies differ in this regard, and we are not confident of the generality of these findings.

shorebirds in our study appeared to eat much smaller *Corophium* than previously reported. Virtually all large *Corophium* were gone by the end of the experiment, possibly due to a combination of predation by birds and fish (Wilson, 1989) and natural mortality of adults (Matthews et al., 1992), so perhaps birds were forced to feed on smaller individuals as well. It is unknown whether there are differences in size-selectivity between adult sandpipers (which migrate early in the season) and juveniles (which migrate later). However, if juveniles were less selective, selective predation by adults that occurred earlier may have been obscured. Based on these possibilities, had birds been more abundant prior to the early August sample, or had we collected additional samples between the second and third sampling periods, we may have detected some selectivity. It is also possible that birds were selective and that interactions with other species obscured this result (see *Indirect effects and compensatory interactions* below). Further research is needed to clarify this result and

identify the timing and level of size-selective predation by shorebirds on different mudflats.

Although shorebird predation reduced *Corophium* densities, much of the change in the *Corophium* population would have occurred even if shorebirds had been absent. From the beginning to the end of the experiment in controls of unfertilized plots, *Corophium* number declined by 85% and biomass by 84%. Based on a comparison of declines in exclosures and controls, shorebirds were responsible for approximately 55% of the decline in number and 13% of the decline in biomass. Natural mortality of adult *Corophium* (the majority of the biomass) after reproduction (Matthews et al., 1992) probably explains much of the large decline in biomass observed independent of bird predation, and the discrepancy in effects of birds on *Corophium* number and biomass. Because exclosures were not 100% effective, it is also possible that selective predation by the few birds that got into exclosures, if it occurred, could have obscured some of the apparent effect of birds on biomass (though this effect is expected to be minor given the overall effectiveness of the exclosures). Further, predation by demersal fish, some of which are known to prefer adult *Corophium* (Gilmurray & Daborn, 1981; Dadswell et al., 1984; Wilson, 1989), may also have contributed to the result. Fish could move freely through bird exclosures. If they fed selectively on large *Corophium* in both exclosures and controls, this could have obscured or limited (through competition) size-selective predation by birds, as described above, and contributed to the overall decline in *Corophium* biomass in the system. However, because our exclosures affected only birds and therefore essentially controlled for effects of fish predation, we can isolate the magnitude of bird effects and tentatively conclude (given the above caveats), that the main season-long effect of shorebird predation at Avonport may be on juvenile *Corophium*.

Although birds do appear to have a substantial effect on at least part of the *Corophium* population, it is questionable whether or not they have any long-term effects. Avian predators can have significant, lasting effects on their prey (e.g., Cooper et al., 1984; Quammen, 1984; Meese, 1993; Wootton, 1995; Hamilton, 2000). However, when

predation is intermittent or limited to one season, and the generation time of the prey is short, effects can be short-lived (Marsh, 1986a; Hamilton et al., 1994; but see Navarrete (1996) and Berlow (1997) for a different view). *Corophium* in this ecosystem has two generations annually and shorebirds affect only one of them, so long-term effects of bird predators may be limited. If there is any degree of intra- or interspecific competition involving *Corophium* and other invertebrates (see *Indirect effects and compensatory interactions* below), birds may alleviate it during the period they are present, but have little overall effect on the amphipod population.

Effects of fertilizer

Primary producers in this mudflat community were clearly nutrient-limited; chlorophyll *a* concentration in the sediment increased significantly within 3 weeks of fertilizer application. The rapid response to fertilizer is consistent with the behaviour of diatoms, which are capable of quickly generating blooms when favourable conditions develop (Underwood & Paterson, 1993). However, the response did not persist; 6 weeks after fertilizer application diatom densities (as measured by chlorophyll *a*) returned to ambient levels. A small reduction in fertilizer effectiveness by that time may partially explain this, but herbivores probably also played a role (see below). Based on measured ammonium levels (Fig. 2), and the lack of an increase in chlorophyll *a* concentration in unfertilized plots from early to late August (Fig. 4), loss of the fertilizer effect was not due to diffusion of fertilizer to unfertilized plots. Similarly, the change was probably not because the system was overloaded (i.e., unable to support a diatom population at that level), because observations at Avonport and elsewhere in the Bay of Fundy have revealed chlorophyll *a* concentrations well in excess of those observed in this study (Hamilton, Barbeau, and Diamond, unpublished data).

The response of primary producers to fertilizer indicates a bottom-up effect. However, it did not translate into an increase in *Corophium* abundance in exclosures, or bird predation where they fed freely, as predicted under models of trophic dynamics (Power, 1992) (Fig. 8). There are several

possible explanations for this. First, although *Corophium* in other systems can be food-limited (Smith et al., 1996), that may not be the situation here, and top-down processes may be more important. Second, the high ammonium concentration in the fertilizer may have had a negative effect on *Corophium* (Peletier, 1996). This may have reduced herbivory in fertilized plots, and artificially generated what appeared to be a bottom-up effect of fertilizer on diatoms. However, this scenario is unlikely because diatoms are known to respond to fertilizer high in nitrogen (Fisher & Cowdell, 1982). Similarly, fertilizer enhanced the ability of medium and large *Corophium* to co-exist with mud snails (see *Indirect effects and compensatory interactions* below), indicating that it was not harmful to the amphipods. It is also possible that the duration of the fertilizer treatment was not sufficient to elicit a response from *Corophium*, or that the experiment was too short to detect the response. Although not completely excluded, this explanation seems unlikely because the study covered nearly a full generation of *Corophium* growth and reproduction. Finally, another species may have responded to the fertilizer and either blocked the bottom-up effect or disturbed *Corophium* through competition (see below).

The lack of a bottom-up effect on *Corophium* was followed by no response by birds to the increase in chlorophyll *a* (diatoms), further indicating that bottom-up effects did not transmit through this food chain (Fig. 8). Although the functional response of shorebirds may have been saturated, preventing increases in predation with an increased food supply, in that situation *Corophium* abundance would have increased in fertilized control areas (where birds fed freely), and that was not the case.

Indirect effects and compensatory interactions

There were both top-down and bottom-up effects in the mudflat community at Avonport, but neither crossed the *Corophium* – diatom link (Fig. 8). Bird predation reduced *Corophium* abundance, but this led, by the end of the experiment, to a higher chlorophyll *a* concentration in exclosures than in controls. That result is the opposite of what would be expected under a top-down trophic cascade (McQueen et al., 1989). It is also surprising

because *Corophium* has been shown to reduce abundance of benthic diatoms (Gerdol & Hughes, 1994a, b; Smith et al., 1996; Hagerthey et al., 2002; but see Mouritsen et al. (1998) for a different view). There were no other effects of predation by shorebirds on the invertebrate community, indicating that indirect effects in this system were limited. Similarly, fertilizer had no demonstrated effect on the community beyond increasing the abundance of benthic diatoms and a small, short-term positive effect on *Heteromastus*. Multivariate analyses revealed no major interactions between *Corophium* and polychaetes in the community. This finding should be revisited in future studies, because other authors have identified negative relationships between *Corophium* and several polychaetes (e.g., Commito, 1982; Wilson, 1988; Jensen & André, 1993). In particular, *Nereis virens*, which is often common in soft-bottom communities in Atlantic Canada and Maine, is known to feed on *Corophium* (Commito, 1982; Ambrose, 1984). This species was not common in the study plots at Avonport, and, perhaps as a result, in this study responses by polychaetes had no bearing on the apparent blockage of top-down and bottom-up effects.

The single clear indirect effect of both fertilizer and predator exclusion was the response of mud snails to these manipulations. Snails, which feed on benthic microalgae as well as dead animal material (Pace et al., 1979; Connor et al., 1982), increased in abundance in fertilized plots within 3 weeks of fertilizer application. Individual snails can follow the mucus trails of others across the mud (Bretz & Dimock, 1983), facilitating rapid assembly of large groups on abundant food resources. Because they are highly mobile, mud snails responded much more quickly to the increased food supply than could *Corophium*, which would display a primarily developmental (*sensu* Murdock, 1971), rather than aggregative, response. By consuming the excess microalgae, snails may have prevented an increase in *Corophium* abundance, and a resulting increase in bird predation, in fertilized plots. They appear to have acted as compensating herbivores in this system, blocking transmission of indirect effects and truncating both species and community-level bottom-up interaction chains (Fig. 8). Similarly, by late August, snails were more abundant in controls, where birds reduced *Corophium*

abundance, than in exclosures, suggesting that snails responded to an enhanced feeding opportunity provided by removal of *Corophium*. Feeding by snails blocked transmission through the community of top-down effects of shorebird predation, preventing a trophic cascade and further indirect effects (Fig. 8). Snails probably over-compensated somewhat for the removal of *Corophium*, generating the reduction in chlorophyll *a* in controls relative to exclosures. It is theoretically possible that snails, as omnivores, also consumed *Corophium* and therefore contributed directly to either the lack of response of amphipods to fertilizer application or the *Corophium* decline in control areas. However, we have neither observed this in the field nor noted it in the literature, so we strongly suspect that the activities of mud snails in this system had strictly indirect effects on community dynamics.

The indirect effects of predation and fertilizer on mud snails probably involved competition between snails and *Corophium*. We did not explicitly test this, but knowledge of feeding habits of both species, combined with previous research (Wilson, 1988) and the observed negative relationships between them in this study and on a broader scale (Hamilton et al., 2003), suggests that they did compete. Assuming that is the case, the competition was probably a combination of exploitation and interference. Exploitation competition is suggested by the response of snails to an enhanced food source, and by the fact that both species feed on benthic microalgae (Wilson, 1988). Similarly, during the period when fertilizer was most effective (early August), it enhanced the ability of large juvenile and adult *Corophium* to coexist with snails, suggesting that food was limiting.

Interference competition is suggested by the fact that the smallest *Corophium* did not benefit from fertilizer application in the way larger individuals did; it did not enhance their ability to coexist with mud snails. *I. obsoleta* is known to reduce abundance of several species of intertidal invertebrates (DeWitt & Levinton, 1985; Hunt et al., 1987), and to disrupt settlement of invertebrate larvae (Dunn et al., 1999). Wilson (1988) found that when snails were added to cores of sediment containing *Corophium*, juvenile amphipod abundance declined. By moving through the upper 2 cm of intertidal sediment, snails collapse or destroy burrows of tube-dwelling amphipods

(DeWitt & Levinton, 1985). In our study, small *Corophium*, which build shallow burrows (Meadows, 1964), might have been unable to benefit from the enhanced food supply provided by fertilizer because of physical disturbance by snails.

Corophium also compete intraspecifically, with adults reducing the relative abundances of smaller conspecifics (Limia & Raffaelli, 1997; Wilson, 1989). However, this was probably not a factor in our study, because there was no evidence of a reduction in small *Corophium* in exclosures (where more adults were present) relative to controls. The effects of mud snails on *Corophium* likely kept amphipod densities at levels low enough to prevent intraspecific competition in this system. However, intra- and interspecific competition can have similar effects on small *Corophium*, so future studies should be designed to clearly separate the two.

The *Corophium*–snail relationship may provide an alternate explanation for the apparent lack of size-selectivity in shorebird predation. It is possible that the higher snail density in control plots in late August increased mortality of small *Corophium* which, combined with bird predation, resulted in a decline in *Corophium* of all sizes. This possible indirect chain of events highlights the importance in ecological studies of considering the mechanisms of trophic interactions, as well as both direct and indirect effects (Wootton, 1994). Indirect effects can either obscure direct effects among species (e.g., Hamilton, 2000) or create the appearance of direct effects when they are really mediated by other processes (this study). Further study of these interactions in intertidal mudflats is warranted.

Trophic cascades

There was no evidence of a trophic cascade, as it is usually viewed (Persson, 1999), in the mudflat community at Avonport. Although indirect effects can be slow to develop (Yodzis, 1988; Wootton, 1992; Hamilton, 2000; see Menge (1997) and Schmitz et al. (2000) for an alternative view), because mud snails responded rapidly to both predation and fertilizer application, short experimental duration probably was not a factor in this result. More likely, as described above, snails compensated for the experimental manipulations

and prevented transmission of indirect effects across trophic levels (Fig. 8), possibly contributing to community stability. This is consistent with Menge's (1995, 1997) conclusion that pathways of indirect effects are usually short.

Such compensatory activities by invertebrates have been well documented in other studies (Marsh, 1986a; Navarrete & Menge, 1996; Hamilton, 2000), and are thought to be important in limiting trophic cascades (Strong, 1992; Polis & Strong, 1996; Pace et al., 1998, 1999; Persson, 1999). Pace et al. (1999) concluded that the expression of compensation depends on the ability of a species to respond to manipulations. Our results support this view. Snails responded rapidly to the experimental manipulations, enabling them to compensate quickly for changes in the system.

Though the prevalence of trophic cascades in nature continues to be debated (Strong, 1992; Polis & Strong, 1996; Persson, 1999; Pace et al., 1999; Schmitz et al., 2000), it is generally agreed that cascades are most likely to appear in simple communities with relatively few species in each trophic level, and limited opportunities for compensation. The Avonport mudflat is simple, and has many of the attributes commonly associated with a top-down trophic cascade. However, in this case the cascade was prevented by the activities of mud snails. This result strengthens the conclusion of Hamilton (2000) that, although compensatory interactions and indirect effects may be more common in species-rich communities, they certainly are not limited to them.

Implications for shorebird–Corophium interactions in the Bay of Fundy

The intertidal mudflat community at Avonport is probably stabilized by the activities of mud snails. Bird predation may reduce *Corophium* densities, but the effects are limited to one or two months per year and at least on a small scale, snails quickly compensate for changes caused by shorebirds. Both diatoms (Grant et al., 1986; Underwood & Paterson, 1993) and *Corophium* (Mouritsen et al., 1998) contribute to mudflat stability. Therefore, by buffering effects of changes in *Corophium* abundance on diatoms and the rest of the community, snails may contribute indirectly to sediment stability.

Our results show no evidence of the top-down trophic cascade envisioned by Daborn et al. (1993) for this ecosystem. However, Daborn et al. (1993) did not quantify effects of shorebirds in the system, so direct comparisons are difficult. Their study was conducted on a different mudflat (Starr's Point) several km from Avonport, raising the possibility that our results may be site-specific. Further, it is questionable whether the compensatory response by snails can be generalized from small study plots to whole mudflats. However, recent surveys of other mudflats revealed the same relationships, on both fine and broad scales, between snails and *Corophium* (Hamilton et al., 2003), suggesting that what is occurring at Avonport may be a general pattern in the upper Bay of Fundy.

Based on our results, a change in the distribution of foraging shorebirds on mudflats in the upper Bay of Fundy may have little long-term effect on mudflat communities. Potential disturbance of shorebirds is certainly an issue, because this region is a critical staging area for them (Shepherd & Boates, 1999), but large-scale bird movements would probably not jeopardize mudflat stability. This is an important finding, because in recent years shorebird distributions have changed (P. Hicklin, personal communication), and there is concern about the implications of these changes.

Conclusions and future work

Both top-down and bottom-up effects were found in this Bay of Fundy mudflat ecosystem, but because the compensatory response of mud snails was driven by food availability, bottom-up forces were probably dominant. Our results indicate that compensatory interactions that block trophic cascades and stabilize communities need not be limited to diverse or complex communities. As more examples of compensation in simple systems emerge, it becomes increasingly clear that the presence of individual species capable of compensatory interactions, rather than community complexity per se, is of prime importance in stabilizing such communities.

Future research on intertidal mudflat communities in the upper Bay of Fundy should include a detailed analysis of the relationship between *Corophium* and snails. In particular, the nature of

the relationship between these two species should be assessed experimentally by excluding snails from fertilized and unfertilized plots, as we did with shorebirds in this study. The role of parasites in this ecosystem should also be considered in conjunction with *Corophium*-snail-shorebird interactions. Parasites are known to affect interactions among free-living species (Poulin, 1999). On intertidal mudflats, nematodes that use *Corophium* as intermediate hosts and shorebirds as their definitive host alter the behaviour of *Corophium* to make them more susceptible to bird predation (McCurdy et al., 1999a), and can affect reproductive behaviour of female *Corophium* (McCurdy et al., 1999b) and subsequent population dynamics. Further, trematodes that infect mudsnails, *Corophium*, and shorebirds may influence the distribution of mudsnails, bringing them into contact with *Corophium* (McCurdy et al., 2000) and possibly leading to the interactions described in this paper.

Additional manipulative experiments on the species described here, combined with quantitative studies on other components of the mudflat community, would facilitate further development, parameterization, and testing of the conceptual model initiated in this study (Fig. 8). A quantitative model of intertidal trophic interactions would greatly enhance our ability to predict the response of mudflat communities in the upper Bay of Fundy to a variety of natural and human-induced changes and disturbances, especially needed in this period of climate change and extensive coastal development.

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Trophic structure and avian communities across a salinity gradient in evaporation ponds of the San Francisco Bay estuary

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Abstract

Commercial salt evaporation ponds comprise a large proportion of baylands adjacent to the San Francisco Bay, a highly urbanized estuary. In the past two centuries, more than 79% of the historic tidal wetlands in this estuary have been lost. Resource management agencies have acquired more than 10 000 ha of commercial salt ponds with plans to undertake one of the largest wetland restoration projects in North America. However, these plans have created debate about the ecological importance of salt ponds for migratory bird communities in western North America. Salt ponds are unique mesohaline (5–18 g l⁻¹) to hyperhaline (>40 g l⁻¹) wetlands, but little is known of their ecological structure or value. Thus, we studied decommissioned salt ponds in the North Bay of the San Francisco Bay estuary from January 1999 through November 2001. We measured water quality parameters (salinity, DO, pH, temperature), nutrient concentrations, primary productivity, zooplankton, macroinvertebrates, fish, and birds across a range of salinities from 24 to 264 g l⁻¹. Our studies documented how unique limnological characteristics of salt ponds were related to nutrient levels, primary productivity rates, invertebrate biomass and taxa richness, prey fish, and avian predator numbers. Salt ponds were shown to have unique trophic and physical attributes that supported large numbers of migratory birds. Therefore, managers should carefully weigh the benefits of increasing habitat for native tidal marsh species with the costs of losing these unique hypersaline systems.

Introduction

Several tidal marsh species are now endangered because more than 79% of historic tidal wetlands have been lost to urbanization, agriculture, and salt production (Goals Project, 1999). The San Francisco baylands comprise a fragmented

landscape of non-tidal salt, brackish and freshwater wetlands; agricultural lands; seasonal ponds; vernal pools; riparian scrub; and commercial salt ponds (Goals Project, 1999). Although salt ponds were not a natural feature of the landscape, they have existed in the San Francisco Bay estuary for more than 150 years (Ver Planck, 1958). These

non-tidal hyperhaline ponds vary seasonally in salt content from brackish to saturated, range from a few centimeters to a few meters in depth, and are composed of relatively simple but productive assemblages of algae and invertebrates (Carpelan, 1957; Lonzarich & Smith, 1997).

The San Francisco Bay ecosystem is an important staging and wintering area for migratory waterfowl and shorebirds in the Pacific Flyway (Harvey et al., 1992). It is recognized as a site of hemispheric importance for shorebirds because it supports at least 30% of some populations in the flyway (Page et al., 1999), and also up to 50% of many diving duck populations (Accurso, 1992). Many migratory waterbirds use the baylands, which consists of the area between the historic high and low tide lines and comprises about 85 830 ha in the estuary (Goals Project, 1999). The ponds have become an integral part of the landscape, as well as essential habitats for large numbers of waterbirds during migration and winter (Anderson, 1970; Accurso, 1992; Takekawa et al., 2001; Warnock et al., 2002).

