

Community concordance between the fish and aquatic birds of lakes in northern Alberta, Canada: the relative importance of environmental and biotic factors

CYNTHIA A. PASZKOWSKI AND WILLIAM M. TONN

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

SUMMARY

1. Community concordance measures the degree to which patterns in community structure in a set of sites are similar between two different taxonomic groups. Although seldom incorporated into studies of lake ecosystems, aquatic birds can be influenced by the same environmental features of lakes which affect fish and invertebrates, and can interact with these organisms directly as predators, competitors or prey. We surveyed lakes in north-central Alberta, Canada, to determine if co-occurring fish and aquatic bird assemblages displayed concordance, and assessed the relative importance of environmental and biotic factors in contributing to observed concordance.

2. In 41 lakes (3–305 ha), we encountered seven species of fish and thirty-one avian taxa which subsequently were used in multivariate analyses. Fish assemblages dominated by large piscivores were in large deep lakes, whereas fishless lakes and lakes with only small-bodied fish were small and shallow, and thus, prone to winter hypoxia. Bird assemblages displayed three general patterns: (a) small shallow lakes supported a 'core' of widespread species (between three and eight species per lake); (b) large, deep lakes supported more species (between 11 and 16), including large, aerially foraging piscivores; and (c) large, shallow lakes supported the most species (between 15 and 23), including many ducks.

3. Randomization tests of matrix concordance and Mantel tests both showed that fish and bird assemblages were significantly concordant. Concordance reflected the fact that both groups were strongly affected by the same key environmental factors, principally lake size and maximum depth, and to a lesser extent, productivity and geographic isolation. Direct interactions between birds and fish, such as predation and competition, appeared to play much smaller roles in shaping the two assemblages.

Keywords: boreal lakes, multivariate analyses, piscivory, waterfowl assemblages, winterkill

Introduction

The concept of coherence (or synchrony) has recently been developed in aquatic ecology as a means of detecting general, unifying forces among ecosystems while recognizing site-to-site diversity (Magnuson, Benson & Kratz, 1990; Kratz *et al.*, 1998). Coherence

can be defined as the degree to which different ecosystems within a region behave similarly through time (Magnuson *et al.*, 1990). Patterns of temporal coherence among lakes in a district generally progress from strong coherence for physical, climate-controlled factors (e.g. temperature), moderate coherence for chemical variables (e.g. conductivity and dissolved organic carbon; Webster *et al.*, 1996), and weak or no coherence for biological responses (e.g. total zooplankton biomass; Kratz *et al.*, 1998). With access to longer-term data sets and an improved understanding of the forces which influence various components of lake ecosystems, even some biological phenomena,

Correspondence: Cynthia A. Paszkowski, Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada. E-mail: cindy.paszkowski@ualberta.ca

such as chlorophyll dynamics, can be shown to display significant interannual synchrony (Baines *et al.*, 2000).

In a spatial, community-level context, the concept of concordance parallels the concept of coherence. Community concordance measures the degree to which patterns in community structure in a set of locations (e.g. lakes) are similar among different taxonomic groups (Jackson & Harvey, 1993). Numerous studies have described multilake patterns in the community structure of a single taxonomic group and linked that structure to patterns in the abiotic environment (e.g. Tonn & Magnuson, 1982; Johnson & Wiederholm, 1989; Kauppinen & Väisänen, 1993; Toivonen & Huttunen, 1995). A number of studies have also included data from one taxonomic group in the suite of environmental variables used to explain community-level patterns in a second group (e.g. Mills & Schiavone, 1982; Rodríguez, Magnan & Lacasse, 1993; Pinel-Alloul, Niyonsenga & Legendre, 1995). Very few studies (e.g. Jackson & Harvey, 1993) have explicitly examined the issue of concordance between two distinct communities in freshwater ecosystems.

Following logically from the community-environment framework, strong concordance could suggest that the two communities are responding similarly, but independently, to the same suite of environmental conditions. Based on the physical-chemical-biological gradient of coherence strength (Kratz *et al.*, 1998), we might expect stronger concordance among communities which occupy lower trophic levels, where component organisms are more directly under the influence of physical and chemical factors, than among communities at higher trophic levels. Alternatively, because species at lower trophic levels, such as phytoplankton and zooplankton, are small and short-lived and respond quickly (but not instantaneously) to environmental change, simultaneous 'snapshots' of contemporary assemblages are more likely to be 'out of phase' in their response to physical or chemical perturbations. Therefore, concordance would be more likely between the stabler, less dynamic assemblages of larger, longer-lived organisms occupying higher trophic levels.

In addition, strong community concordance could result from biotic interactions, often direct interactions between the member species of two communities. Although biological variables typically show weak or no temporal coherence, trophic cascades (Carpenter,

Kitchell & Hodgson, 1985) and community-wide effects of strong interactors (Paine, 1980) are well documented in lake ecosystems and could produce concordance. Based on large-scale empirical surveys (e.g. McQueen, Post & Mills, 1986), one might predict a gradient in concordance strength which parallels differences in trophic-level, body size or life-history traits between the pairs of communities under comparison.

Interestingly, in 40 lakes in Ontario, Canada, Jackson & Harvey (1993) found fish species composition to be significantly related to lake morphometry, whereas invertebrate community structure was linked closely to water chemistry. Nevertheless, there was significant concordance between the fish and benthic invertebrate communities. Jackson & Harvey (1993) suggested that this paradox was a result of complex interactions between the biotic and abiotic environment, leaving unresolved the issue of the relative strength of abiotic forces versus biotic interactions in creating concordance.

In the present study, we assess concordance between two communities of vertebrates, fish and aquatic birds on lakes in north-central Alberta, Canada. Until recently, concordance between fish communities and coexisting bird communities would have been viewed as unlikely (if thought of at all). However, there is growing recognition that aquatic birds are members of lake ecosystems, can be influenced by the same physical and chemical features of lakes which affect other vertebrate and invertebrate organisms, and can interact with these organisms directly (Kerekes, 1994).

A second objective of our study is to evaluate separately the relationships of each of the two communities to local and landscape-level environmental characteristics of the lakes. Our previous research on fish communities in the region uncovered two distinct assemblage types (plus fishless lakes) shaped by both abiotic (winterkill) and biotic (piscivory) factors (Robinson & Tonn, 1989; Tonn, Vandenberg & Paszkowski, 1995).