A large proportion of the salt ponds was purchased and taken out of salt production in 1994 (North Bay: 4045 of 4610 ha) and 2002 (South Bay: 6110 of 10 520 ha, North Bay: the remaining 565 ha). Resource management agencies have proposed converting the salt ponds into tidal marshes to restore populations of tidal marsh species of concern and to minimize management costs. A planning report for the future of wetlands in the estuary (Goals Project, 1999) suggested that only a few hundred ha of more than 10 000 ha of salt ponds in the estuary would likely remain through the next century. However, it is not well understood how these ponds support such large numbers of wintering and migratory birds, and it is unknown whether sufficient alternative habitats remain in this highly urbanized estuary. Thus, we initiated a study to document the limnological character of salt ponds in the estuary. We examined water quality, nutrient concentrations, primary productivity, zooplankton, macroinvertebrates, fish, and birds across a salinity gradient to examine the ecological character and trophic structure of salt ponds in the estuary and to determine the relationship between salinity and community structure.

Study area

We examined salt ponds in the North Bay sub-region (37.90° N–38.25° N; 122.25° W–122.50° W) of the San Francisco Bay estuary (Fig. 1). The salt ponds were located 5 km northwest of Vallejo, California (38° 10' W, 122° 20' N) and comprised about 4000 ha. They were acquired in 1994 by the California Department of Fish and Game as part of the Napa-Sonoma Marshes Wildlife Area. Although salt production ceased in 1993, the system remained intact with lower salinities and muted tidal flow in primary ponds and higher salinity and very little tidal flow in ponds farther inland (Takekawa et al., 2000; Lionberger et al., 2004).

Methods

A sub-sample of five ponds was selected for study, representative of the salinity gradient in the salt pond system (Fig. 1). Ponds 1 (P1), 2 (P2), 3 (P3), 4 (P4), and 7 (P7) ranged in size from 127 to 534 ha and varied in mean salinity from 23 to 224 g l⁻¹ (Table 1), similar to the salinity range found in commercial salt production systems. Originally, P1 was the intake pond from a channel to the North Bay, whereas ponds with higher numbers had increasing salinity. Water entered P1, primarily by tidal influence through a one-way gate and was pumped into P2 intermittently during the study period (T. Huffman, California Department of Fish and Game, personal communication). Increased water elevation in P2 supplied water into P3 via an inverted siphon except when density differences and small hydraulic head prevented flow (Lionberger et al., 2004). Density differences and small hydraulic head usually prevented flow through an inverted siphon between P3 and P4 (Lionberger et al., 2004). During salt production, the supernate was removed from the brine and stored in P7, the bittern pond.

We superimposed a 250×250 m (6.25 ha) Universal Transverse Mercator (UTM) grid upon the sampled ponds to provide a framework for integrated sampling (Takekawa et al., 2000). This grid system provided the basis for identifying sampling locations in each pond (Matveev, 1995; Posey et al., 1995). Individual gridcells where birds were located

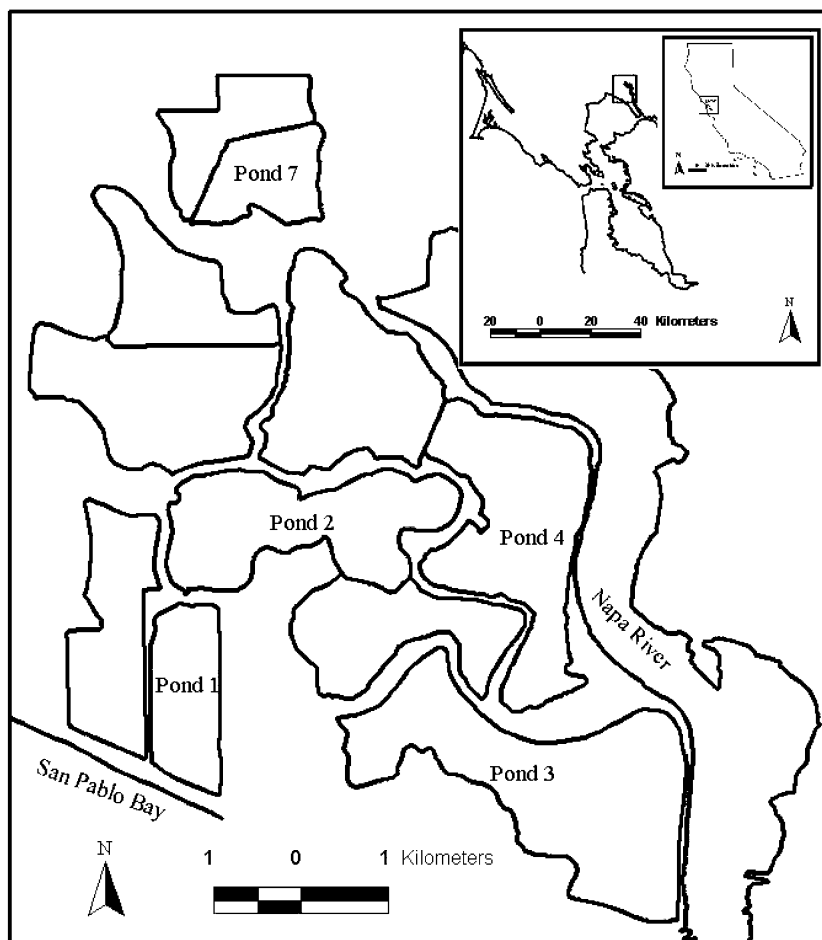


Figure 1. Former salt evaporation ponds in the Napa-Sonoma Wildlife Area located 5 km northwest of Vallejo, California, USA on the northern edge of San Pablo Bay in the San Francisco Bay estuary.

in monthly surveys were identified and selected as sampling locations in each pond to facilitate the study of trophic level relationships. Beginning in March 1999, 10 gridcells in which birds were observed during monthly surveys were randomly selected from each pond for nutrient, primary productivity, invertebrate and fish sampling. If

< 10 gridcells were used by birds within a pond, additional gridcells were selected randomly.

Water quality

From February 1999 until November 2001, water quality parameters were measured monthly in P1,

Table 1. Average water quality values \pm SD in milligrams per liter for Napa-Sonoma Ponds 1, 2, 3, 4 and 7 during 1999, 2000 and 2001

Pond	Salinity (PPT)	D.O. mg l ⁻¹	pH	Turbidity (NTU)	Temp. (°C)
1	23.1 \pm 9.4	8.7 \pm 1.5	8.1 \pm 0.3	253.9 \pm 227.0	18.2 \pm 4.8
2	23.1 \pm 8.2	8.5 \pm 1.5	8.6 \pm 0.3	82.0 \pm 44.1	16.8 \pm 4.3
3	47.6 \pm 16.1	8.3 \pm 2.2	8.4 \pm 0.2	198.4 \pm 94.8	18.0 \pm 4.7
4	169.7 \pm 70.6	6.0 \pm 4.6	7.7 \pm 0.5	96.8 \pm 97.1	19.6 \pm 5.8
7	224.3 \pm 66.4	3.6 \pm 1.8	5.9 \pm 0.8	163.4 \pm 74.4	20.5 \pm 5.4

P2, P3, P4 and P7. Four or five sampling locations were established for each salt pond with measurements taken at the corners of the ponds. Water quality sampling locations were chosen to maximize the detection of spatial variability in the ponds, and measurements were timed to occur within a week of the bird surveys. Sample locations were referenced to the 250×250 m UTM grid.

A Hydrolab Minisonde[®] (Hydrolab-Hach Company, Loveland, CO) was used to measure conductivity (internally converted to salinity with the 1978 Practical Salinity Scale), pH, turbidity, temperature, and dissolved oxygen at each location. The sensors on the Hydrolab were calibrated prior to each use and a calibration check was performed after sampling. Because the salt ponds are known to stratify under certain conditions, readings from near-surface and near-bottom of the water column were collected at sampling locations where water depth exceeded 60 cm. When salinity in the ponds exceeded 70 g l⁻¹, specific gravity was measured with a hydrometer (Ertco, West Paterson, NJ) scaled for the appropriate range. These data were corrected for temperature and converted to salinity.

Chlorophyll and nutrients

We collected a sub-surface sample of water from each of the sampled gridcells on each survey date. Water samples were immediately placed on ice in a cooler and frozen within 8 h. Water samples were subsequently divided for analyses of chlorophyll *a* (chl *a*) and nutrients. Chl *a* concentration was determined with the monochromatic method described by Wetzel & Likens (1991). Each sample was passed through a 0.45 μm filter, and the filter was immediately ground in a tissue grinder with 3–4 ml of 90% alkaline acetone. Contents were transferred to a 20-dram vial, capped and placed in a darkened refrigerator. After 12 h, supernatant in vials was decanted into a glass cuvet (light path 2.0 cm) and absorption measured at 750 and 665 nm on a spectrophotometer with maximum spectral bandpass width of 8 nm and wavelength accuracy of ±2 nm (Model 401, Spectronic Instruments, Inc., Rochester, NY). For each sample, we then added 0.1 ml of 1 N HCl ml⁻¹ extract, mixed the solution and repeated absorption measurements at the same wavelengths. Chl *a* was then calculated (Wetzel & Likens, 1991).

The remainder of the water sample was analyzed for concentrations of nitrogen and phosphorus. Nitrate was measured with an ultraviolet screening method, and ammonia nitrogen was determined following the Nesslerization method (American Public Health Association, 1989). Soluble reactive phosphorus concentration was determined with persulfate digestion after filtering the sample through a 0.45 μm filter, and total phosphorus concentration was determined with persulfate digestion on unfiltered samples (APHA, 1989).

Zooplankton

Zooplankton samples were collected with a Miller high-speed plankton sampler fitted with a 149 mm mesh net and flow meter. Samples were collected by pulling the sampler about 10 m off the side of a small boat at a depth of about 0.25 m. Zooplankton samples were immediately concentrated with a 149 mm mesh screen and preserved in 5% formalin, then later transferred to 70% alcohol. Zooplankton in samples were identified and enumerated under a stereo-zoom microscope with 10–100× magnification. When the number of individuals was >1000, sub-sampling was performed (Wetzel & Likens, 1991). In sub-sampling, we first enumerated all *Ephydra* (brine flies) and *Artemia* (brine shrimp) in the sample. We then diluted the remainder of the sample to 200 ml, mixed it on a magnetic stirrer and withdrew five 1 ml sub-samples in a Hansen-Stempel volumetric pipet.

Sub-samples were transferred to a grid-lined petri dish and zooplankton were enumerated. Nauplii (larvae) and juvenile stages of *Artemia* were distinguished by the presence and length of filtering appendages. Individual organisms within each sample were categorized as adults or as 1st, 2nd or 3rd instar larvae. In addition, larvae were measured and separated into 1 mm size classes ranging from 1 to 7 mm. Adult males were distinguished by the presence of claspers, whereas females were distinguished by the presence of extended ovisacs. Larval instars of *Ephydra* were determined by size and by the presence of respiratory siphons and appendages. *Ephydra* larvae were also measured and separated into 1 mm size classes. Other taxa were identified to a practical taxonomic level and counted.

Biomass of *Artemia* and *Ephydra* was calculated from length to weight relationships and abundance. Length–weight regressions were determined from 60 *Artemia* and 32 *Ephydra*. We recorded lengths (nearest 0.01 mm) under the stereomicroscope fitted with an ocular micrometer and preserved weight of individuals (nearest 1.0 μg) on a Mettler model M1 microbalance (Mettler-Toledo, Inc., Columbus, OH). We determined fresh weight from preserved weight with a conversion of 0.8, and dry weight from fresh weight with a conversion of 1.1 (Wetzel, 1983).

Macroinvertebrate surveys

Benthic macroinvertebrates were sampled in P1, P2, P3 and P4. P7 was sampled on three occasions, but sampling was discontinued because invertebrates were rare or not found at such high salinities. Monthly waterbird surveys were used to randomly select 10 gridcells identified by GPS location to sample for benthic macroinvertebrates within each pond. P1–P4 were sampled every other month beginning April 1999 to November 2000, and then in February, June and November 2001 (sample frequency changed with very low water levels in some ponds in summer or during inclement weather conditions in winter).

Within each gridcell, we located the center with a GPS unit, allowed the boat to drift, and then collected three cores (about 3 m apart) with a standard Ekman grab sampler (15.2 cm³). A standard (USA ASTM E-11 Number 18) 1.0 mm mesh sieve was used to reduce cores to invertebrates and debris that were preserved in 70% ethanol and Rose Bengal dye. The qualitative procedure for estimating the texture of the substrate was developed by a single observer, who trained others in this characterization. Substrate was characterized as soft, medium, or hard in penetrability, and as primarily clay, sandy, or silty in appearance. We noted outstanding features, such as abundant shell fragments, large organic debris, or encrusted crystalline salt.

Field samples were processed using binocular microscopes (3–10 \times power) by sorting individual invertebrates from debris and residual sediment. Invertebrates were identified and enumerated to genus or species (when common) or family (when uncommon) with appropriate keys (e.g., Smith &

Carlton, 1975; Morris et al., 1980). As a quality control measure, a second observer verified the identification of 5–10% of these samples. Blotted wet weight biomass of organisms was determined with an Ohaus, Model 3130 scale (Pine Brook, NJ). Samples were dried in a Precision convection oven (Winchester, VA) at 15.5 °C for 24 h to determine dry weight.

Fish surveys

Fish species assemblages were surveyed bimonthly from July 1999 until December 2000 in P1–P3 (sampling in P4, which ranged to salinity 100, was discontinued after no fish were detected in initial samples; P7, with salinity >250, was presumed not to support fish life). We used bag seines to sample shallow areas near shore and gill nets to sample deeper areas offshore to assess the distribution and relative abundance of both juvenile and adult fishes. Fishing effort for each gear type was standardized and replicated to allow for statistical comparisons of fish catch among dates and sites. A 5.5 m bag seine with 6.4 mm mesh in the bag and 12.7 mm mesh in the wings was used along shorelines in water <1.5 m deep. Six sites were sampled with five hauls of a bag seine at each site by manually dragging the seine about 8 m perpendicular or parallel to shore.

In addition, six 38.1 m long (1.8 m deep) variable-mesh monofilament gill nets with 12.7, 15.4, 38.1, 50.8 and 63.5 mm square mesh panels were fished for a maximum of 6 h, checking them every 1–2 h to release protected fish species such as Sacramento splittail (*Hypomesus transpacificus*) and delta smelt (*Pogonichthys macrolepidotus*). Individuals were identified to species in the field with taxonomic keys (Miller & Lea, 1972; Moyle, 1976; Eschmeyer et al., 1983; McGinnis, 1984). Fish that were not reliably identified in the field were preserved and later identified by taxonomic specialists. The first 25 individuals of each species were measured for standard length (to the nearest mm) and weighed (blotted wet weight biomass to the nearest 0.1 g).

Bird surveys

We conducted monthly complete counts of the five ponds from January 1999 to June 2001, and then

bimonthly counts thereafter through November 2001. Observers conducted counts of species with binoculars and spotting scopes from vantage points at the edge of ponds during the first week of each month, and locations of waterbirds were placed within the gridcells of each pond. Surveys were conducted during the day within 3 h of the highest high tide when the largest number of waterbirds was roosting in the salt ponds.

Identified waterbirds were separated into guilds to examine differences among foraging groups rather than differences among species. These foraging guilds included: (1) sweepers – obtained prey from the surface, e.g., *Recurvirostra americana* (American avocet); (2) shallow probers – foraged in the top layer (< 3 cm) of sediments, e.g., *Calidris mauri* (western sandpiper); (3) deep probers – reached deeper into the substratum than shallow probers, e.g., *Limosa fedoa* (marbled godwit); (4) dabblers – fed in the upper water column, e.g., *Anas acuta* (northern pintail); (5) diving benthivores – fed in deeper water on benthic invertebrates, e.g., *Aythya affinis* (lesser scaup); (6) piscivores – fish consumers, e.g., *Pelecanus erythrorhynchos* (American white pelican); and (7) other – omnivores and incidental species including gulls.

Statistical analyses

We examined differences in salt ponds during the winter (Dec–Feb), spring (Mar–May), summer (June–Aug), and fall (Sep–Nov) seasons, 1999–2001. Months were assigned to seasons to encompass the major bird migration chronology in spring and fall. We computed means from repeated monthly water quality measurements but did not make statistical comparisons, because sampling locations were fixed and non-random. We computed means from repeated monthly or bimonthly nutrient measurements for each pond and examined between-pond differences with univariate analysis of variance (ANOVA) or multivariate (MANOVA) tests (SAS Institute, 1990). We tested for equal variances using Levene's test and then used the multiple variance mixed procedure (SAS Institute, 1990) if data violated the equal variance assumption. Because sample sizes often differed among ponds, significant ANOVA results were investigated with the Tukey–Kramer procedure

(SAS Institute, 1990) to make multiple comparisons among pairs of means (Sokal & Rohlf, 1995).

Sampling effort for chl *a*, zooplankton, invertebrates, and fish was standardized and replicated to allow for statistical comparisons among ponds. The results of fish sampling methods were not directly comparable because species composition, numbers, and biomass differed strongly between gear types. However, samples were standardized for sample size and then combined for biomass and species diversity comparisons. To ensure equal representation of sampling methods in comparisons of fish species composition between ponds, catch data were converted to proportions of the total catch for each gear type and then combined. Complete counts of birds were standardized by conversion to density (birds ha⁻¹) because salt ponds varied in size. We used the Shannon–Weiner index (Krebs, 1999) to assess species diversity for birds, fish, and invertebrates for each independent sampling event. For invertebrates, we used a MANOVA model to compare diversity indices over time by pond (model effect) with least squares and mean response design. ANOVA was then used to compare individual differences among ponds or time.

We elaborated on the between-pond comparisons by directly examining the relationship between salinity and other parameters. We independently examined chl *a* concentrations and zooplankton biomass in addition to invertebrate, fish, and bird concentrations and diversity by applying a best-fit quadratic function to the relationship with salinity. Non-metric Multidimensional Scaling (NMDS), a distance-based ordination method that displays multi-dimensional data by maximizing rank–order correlation, was used to present similarity matrix distances and distance in ordination space on two-dimensional plots (Clarke & Warwick, 2001). We used the PRIMER program (Plymouth Routines in Multivariate Ecological Research, Plymouth, England) to perform NMDS on transformed data based on a Bray–Curtis similarity matrix (Bray & Curtis, 1957), and visually compare species composition among samples in two dimensions. We averaged sample values by season to simplify the display and associated larger diameter circles with increased salinity to accentuate the relationship

between salinity and species composition (Clarke & Warwick, 2001). We used analysis of similarities (ANOSIM, PRIMER) to further investigate community differences among ponds with 5000 permutations to compare overall and pair-wise effects of pond differences on species composition. PRIMER provides Global R and pairwise R statistics that provide a measure of the difference between rank dissimilarities within and among groups (Sommerfield et al., 2002). Stress values represent how well the multi-dimensional relationship between variables is represented in the two-dimensional plot; although stress parameters change according to quantity of data as well as the number of dimensions, Clarke & Warwick (2001) suggest that stress < 0.05 is excellent but stress < 0.10 is a good ordination, whereas stress > 0.3 suggests that the ordination plot is not interpretable. For all analyses, results were deemed significant when $p \leq 0.05$.

Results

Water quality

Salinity varied widely throughout the study, ranging from 23.1 to 224.3 g l⁻¹ (Table 1, Fig. 2). The intake pond (P1) and an interior pond (P4) showed the greatest temporal variation in salinity. Ponds varied more seasonally than they did annually, especially in the higher salinity ponds (Fig. 2). Salinity was lowest following late winter rainfall and increased to peak concentrations in the late summer. The pH of the system was alkaline, but the water in P7, a bittern pond that was often very shallow with few areas to sample, was acidic throughout the year (Table 1). Turbidity was generally high in P3, coincident with seasonal winds. Water temperature ranged from 9 to 30 °C, with greatest extremes in P1 and P4, ponds that also had the greatest changes in water levels. Decreased water levels combined with elevated temperatures resulted in low dissolved oxygen readings in P4 during the summer months.

Nutrients

Nutrient concentrations varied among ponds and seasons (Table 2). Nitrate (NO₃-N) concentration

ranged from 0.306 to 8.05 mg l⁻¹ (Fig. 3). Nitrate was greater in P4 than in P1 and P2 ($F_{3,25} = 3.89$, $p < 0.021$). Ammonia (NH₃-N) concentrations ranged from 0.409 to 18.2 mg l⁻¹ (Fig. 3). Ammonia was greater in P4 than in P1–P3 ($F_{3,24} = 25.23$, $p < 0.0001$). Average soluble reactive phosphorus (SRP) concentration ranged from 0.151 to 3.21 mg l⁻¹ (Fig. 3). Overall, SRP concentration was lower in P4 than in P2 or P3 ($F_{3,25} = 3.33$, $p = 0.036$). Average total phosphorus (TP) concentration ranged from 0.29 to 4.88 mg l⁻¹ (Fig. 3). TP concentration was greater in P2 and P3 than in P4 ($F_{3,25} = 4.72$, $p = 0.0096$). Nitrogen to phosphorus (N:P) ratios ranged from 0.3 to 3.2 in P1, from 0.7 to 3.4 in P2, from 0.9 to 7.5 in P3 and from 2.3 to 30.3 in P4. N:P ratios in P4 were > 10.0 on 4 of 7 dates, but < 10.0 in the other ponds on all dates.

Primary productivity

Mean annual chl a concentration was higher in P3 and P4 than in P1 (Table 3). Seasonal change in chl a concentration was most pronounced in P4, and least pronounced in P1 and P2 (Fig. 4a). Chl a concentration was greater in P3 and P4 than in P1. However, the mean annual concentration in P4 reflected exceptionally high chl a concentrations (130.0 mg m⁻³) measured in the winter (Fig. 4a). Overall, chl a generally increased with salinity, but only P1 was significantly lower than the other ponds (Table 3; $F_{3,164} = 4.46$, $p = 0.0048$). Patterns in phaeophyton concentrations by pond were similar to chl a ($F_{3,164} = 4.46$, $p = 0.0049$) and were higher in P2, P3, and P4 than in P1 (Table 3).

Among all ponds, chl a concentration was negatively correlated with total zooplankton biomass (intercept = 1.2266, slope = -0.4547, adjusted $r^2 = 0.17$, $p < 0.0001$). Similarly, chl a concentration in P4 was negatively correlated with *Artemia* biomass (intercept = 12.333, slope = -0.7689, adjusted $r^2 = 0.331$, $p < 0.0001$).

Zooplankton

Twenty zooplankton taxa were identified in the salt ponds. Eight taxa were recorded in lower salinity ponds (P1 and P2), seven were recorded in P3 and only five taxa were recorded in P4 and P7. Seasonally, more taxa were recorded during

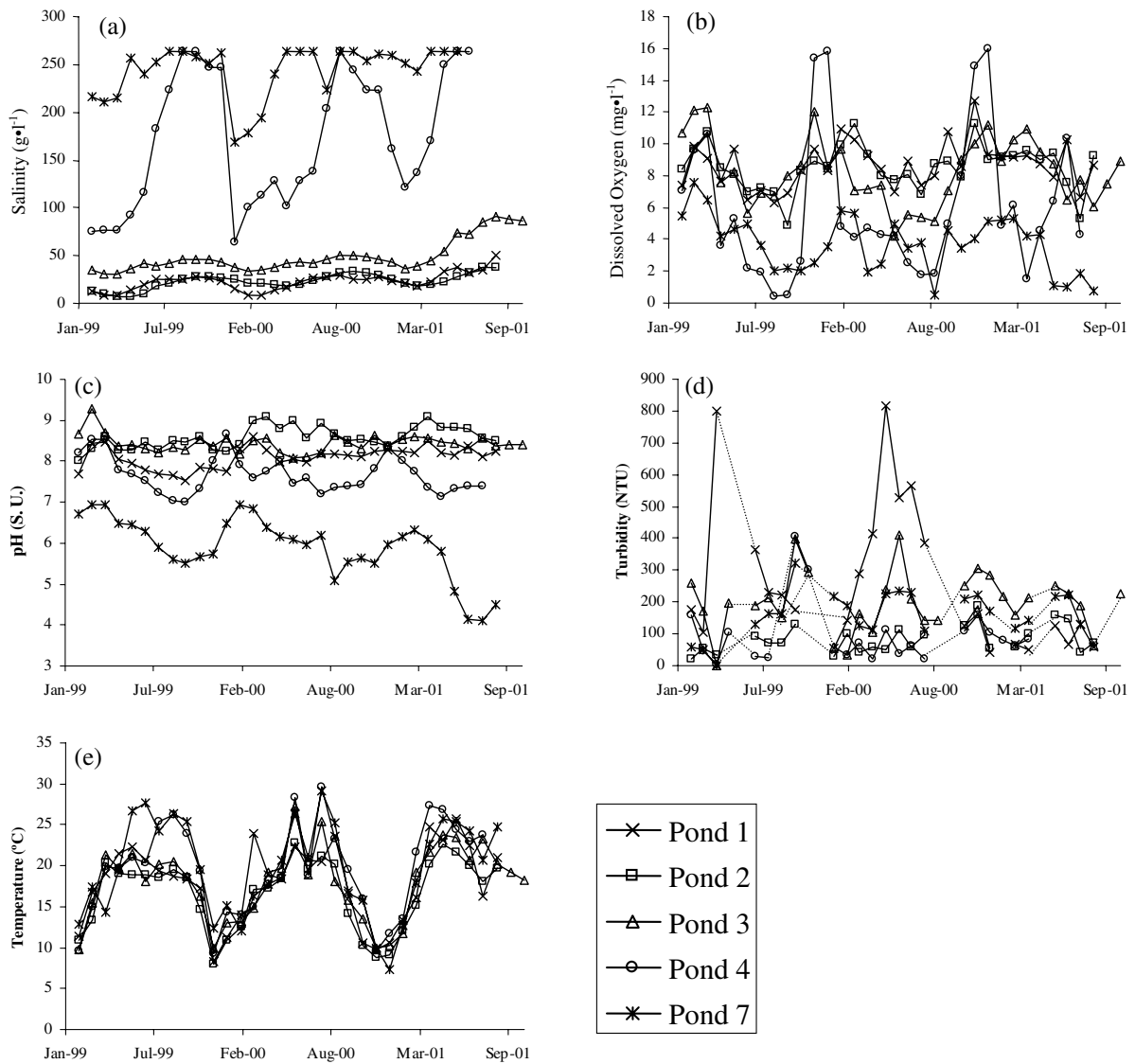


Figure 2. Salinity (g l^{-1}), dissolved oxygen (mg l^{-1}), pH (SU), turbidity (NTU), temperature ($^{\circ}\text{C}$) for Ponds 1, 2, 3, 4 and 7 in the Napa-Sonoma Marshes from 4 to 5 sampling locations per pond, Feb 1999–Nov 2001.

Table 2. Average dissolved nutrient concentrations \pm SD ($\mu\text{g l}^{-1}$) for Napa-Sonoma Ponds 1–4 during 1999 and 2000. Means that are not significantly different (Tukey–Kramer) are indicated by similar superscripts

Pond	$\text{NO}_3 \text{ mg l}^{-1}$	$\text{NH}_3\text{-N mg l}^{-1}$	SRP mg l^{-1}	TP mg l^{-1}
1	$1.57^a \pm 1.1$	$5.56^a \pm 2.8$	$2.18^{ab} \pm 0.8$	$2.17^{ab} \pm 0.8$
2	$1.47^a \pm 1.7$	$6.24^a \pm 1.1$	$3.21^b \pm 1.3$	$3.34^b \pm 1.4$
3	$3.30^{ab} \pm 2.6$	$7.21^a \pm 3.0$	$2.57^b \pm 0.9$	$2.71^b \pm 1.2$
4	$4.02^b \pm 1.3$	$15.42^b \pm 2.2$	$1.25^a \pm 1.7$	$1.16^a \pm 1.2$

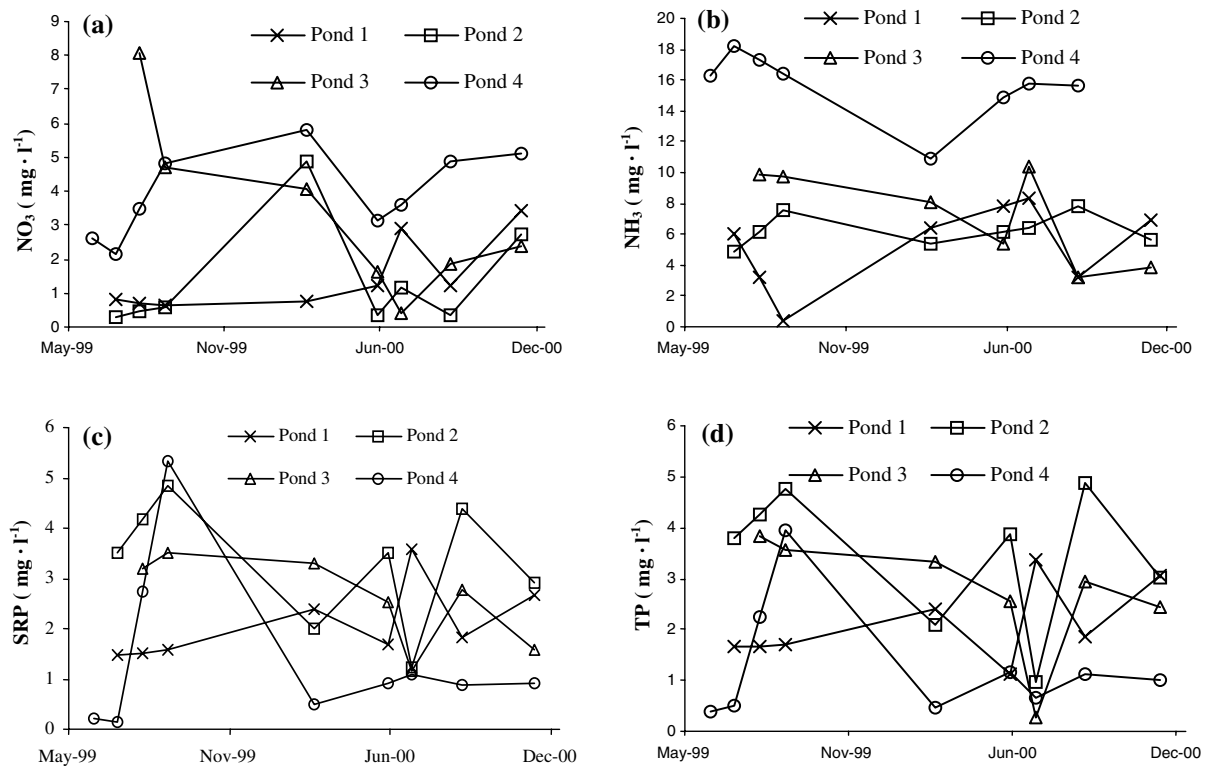


Figure 3. Nutrients (mg l⁻¹) including nitrate (NO₃-N), ammonium (NH₄-N), soluble reactive phosphorus (SRP) and total phosphorus (TP) in Ponds 1-4 of the Napa-Sonoma Marshes during May 1999-Sep 2000.

Table 3. Average chlorophyll *a* and phaeophyton values \pm SD (mg m⁻³) for Napa-Sonoma Ponds 1-4 during 1999, 2000 and 2001. Means that are not significantly different (Tukey-Kramer) are indicated by similar superscripts

Pond	Chl <i>a</i> mg m ⁻³	Phaeophyton mg m ⁻³
1	25.5 ^a \pm 24.9	43.4 ^a \pm 42.3
2	37.9 ^{ab} \pm 26.3	64.4 ^{ab} \pm 44.8
3	47.9 ^b \pm 33.7	81.5 ^b \pm 57.2
4	52.4 ^b \pm 61.9	89.1 ^b \pm 105.2

May-Jun and fewest during Sep-Mar. Two taxa comprised 94.3% of the zooplankton counted: copepods comprised 66.1% and *Artemia* 28.2%. Copepod abundance differed among ponds ($F_{3,465} = 13.80$, $p < 0.001$) and were more abundant in P3 than in P2 or P4 (T-K, $p < 0.001$). Average number of copepods during the entire sampling period ranged from 82 to 301 m⁻³ in P1-P3, but was < 1.0 m⁻³ in P4. Copepods were not found in P7. *Artemia* comprised $< 0.05\%$ of organisms in P1-P3, but comprised $> 98\%$ of organisms in P4. The

single other taxon considered common was *Ephydra*. Like *Artemia*, *Ephydra* appeared to be incidental in P1-P3 (0-0.1%), but was more common in P4 (1.5%). Average abundance of zooplankton in P2 (87 m⁻³) was less than in other ponds (range: 236-323 m⁻³) ($F_{3,465} = 6.00$, $p = 0.0005$; T-K, $p = 0.012$). Seasonally, total zooplankton abundance was greatest in spring and early summer with peak biomass 3-5 magnitudes higher in P4 than in all other ponds (Fig. 4b).

Zooplankton biomass in ponds reflected the numerical distribution of taxa. Copepods comprised 73-90% of the zooplankton biomass in P1-P3, but almost none of the biomass in P4. Average copepod biomass in P1-P4 was 0.23, 0.09, 0.32 and < 0.01 mg m⁻³, respectively. Copepod biomass differed among ponds ($F_{3,465} = 13.77$, $p < 0.001$) and was greater in P3 than in either P2 or P4 (T-K, $p < 0.001$). Biomass of total zooplankton in P4 (96.0 mg m⁻³) was greater than in any other pond (range 0.1-0.3 mg m⁻³). In P4, *Artemia* comprised 99% and *Ephydra* 1% of the

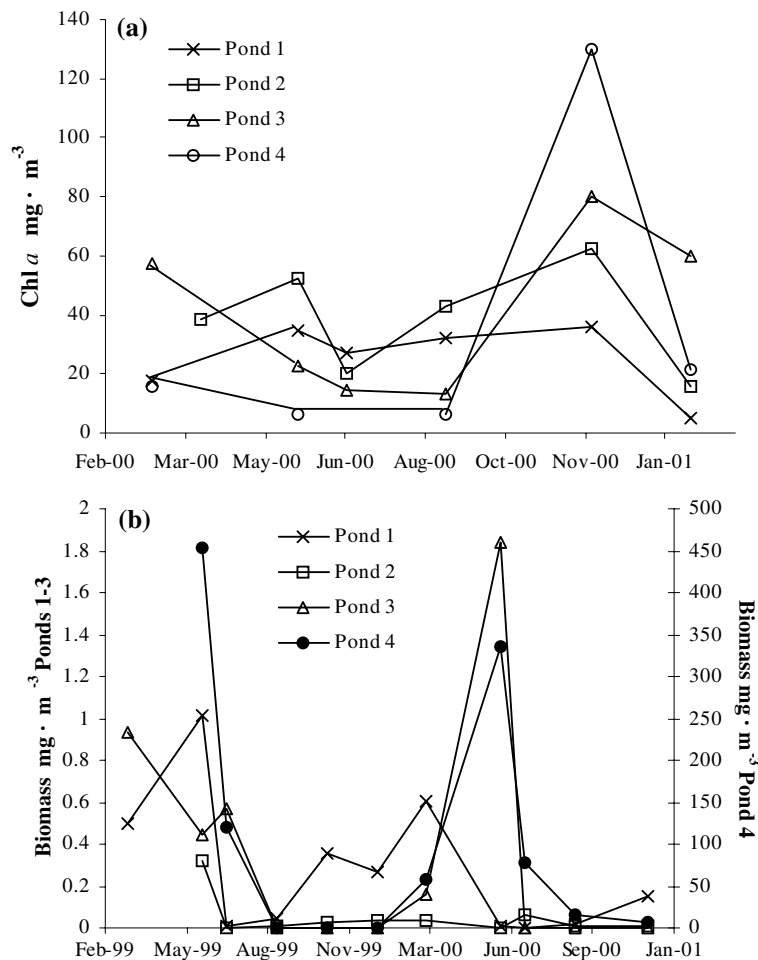


Figure 4. (a) Chlorophyll *a* (mg m⁻³) and (b) zooplankton (mg m⁻³) in Ponds 1–4 of the Napa-Sonoma Marshes, May 1999–Sep 2000.

biomass. Seasonally, total zooplankton biomass was greatest in spring and summer, except in P2 where it was low on most dates.

Macroinvertebrates

Species diversity (Shannon–Wiener) of benthic macroinvertebrates among ponds and time periods sampled (approximately bimonthly) differed significantly (MANOVA, $F_{36,299} = 23.90$, Wilk's $\lambda = 0.02$, $p < 0.0001$). Mean overall diversity differed significantly among ponds ($F_{3,48} = 17.80$, $p < 0.001$). P1 and P2 were different from P3 and P4 (T–K $p = 0.0002$; Table 4). Diversity was generally higher and similar in P1 and P2 relative to P3 and P4. One-way ANOVA and Tukey–Kramer tests indicated that diversity in P1 and P2 did not

differ significantly in 1999 and early 2000 ($F_{3,116} = 10.99$ – 205.51 , $p < 0.0001$) but were significantly higher in P1 than P2 in May 2000 ($F_{3,116} = 34.30$, $p < 0.0001$) and higher in P2 after May 2000

Table 4. Mean Shannon–Wiener diversity indices \pm SD from 1999 to 2001. Fish were not detected in Napa-Sonoma Ponds 4 and 7. Invertebrates were collected too infrequently in Pond 7 for comparison. Means that are not significantly different (Tukey–Kramer) are indicated by similar superscripts

Pond	Mean bird H'	Mean fish H'	Mean invert H'
1	1.75 ^c \pm 0.5	1.31 ^b \pm 0.5	0.96 ^b \pm 0.3
2	1.40 ^b \pm 0.7	0.53 ^a \pm 0.3	1.12 ^b \pm 0.3
3	1.58 ^{bc} \pm 0.4	0.84 ^a \pm 0.2	0.54 ^a \pm 0.3
4	1.83 ^c \pm 0.8	–	0.51 ^a \pm 0.2
7	0.60 ^a \pm 0.9	–	–

($F_{3,116} = 57.11\text{--}139.05$, $p < 0.0001$). Mean separation tests indicated that diversity in P3 and P4 was similar on 6 of 10 intervals sampled in 1999 and 2000, but like P1 and P2, differed significantly in 2001. Diversity in P1 and P4 were similar (Jul 1999, Jan and Mar 2000) until 2001 when all ponds were dissimilar during all sampling intervals.

Diversity in P1 and P2 was represented by 50–55 taxa, many of which were uncommon, and high densities of individuals from just 3–4 taxa. P3 (25 taxa) and P4 (12 taxa) usually had lower numbers of taxa and similarly high densities in 2–4 taxa. *Heteromastus* sp. (polychaete), *Gemma* sp. (bivalve), *Corophium* sp. and *Erichthonius* sp. (amphipods) dominated taxa in P1 and P2, *Polydora* sp., *Capitella* sp. (polychaetes), *Corophium* sp., and occasionally *Streblospio* sp. (polychaete) and Corixidae (waterboatman insect) dominated P3, and *Artemia* and *Ephydra* dominated P4.

Fish

From July 1999 to December 2000, a total of 4334 fish representing 16 species was captured from P1 to P3. Gill netting yielded 730 fish (16.8%), whereas bag seining yielded 3604 fish (83.2%). Fish abundance from gill nets was high in both P1 (343 fish) and P2 (368 fish), with far fewer fish captured in P3 (19 fish). No fish were captured in P4. By comparison, bag seines indicated that fish abundance was highest in P1 (2694 fish), followed by P3 (779 fish), and P2 (131 fish). Combined biomass was greatest in P1 and P2, and much lower in P3.