In contrast to fish, the structure and functioning of aquatic bird communities are often poorly documented and understood, and those on Alberta lakes are no exception. Studies in North America and Europe on lake acidification (Eriksson, 1985; Blancher *et al.*, 1992; Mallory *et al.*, 1993) and eutrophication (Nilsson & Nilsson, 1978; Hoyer & Canfield, 1994; Suter, 1994)

have begun to demonstrate direct and indirect responses of bird populations to changes in water quality. Similarly, biotic interactions between primary producers, aquatic invertebrates, fish and birds are gradually becoming better understood and appreciated, especially the impact of trophic interactions on avian reproductive success (Giles, 1990; Hargeby *et al.*, 1994; Hanson & Riggs, 1995). However, aquatic birds on Alberta lakes do not always follow patterns described for other regions (Gingras & Paszkowski, 1999), and it is important to begin to quantify community-level patterns and identify the environmental factors which contribute to these patterns.

Acknowledging that birds and fish are fellow members of a number of trophic levels in lake ecosystems, we predict that these two vertebrate groups will display strong community concordance in Alberta lakes. Because birds are highly mobile, air-breathing endotherms and fish are less mobile, gilled ectotherms, we predict that fish communities will show stronger relationships with the environmental characteristics of lakes, particularly landscape and chemical variables, than bird communities. However, given the increasing documentation of trophic interactions between birds and fish, and the abundance and diversity of piscivorous birds in Alberta, we predict that biotic interactions between birds and fish, specifically competition and predation, will best explain patterns of concordance which are detected between these taxa.

Methods

Study area

The study took place in Athabasca County, Alberta, and surrounding areas (54.2–55.0° N, 112.5–113.8° W). This region is a mosaic of agricultural land, primarily in pasture and grain production, and boreal mixed-wood forest (Rowe, 1972). A flat landscape and poorly drained soils have produced numerous wetlands and peatlands.

Lakes in this region tend to be circumneutral to basic, nutrient-rich and productive, even in forest- or peatland-dominated catchments (Mitchell & Prepas, 1990). The limited topographical relief results in most of the smaller lakes being shallow (< 10 m), with broad littoral zones and abundant macrophytes. The semiarid climate, low relief and an abundant beaver,

Castor canadensis L., population result in many lakes lacking free-flowing outlet streams. Shallow productive lakes, combined with a long (5–6 months) ice-covered period result in frequent hypoxic conditions during winter. Because of regional (climatic) and historic factors (e.g. distance from glacial refugia), the regional fish fauna is depauperate (Nelson & Paetz, 1992); combined with seasonally harsh conditions within lakes and a paucity of refuges, this contributes to local fish assemblages which are also depauperate (Robinson & Tonn, 1989). In contrast, both the regional fauna and local assemblages of aquatic birds are relatively speciose (Semenchuk, 1992); the abundant wetlands and shallow productive lakes offer attractive breeding habitat for Gaviiformes, Podicipediformes, Anseriformes, Charadriiformes and Gruiformes.

Field techniques

Forty-one study lakes (Table 1) were chosen based on (1) size (< 300 ha), (2) a predominance of undeveloped shoreline, (3) permanence and (4) access. Thirty lakes were sampled for fish in May–August 1993 or 1994. The sampling gear consisted of multimesh gill nets (6.25–75 mm square mesh), minnow traps and small fyke nets set overnight. Fish data from the remaining eleven lakes came from an earlier study (Robinson & Tonn, 1989) which used similar methods and gear; for five of these lakes, limited sampling in 1993–1994 agreed with the earlier community descriptions (W. Tonn, unpublished data).

Birds were sampled between 4 May and 9 July 1993. On most lakes, a canoe was slowly paddled around the perimeter of a lake, 3–8 m from shore or from dense beds of emergent vegetation. A running record of time, location, and behaviour was kept for all individual birds encountered to decrease the likelihood that individuals were counted more than once. Birds were viewed through binoculars, identified to species, sexed and aged (mature versus immature) when possible. Any nests encountered were recorded. One circuit took 0.5–3 h. A few of the smallest lakes were surveyed from shore (20–30 min) with a × 45 spotting scope. Twenty-eight of the 41 lakes were visited one or two additional times in July and August 1993. Agreement in the number and identity of species seen across multiple visits was good (C. Paszkowski, unpublished data).

Table 1 Lake names, fish species and bird taxa (species and multispecies categories) used in community analyses of forty-one lakes in north-central Alberta. The codes refer to those used in Figs 1–3)

Lakes (code)	Fish species	Fish code	Bird species	Bird code
Bambi	Brook stickleback, <i>Culaea inconstans</i> (Kirtland)	BRST	American coot, <i>Fulica americana</i> Gmelin	AMCO
Beaver	Fathead minnow, <i>Pimephales promelas</i> (Rafinesque)	FTMN	American widgeon, <i>Anas americana</i> Gmelin	AMWI
Bilsky	Iowa darter, <i>Etheostoma exile</i> (Girard)	IWDR	Bald eagle, <i>Haliaeetus leucocephalus</i> (L.)	BAEA
Bobier	Northern pike, <i>Esox lucius</i> (L.)	NRPK	Belted kingfisher, <i>Ceryle alcyon</i> (L.)	BEKI
Chump	Spottail shiner, <i>Notropis hudsonius</i> (Clinton)	SPSH	Black tern, <i>Chlidonias niger</i> (L.)	BLTE
Cloudberry (Cloudb)	White sucker, <i>Catostomus commersoni</i> (Lacépède)	WHSC	'Black-headed gull': Bonaparte's gull, <i>Larus philadelphia</i> (Ord) &	
Canoe	Yellow perch, <i>Perca flavescens</i> (Mitchell)	YLPR	Franklin's gull, <i>Larus pipixcan</i> Wagler	BHGU
Duggans (Duggan)			Blue-winged teal, <i>Anas discors</i> L.	BWTE
Ghost			Bufflehead, <i>Bucephala albeola</i> (L.)	BUFF
Gilbert			Canada goose, <i>Branta canadensis</i> (L.)	CAGO
Gods			Canvasback, <i>Aythya valisineria</i> (Wilson)	CANV
Grochowski (Grocho)			Common goldeneye, <i>Bucephala clangula</i> (L.)	COGO
Hope			Common loon, <i>Gavia immer</i> (Brünnich)	COLO
Hutterite (Hutter)			Eared grebe, <i>Podiceps nigricollis</i> Brehm	EAGR
Jackfish (Jack)			Gadwall, <i>Anas strepera</i> L.	GADW
Jenkins			Great blue heron, <i>Ardea herodias</i> L.	GTBH
Joseph			Green-winged teal, <i>Anas crecca</i> L.	AGWT
Jumping Deer (JDeer)			Horned grebe, <i>Podiceps auritus</i> (L.)	HOGH