Gill netting and bag seining sampled different segments of the fish species assemblage in each pond. In P1, American shad (*Alosa sapidissima*, 37.3%), striped bass (*Morone saxatilis*, 42.9%), and striped mullet (*Mugil cephalus*, 8.5%) were captured in gill nets, whereas Pacific staghorn sculpin (*Leptocottus armatus*, 51.4%) and yellowfin goby (*Acanthogobius flavimanus*, 41.6%) were captured in bag seines. In P2, gill net catches consisted almost exclusively of striped bass (94.3%), while bag seine catches consisted mostly of inland silverside (*Menidia beryllina*, 42.0%) and striped bass (32.8%). In P3, striped bass (47.4%), longjaw mudsucker (*Gillichthys mirabilis*, 36.8%), and yellowfin goby (15.8%) were caught in gill nets, and longjaw mudsucker (45.3%), Shimofuri

goby (*Tridentiger bifasciatus*, 28.6%), and inland silverside (20.9%) were captured in bag seines. Shannon–Wiener diversity differed significantly among ponds ($F_{2, 22} = 10.40$, $p = 0.0007$). P1 had the highest overall diversity, significantly higher than P2 and P3 ($p = 0.0005$), which did not differ ($p = 0.318$; Table 4).

Birds

Mean diversity differed significantly among ponds ($F_{4,146} = 4.84$, $P = 0.0011$). P7 had the lowest diversity and differed significantly from all other ponds. Sixty-five species were recorded in all ponds, comprising several foraging guilds (see Takekawa et al., 2001). Diving benthivores comprised the majority of birds in all ponds followed by shallow probers. Surface feeders, dabblers, piscivores, and deep probers made up the remainder. P4 contained the greatest density of birds, whereas P1–P3 and P7 contained substantially less.

P1–P4 supported the majority of diving benthivores, primarily diving duck species. P2 supported almost exclusively diving ducks, representing over 95% of the birds counted in the pond. In P3, diving ducks comprised 70% of the birds counted in the pond. P7 had very few birds present year-round. Density of non-piscivorous birds was highest in Pond 1, and lowest in Pond 3. Piscivorous birds were much higher in Pond 1 compared with other ponds.

Waterbirds were most diverse and abundant on P1 (48 species and 23% of the total birds) and P4 (46 species and 46% of the total birds), but diversity on these ponds did not differ significantly from P3 (T–K_{P3,P4}, $p = 0.1293$; Table 4). In summer, P4 contained few diving benthivores relative to shorebirds, particularly shallow probers.

Trophic variation and the salinity gradient

The relationship between salinity and chl *a* (Fig. 5a) fit a quadratic equation with lowest concentrations at mid salinity ($r^2 = 0.4201$, $p = 0.0499$). Conversely, the relationship between salinity and zooplankton (Fig. 5b) was inverse, with highest concentrations of zooplankton at mid-salinities ($r^2 = 0.3661$, $p = 0.0002$). A test of the relationship between invertebrate biomass and

salinity (Fig. 5c) showed that salinity explained 16.8% of the variation in biomass ($p=0.0176$) and 27.8% of the variation in invertebrate diversity ($p=0.0008$). Macroinvertebrate biomass and diversity fit a quadratic curve similar to chl *a* (Fig. 5c), but with much higher levels at low salinities. Biomass of fishes decreased with salinity ($r^2=0.5667$, $p=0.0002$; Fig. 5d), but the relationship between salinity and diversity was not significant ($r^2=0.0895$, $p=0.3913$). Finally, bird density and diversity fit quadratic equations with highest levels at mid-salinities (Fig. 5e); density was not well explained by salinity ($r^2=0.0501$, $p=0.0312$), whereas bird diversity (Fig. 5e) fit a quadratic equation with highest levels at mid-salinities ($r^2=0.2308$, $p<0.0001$).

Trophic similarity by season and salinity

The NMDS ordination showed that macroinvertebrate community composition was consistent within ponds across seasons and varied with salinity (Fig. 6a). Each pond had a cluster in Figure 6a, indicating that macroinvertebrate community composition was consistent within ponds for all seasons. Composition also varied with salinity, as indicated by left to right increase in salinity (bubble size) in Figure 6a. The macroinvertebrate ordination had a fairly good relationship with a low stress value of 0.12. P1 and P2 had comparable composition of taxa, but abundances of these common taxa differed over time. P3 had a distinct invertebrate community that differed from P1, P2 and P4, and the community of P4 vastly differed from P1, P2 and P3, reflecting the much higher salinity in P4 (Table 1).

Seasonal differences in invertebrate communities were not consistent, but spring was most often represented on the perimeter of pond groupings in ordination space (Fig. 6a). ANOSIM determined that the composition of invertebrate communities differed significantly among ponds (Global $R=0.779$, $p<0.0001$; Clarke & Warwick, 2001). In pairwise tests of the ponds, P1 and P2 community composition differed significantly but at a lower level of significance ($p=0.001$) than all other pond pairs ($p<0.0001$).

Fish community composition differed significantly among ponds overall (Global $R=0.313$, $p<0.0001$) and across pairwise comparisons

($p<0.0001$). The excellent fit for the NMDS relating fish communities across ponds (stress=0.07) suggests that seasonal variation in species composition may be closely related to salinity. Samples with similar salinity values had dissimilar species composition, whereas samples with dissimilar salinities had similar species composition, but within-pond samples were most similar across seasons (Fig. 6b). During summer and fall, the fish ordination plot suggested that P3 had the most dissimilar fish species composition from other ponds, and its community composition was closer to P3 in winter and spring than to any other pond (Fig. 6b).

Although species composition within ponds was less clearly delineated for birds than other taxa (except P7), community composition differed significantly among ponds overall (Global $R=0.398$, $p<0.0001$) and across pair-wise comparisons ($p<0.0001$). The NMDS analysis (stress=0.13) suggested a strong influence of salinity on avian species composition in P7 and in P4 (Fig. 6c), but P4 values were more similar to P1–P3. P7 in the spring was most dissimilar to all other pond and season combinations.

Discussion

The wetland classification system for the United States (Cowardin et al., 1979) recognizes estuarine wetlands modified by salinity, but poorly distinguishes the hyperhaline (haline is used to indicate an ocean salt source, but salinity is used interchangeably here unless referring to a specific wetland type) communities that we studied in the San Francisco Bay salt ponds. For example, P1 and P2 had very similar salinity, dissolved oxygen, and pH patterns, but they would be separated into mixohaline (0.5–30 g l⁻¹) and euhaline (30–40 g l⁻¹) classes. P3, P4 and P7 would be classified under the single modifier of hyperhaline (>40 g l⁻¹), despite great differences in their ecological communities. Inland saline classification systems also were inappropriate for classifying the ecological communities we studied. Javor (1989) used microorganisms to describe four hyperhaline classes characterized by macroalgae and fish (60–100 g l⁻¹), halophilic species (100–140 g l⁻¹), *Dunaliella* and *Artemia* (140–300 g l⁻¹), and low

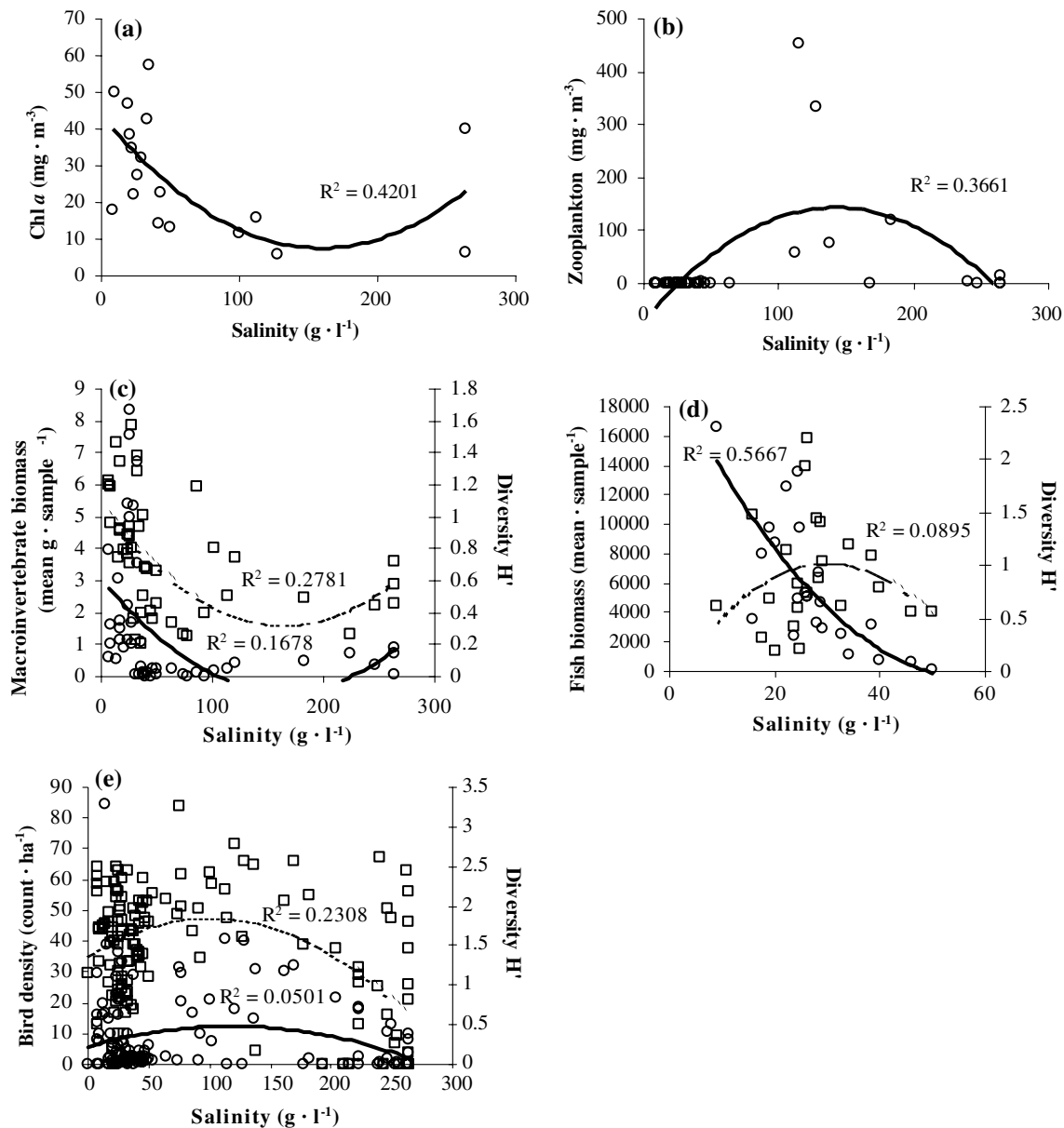


Figure 5. (a) Chlorophyll *a* (mg m^{-3}); (b) zooplankton (mg m^{-3}); (c) macroinvertebrate biomass (mg m^{-3}) and diversity (H'); (d) fish biomass (mg m^{-3}) and diversity (H'); and (e) avian counts (birds ha^{-1}) and diversity (H') across salinities in Ponds 1–4 of the Napa-Sonoma Marshes. Biomass (circles; solid line) and Shannon–Weiner species diversity (H' : squares; broken line) are shown for (c) macroinvertebrates, (d) fish and (e) birds along with the best-fitting curves and regression coefficients for each. All relationships were significant ($p < 0.05$) except for fish species diversity ($p = 0.3913$).

productivity *Dunaliella* and bacteria ($300\text{--}360 \text{ g l}^{-1}$), but higher trophic levels were not considered in his definitions. Thus, we used mixohaline ($0.5\text{--}30 \text{ g l}^{-1}$), and low ($31\text{--}80 \text{ g l}^{-1}$), mid ($81\text{--}150 \text{ g l}^{-1}$), and high ($>150 \text{ g l}^{-1}$) hyperhaline

classes to better represent the distinctive trophic communities we observed.

Most studies of hypersaline systems have been conducted in interior salt lakes where species richness decreases steeply from freshwater to

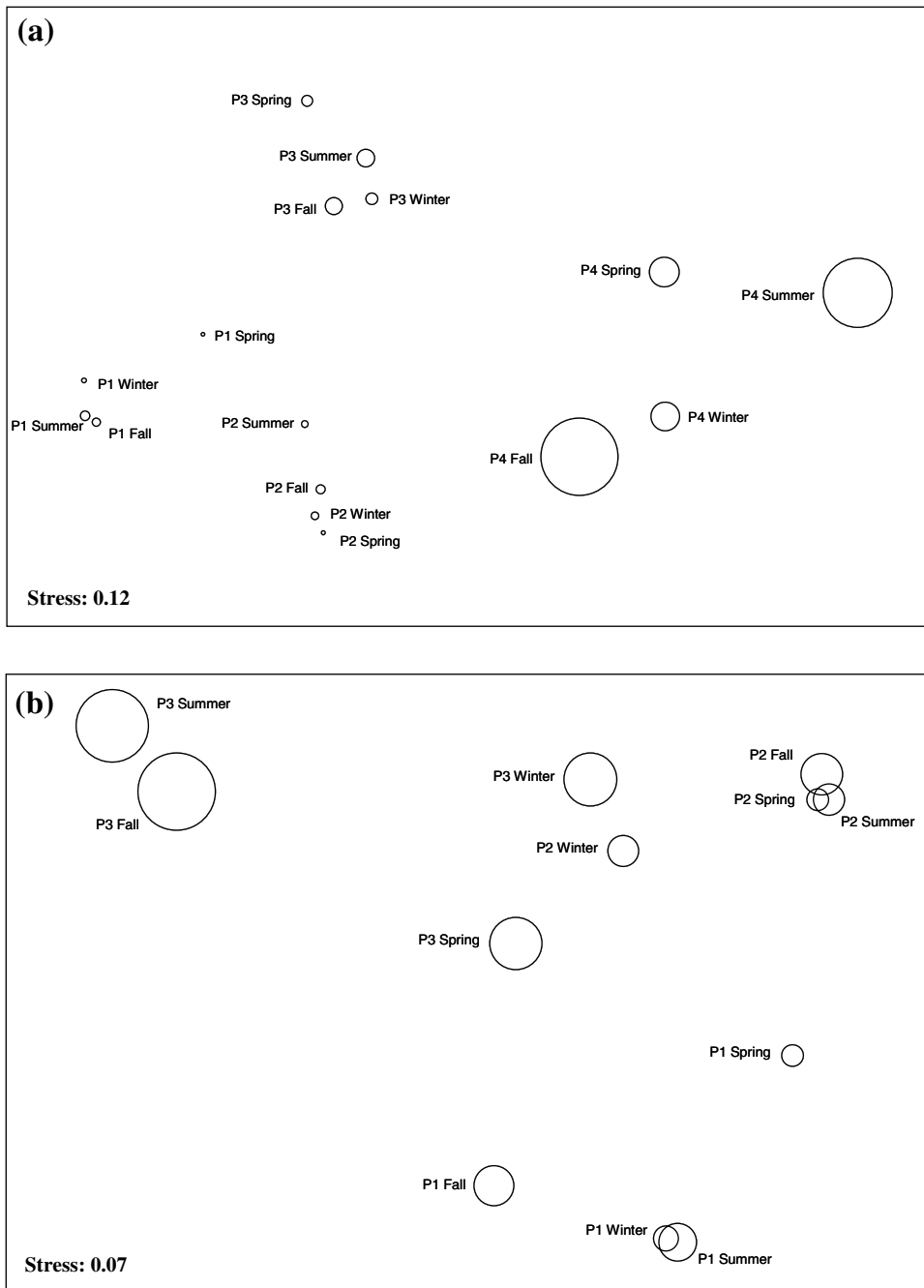


Figure 6. a and b

10 g l⁻¹ and then gradually at higher salinity levels (Hammer, 1986). Our studies were conducted where salinities generally exceed mesohaline levels (5–18 g l⁻¹), and range as high as 224 g l⁻¹. Al-

though hypersaline waters have been characterized as having low biological diversity determined by increasing salinity (Velasquez, 1992), we found that quadratic curves rather than inverse linearity

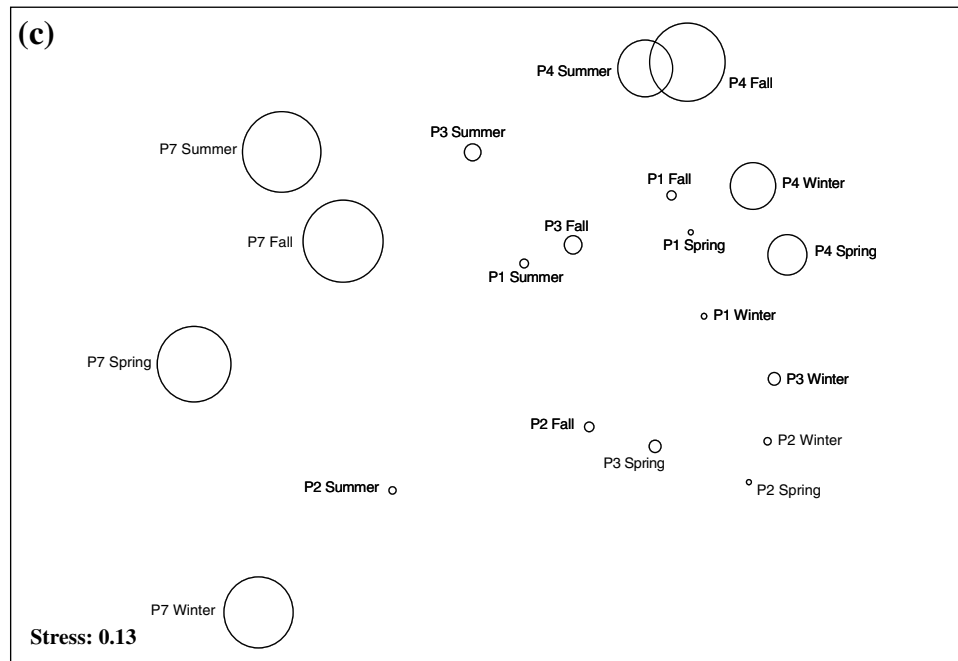


Figure 6. Non-metric Dimensional Scaling (NMDS) bubble plots across salinities (increasing diameter bubble with higher salinity) and seasons in Ponds 1–4 of the Napa-Sonoma Marshes, 1999–2001 for (a) macroinvertebrates (stress = 0.12), (b) fishes (stress = 0.07), and (c) birds (stress = 0.13). Low stress (excellent < 0.05; good < 0.10; uninterpretable > 0.3; Clark & Warwick, 2001) indicates a close representation of species composition differences in ordination space.

best described the relationship of biomass to salinity in salt ponds of the San Francisco Bay estuary (Fig. 5). A large proportion of the variation in biomass was explained by salinity for primary producers and primary consumers, and this relationship changed at higher salinities. Primary productivity biomass was highest under mid and high salinity conditions, whereas zooplankton biomass was highest under mid-salinity conditions. Changing biomass at higher salinities was likely often preceded by a shift in species composition. Copepods predominated in mid-salinity ponds P1–P2, but were replaced by *Artemia* and *Ephydra* in P4. Average zooplankton biomass in P4 was several orders of magnitude greater than in less saline ponds, due primarily to large concentrations of *Artemia* in this hyperhaline system.

Our analyses showed that salinity explained less of the variation in biomass for higher trophic levels than for lower ones. Macroinvertebrate biomass was highest in mixohaline P1, but the biomass of hypersaline ponds (P4, and also P3

toward the end of the study) was only slightly lower because they included large numbers of *Artemia* and *Ephydra*. Invertebrates underwent a change in community composition that resulted in an increase in biomass of *Artemia* following a decline in biomass of copepods, but fish as a group exhibit less variability in salinity tolerance and cannot survive > 80 g l⁻¹; thus, they cannot shift species composition. Although the relationship between fish biomass and salinity was strong ($r^2 = 0.5667$), this was an exception to the quadratic relationships because no fish were found above the low hyperhaline ponds. The relationship between bird density (as an index of biomass) and salinity was weak ($r^2 = 0.0360$), but the highest density of birds was found in the low to mid hyperhaline ponds (Fig 5e). Bird density and salinity followed a similar quadratic model at South Bay salt ponds (Warnock et al., 2002). Warnock et al. (2002) found a poorer fit for piscivorous than for non-piscivorous birds, possibly reflecting the greater numbers of fish in mixohaline ponds.

Descriptions of hypersaline systems suggest that as a general rule, species diversity decreases with salinity (Hammer, 1986; Williams et al., 1990; Williams, 1998). However, we found that similar to biomass, the relationship of salinity and species diversity in upper trophic levels followed quadratic curves (Fig. 5c–e). This was probably due to shifts in species composition, following salinity regimes, within these larger taxonomic groups. However, macroinvertebrates and fish did not respond to salinity changes as quickly as birds because community composition inside the ponds was dependent upon the source populations within the ponds and the opportunistic immigration of organisms into the ponds.

Diversity in the mid hyperhaline was lowest for macroinvertebrates and highest for fishes and birds. Similar to our findings, Britton & Johnson (1987) found highest biodiversity at mid hyperhaline salt ponds in the Camargue estuary in southern France, but decreasing species richness with increasing salinity.

Seasonal variation

Britton & Johnson (1987) found that the regular seasonal cycle of salinity in salt ponds resulted in a predictable food supply and abundant avifauna. We found cyclical patterns of physical and biological variables with salinity, but the regularity of these patterns was obscured by changes in water management during our studies. Water quality (Fig. 2) generally followed annual weather patterns. The lowest salinity levels were recorded in winter (February) and highest in late summer (August), but salinities gradually increased overall during the study (Fig. 2a). Dissolved oxygen was inversely related to salinity and temperature and reached anoxic levels ($<2 \text{ mg ml}^{-1}$) in P4 and P7.

The limited inflow to the pond system created greater dependence on nutrient recycling through remineralization and N-fixation in higher salinity ponds. Intake water accounted for the primary input of nutrients into P1 available for transformation by microbial organisms. Allochthonous nutrient sources also increased in importance as water was moved through the ponds and nutrients were transformed and depleted. Bacterial N-fixation and transformation of phytoplankton may have influ-

enced the gradual increase in nitrate in higher salinity ponds.

Effects of salinity and evaporation were greatest on P4 with the lowest influx of water, contributing to the higher concentrations of both measured forms of nitrogen. Ammonia gradually increased from P1 to P3, but doubled from P3 (7.21 mg l^{-1}) to P4 (15.42 mg l^{-1}). This may be attributed to animal waste (i.e., zooplankton, birds) or decomposition of *Artemia* that exceeded bacterial oxidation and phytoplankton uptake. A simple feedback loop in the form of primary producers, grazers, higher consumers, and decomposers may be occurring in P4. Also, phosphorus was slightly higher in P2 than in other ponds; this pond was managed to attract waterfowl for hunting and stocked with fish, which may explain the elevated phosphorus.

Seasonal maximum macroinvertebrate biomass was recorded in mid hyperhaline P4 during spring and coincided with the largest number of foraging birds at the ponds. Salinity changes in the ponds followed a seasonal pattern, but changes in macroinvertebrate diversity did not. The water regime on P1 was muted tidal flow influenced largely by changes in adjacent estuarine waters, and the diversity of taxa in this pond was generally similar to that found in the North Bay sub-region (Miles, unpublished data). Water quality and diversity in P2 was similar to that in P1, except in September 2000; water management on P2 may have been altered around that sampling interval. The temporal pattern of species diversity was similar in P3 and P4, but changes in P3 were followed by changes in P4 at subsequent sampling intervals, e.g., peaks in diversity in P3 during Jul 1999, Mar 2000, and Feb 2001 were followed by peaks in P4 during Sep 1999, May 2000 and after Jun 2001.

The largest densities of waterbirds were seen in spring, with the next largest number of birds observed in winter (Takekawa et al., 2001). Most migratory bird species were not present in the estuary during summer, and we counted fewer birds in fall compared with spring when the largest number of waterbirds was counted. Although species composition did exhibit some seasonal variability, there was a greater degree of similarity within ponds than within seasons, even when salinity levels were similar (Fig. 6). Thus, factors

other than salinity seemingly influenced species composition in ponds.

Factors other than salinity

We measured seasonal variation in biomass and diversity among trophic levels across a salinity gradient, but we did not control for differences among or within ponds because we lacked replication in this single system. Factors other than salinity may have greatly influenced the system, such as hydrologic patterns, ionic composition, oxygen content, biological interactions, and water depth that might affect community structure (Carpelan, 1957; Anderson, 1970; Williams et al., 1990; Velasquez, 1992; Williams, 1998).

Hydrologic patterns

In northern San Francisco Bay, salinities may become diluted to oligohaline levels ($0.5\text{--}5\text{ g l}^{-1}$) in late winter, but average salinities in the salt ponds typically remained above mesohaline levels and were influenced by rainfall and evaporative loss. Fauna in even the mixohaline salt ponds differed from euryhaline estuarine species in salt ponds of southern France (Britton & Johnson, 1987) and impoverished fauna at hypersalinity was attributed to lagoon-type confinement. Similarly, Carpelan (1957) described South Bay salt ponds as more similar to littoral lagoons than estuarine wetlands.

Ionic composition and nutrients

Species diversity quickly decreases in low hyperhaline ponds when carbonates precipitate (70 g l^{-1}), remains constant in mid hyperhaline ponds when CaSO_4 precipitates (150 g l^{-1}), and declines in high hyperhaline ponds where few species of invertebrates survive (300 g l^{-1} ; Britton & Johnson, 1987). Fish are absent above the low hyperhaline, but *Artemia* and *Ephydra* reach maximum density at high hyperhaline, although they may survive across a much wider range of salinities (Maffei, 2000). Molluscan species with carbonate shells tend to disappear above low hypersalinity, and our collections indicated few clams in P3 and P4. Salt ponds typically have low N and P, restricting plant growth (Britton & Johnson, 1987) and increasing nitrate with salinity,

although our results showed nitrates were highly variable (Fig. 3). P1–P2 had beds of *Ruppia maritima*, but hyperhaline ponds lacked any submergent macrophytes.

Dissolved oxygen

Sherwood et al. (1992) reported an inverse relationship between oxygen content and salinity ranging from 8.85 mg l^{-1} at 5 g l^{-1} to 1.7 mg l^{-1} at 260 g l^{-1} . Williams (1998) suggested that respiratory breakdown occurs at $\sim 2\text{ mg l}^{-1}$. In the mid and high hyperhaline ponds, oxygen dropped below the respiratory threshold in summer months. The lack of oxygen in those ponds may have influenced the biomass of invertebrates.

Biological interactions

Our chl *a* and zooplankton data illustrate food web interactions at several trophic levels. First, we found a weak negative correlation of zooplankton biomass with chl *a*. The negative relationship between biomass of *Artemia* and chl *a* was stronger in P4. Grazing by *Artemia* probably reduced algal densities, resulting in low chl *a* concentrations during summer. In turn, increased chl *a* concentrations in winter were probably influenced by decomposition of *Artemia* and subsequent increased ammonia that benefited phytoplankton. *Artemia* was the key taxon in the simple food web of P4. In this fishless pond, high densities and biomass of *Artemia* likely contributed to the high use by foraging birds.

Replacement of copepods in the hyperhaline ponds by *Artemia* is likely the result of both salinity and food web effects. Although *Artemia* may tolerate salinities near sea-water (35 g l^{-1}) (Persoone & Sorgeloos, 1980), *Artemia* predators occupy lower salinity environments (Wurtsbaugh, 1992). When salinity in the Great Salt Lake, Utah, declined from >100 to $\sim 50\text{ g l}^{-1}$, Wurtsbaugh (1992) reported that the predaceous insect *Trichorixa verticalis* became abundant in the open waters of the lake and *Artemia* declined dramatically. Wurtsbaugh (1992) subsequently reported corixids attacking adult *Artemia*, but more importantly preying on nauplii or other juvenile stages of *Artemia*, therefore limiting the development of the population. In a similar study, Herbst (2001) observed *Artemia* and *Ephydra* were restricted to moderate to high salinity

salt ponds located in the Mojave Desert, California, while *Trichorixa* adults occupied lower salinity ponds.

Soluble and total P concentrations seemed to be higher in mixohaline P2 than elsewhere, chl *a* concentration was intermediate, and copepod abundance and biomass was low. P2 has been the subject of manipulations for sport fishery purposes and had higher densities of potentially zooplanktivorous fishes than any other pond. Thus, it appears that fish predation on zooplankton may have contributed to a trophic imbalance in P2 (Carpenter, 1988), where reduced zooplankton biomass resulted in greater algal growth than in P1, and algal growth in P2 reduced nitrogen, the limiting nutrient in these ponds.

Water depth

Velasquez (1992) noted that while bird abundance was related to salinity, availability of habitat to birds depended on depth. Ponds that contained islands and were more spatially variable in depth overall contained a wider variety of foraging guilds, particularly shorebirds. P2 and P3 were more homogenous and invariant in depth than the other ponds and supported diving birds almost exclusively in 1999–2001. P2, which contained few islands, supported almost exclusively diving ducks whereas P3, which had more islands and exhibited more variability in depth overall, contained fewer relative to other guilds. Dabblers and diving benthivores were present in P1–P3, but the two guilds were mostly spatially separated within the ponds. Water depths varied spatially in P1, which was very shallow at the southern end and deeper on the northern end. Diving benthivores were more common on the deep northern end of P1 while dabbling ducks used the shallower southern end. Water depth varied temporally in P4, which was deep (0.5–2.0 m) in the winter and much shallower or dry in the summer. P4 had more overlap of dabblers and diving benthivores, in part explained by the water fluctuation in this pond throughout the year. The water depth was more variable and there may have been times when the water level was acceptable for both guilds. Water was not flowing through the siphon pipe to P4 in the summer, and as a result, P4 was more than 50% dry during summer months. This caused a decline in diving benthivores numbers and an in-

crease in the number of shorebirds, particularly shallow probers.

Anderson (1970) noted that birds such as diving ducks, grebes, phalaropes, and Bonaparte's gulls (*Larus philadelphia*) in the South Bay salt ponds used high hyperhaline ponds, and shorebirds seemed to use ponds of suitable water depth regardless of the salinity. Other researchers have suggested that shorebirds require water depths of < 8 cm (Collazo et al., 1995; Davis & Smith, 1998). However, shallow water depths may also indicate warmer temperatures and less DO, reducing populations of macroinvertebrate and fish prey species.

Optimizing salt ponds for waterbirds

Salt ponds are synonymous with large populations of migratory waterbirds (Takekawa et al., 2001; Paracuellos et al., 2002; Warnock et al., 2002), yet the unique ecology of these hyperhaline systems has not been well described, especially within estuaries. Artificial salt ponds have existed in the estuary since the mid-1800s (Ver Planck, 1958). Our study indicated that salinity was a major driver in the system for lower trophic levels, but it was more variable at higher trophic levels. Seasons and salinity were more similar than pond for macroinvertebrates (Fig. 6a), but for fish (Fig. 6b), salinity was a major driver. In contrast, mixohaline and high hyperhaline avian communities were distinct, while mid hyperhaline ponds were similar (Fig. 6c). Most birds were found in the mid hyperhaline (Fig. 5e). We found that the density of benthivores was four times greater in the salt ponds compared with the baylands in the winter and spring (Takekawa et al., 2001).

Salt ponds were heavily used during migration, and populations of waterbirds were higher in spring than in fall, possibly because invertebrate populations tended to increase during winter and into spring. Studies of western sandpipers (*Calidris mauri*; Warnock & Takekawa, 1996) confirmed that this species used salt ponds more during spring. Shallow probers were found to be denser in spring, primarily because of the migration of large numbers of western and least sandpipers. Salt ponds provided these species with multiple advantages. The large expanses of water facilitated

taking flight, and predator avoidance without human disturbance and the shallow, sheltered impoundments likely created a favorable microclimate for roosting and foraging.

The salt ponds generally decreased in depth and increased in salinity from summer through fall, which may have reduced invertebrate biomass and foraging value for many waterbirds. In salt ponds, the largest densities of waterbirds were seen in spring, with the next largest number of birds observed in winter. Most migratory bird species were not present in the estuary during summer, and we counted fewer birds in fall than in spring.

Historic wetland habitats that were converted to agriculture or urban development now have limited value for waterbird species, with the exception of areas inundated seasonally during winter and spring. Restoring or rehabilitating these agricultural and urban areas is likely beneficial for waterbirds. However, converting from one wetland habitat type to another, such as converting salt ponds to tidal marsh, will likely benefit some species at the expense of others. Most shorebirds prefer more open habitats rather than tidal marsh plain habitats (Warnock & Takekawa, 1995). Development of coastal zones and interior valley wetlands have resulted in fewer areas available for migratory waterbirds in the flyway, and alternative wetlands may not exist outside of the San Francisco Bay estuary to compensate for loss of waterbird habitats in the ecosystem.

Our results suggest that the Napa salt ponds provide a unique habitat for waterbirds. *Artemia* represents an important food resource in mid hypersaline ponds, with biomass exceeding the combined biomass of other ponds by several orders of magnitude. Because *Artemia* was so abundant in the diversity-poor mid hypersaline ponds, its demise probably would substantially affect upper trophic level organisms. Although zooplankton species richness decreased with increased salinity, the ability of the larger bodied *Artemia* to successfully occupy hypersaline waters allows it to escape predators and competitors found in lower salinity ponds (Herbst, 2001; Wurtsbaugh, 2002). Changes that reduce salinity will eradicate *Artemia*, as well as *Ephydra*, and result in a dramatically different food web. Proper management of hyperhaline salt ponds must include water depth and hypersalinity as elements important for waterbirds. Eliminating artifi-

cial salt ponds without providing alternative habitats may reduce or extirpate avian species from the ecosystem.

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Spatial and temporal fluctuations in presence and use of chironomid prey by shorebirds in the Odiel saltpans, south-west Spain

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Key words: saltpans, *Chironomus salinarius*, salinity, shorebirds, foraging habitat, Odiel marshes

Abstract

We studied the seasonal variation in abundance and distribution of shorebirds and chironomid *Chironomus salinarius* larvae in both traditional and industrial salines in the Odiel marshes, south-west Spain, in 2001. We selected 12 ponds that were representative of the different phases of the salt production process. The benthic chironomids were sampled in each pond every 2 months, and the birds were counted weekly. Chironomid larvae were most abundant in spring and autumn, and in the ponds of lower salinity. The density of larvae averaged $7023 \pm 392 \text{ m}^{-2}$ (\pm SE) over the six sampling events. Shorebirds were always more abundant at high tide than at low tide, and were especially abundant during the spring and autumn migration periods when up to 20,775 birds were counted. A total of 24 species were recorded, six of which were present in internationally important numbers. The salines were especially important as foraging and roosting habitat during migration. The percentage of birds that were feeding in the ponds was positively correlated with the abundance of chironomid larvae at accessible depths. The number of feeding birds was also higher in ponds with more chironomid larvae available. Despite more intensive management, industrial salines held higher densities of birds and a similar abundance of chironomids when compared with traditional salines.

Introduction

Many shorebirds or waders (Charadrii) are long distance migrants which migrate thousands of kilometres between breeding and wintering sites and are heavily dependent on passage sites along the flyways, where they can rest and refuel (Alexander et al., 1996; Iverson et al., 1996). Natural and artificial coastal wetlands tend to be highly productive and are a vital habitat for these birds (Velasquez, 1992; Masero et al., 1999), which are very sensitive to habitat change (Alexander et al., 1996). In recent decades, many coastal

wetlands have been destroyed or transformed, resulting in major impacts on shorebird populations (Goss-Custard et al., 1977a, b; Goss-Custard & Moser, 1988).

Artificial wetlands such as salines can provide important foraging habitats for shorebirds, especially at high tide when intertidal marshes are flooded and inaccessible (Pérez-Hurtado & Hortas, 1991). Salt production via the circulation of sea water through a system of ponds in salines is an ancient activity in the Mediterranean region and other warm coastal areas (Britton & Johnson, 1987). Aquatic invertebrates in saltpans represent

abundant prey for shorebirds (Velasquez, 1992), although there are relatively few invertebrate taxa owing to the extreme salinities. Amongst these taxa, chironomid larvae are particularly important (Velasquez, 1992; Pérez-Hurtado et al., 1997).

The Odiel marshes in south-west of the Iberian peninsula are one of the most diverse and productive coastal marsh systems in southern Europe (Castellanos et al., 1998). They are situated on the East Atlantic flyway (Smit & Piersma, 1989), and their importance for waterbirds has led to their protection as a Natural Park, Ramsar site (Bernués, 1998) and Biosphere Reserve. The salines represent 16% of the surface area of the marshes, and are an important feeding and roosting area for shorebirds. During the migration periods and in winter, flocks of over 12,000 birds can regularly be observed. However, there are no previous studies of the shorebird and invertebrate communities in the salines, or of shorebird habitat use.

In this study, we describe the seasonal variation in the abundance and distribution of shorebirds in the Odiel salines, as well as in the abundance and distribution of one of their principle prey species, the chironomid *Chironomus salinarius*. We assess the differences between salt pans of different salinities and between industrial salines (with an intensive salt production process) and traditional salines in their value for shorebirds and their prey. We test whether or not chironomid abundance predicts the abundance of foraging shorebirds in space and time. We consider what changes to current management may increase the shorebird carrying capacity of our study site.

Study area

The Odiel marshes (37°17' N 06°55' W), found in the combined estuaries of the Tinto and Odiel rivers, are tidal marshes with a total surface area of 7,185 ha. The salines occupy 1,185 ha, of which c.1,118 is an industrial saline complex and c.56 ha is a traditional saline (Fig. 1).

In both kinds of salines, sea water is introduced via a tidal canal to a complex of large and deep ponds which act as reservoirs (the primary evaporation ponds PEPs), where the salinity is relatively low and the diversity of invertebrates

relatively high. From there, the water circulates into a system of shallower ponds (the secondary evaporation ponds SEPs) with intermediate salinity and where the invertebrate community is dominated by *C. salinarius* in the benthos and the brine shrimp *Artemia parthenogenetica* in the water column. These two species are the most abundant prey for waterbirds in the salines. *C. salinarius* is actually a species complex requiring further taxonomic study (Armitage et al., 1995). The brine shrimp population is dominated by the diploid form of *A. parthenogenetica* (F. Amat pers. comm., Amat et al., 1995).

From the secondary evaporation ponds, the water passes to the pre-crystallization ponds (PCPs), a group of shallow and hypersaline ponds where water is stored until it approaches saturation point. Finally, the water then enters the crystallization ponds (CPs), where the salt precipitates and is harvested (Fig. 1). The abundance of invertebrates in these last two classes of ponds fluctuates according to the salt concentration.

Methods

Invertebrate sampling

Twelve ponds covering the range of salinities were selected and sampled throughout 2001, including nine in the industrial salines and three in the traditional salines (Fig. 1). The ponds included two PEPs, six SEPs, two PCPs and two CPs. The traditional saline is more a labyrinth of canals than a complex of ponds, through which the water flows continuously. We did not sample the traditional PEP, which was too deep for shorebirds.