Little Buck (LBuck)	Lesser scaup, <i>Aythya affinis</i> (Eyton)	LESC
Lodge	'Large white gull': California gull, <i>Larus californicus</i> Lawrence	LWGU
Lofty	Herring gull, <i>Larus argentatus</i> Pontoppidan &	
Long Island (LongIs)	Ring-billed gull, <i>Larus delawarensis</i> Ord	
Lower Chain (LChain)	Mallard, <i>Anas platyrhynchos</i> L.	MALL
Middle Chain (MChain)	Northern pintail, <i>Anas acuta</i> L.	NOPI
Mystic	Northern shoveler, <i>Anas clypeata</i> L.	NSHO
Pike	Osprey, <i>Pandion haliaetus</i> (L.)	OSPR
Narrow	Pied-billed grebe, <i>Podilymbus podiceps</i> (L.)	PBGR
Nelson	Redhead, <i>Aythya americana</i> (Eyton)	REDH
North Crooked (NCrook)	Red-necked grebe, <i>Podiceps grisegena</i> (Boddaert)	RNGR
Orrin	Ring-necked duck, <i>Aythya collaris</i> (Donovan)	RNDU
Rochester (Roch)	Ruddy duck, <i>Oxyura jamaicensis</i> (Gmelin)	RUDU
Schumaker (Shumak)	'White tern': common tern, <i>Sterna hirundo</i> L. &	
Shelly	Forester's tern, <i>Sterna forsteri</i> Nuttall	WHITE
South Crooked (SCrook)	White-winged scoter, <i>Melanitta fusca</i> (L.)	WWSC
Spear	Wilson's phalarope, <i>Phalaropus tricolor</i> (Vieillot)	WIPH
Tawatnaw (Tawat)		
Teen		
Tempo		
Tipetary (Tiper)		
Turkawski (Turkaw)		
Two Island (Twols)		

For community analysis, we used only non-passerine birds which feed at or beneath the surface of the water. We chose these species because they are most strongly and unambiguously linked to lake characteristics, and were most reliably visible and identifiable by sight alone. We included only birds known to breed in the study area (Semenchuck, 1992); for most species, young were seen on at least one of the study lakes. However, we did not assume that a species seen on a lake was necessarily nesting there, only that it regularly used that site for feeding during the breeding season. In a few cases, two or more species which were identified inconsistently from a distance were combined into a single category; for example, 'black-headed gull', 'large white gull' and 'white tern'.

Water chemistry data (i.e. colour, conductivity, pH and total phosphorus concentration [TP]) for lakes sampled in 1993–1994 were measured during fish sampling with a Hydrolab Surveyor II (Hydrolab Corp., Austin, TX, U.S.A.) or from water samples collected from just below the surface. Data for other lakes came from previous studies (Prepas, Dunnigan & Trimbee, 1988; Robinson & Tonn, 1989) or from ongoing projects on the survey lakes (W. Tonn, unpublished data).

Morphometric measurements for lakes were based on 1:50 000 topographic maps. Area and perimeter were measured for each lake by tracing photocopied enlargements of map images on a Summasketch Plus digitizing tablet (Summagraphics Corp., Fairfield, CT, U.S.A.) and converting input using Sigma Scan. (Jandel Scientific Software, San Rafael, CA, U.S.A.) Shoreline development, an index of shoreline irregularity (Horne & Goldman, 1994), was calculated based on the aforementioned values. Maximum depth was estimated from thirty or more soundings made with a calibrated, weighted rope during fish samplings or during previous surveys (Prepas *et al.*, 1988; Robinson & Tonn, 1989).

Landscape variables (i.e. altitude, latitude, longitude and presence of inlet/outlet) were obtained from topographic maps. Three indices of lake isolation (Tonn *et al.*, 1995) were also obtained from maps by measuring the shortest map distance from each study lake to the nearest lake which was greater or equal in area to the (1) smallest (3 ha, 'distance-small lake'), (2) median-sized (55 ha, 'distance-medium lake') and (3) largest (305 ha, 'distance-large lake')

study lake. Distances were measured between the centres of the two lakes.

Data analysis: patterns of fish and bird assemblages

We used correspondence analysis (CA, also called reciprocal averaging) on both the fish- and bird-assemblage data sets to summarize the multivariate data resulting from the fish and bird surveys, to detect patterns in these community data sets, and to graphically represent the results, (McCune & Mefford, 1997). Fishless lakes were not included in these analyses. Community analyses were restricted to presence/absence data, and rare species, i.e. those found on only one lake, were omitted from analyses (Gauch, 1982; Jackson & Harvey, 1993).

Community–environment relations were examined in a number of ways. Firstly, we assessed the significance of overall community–environment relations for both fish and birds using Mantel tests and the PROTEST procedure (see below). For the latter, comparisons were made between lake scores from the first three axes from CAs (fish and birds) and principal component analyses (PCAs; lake environment). All environmental variables, except pH, were transformed [$\log_{10}(x + 1)$]. Inlet/outlet was a categorical variable, receiving a score of 1 if any stream connection was present or 0 if absent. Initial interpretations of community–environment relations were aided by calculating correlation coefficients (r) between CA ordination scores (fish and birds) and transformed environmental variables.

Canonical correspondence analysis (CCA; ter Braak, 1991) was used for direct analysis of community–environment relations. Preliminary analyses of species data for fish and bird assemblages using detrended CA indicated that the length of the ordination gradient on the first axis was appropriate for CCA in each case (4.0 and 2.0, respectively; ter Braak, 1987). Canonical correspondence analysis was performed with latitude and longitude as co-variables to account for any (coincidental) geographic pattern imbedded in the data. Environmental variables incorporated into final models were chosen via a forward selection procedure (ter Braak, 1991); for birds, a cut-off of $P < 0.10$ for variable inclusion was used (Magnan *et al.*, 1994), which led to an ordination based on three environmental variables (see 'Results'). To produce a comparable three-variable analysis, a cut-off of

$P < 0.11$ was needed in the fish CCA. Significance of the overall CCA model and of the first two ordination axes was assessed by Monte Carlo permutation tests (9999 permutations; ter Braak, 1991).

Data analysis: community concordance between fish and birds

To assess concordance of community-level patterns between fish and aquatic birds, we used two basic techniques. The more common of the two, the Mantel test (Mantel, 1967), evaluates the relationship between two matrices; in this case, Euclidean-distance matrices were constructed from the original lake-by-fish and lake-by-bird matrices. The significance of the relationship between the fish and bird distance matrices was assessed with a Monte Carlo randomization method, using 9999 permutations (McCune & Mefford, 1997).

To avoid problems that can result from choosing different distance measures in Mantel tests, Jackson (1995) developed PROTEST, a randomization test of matrix concordance based on Procrustean matrix rotation. The method tries to match the position of each lake in one multivariate space (defined here by the first three CA axes of the bird data) to the position of the same lake in a second multivariate space (the first three CA axes of the fish data), thereby assessing the degree to which both communities have similar interlake patterns (Jackson & Harvey, 1993). In addition to eliminating variation as a result of choice of distance measure, PROTEST has recently been shown to have more power than the Mantel test (D. Jackson, personal communication). The significance of the analysis was assessed with a Monte Carlo randomization method, using 9999 permutations.

If there is significant community-level concordance, then patterns described for one taxon might allow for predictions of patterns in the second. To examine for this possible predictive power, we classified the study lakes into three groups based on their fish communities: (1) lakes which contained large-bodied piscivores; (2) lakes containing only small-bodied fish; and (3) lakes which were fishless (Robinson & Tonn, 1989). We then applied a multi-response permutation procedure (MRPP), a non-parametric test analogous to discriminant analysis (McCune & Mefford, 1997), to test the hypothesis that bird communities did not differ across these

three groups of lakes. The analysis was performed, using Euclidean distance, on the bird community data from all forty-one lakes.

To examine the strength of associations between individual bird species and fish community types, we performed indicator species analysis (McCune & Mefford, 1997; Dufrêne & Legendre, 1997) on presence/absence data for each avian taxon. This analysis generates an indicator value for each species in an assemblage. This value is maximum (100) when a species occurs only at a single type of site (in this case, fish community) and at all sites of that type. We evaluated the statistical significance of the maximum indicator value of each bird taxon using a Monte Carlo randomization procedure (9999 permutations; McCune & Mefford, 1997).

Finally, to assess simultaneously the relative contributions of environmental and biotic factors to patterns in each assemblage, we partitioned the variation in the fish and bird data sets which could be explained by these two classes of factors (and their overlapping influence) by performing a series of partial CCAs (e.g. Borcard, Legendre & Drapeau, 1992; Tonn *et al.*, 1995). Abiotic factors included morphometric, chemical, and landscape variables, whereas biotic factors included the species composition data of the 'other' taxonomic group (i.e. bird data for the fish analysis and *vice versa*); as before, latitude and longitude were used as covariables. Because the bird and environmental data sets contained more variables (thirty-one and twelve, respectively) than there were fish species (seven), we first used forward selection (ter Braak, 1991) to identify a reduced set of seven bird species and seven environmental factors for use in the CCAs.

Results

A total of nine fish species were captured in the forty-one lakes; however, only seven were included in analyses because lake whitefish, *Coregonus clupeaformis* (Mitchill), and rainbow trout, *Oncorhynchus mykiss* (Walbaum), each occurred in only a single lake (Table 1). Eight lakes were fishless. The mean ($\pm$ SD) number of fish species per lake (excluding fishless lakes) was 2.3 ± 1.1 . Forty-two aquatic bird species were observed during surveys, but only thirty-one taxa were included in our analyses (Table 1). Seven species were excluded because they were observed on

Table 2 Medians and range for environmental variables from forty-one lakes in north-central Alberta used in analyses of fish and bird assemblages. For each lake, inlet/outlet was simply scored as present or absent

Variable	Median	Range
<i>Morphometric variables</i>		
Area (ha)	54.8	2.7–304.8
Perimeter (km)	3.9	0.8–15.5
Shoreline development index	1.45	1.02–3.65
Maximum depth (m)	2.8	0.6–38.0
<i>Chemical variables</i>		
Colour (Pt L ⁻¹)	30.0	2.5–160.0
Conductivity (µS cm ⁻¹)	268	80–535
pH	8.3	6.4–9.9
Total phosphorus (µg L ⁻¹)	46.4	11.0–500.0
<i>Landscape variables</i>		
Distance to small lake (km)	2.0	0.7–5.8
Distance to medium-sized lake (km)	3.8	1.3–17.9
Distance to large lake (km)	13.4	1.6–25.6
Altitude (m)	636.4	567.8–689.5
Latitude (°N, expressed as a decimal)	54.63	54.22–54.97
Longitude (°W, expressed as a decimal)	113.32	112.45–113.78
Inlet/outlet	NA	NA

only one lake: American bittern, *Botaurus lentiginosus* (Rackett), common merganser, *Mergus merganser* L., double-crested cormorant, *Phalacrocorax auritus* (Lesson), hooded merganser, *Lophodytes cucullatus* (L.), sandhill crane, *Grus canadensis* (L.), surf scoter, *Melanitta perspicillata* (L.), and western grebe, *Aechmophorus occidentalis* (Lawrence). Seven additional species were encompassed within three composite taxa (Table 1). The mean ($\pm$ SD) number of bird taxa per lake was 12.0 ± 5.2 . Table 2 summarizes environmental characteristics for the forty-one lakes.

Patterns of fish and bird assemblages

The first CA axis divided the fish assemblages into two types: (1) assemblages characterized by the small-bodied species, fathead minnow and/or brook stickleback; and (2) assemblages with a large-bodied piscivore (northern pike), sometimes accompanied by yellow perch and/or white sucker (Fig. 1a). In one exceptional lake (Gods), pike co-occurred with both fatheads and sticklebacks. Two other small-bodied species, spottail shiner and Iowa darter, occurred only in lakes with pike.