The benthos was sampled every 2 months, selecting four points at random from each pond within the depth range accessible to shorebirds (0–20 cm, Ntiamoa-Baidu et al., 1998). At each point, three core samples were taken to a depth of 3 cm with a 19.6 cm² corer. The salinity was measured at the same time using a densimeter. In the laboratory, the sample was filtered through 0.5 and 0.1 mm sieves. In order to separate chironomids from the sediments retained in the sieves, we floated them in saturated salt solution collected

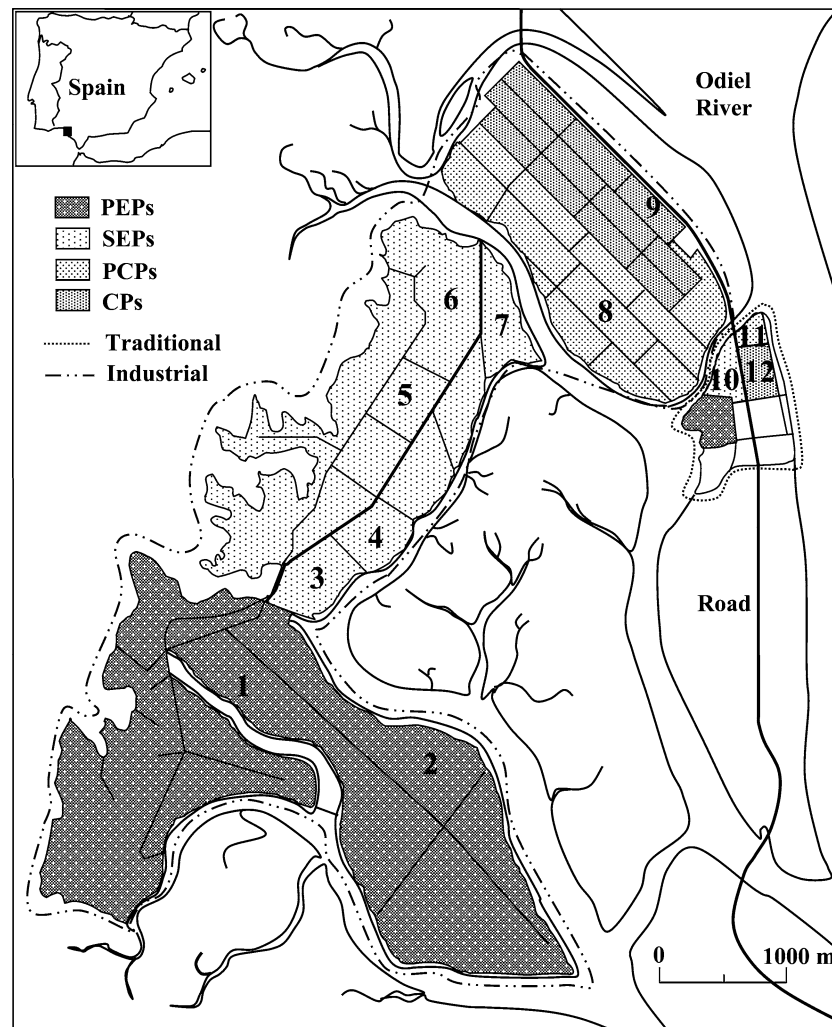


Figure 1. The location of the Odiel salines in SW Spain, and of our study ponds in the traditional and industrial salines.

from a CP. The larvae and pupae were collected from the surface and preserved in 70% ethanol.

Shorebird counts

In each of the study ponds we counted the number of shorebirds of each species that were feeding and resting 1 day each week, using a 20–60 × telescope. On each day, we carried out two counts of 3 h duration, one centred around high tide and the other around low tide. The ponds were always counted at the same time (by choosing to count on the day that high or low tide occurred around

09:00 h) and always following the same route between ponds.

Calculation of the available surface area

In most of the ponds, only shallow areas of 0–20 cm around the edge and around islands are available to foraging shorebirds. The accessible surface area varies with fluctuations in the overall water level, which were monitored by recorded depth at a reference point in each pond at the time of conducting surveys. The depth profile of each pond was established by conducting various

transects, and the surface area accessible for foraging at the time of survey was estimated via image analysis (Sigma Scanpro, version 4.0).

Statistical analysis

The abundance of chironomid larvae and pupae and of shorebirds were analyzed using generalized linear models (GLMs) following GENMOD procedure in SAS (v. 8.2, SAS Institute, 2000). POND and MONTH were included as fixed factors. POND had 12 levels for the shorebird model, but only nine for the chironomid models as three ponds where chironomids were absent in all but one month were removed. MONTH had 12 levels for shorebirds and six for chironomids. For the shorebird model, we also include TIDE as a fixed factor of two levels (low or high). Owing to overdispersion observed in the data for larvae and shorebirds, we used a negative binomial error distribution (Bliss & Fisher, 1953; Kopocinski et al., 1998), log link function and type III tests. Such a model for pupae did not converge owing to the high proportion of zeros, so we conducted a non-parametric analysis using ranks in GENMOD with an identity link (RANK procedure in SAS).

The deviance of each fitted GLM model is analogous to the residual sum of squares in ordinary linear regression. The reduction in deviance compared to the null model is used to assess

the contribution of the model to the explanation of the variance in the data set. The significance of the reduction in deviance can be estimated by comparison with the distribution of the chi-square statistic, with degrees of freedom (df) equal to the change in df compared to the null model. *Post-hoc* differences between two levels of a factor were tested with the Wald chi-square test for differences between least-squares means (SAS Institute Inc., 1997).

Spearman's rank correlations were conducted between the proportion of shorebirds that were feeding and the number of chironomid larvae available, and between salinity and the density of larvae.

Results

Abundance of chironomids

Chironomid larvae were present in the sediments all year round but with a marked pattern in seasonal abundance (Fig. 2) with the first and strongest peak in May (mean of $11,835 \pm 1470$ larvae m^{-2} , mean \pm SE, $n = 804$) and a second peak in November (9933 ± 1063 m^{-2}). The same patterns were observed for large and small larvae collected from the 0.5 and 0.1 mm sieves, although the larger larvae were relatively more abundant when the

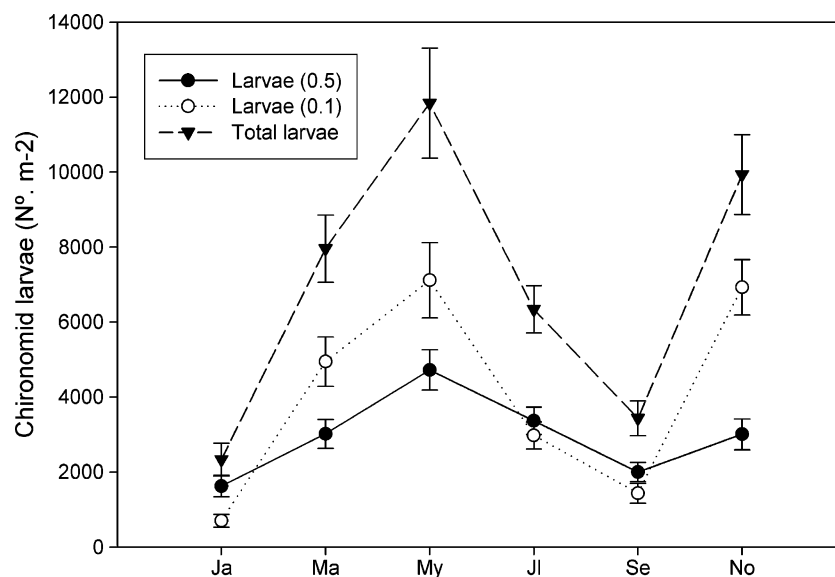


Figure 2. Seasonal variation in the density of chironomid larvae (mean \pm SE, $n = 144$ for each month), in the Odiel salt pans in 2001.

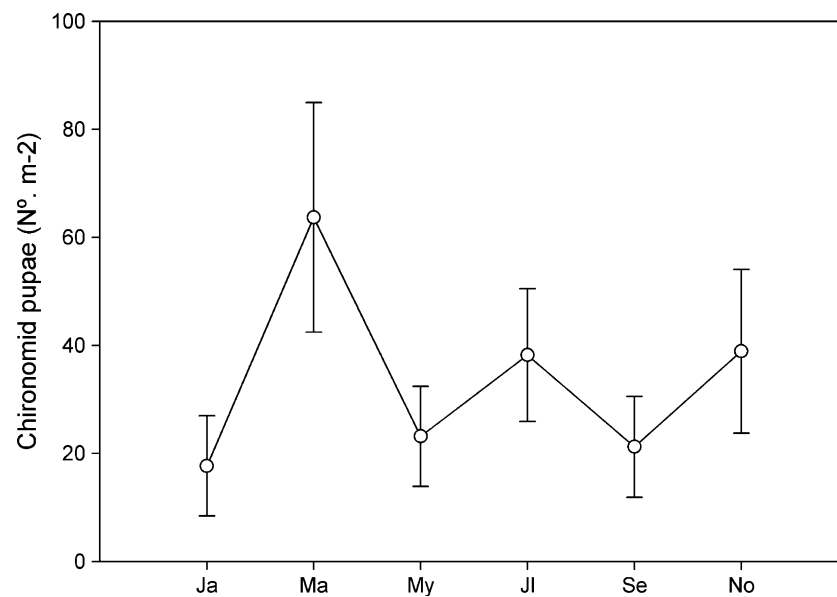


Figure 3. Seasonal variation in the density of chironomid pupae (mean \pm SE, $n = 144$ for each month), in the Odiel salt pans in 2001.

total number of larvae was lower (Fig. 2). Larvae were only recorded in the CPs and the industrial PCP during one month (November for the traditional CP, March for the other two ponds). In the CPs, this was probably owing to the compacted sandy nature of the sediments and the effects of salt crystallization, while in the PCP it was owing to incrustations of gypsum salts on the sediment surface which made it impossible for larvae to enter the sediments and construct their tubes.

The annual average density of chironomid larvae varied between different ponds, with the highest densities recorded in PEPs and SEPs and the lowest in the CPs (Table 1). This suggests a gradual decrease in larval density during the evaporation and crystallization process, as confirmed by a significant negative correlation between average salinity in each pond and the average larval density ($r_s = -0.713$, $p = 0.008$, $n = 12$). There were no consistent differences between industrial and traditional salines in the abundance of larvae for a given salinity type (Table 1).

GLMs revealed highly significant effects of POND, MONTH and the POND*MONTH interaction on the abundance of benthic chironomid larvae (Table 2). Thus, there were strong differences in abundance between different ponds and times of the year, while seasonal differences varied between ponds (as shown by differences between

ponds in the month when abundance peaked, Table 1). Similar results were recorded for GLMs analysing the numbers of large (those retained on a 0.5 mm sieve) and small (those retained on a 0.1 mm sieves) larvae (Table 2). In a GLM for benthic pupae, the POND*MONTH interaction was highly significant (Table 2), indicating that seasonal patterns in chironomid emergence (Fig. 3) were not consistent between ponds.

Abundance of shorebirds

A total of 24 shorebird species were recorded in the study area, the most abundant being dunlins (*Calidris alpina* (L.)), black-tailed godwits (*Limosa limosa* (L.)), and curlew sandpiper (*Calidris ferruginea* (Pontoppidan)) (Table 3). The highest count was of 20,775 birds in April. The total numbers of shorebirds showed a strong seasonal pattern, with peak counts in April and August coinciding with the pre- and post-breeding migration periods (Fig. 4). The post-breeding migration was the stronger and more prolonged, with high counts being recorded from July to September. In contrast, the pre-breeding migration was only marked during April (Fig. 4). The number of birds recorded in the salines was always higher at high than at low tide (Fig. 4). The proportion of birds that remained at low

Table 1. Annual average salinity, size and density of chironomid larvae recorded in individual saltpans in Odiel, 2001

Pond	Pond type	Management	Salinity (g/l)	Total surface area (m ²)	Available surface (m ²)	Chironomid density (m ⁻² , mean ± SE)	Peak density (month)
1	PEP	I	30	842,200	550 ± 400	3984 ± 1267	8068 (Nov)
2	PEP	I	40	790,700	5787 ± 1229	20,396 ± 5688	44,671(May)
3	SEP	I	90	196,100	48,039 ± 5948	2505 ± 951	5817(Mar)
4	SEP	I	90	171,900	37,165 ± 14641	5846 ± 1814	13,461 (Mar)
5	SEP	I	70	176,300	34,215 ± 2168	9193 ± 2806	19,873 (Nov)
6	SEP	I	70	512,200	43,552 ± 3170	13,234 ± 3144	25,223 (Nov)
7	SEP	I	70	179,100	13,434 ± 951	10,389 ± 3564	23,524(Nov)
8	PCP	I	100	164,500	77,109 ± 969	106 ± 106	637(Mar)
9	CP	I	160	90,253	51,828 ± 40623	64 ± 44	255(Mar)
10	SEP	T	40	41,938	8943 ± 0	6723 ± 3563	24,331(Nov)
11	PCP	T	80	28,092	6154 ± 0	5761 ± 2619	17,028(May)
12	CP	T	90	37,579	11,428 ± 0	226 ± 226	1359 (Nov)

See methods for details of pond type and how available surface area was calculated. I = industrial, T = traditional.

tide varied between seasons, and was higher during spring migration than autumn migration (Fig. 4).

In a GLM, there were highly significant main effects of POND, MONTH and TIDE on the number of shorebirds (Table 2). All two way

Table 2. Summary of GLM models testing the effects of POND, MONTH and TIDE on the abundance of Chironomidae larvae and pupae and shorebirds in the Odiel salines

	Effect	df	Chi-Square	<i>p</i>
Total larvae	Pond	8	71.84	< 0.0001
<i>n</i> = 216	Month	5	67.56	< 0.0001
D = 4.92%	Pond*Month	40	99.65	< 0.0001
0.5 Larvae	Pond	8	44.6	< 0.0001
<i>n</i> = 216	Month	5	27.25	< 0.0001
D = 4.32%	Pond*Month	40	97.25	< 0.0001
0.1 Larvae	Pond	8	85.6	< 0.0001
<i>n</i> = 216	Month	5	101.03	< 0.0001
D = 8.30%	Pond*Month	40	129.48	< 0.0001
Pupae	Pond	8	10.25	0.2477
<i>n</i> = 216	Month	5	6.25	0.2823
D = 35.03%	Pond*Month	40	76.94	0.0004
Shorebirds	Pond	11	671.93	< 0.0001
<i>n</i> = 467	Month	11	213.73	< 0.0001
D = 14.99%	Tide	1	84.24	< 0.0001
	Pond*Month	121	758.19	< 0.0001
	Pond*Tide	11	71.4	< 0.0001
	Month*Tide	11	44.65	< 0.0001

For larvae, totals are modelled as well as the number of larvae retained on 0.5 mm and 0.1 mm sieves. Main effects shown are those observed when interactions are not included in the model. D = percentage of additional deviance explained by the final model in comparison to null models. See methods for more details.

Table 3. Shorebird species recorded in our study site and their abundance

Common name	Latin name	Mean count ±SE	Range of counts	Mean number of feeding birds ±SE	Range of feeding birds	% feeding in traditional salines
Dunlin*	<i>Calidris alpina</i>	1750 ± 453	17–15,689	803 ± 262	7–1068	0.3
Black-tailed godwit*	<i>Limosa limosa</i>	1209 ± 254	0–6684	232 ± 56	0–1309	9.5
Curlew sandpiper	<i>Calidris ferruginea</i>	925 ± 220	0–5567	459 ± 122	0–3214	0.0
Redshank	<i>Tringa totanus</i>	693 ± 91	5–2170	366 ± 50	2–1310	5.3
Ringed plover*	<i>Charadrius hiaticula</i>	332 ± 67	0–1780	97 ± 32	0–1182	0.2
Avocet*	<i>Recurvirostra avosetta</i>	309 ± 43	2–1155	42 ± 9	0–227	1.4
Grey plover	<i>Pluvialis squatarola</i>	253 ± 56	0–1313	30 ± 14	0–480	0.2
Kentish plover*	<i>Charadrius alexandrinus</i>	179 ± 50	0–1561	72 ± 30	0–1180	0.0
Little stint	<i>Calidris minuta</i>	166 ± 36	0–888	143 ± 29	0–885	1.0
Black-winged stilt*	<i>Himantopus himantopus</i>	148 ± 33	0–817	97 ± 23	0–572	5.3
Bar-tailed godwit	<i>Limosa lapponica</i>	68 ± 21	0–754	16 ± 13	0–507	0.0
Sanderling	<i>Calidris alba</i>	63 ± 14	0–364	47 ± 11	0–332	0.2
Curlew	<i>Numenius arquata</i>	58 ± 22	0–830	0.07 ± 0.05	0–2	0.0
Spotted redshank	<i>Tringa erythropus</i>	43 ± 12	0–351	28 ± 10	0–306	5.0
Greenshank	<i>Tringa nebularia</i>	25 ± 6	0–202	15 ± 4	0–162	6.3
Turnstone	<i>Arenaria interpres</i>	17 ± 5	0–143	10 ± 3	0–101	4.6
Red knot	<i>Calidris canutus</i>	7.32 ± 4.43	0–166	2.97 ± 1.47	0–47	0.0
Whimbrel	<i>Numenius phaeopus</i>	5.5 ± 3.07	0–121	0.07 ± 0.05	0–2	0.0
Oystercatcher	<i>Haematopus ostralegus</i>	3.95 ± 0.79	0–17	0	0	...
Ruff	<i>Philomachus pugnax</i>	3.1 ± 1.79	0–71	2.2 ± 1.22	0–48	21.6
Little ringed plover	<i>Charadrius dubius</i>	2.07 ± 1.70	0–68	1.65 ± 1.57	0–63	0.0
Common sandpiper	<i>Actitis hypoleucos</i>	0.25 ± 0.08	0–2	0.2 ± 0.07	0–2	75.0
Marsh sandpiper	<i>Tringa stagnatilis</i>	0.15 ± 0.10	0–4	0.02 ± 0.02	0–1	0.0
Red-necked phalarope	<i>Phalaropus lobatus</i>	0.1 ± 0.06	0–2	0.1 ± 0.06	0–2	0.0
Total		6253 ± 758	53–20775	2466 ± 368	49–13,438	2.2

Note figures refer to counts made in the ponds selected for our study (i.e. only part of the salines).

*Highest counts exceeded the 1% threshold for the flyway population used to identify wetlands of international importance for a given species (Delany & Scott, 2002).

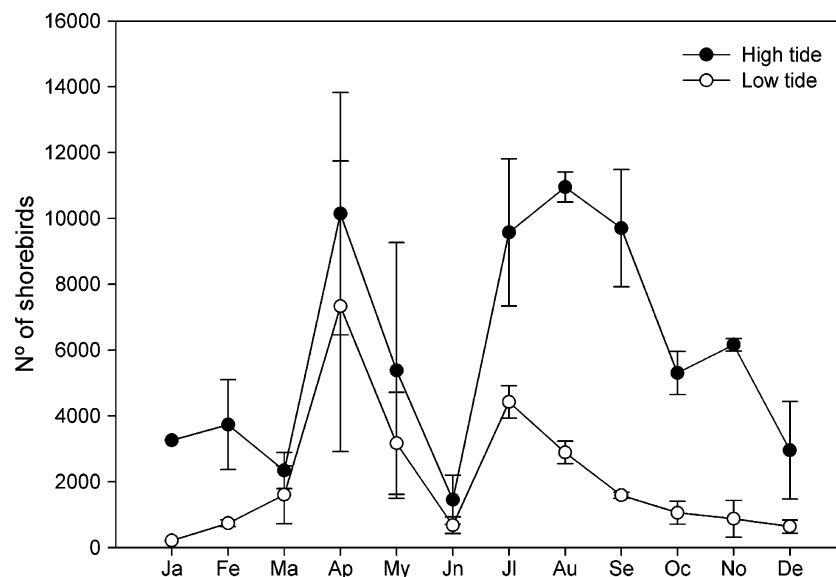


Figure 4. Total number of shorebirds counted (mean \pm SE, $n=4$ counts for each month) in our 12 study ponds in the Odiel salt pans at high and low tide, 2001.

interactions were also highly significant. Thus, we recorded strong spatial, temporal and tidal effects on the distribution of shorebirds that interacted in a complex way.

The seasonal patterns in abundance varied greatly between shorebird species. Amongst the more abundant species (Table 3), dunlins (*Calidris alpina*) and little stilts (*Calidris minuta* (Leisler)) showed only a strong spring migration. In contrast, black-tailed godwits (*Limosa limosa*), curlew sandpipers (*Calidris ferruginea*), redshanks (*Tringa tetanus* (L.)), avocets (*Recurvirostra avosetta* (L.)), kentish plovers (*Charadrius alexandrinus* (L.)) and black-winged stilts (*Himantopus himantopus* (L.)) showed only a strong autumn migration. Ringed plovers (*Charadrius hiaticula* (L.)) and grey plovers (*Pluvialis squatarola* (L.)) showed both a strong spring and a strong autumn migration.