Lake scores on axis 1 (eigenvalue = 0.85, 51.8% of variance explained) were significantly correlated with

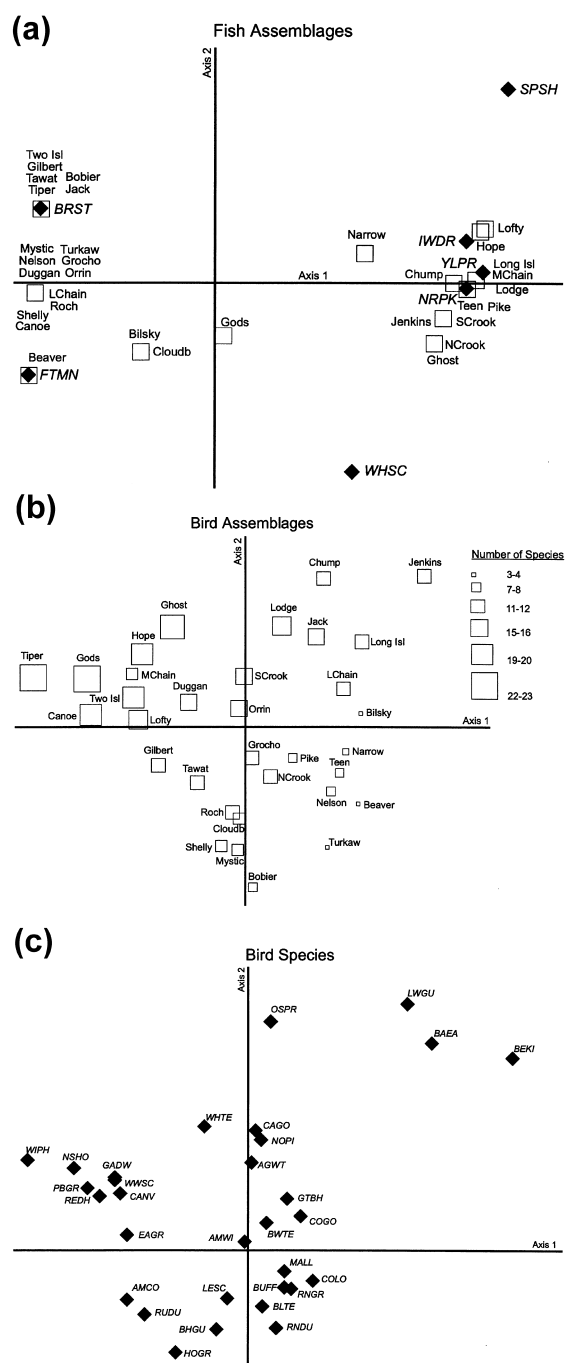


Fig. 1 Correspondence analysis ordinations of sites (□) and species (◆) for 33 lakes in north-central Alberta based on (a) the presence/absence of seven fish species and (b & c) for the same lakes based on the presence/absence of 31 bird taxa. For the lake ordination based on bird assemblages (b), the size of each square is proportional to the richness of the assemblage (from three to 23 species) presented in richness increments of two species. See Table 1 for lake and species codes.

Table 3 Correlations between the environmental characteristics of the thirty-three study lakes containing fish with the scores of the first two ordination axes from correspondence analyses of fish and bird assemblages

Environmental factor	Fish		Bird	
	Axis 1	Axis 2	Axis 1	Axis 2
Area	0.527**	NS	NS	0.787**
Perimeter	0.595**	NS	NS	0.746**
Shoreline development	0.392*	NS	0.365*	NS
Maximum depth	0.734**	NS	0.381*	0.645**
Colour	-0.678**	NS	NS	-0.752**
Conductivity	0.417*	NS	NS	0.435*
pH	NS	NS	NS	0.519**
Total phosphorus	-0.399*	NS	NS	NS
'Distance-small'	NS	NS	NS	NS
'Distance-medium'	NS	NS	NS	NS
'Distance-large'	-0.487*	NS	NS	-0.349*
Altitude	NS	NS	NS	-0.410*

* $P < 0.05$. ** $P < 0.01$. NS: $P > 0.05$.

all morphometric variables (Table 3), reflecting the fact that large, deep lakes with complex shorelines supported the pike-dominated assemblage type. Chemical variables with significant correlations were colour, conductivity and TP; pike lakes were less coloured and had lower phosphorus values, but higher conductivity, than lakes supporting the small-fish assemblage type. The only landscape variable with a significant correlation was 'distance-large' lake; pike lakes were less isolated from large bodies of water than were fathead-stickleback lakes. No environmental variables were significantly correlated with axis 2 (eigenvalue = 0.21, 14.2% of variance explained)

which separated lakes containing spottail shiners from those with suckers among large-piscivore assemblages and lakes containing fathead minnows from those with brook stickleback among small-fish assemblages (Fig. 1a).

Canonical correspondence analysis results for fish assemblages were consistent with CA results. The three environmental variables included by forward selection were perimeter, maximum depth and 'distance-small lake'. The overall ordination and axis 1 were both significant ($P < 0.001$), but axis 2 was not ($P = 0.208$; Table 4). Similar to, but less distinct than the pattern display by CA, axis 1 separated small,

Table 4 Results of canonical correspondence analysis for fish and bird assemblages. The significance values for the sum of all eigenvalues (permutational probabilities estimated by Monte Carlo simulations) are $P < 0.001$ for both fish and bird ordinations

	Fish		Bird	
	Axis 1	Axis 2	Axis 1	Axis 2
<i>Summary statistics for first two axes</i>				
Eigenvalue	0.311***	0.052 (NS)	0.095***	0.079***
Percentage of variance explained	26.4	4.4	9.6	7.9
Species:environment correlation	0.754	0.547	0.803	0.838
<i>Correlations with first two axes</i>				
Area	–	–	-0.556**	0.604**
Perimeter	0.696**	-0.014	–	–
Maximum depth	0.685**	-0.109	0.056	0.750**
Conductivity	–	–	-0.404*	0.026
'Distance-small'	-0.003	-0.500**	–	–

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$. NS: $P > 0.05$.