Relationship between the abundance of chironomids and of shorebirds

When we analyze the use of the salines by shorebirds throughout the year, we find that the proportion of birds observed feeding was strongly correlated with the availability of chironomid larvae ($r_s=0.88$, $p=0.033$, $n=6$). The proportion of birds feeding was highest in May when the

abundance of chironomid larvae was greatest (Fig. 5). There was also a strong positive correlation between the number of larvae available in each pond and the number of feeding shorebirds (using annual means, $r_s=0.66$, $p=0.019$, $n=12$).

In the traditional salines, a higher proportion of the surface area of ponds is available for foraging (25% on average, compared with 10% for industrial salines, Table 1). Nevertheless, the highest densities of shorebirds were recorded in the industrial salines, where the peaks corresponding to the spring and autumn migrations were very pronounced (Fig. 6). In the traditional salines the highest density was recorded during the winter period in February (Fig. 6). On average, 8.5% of available foraging habitat was found in the traditional salines (Table 1). Thus, 15 of 16 shorebird species with average counts of more than 10 individuals made more use of the industrial salines for foraging than would be expected at random (Table 3).

Discussion

Chironomus salinarius is a chironomid species (complex) that is particularly tolerant of high salinities (Armitage et al., 1995) and is often recorded as the only benthic invertebrate species. In

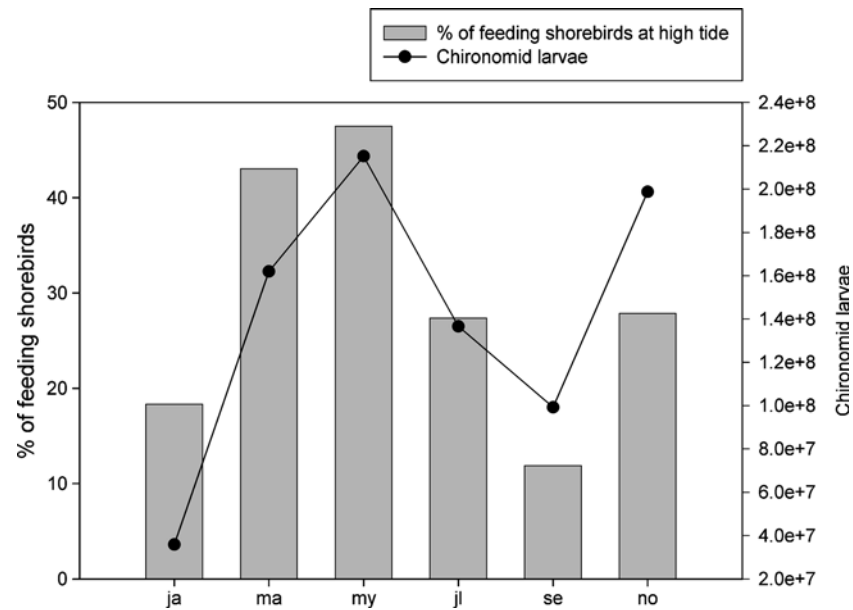


Figure 5. Fluctuations in the percentage of shorebirds that are feeding, compared with changes in the number of chironomid larvae available. Using the bird census conducted at that date closest to the date of benthic sampling, we calculated the proportion of birds present at high tide that were feeding. Using densities of larvae and the surface area of ponds that were available to shorebirds (i.e. ≤ 20 cm), we estimated the number of larvae available.

the nearby Cádiz Bay, this species is thought to have about five generations a year (Arias & Drake, 1994). Such multivoltinism is characteristic of latitudes such as those of southern Spain, where

high temperatures allow high growth rates (Huryn, 1990). The presence of pupae throughout the annual cycle in our samples confirms that this species must have many generations a year, since the

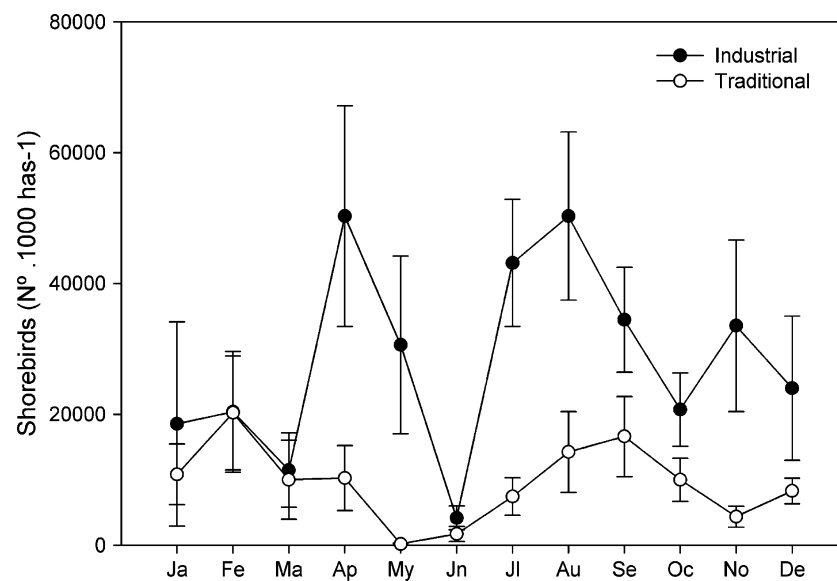


Figure 6. Average monthly density of shorebirds recorded at high tide in industrial and traditional salines. Densities were recorded based on the total surface area of salines.

benthic pupal stage lasts a few days at most (Armitage et al., 1995).

For the salines as a whole, we observed a marked seasonality in the abundance of larvae of this species, with peaks in May and November. This pattern contrasts with those observed in marine soft-bottom habitats in temperate regions, where abundance of invertebrates peaks in winter and spring (Service & Feller, 1992). Our results are also different to those found in a tidal lagoon in Cádiz bay, where the abundance of larvae peaked from late summer until winter (Drake & Arias 1995). This difference is probably related to the differences in habitat and management of water levels at each site (see Drake & Arias 1995). Differences in management of water levels between individual ponds are also likely to explain the strong POND*MONTH interaction we observed at our site.

In our study site, the main salinity gradient is spatial between ponds rather than temporal between months of different temperatures (as observed in other Mediterranean aquatic systems), and we recorded a negative correlation between the salinity of each pond and the larval density. Thus, high salinities allow *C. salinarius* to monopolise benthic resources, but further increases appear to reduce growth and/or survival rates. Similar effects of extreme salinities on the density of chironomid larvae have been recorded in other wetland types (Galat et al., 1988; Hammer et al., 1990). A negative correlation between larval abundance and salinity was also recorded in Cádiz Bay (Arias & Drake, 1994), but it confounds spatial and temporal variation and is hard to interpret.

Chironomid larvae are one of the principal food items of shorebirds in the coastal wetlands of southern Europe (Pérez-Hurtado et al., 1997), unlike northern Europe where polychaetes, gastropods and bivalves tend to be dominant prey (Goss-Custard et al., 1977a; Worrall, 1984; Dit Durell & Kelly, 1990; but see Rehfisch, 1994). The high density and availability of *C. salinarius* (together with that of *Artemia*) makes the Odiel salines an important foraging habitat for shorebirds, especially during the migration periods. During autumn passage, most birds used the salines only at high tide when the tidal marshes were unavailable, leaving to feed in the tidal marshes at low tide. Similar results have been reported in salines

elsewhere (Masero et al., 2000). However, during spring passage we found most shorebirds to remain in the salines at low tide, suggesting that the salines provided a relatively better foraging habitat in spring than in autumn. The strong relationship detected between changes in the density of chironomid larvae and in the numbers of feeding shorebirds suggests that the birds make decisions about feeding in salines and which pond to feed in based largely on the availability of chironomids. Previous studies in other regions have shown that shorebirds respond to variation in prey density, with a positive correlation between prey density and bird density (Goss-Custard, 1970; Goss-Custard et al., 1977a, 1991; Velasquez, 1992). The same pattern appears to occur in the Odiel salines.

Further evidence that changes in the density of chironomid prey determine these changes in the use of salines by foraging shorebirds comes from a diet study of the redshank (Sánchez et al., 2005). Pellets collected in spring 2001 were dominated by invertebrate prey from the salines (chironomid larvae and pupae, and Coleoptera), while those collected in autumn were dominated by prey from the tidal marshes (isopods, bivalves and polychaetes). Of 39 pellets collected in spring, 59% contained chironomid larvae, compared to only 6.6% of 121 pellets from the autumn (Sánchez et al., 2005). Nevertheless, the abundance of chironomid pupae in these pellets (found in 74.4% of pellets in spring and 9.9% in autumn), despite the relative rarity of pupae in the benthos suggests that, as well as feeding on chironomids in the sediments, shorebirds also take pupae as they come to the surface and before the adults have had time to emerge (Sánchez et al., 2005).

Changes in use of the salines by shorebirds will also depend on fluctuations in the availability of prey in tidal marshes between seasons. We have no data to assess how prey abundance in tidal marshes differed between spring and autumn. Between the spring and autumn migrations, we also observed an important shift in the composition of the shorebird community, e.g. with relatively more dunlins and little stints in spring and more black-tailed godwits, avocets and black-winged stilts in autumn. Given the differences in diet and habitat use by these species, these changes may also have influenced the relative increase in the use of salines for foraging during the spring migration.

We found that the more traditional manner of salt production did not produce a higher availability of chironomid prey, and did not provide a preferred habitat for waders. Waders were found at a higher density in the industrial salines, perhaps because these ponds were larger than traditional ones (Fig. 1) and thus permit more effective vigilance against predators (Cayford, 1993), and because the traditional salines suffered more disturbance from a road.

The extent to which a high production of chironomid larvae is translated into a good foraging habitat for shorebirds depends largely on appropriate management of water levels (Velasquez, 1992; Rehfish, 1994). Smaller shorebird species are those that are most limited in the depth range where they can feed, and also those most dependent on alternative, artificial habitats such as salines since their low body mass and high metabolic rate requires them to feed practically all day round (Goss-Custard et al., 1977b; Fasola & Canova, 1993). Some species such as avocets are less limited by water depth, as they also feed on *Artemia* in deeper parts of our study site (by swimming and taking brine shrimps close to the surface).

The high ecological and conservation value of the Odiel salines is obvious given the numbers and diversity of birds that it supports. For six different species, our partial counts sometimes exceeded the 1% threshold for the flyway population used to identify wetlands of international importance for a given species (Table 3). The salines offer both a good food supply and disturbance-free areas for resting, two key factors that determine the habitat use by shorebirds (Goss-Custard, 1969). Nevertheless, the quality of the habitat as a foraging area could be increased by changing management practices to increase the accessibility of chironomids to shorebirds, and particularly by using drawdowns to increase access to deeper areas during the migration periods. At the moment, the proportion of chironomid production that is consumed by birds is relatively low compared to lagoons managed specifically for birds (Rehfish, 1994). In most of the ponds, the majority of the benthos is inaccessible to shorebirds throughout the year (Table 1). On the other hand, in those areas of our study ponds where shorebirds are able to feed, enclosure experiments show that shorebird predation has a “top-down” effect in regulating

the density of chironomid larvae (Sánchez et al., 2006). This suggests that the foraging intake of a shorebird feeding at a given moment is likely to be limited by shorebird use of the site in the previous weeks, and underlines the potential benefits of drawdowns so that the Odiel salines can provide a more efficient refuelling site for a larger number of migratory shorebirds.

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Anostracans and microcrustaceans as potential food sources of waterbirds on sodic pans of the Hungarian plain

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Key words: dabbling-filter feeding waterfowl, pelagic foraging wader, sodic crustacean biomass, sodic pan, natronophile Anostracans, natronophile microcrustacean

Abstract

Hungarian sodic water bodies have a rich macro- and microcrustacean fauna due to the lack of fish populations. The crustacean population is very abundant, for this reason these wetlands provide good feeding resources for waterbirds. The density of macro- and microcrustacean populations together with feeding waterbirds was investigated in March, April, and May of 2002, on two characteristic sodic pans, “Kelemen-szék” and “Zab-szék”. The following dabbling-filtering waterfowls and pelagic forager wader species were counted: northern pintail (*Anas acuta*), northern shoveler (*Anas clypeata*), garganey (*Anas querquedula*), common teal (*Anas crecca*), avocet (*Recurvirostra avosetta*), spotted redshank (*Tringa erythropus*), greenshank (*Tringa nebularia*), and marsh sandpiper (*Tringa stagnatilis*). The dominant macrocrustacean species was the [Anostraca – Branchinectidae] natronophile *Branchinecta orientalis*, and its density was significantly higher in Zab-szék than in Kelemen-szék. The microcrustacean zooplankton community was also different in the pans, [Cladocera] *Daphnia magna* density was significantly higher in Kelemen-szék than in Zab-szék, but the density of the [Copepoda] natronophile *Arctodiaptomus spinosus*, was higher in Zab-szék than in Kelemen-szék. The density of the investigated waterbird species was also significantly higher in Zab-szék than in Kelemen-szék during spring. We can conclude that the macrocrustacean *B. orientalis* is one of the most important potential food resources for migrating pelagic foraging waders in spring on characteristic Hungarian sodic pans. However, the most abundant available food item for waterbirds are copepod microcrustacean zooplankton, which have a biomass that is larger by approximately one order of magnitude than the macrocrustacean zooplankton biomass. Considering the lack of submerged water vegetation, we suggest that planktonic microcrustaceans are an important food resource for dabbling-filtering ducks because they can utilise the small crustacean biomass more effectively than the less abundant and rapidly moving macrocrustacean *B. orientalis*.

Introduction

Hungarian continental intermittent shallow periodical sodic water bodies have rich macro- and microcrustacean fauna due to a lack of fish populations and scarce amphibians. The composition and volume of the microcrustacean fauna in these pans was characterised by Forró (2001, 2003). The composition and volume of the macro-nektonic

invertebrate population was characterised by Kiss et al. (2001), and the more limited benthic fauna was characterised by Andrikovics (2001) and Andrikovics & Murányi (2003).

In contrast with data of sodic planktonic, nektonic, and benthic invertebrate communities, there were no clear quantitative data about the density of sodic anostracan macrocrustacean populations in Hungary, as the plankton net used

in zooplankton studies was not suitable for taking representative samples of actively moving anostracans. Nevertheless it is known that natronophile anostracan species such as *Branchinecta orientalis* (G.O. Sars) can be commonly found in most characteristic Pannonic sodic wetlands (Metz & Forró, 1989; Forró, 2000).

The crustacean food of waterbirds has been studied in many investigations on wetlands. However, there are only a few studies about sodic crustacean food resources in Hungary. Most of them were based on stomach content analyses and field feeding behaviour observations, for example Sterbetz (1988) found anostracan *B. orientalis* in large amounts and high frequencies in the stomachs of 15 shorebird (Scolopacidae) species' stomachs on a characteristic sodic pan (Kardoskut, "Fehérszék" pan in the South part of Great Hungarian Plain). This finding suggests that this anostracan species was easily available for shorebirds on that pan, but unfortunately the anostracan population was not investigated simultaneously. He predicted that the invertebrate population of Pannonic sodic wetlands provides good feeding resources for shorebirds (e.g.) dunlin, *Calidris alpina* (L.), and curlew sandpiper, *Calidris ferruginea* (Pontoppidan), during migration period, (Sterbetz, 1992, 1993). Sterbetz (1972, 1991) also investigated dabbling-filtering duck stomach contents, but this investigation comprised many types of wetland habitats including sodic waters. He found mainly plant material in ducks guts and only a small amount of crustacean and no *Branchinecta* at all.

More data are given by Glutz et al. (1968, 1997) and Cramp & Simmons (1977, 1983) about small microcrustaceans and anostracans as diet for waterbirds, and only a few studies were carried out investigating crustacean and waterbird populations simultaneously in these sodic habitats.

Clear positive correlations were indicated between sodic microcrustacean density and avocet, *Recurvirostra avosetta* (L.), density on the feeding sites (Forró & Boros, 1997) in early spring, as well as between benthic and nektonic species density and migrating shorebirds (Charadriiformes) in late spring, summer and autumn on the same sodic pans (Boros, 2001).

Winkler (1980) reported that certain shorebird species fed on the *B. orientalis* population on sodic pans in Austria. Furthermore he reported that the energy of a 2 cm long *Branchinecta* is 38 J ind.⁻¹,

and that the density of 20–115 individuals m⁻² was reduced by half in a week from shorebird predation.

In this study we predict that anostracans and microcrustaceans are almost the exclusive food resources of sodic ponds in early spring. These ponds are very important stopover sites for waterbirds, because there are no other profitable food resources during this early spring period. We also predict that large number of feeding waterbirds prefer the pans which have more abundant crustacean population. Based on former experiments we selected two characteristic sodic pans for investigating potential crustacean food resources and waterbird populations.

Study site

Sodic pans are a special type of continental saline water body. These open water bodies have a characteristic chemical composition, and develop from groundwater seepage and rainfall.

They have intermittent shallow waters (average depth = 0.4–0.5 m), notable seasonal water level fluctuations, and frequently dry out entirely in midsummer or fall. The salinity varies between hypo- (3–20 g l⁻¹) and mesosaline (20–50 g l⁻¹) ranges depending on the water level. The total dissolved solids are dominated by sodium (Na⁺), calcium (Ca²⁺), and carbonate (CO₃²⁻) ions, and high grey-brown coloured turbidity (0.01–0.03 m) permanently suspended by colloidal ion complexes. The characteristic sodic-alkaline soil is made evident around the shoreline by the marshland *Bolboschoenus-Phragmitetum* and wet meadow *Lepidio-Puccinellietum* association. There is no vegetation in the major part of the pan-bed during the wet periods.

The investigated pans were Zab-szék (105 ha open water) [N: 46° 50' E: 19° 10'] and Kelemen-szék (135 ha open water) [N: 46° 48' E: 19° 11']. They are included in the Hungarian Waterfowl Monitoring program (Faragó, unpublished data). The waters are hypertrophic based on total phosphorus concentrations (≥100 µg l⁻¹) according the OECD trophic classification system (Vollenweider & Kerekes, 1980). These pans are important stopover sites for waterbirds (Anseriformes, Charadriiformes) in the middle reaches of the River-Danube basin. For this reason the ponds are strictly

protected parts of the Kiskunság National Park, and they were designated as Ramsar sites in 1979. The geographical location of the investigated pans can be seen in Figure 1.

Methods

The density of anostracan macrocrustacean and microcrustacean populations and feeding waterbirds were investigated during March, April and May of 2002, on two characteristic sodic pans, Kelemen-szék and Zab-szék.

Three sampling points were marked on the characteristic feeding territories in each pan. Three random repeating samples were taken within a circle of 100 m radius around each marked point ($n=9$ within a pan per sampling event). The distances (m) between random and marked points were generated by means of a random table in the field, and random sampling points were approached by wading in the shallow water. The water depth and conductivity were also measured at each random sampling point.

The conductivity was measured by WTW MultiLine P4 universal field instrument. Salinity

was calculated on the basis of conductivity data (Freeze & Cherry, 1979) by means of experimental equation ($\text{TDS (mg l}^{-1}\text{)} = A \text{ (constant)} * \text{EC (}\mu\text{S cm}^{-1}\text{)}$). The 'A' constant was calculated by regression of conductivity and TDS laboratory measures separately for each pan ($n_{1,2}=12-12$), and the same value ($A=0.8$) was found for both pans. The difference in median salinity between the two pans was tested by means of a non-parametric Mann-Whitney U test.

Crustaceans were sampled with a cylindrical plastic tool (diameter: 0.58 m heights: 0.60 m). This is a modified type of "Aqualax" sampling method (Nagy et al., 1998) developed for water invertebrate sampling in Hungary.