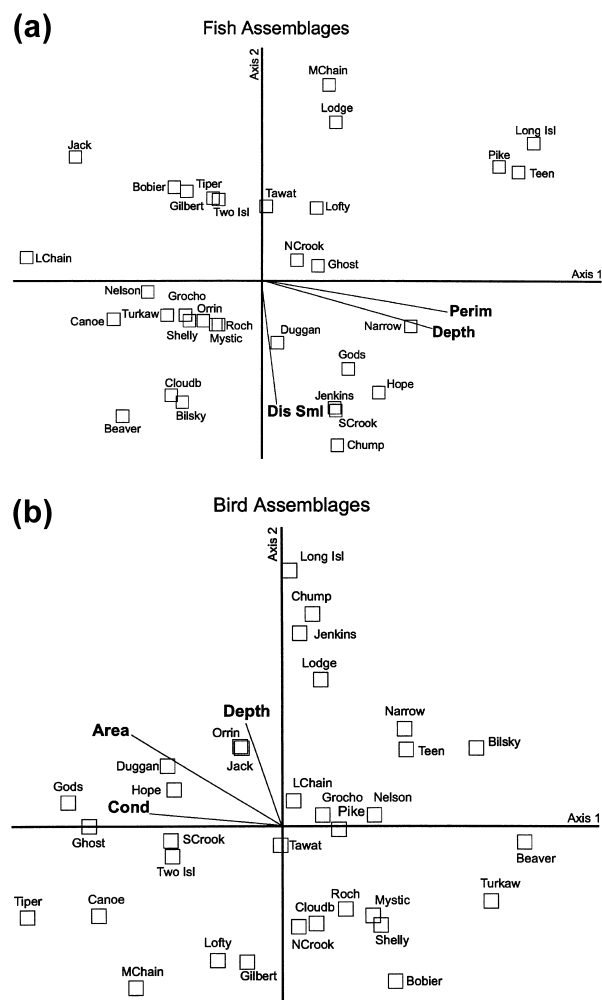


Fig. 2 Canonical correspondence analysis ordination biplots of environmental variables, and (a) fish assemblages and (b) bird assemblages from the 33 study lakes in north-central Alberta which contained fish. Environmental variables were selected via forward selection procedures (see text): (Area) lake area; (Perim) lake perimeter; (Depth) maximum depth; (Cond) conductivity; and (Dis Sml) distance to nearest small lake. See Table 1 for lake codes.

shallow lakes with small fish (fathead-stickleback assemblages) from larger, deeper lakes with large-piscivore (pike) assemblages (Fig. 2a; Table 4). Axis 2 weakly distinguished among subcategories of the two main fish assemblage types (e.g. stickleback lakes versus fathead lakes and lakes with white sucker versus those with yellow perch). Lakes with the lowest scores on axis 2 (containing fatheads or suckers) were generally more isolated (Table 4).

The patterns uncovered by CA for bird assemblages in lakes containing fish were more complex than the patterns displayed by the fish assemblages.

Scores on both axes 1 (eigenvalue = 0.20, 17% of variance explained) and 2 (eigenvalue = 0.13, 11.2% of variance explained) were significantly ($P < 0.01$) correlated with the total number of bird species present ($r = -0.721$ and 0.544 , respectively), with the resulting ordination of lakes being roughly triangular in shape (Fig. 1b). Assemblage richness reflected an additive pattern; species-poor lakes were inhabited by a core cohort of widespread birds, with richer lakes adding species to this core.

The cluster of de-pauperate (three to eight species) lakes (lower-right in Fig. 1b) was characterized by the occurrence of ubiquitous species seen on at least 75% of the lakes: common loon, red-necked grebe, mallard, ring-necked duck, bufflehead and black tern (Fig. 1c). Lakes with somewhat richer assemblages (eight to thirteen species), in the lower centre of the ordination, had additional duck species (i.e. American widgeon, blue-winged teal, lesser scaup and common goldeneye) and great blue heron. A second group of assemblages (eleven to sixteen species), with high scores on both axes 1 and 2 (Fig. 1b), added a group of aerially foraging piscivores: large *Larus* gulls, bald eagle, osprey and belted kingfisher. A third cluster, with low scores on axis 1 but high scores on axis 2 (Fig. 1b), represented the most speciose lakes (15 to 23 species). These were the only sites to include species more typical of the prairie and parkland ecoregions south of the boreal forest: eared grebe, pied-billed grebe, gadwall, northern shoveler, redhead, canvas-back, white-winged scoter and Wilson's phalarope (Fig. 1c).

Lake scores on axis 1 (Fig. 1b) were significantly correlated with only two morphometric variables, i.e. maximum depth and shoreline development (Table 3); TP was nearly significant, negatively correlated at $0.05 < P < 0.10$. Lake scores on axis 2 displayed stronger relationships with a wide variety of environmental factors, including morphometric, chemical and landscape variables (Table 3). Significant correlations between CA scores and morphometric variables coincided with species richness patterns: large lakes supported more species than small lakes, and large, relatively shallow lakes supported more species than large deep lakes. Correlations with landscape variables indicated that speciose lakes were at lower altitudes, potentially associated with more wetland habitat, and were nearer large lakes, which may have provided addi-

tional resources for some species. Finally, lakes supporting the aerially foraging piscivores were considerably less coloured than those lacking this guild.

The three environmental variables included by forward selection in the CCA of bird assemblages were area, maximum depth and conductivity. The overall analysis, and both axes 1 and 2, were significant ($P < 0.001$; Table 4) and the resulting ordination (Fig. 2b) was similar to the CA results. Axis 1 reflected the additive pattern of species richness. Lakes with high-to-moderate scores contained the core collection of widespread species. These lakes were generally smaller and had low conductivity. Larger lakes with richer assemblages in the centre of the ordination had additional duck species and great blue heron. Lakes with low scores on axis 1, representing the most speciose lakes, were large, relatively shallow lakes with high conductivity. A group of large and deep lakes, with high scores on axis 2 and moderate scores on axis 1, supported the distinctive group of aerially foraging piscivores.

Community concordance between fish and birds

Both the Mantel test and PROTEST showed significant concordance between the CA ordinations of the fish and bird assemblages (Mantel: $P = 0.014$; PROTEST: $P = 0.016$), indicating that arrangements of lakes in the two ordinations (fish and bird assemblages) were more similar than expected as a result of chance. Both the Mantel test and PROTEST also showed significant concordance between an environmental ordination of the lakes (PCA) and the fish (Mantel: $P = 0.0001$; PROTEST: $P = 0.0009$) and bird species ordinations (Mantel: $P = 0.006$; PROTEST: $P = 0.0001$).

The null hypothesis that no differences existed among bird assemblages found on lakes containing different fish-assemblage types (i.e. large piscivores, small fish and fishless) was rejected (MRPP; $P = 0.016$; Fig. 3). Pairwise comparisons by MRPP showed that bird assemblages on fishless lakes and lakes with small-bodied fish did not differ ($P = 0.522$), but that significant differences in bird assemblages occurred between lakes with large piscivores and those which were either fishless ($P = 0.019$) or contained the small-fish assemblage ($P = 0.010$).

Out of the thirty-one avian taxa subjected to indicator species analysis, observed maximum indi-

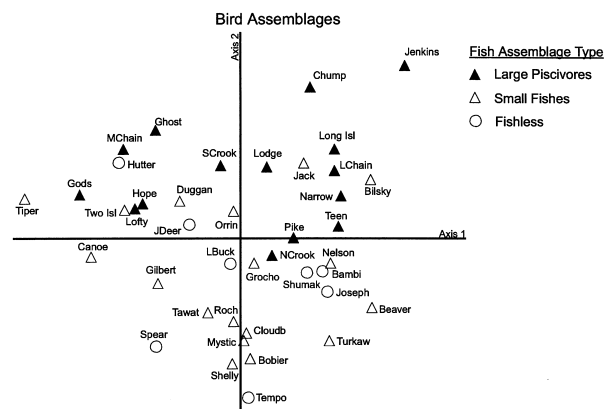


Fig. 3 Correspondence analysis ordination of bird assemblages from all 41 study lakes in north-central Alberta. Lakes were classified into three groups based on the type of fish assemblage the water bodies contained (see text). See Table 1 for lake codes.

cator values for common goldeneye, great blue heron, 'large white gull', osprey and ring-necked duck equalled or exceeded randomly generated indicator values at $P < 0.05$, and observed maximum values for belted kingfisher and white-winged scoter differed from random values at $0.05 < P < 0.10$. Ring-necked duck was an indicator of fishless lakes (indicator value = 40.2); all other taxa were indicators of lakes with the distinctive large-fish assemblage (indicator values = 20.0–53.9).

In assessing the relative contributions of environmental and biotic factors to assemblage-level patterns, forward selection chose two morphometric, four landscape and one chemical variable for inclusion in the partial CCAs of the fish assemblages; bird species selected included two of the widespread 'core' species, one diving duck, two relatively rare waterfowl, and two aerial piscivores. Overall, the analysis explained 49% of the variation in the composition of fish assemblages among lakes; of this percentage, relatively equal proportions could be attributed to environmental factors, biotic factors (i.e. bird-assemblage composition), and to the overlapping, interactive effects of the environment and birds (Fig. 4).

For analysis of bird assemblages, forward selection chose three morphometric, two chemical and two landscape variables as environmental factors (Fig. 4); all seven fish species were included as biotic variables. The overall analysis explained 48% of the variation in the composition of bird assemblages among lakes. Of this explained variation, three-fifths

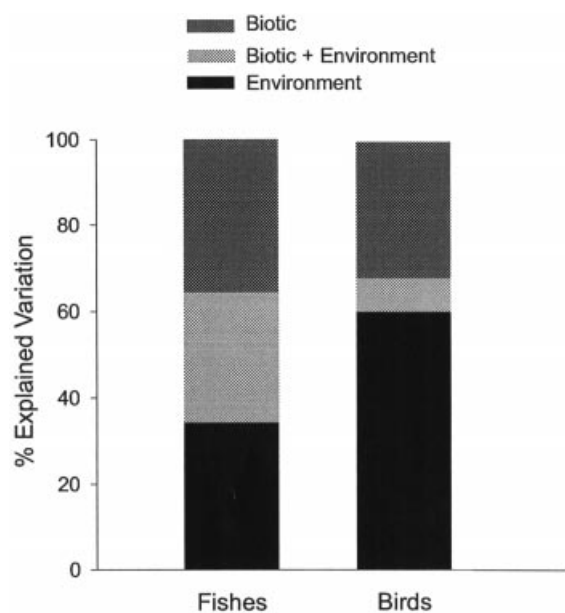


Fig. 4 The percentage of explained variation in the composition of fish and bird assemblages from the 33 study lakes containing fish which could be attributed to environmental variables, biotic variables, and to both environmental and biotic variables, derived from a series of partial canonical correspondence analyses (see text for details). The explained variation is 49% and 48% of the total variation for fish and bird assemblages, respectively.

could be attributed to environmental factors and one-third to fish-assemblage composition (biotic factors), with the remaining 8% caused by the overlapping, interactive effects of the environment and fish assemblage (Fig. 4).

Discussion

As we had predicted, fish and bird assemblages in the lakes of north-central Alberta were clearly concordant with evidence for concordance being consistent across analyses (Mantel test and PROTEST). Furthermore, a classification of lakes based on fish-assemblage type could partially discriminate among bird assemblages, i.e. bird assemblages occurring on large-piscivore lakes were significantly distinguishable from those occurring on either small-fish or fishless lakes (Fig. 3). However, we suggest that community concordance was largely an indirect outcome of parallel responses of each assemblage to lake environments, rather than a direct consequence of biotic interactions between birds and fish. Both assemblages, not only fish

assemblages as we had initially predicted, showed significant concordance with lake environmental features, with lake size (measured as area or perimeter) and maximum depth being especially important to each. Furthermore, analyses involving partial CCAs showed that biotic factors (i.e. the composition of the 'other' assemblage) contributed only about one-third of the explained variation for both fish and bird assemblages.

Concordance was partly an outgrowth of a strong and simple dichotomy among fish assemblages which was driven by a few environmental variables (Robinson & Tonn, 1989; Tonn *et al.*, 1995). For fish assemblages, depth was the primary factor determining species composition and lake size was, in some sense, a co-variate. Small shallow lakes supported small-bodied fish assemblages because minnows and sticklebacks are more tolerant of low winter oxygen levels than are piscivores, but intolerant of high levels of predation (Harvey, 1981; Tonn & Magnuson, 1982). However, large shallow lakes also tended to have the small-fish assemblage; it was the greater depth of many larger lakes which contributed to their distinctive fish assemblage of northern pike and other predation-tolerant species. Unlike other lake districts (e.g. northern Wisconsin, U.S.A.; Tonn & Magnuson, 1982), small deep lakes are virtually non-existent in central Alberta (Mitchell & Prepas, 1990).

For birds, depth and size also play important roles in shaping assemblages, but size appears to be the predominant factor. Differences in the composition of bird assemblages strongly paralleled differences in species richness and reflected species-area relationships reminiscent of those seen among aquatic bird communities in other geographical settings (e.g. Sillen & Solbreck, 1977; Nilsson & Nilsson, 1978; Gibbs *et al.*, 1991; Kauppinen, 1993; Elmberg *et al.*, 1994; Hoyer & Canfield, 1994). Small lakes supported only a core of widespread, generalist species simply because of their size, not because the water bodies were invariably shallow. In contrast to the fish, bird assemblages occurring on large shallow lakes differed from those on small shallow lakes; additional species were added to the generalist core as lake size increased, independent of depth.