The sampling person carries the tool and puts it into the shallow water manually at each sampling point. All crustacean individuals were filtered from the water inside cylinder with a plankton net of 100 μ mesh size. The sampled volume of water was calculated based on water depth inside and diameter of the sampling device. The sampling procedure was carried out four times (09 March, 02 April, 23 April, and 17 May 2002) during the spring season at 9 random points per pan. The sampled crustaceans were preserved in formaldehyde, and later

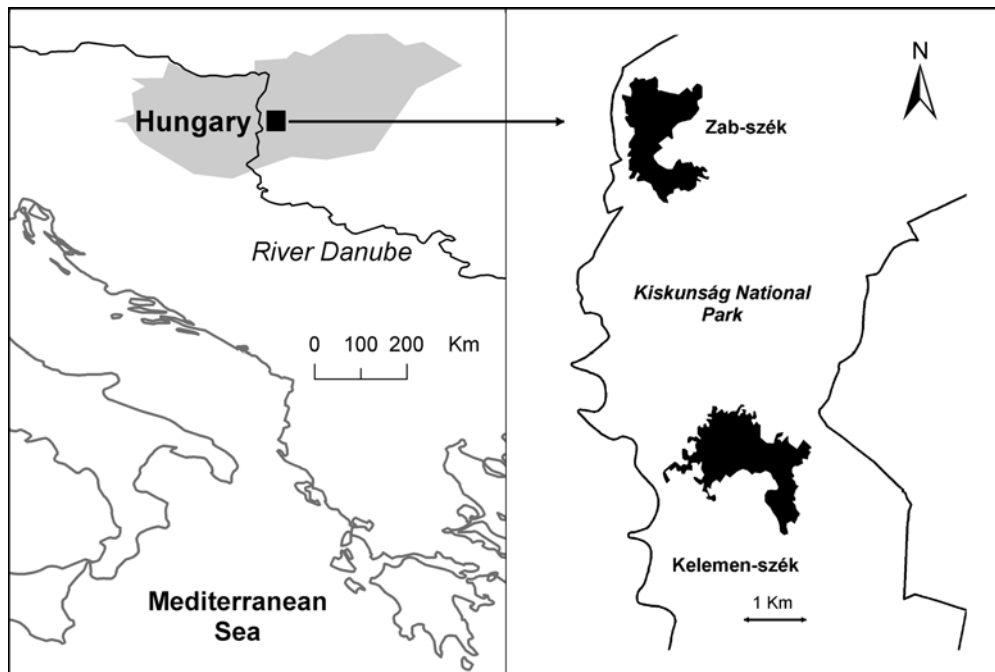


Figure 1. Geographical location of the investigated pans.

identified and counted in laboratory under a dissecting microscope. Only the four dominant species were analysed, and density was expressed as individuals l^{-1} .

Microcrustaceans were identified using Gulyás & Forró (1999, 2001) keys. To determine the number of individuals, the sample was filtered and diluted to 100 ml, after that 5 ml subsamples were taken and individuals were counted. Subsamples were taken from every sample and counted until there was less than a 10% difference between three subsamples. If a sample contained only a few hundred individuals, the whole sample was counted. If a sample contained more than 5000 items, 2 ml subsamples were counted. The length of 50 individuals of the dominant species in each sample was measured using an ocular micrometer. The mass was estimated from the length using the regressions by Bottrell et al. (1976) and Dumont et al. (1975). The dry biomass of the sample was calculated from the mass of 50 individuals and the number of items in the sample.

The body length of 100 individuals of *B. orientalis* (size range 2–31 mm) was measured as the distance from the anterior of the head to the posterior of the last abdominal segment (precision 0.1 mm). For weighing, the individuals were transferred to preweighed aluminium foils and oven dried for 48 h at 60 °C, left to cool in a desiccator, and their dry mass was measured with an analytical balance (precision 0.01 mg). The dry biomass was calculated in each sample by using average body size per sample and a relevant dried/wet weight regression.

The non-parametric Mann–Whitney *U* test was used to study the non-normal and homogeneous crustacean population densities and biomasses between the two studied pans. Crustacean biomass among species populations was tested using the non-parametric Kruskal–Wallis test.

During this investigation, only those waterbird species which fed exclusively on the open water of the pans were taken into account. Total population of predominant dabbling-filter feeding waterfowl and pelagic foraging wader species were counted every week separately on the two pans. Surveyed species include the northern pintail, *Anas acuta* (L.), northern shoveler, *Anas clypeata* (L.), garganey, *Anas querquedula* (L.), common teal, *Anas crecca* (L.), avocet, spotted redshank, *Tringa*

erythropus (Pallas), greenshank, *Tringa nebularia* (Gunnerus), and marsh sandpiper, *Tringa stagnatilis* (Bechstein). The number of waterbird species was transformed to density (individuals ha^{-1}), on the basis of surface area of the open water body. The waterbird density was divided into two feeding guilds based on foraging strategy and predominant prey item groups (Cram & Simmons, 1977, 1983). These are dabbling-filter feeding waterfowl such as northern pintails, northern shovelers, garganeys, common teals, and pelagic foraging waders such as avocets, spotted redshanks, greenshanks, and marsh sandpipers.

Logarithmic transformation for normality and homogeneity were applied. Comparison of the density of the two guilds was tested by two-way ANOVA between pans and guilds. The statistical procedure was carried out by means of Statistica™ Windows software.

Results

Although physical conditions and chemical composition were similar in the two pans, the salinity was significantly higher in Zab-szék than in Kelemen-szék (Mann–Whitney *U* test: $z = -5.299$, $n_{[1,2]} = 36$, $p < 0.0001$). The salinity had increasing trends due to the decrease of water levels (Zab-szék 0.34–0.22 m; Kelemen-szék 0.4–0.27 m) during the study (Table 1).

The cladoceran community was also different between the pans. *Daphnia magna* (Straus) density (Mann–Whitney *U* test: $z = 7.050$, $n_{[1,2]} = 36$, $p < 0.0001$) and biomass (Mann–Whitney *U* test: $z = 5.428$, $n_{[1,2]} = 36$, $p < 0.0001$) were significantly higher in Kelemen-szék (Table 1). The *D. magna* population had a peak in biomass at the beginning of April in Kelemen-szék (Fig. 2). The halophile summer Cladoceran species *Moina branchiata* (Lang) occurred only in the middle of May in Kelemen-szék, but there were not enough data for statistical analysis.

In contrast to *D. magna*, density of the natronophile copepod *Arctodiaptomus spinosus* (Daday) was significantly higher in Zab-szék (Mann–Whitney *U* test: $z = -4.302$, $n_{[1,2]} = 36$, $p = 0.00001$). However, there was no significant difference in the biomass of this copepod species between pans (Mann–Whitney *U* test: $z = -1.261$,

Table 1. Salinity, and density of the crustacean population and bird feeding guilds on the studied pans

	<i>n</i>	Median	Range	Mean	Std. Dev.
"Kelemen-szék" pan					
Salinity	36	4.636	3.064	5.101	1.055
<i>Daphnia</i> density No l ⁻¹	36	101.191	604.567	151.772	154.837
<i>Daphnia</i> biomass g m ⁻²	36	0.132	6.189	0.637	1.527
<i>Arctodiaptomus</i> density No l ⁻¹	36	228.795	1436.465	340.814	361.179
<i>Arctodiaptomus</i> biomass g m ⁻²	36	0.292	9.629	0.948	1.726
<i>Branchinecta</i> density No l ⁻¹	36	0.000	0.059	0.009	0.014
<i>Branchinecta</i> biomass g m ⁻²	36	0.000	0.094	0.009	0.022
Dabbling-filtering waterbird guild density	33	–	–	0.761	1.093918
Pelagic forager wader guild density	7	–	–	0.092	0.103072
"Zab-szék" pan					
Salinity	36	6.680	4.224	7.187	1.457
<i>Daphnia</i> density No l ⁻¹	36	0.000	76.326	4.945	15.590
<i>Daphnia</i> biomass g m ⁻²	36	0.000	0.001	0.000	0.000
<i>Arctodiaptomus</i> density No l ⁻¹	36	2072.207	6665.421	1878.290	1387.493
<i>Arctodiaptomus</i> biomass g m ⁻²	36	1.299	7.718	1.784	1.885
<i>Branchinecta</i> density No l ⁻¹	36	0.297	1.205	0.407	0.402
<i>Branchinecta</i> biomass g m ⁻²	36	0.074	0.520	0.162	0.166
Dabbling-filtering waterbird guild density	35	–	–	2.275	2.577326
Pelagic forager wader guild density	20	–	–	0.537	0.747707

$n_{(1,2)} = 36$, $p = 0.207$) (Table 1). The change in biomass during the season was also in contrast to the relationship between *Daphnia* and salinity.

There was an increase in biomass in Kelemen-szék, while a decreasing tendency was observed on Zab-szék up to May (Fig. 2).

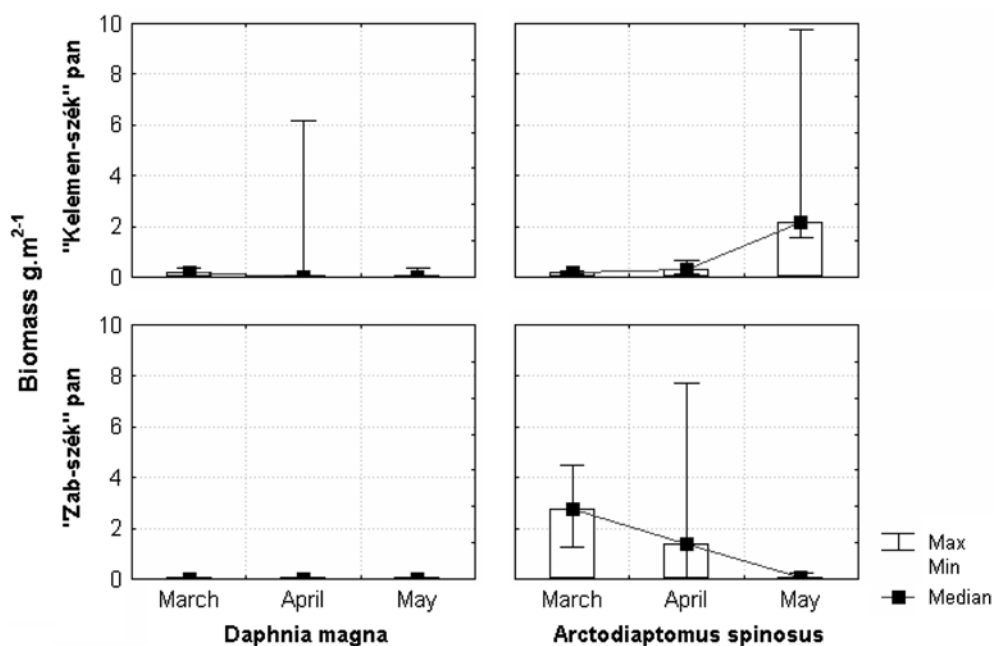


Figure 2. Seasonal changing of predominant planktonic microcrustacean biomass.

The predominant natronophile anostracans were *B. orientalis*, and a few specimens of *Branchinecta ferox* (M. Milne-Edwards) were also found. However, juvenile stages are difficult to identify. Both *Branchinecta* species density (Mann–Whitney *U* test: $z = 5.497$, $n_{[1,2]} = 36$, $p < 0.0001$) and biomass (Mann–Whitney *U* test: $z = 5.496$, $n_{[1,2]} = 36$, $p < 0.0001$) were higher in Zab-szék pan than in Kelemen-szék (Table 1). A biomass population peak was observed at the end of March, followed by a decreasing tendency up to May (Fig. 3).

Comparing the biomass of the three investigated crustacean species, we were also able to find significant differences (Kruskal–Wallis test: $H_{(2,n=216)} = 83.887$; $p < 0.0001$) among species. The figure shows that *A. spinosus* microcrustaceans had the greatest biomass in both pans, but the distribution of other crustaceans was quite different. *D. magna* microcrustaceans had the second highest total biomass in Kelemen-szék, while in Zab-szék it was *B. orientalis* macrocrustaceans. The *B. orientalis* macrocrustacean population biomass in Kelemen-szék, and the *D. magna* microcrustacean population biomass in Zab-szék were almost negligible.

The density of waterbirds was significantly higher (ANOVA: $F_{1,91} = 9.613$; $p = 0.0026$) on Zab-szék than on Kelemen-szék. The dabbling-filtering guild density was significantly higher (ANOVA: $F_{1,91} = 14.472$; $p = 0.0002$) than the pelagic foraging-wader guild density on both pans (Table 1, Fig. 4). The interaction term between pans and guilds was not significant (ANOVA: $F_{1,91} = 0.079$; $p = 0.7791$), suggesting that guild density did not vary between the two areas.

On the basis of average monthly density of waterbirds, species proportions were similar on both pans, but the absolute density was significantly higher (two times) on Zab-szék. The dabbling-filter feeding Anatidae species dominated in March on both pans, especially common teal (max. 8.952 ind. ha⁻¹) and northern shovelers (max. 3.714 ind. ha⁻¹). No other duck species reached a density of 1 individual ha⁻¹. Duck populations decreased towards April and almost totally disappeared by May. There was a migration peak for avocets (max. 8.952 ind. ha⁻¹) and spotted redshanks (max. 1.6 ind. ha⁻¹) on Zab-szék in April. Other waterbird species did not have a notable proportion (density > 1 ind. ha⁻¹) in the feeding guilds.

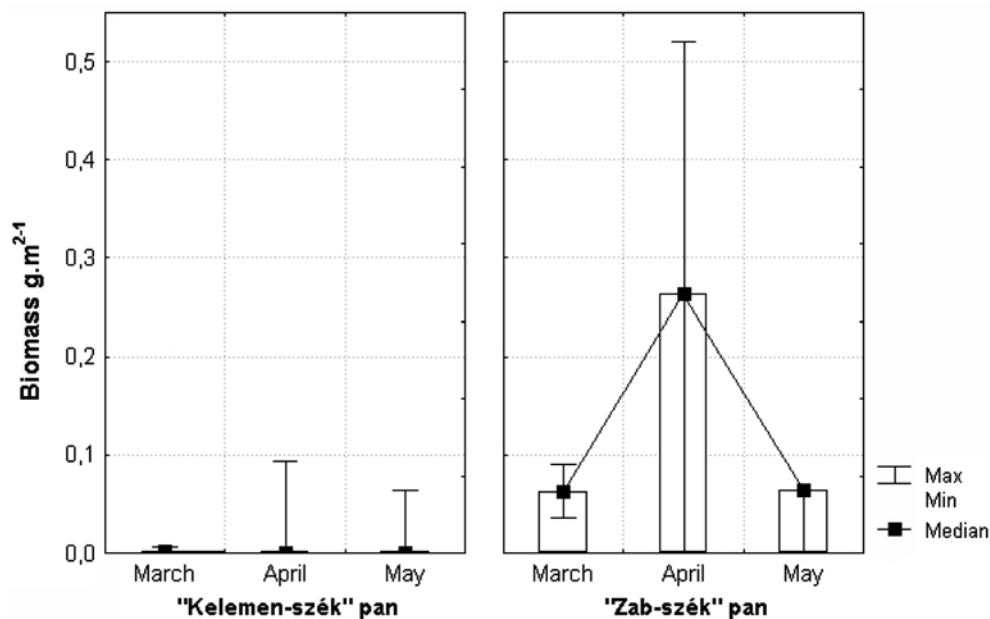


Figure 3. Seasonal changes in predominant anostracan *Branchinecta orientalis* macrocrustacean biomass.

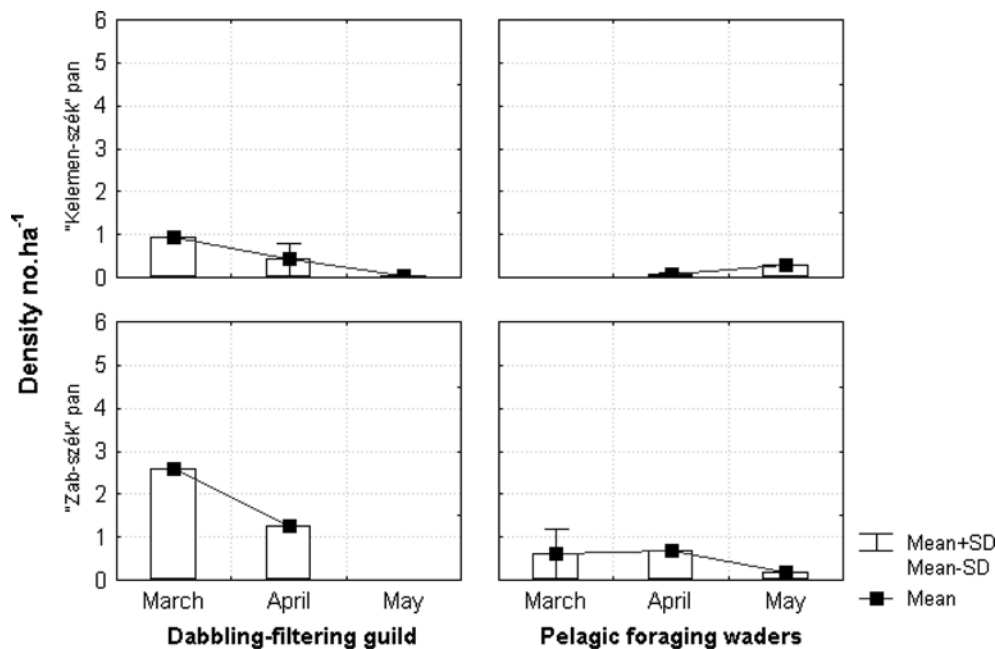


Figure 4. Seasonal changes to density of waterbird feeding guilds.

Discussion

Quantitative population data about *Branchinecta* ssp. macrocrustaceans have not yet been published yet in Hungary, although it is thought to be the most abundant natronophile anostracan genus in Hungarian sodic waters. This investigation suggests that *B. orientalis* macrocrustaceans prefer higher salinity sodic waters than halophile *A. spinosus* microcrustaceans. Metz & Forró (1989) found similar habitat selection of these species in Austria.

The *B. orientalis* macrocrustacean population peak in Zab-szék was coupled with a predominantly *A. spinosus* microcrustacean population peak during March and April. At this time, both dabbling-filtering waterfowl and pelagic foraging waders were present in significantly higher numbers in Zab-szék than in *D. magma* dominated Kelemen-szék. Although there was no significant difference in *A. spinosus* biomass between the pans, *A. spinosus* had a population peak in Kelemen-szék in May, after the main bird migrating season. *A. spinosus* had the largest mean biomass in both pans, which is larger by an order of magnitude than the biomass of *B. orientalis*. The peak biomass of *D. magma* at Kelemen-szék was similar in magnitude to that of *A. spinosus* at Zab-szék in

April. These figures could suggest that the waterbirds did not prefer potentially abundant *D. magma* biomass, or that the dabbling-filtering guild preferred *B. orientalis* macrocrustaceans to microcrustaceans (*D. magma* and *A. spinosus*). Though all investigated waterbird species can consume both micro- and macrocrustaceans, feeding methods suggest that the slow moving dabbling-filtering ducks utilise the most abundant planktonic microcrustaceans (*D. magma* and *A. spinosus*) more effectively than the less abundant and fast moving *B. orientalis* macrocrustacean. Furthermore there was no submerged vegetation in the open water bodies where the investigated ducks fed extensively, and filtering feeding action was more frequent than dabbling.

These observations are supported by Sterbetz's (1972, 1991) stomach data, as he did not find *B. orientalis* macrocrustacean fragments in the gut contents of ducks in Hungary, and by Cramp & Simmons (1977), who reported microcrustaceans in several duck species diet with special emphasis on their importance to northern shovellers.

Significant differences in anostracan biomass and waterbird population densities among the two pans indicate that the natronophile *B. orientalis* macrocrustacean may be one of the most

important food resources in Hungarian mesosaline sodic pans in early spring for pelagic foraging waders such as avocets, spotted redshanks, greenshanks, and marsh sandpipers. This is in accordance with Sterbetz's (1988) stomach content results and Winkler's (1980) observations. Although Forró & Boros (1997) found a positive correlation between avocets and microcrustacean density on a large scale investigation of sodic waters in the Great Hungarian Plain, the *B. orientalis* population was not investigated at the same time. Further research is needed to better quantify the relationship between the dabbling-filtering duck guild and its food resources.

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