Large shallow lakes, typified by the Canoe, Gods and Tiperary lakes, were the most speciose, richer even than large deep lakes, especially in duck species. Because lake depth was negatively correlated with TP

($r = -0.647$, $P < 0.01$), large shallow lakes offered sufficient nutrients to support abundant primary production by phytoplankters and macrophytes (Prepas *et al.*, 1988), with the latter creating excellent foraging conditions for many aquatic birds. Habitat complexity was further enhanced by beds of emergent plants, such as *Scirpus*, which grew along shores and formed vegetation 'islands' which diversified the open lake beds.

Large deep lakes, typified by the Jenkins, Chump and Lodge lakes, had somewhat fewer bird species, but included several unique piscivorous species in their assemblages. Water colour was negatively correlated with both lake area ($r = -0.737$, $P < 0.01$) and maximum depth ($r = -0.825$, $P < 0.01$), suggesting that greater transparency may have made large deep lakes more profitable feeding sites for birds that forage by surface plunging (Eriksson, 1985). The lower species richness of deep versus shallow large lakes may also have been tied to lower TP, hence lower productivity, in the deeper lakes (Nilsson & Nilsson, 1978; Hoyer & Canfield, 1994). Deep lakes did support inshore beds of emergent and submerged macrophytes, but also presented large expanses of open-water pelagic habitat which was less suitable for foraging by most aquatic birds. The central portions of these lakes were used by only a few, deep-diving species, such as common loon, red-necked grebe and common goldeneye, perhaps because of a paucity of true pelagic planktivores among the fish. Thus, depth served as an index of productivity, visibility, habitat complexity and availability of food resources, all of which have been related to species richness and composition of aquatic bird assemblages (Eriksson, 1985; Elmberg *et al.*, 1993). The third environmental factor included in the bird CCA was conductivity. Increased conductivity paralleled increases in lake area and maximum depth, reinforcing distinctions between small versus large, and shallow versus deep lakes.

'Distance-small lake' was the third variable incorporated into the CCA via forward selection for fish assemblages and four of the seven environmental variables used in the partialling analysis were also landscape related. The prevalence of these variables suggests that fish assemblage composition was sensitive to the terrestrial setting of a lake and to the probability of re-colonization following local extinction via winterkill (or drought). For bird assemblages,

only 'distance-small lake' and altitude were included in the partialling-out procedure, and then only as the fifth and sixth variables selected. A detectable but smaller effect of a lake's position in the landscape on its bird assemblage is not surprising given the great disparity in the ability to move among lakes which exists between these two groups of vertebrates (see also Brown & Dinsmore, 1986; Gibbs *et al.*, 1991; Craig & Beal, 1992). Nevertheless, the vegetation and topography immediately surrounding a lake could have determined its use by individual bird species during the breeding season by affecting the availability of appropriate nesting sites. We did not evaluate these factors in our study.

In contrast to our prediction that biotic interactions between birds and fish would best explain community-level concordance, we encountered minimal evidence for direct trophic links between our two taxa. One possible exception was the positive association between large fish species and the avian guild of aerially foraging piscivores. Large gulls, osprey, bald eagle and belted kingfisher occurred exclusively on lakes where large fish species were available as prey. These fish-eating taxa, as well as great blue heron, served as effective indicators of this fish-assemblage type. However, as noted above, greater water clarity in large deep lakes may have contributed to this relationship. In contrast, piscivores which hunted by pursuit diving, such as common loon and red-necked grebe, occurred non-selectively among lakes with large or small fish prey, and even on fishless lakes.

We had expected that bird species which feed primarily on invertebrates would occur less frequently on lakes containing large-bodied fish species than on lakes with no fish or only small fish present, since larger species, like perch and suckers, can compete strongly with birds for benthic invertebrate prey (Giles, 1990; McNicol & Wayland, 1992; Wagner, 1997). Neither grebes nor ducks avoided these lakes. In fact, along with several aerially foraging piscivores, two species of 'sea ducks', i.e. common goldeneye and white-winged scoter, were distinctly associated with the large-fish assemblage. Interestingly, common goldeneye has been repeatedly identified as a species susceptible to competition with *Perca* species on less productive lakes in northern Europe (Eriksson, 1979) and eastern North America (Eadie & Keast, 1982). Furthermore, minnows and sticklebacks do not occur at high enough densities in our study lakes to depress

invertebrate populations and exclude breeding waterfowl from lakes with small-fish assemblages (W. Tonn, unpublished data), unlike conditions reported on prairie wetlands and potholes of the upper Midwest (Hanson & Riggs, 1995; Cox *et al.*, 1998). Indeed, only one bird species, the diving, ring-necked duck, was a reliable indicator of the total absence of fish.

Analyses partialling out sources of variation in fish and bird assemblages further distinguished the role of environmental versus biotic factors. Firstly, the total variation explained by the variables included was similar between fish and bird assemblages (49% versus 48%), and relatively high compared with other community-level studies employing this approach (e.g. Borcard *et al.*, 1992; Pinel-Alloul *et al.*, 1995; Tonn *et al.*, 1995). Such 'convergence' was unexpected given the relative simplicity of the fish assemblages compared to the bird assemblages. In addition, environmental factors accounted for 60% of the explained variation observed for bird assemblages, whereas explained variation in the composition of fish assemblages was nearly equally distributed among environmental factors, bird-assemblage composition and their interaction. This result suggests a much clearer, stronger link between birds and environment than predicted.

The weak and inconsistent ability of direct interactions between fish and birds to account for the observed community concordance may be partly a result of the high littoral productivity of our study lakes. In most of the water bodies, macrophyte beds are both dense and widespread, and macroinvertebrates are abundant (C. Paszkowski, personal observation). Except for specialized species which only consume large fish, such as osprey and bald eagle, resident piscivorous birds can supplement a diet of fish with invertebrates. Even common loons nested and fed on four of the fishless lakes (Gingras & Paszkowski, 1999). Similarly, lakes with invertebrate-feeding fish (e.g. yellow perch or white sucker) still offer attractive sites for nesting and brood-rearing by ducks and grebes. The importance of littoral production to birds was illustrated by the fact that large shallow lakes had richer bird assemblages than large, but relatively deep lakes which contained a greater amount of pelagic habitat relative to littoral zone.

In fact, if fish had negative effects on birds on the study lakes, one might have expected the most unique

bird community to occur on the fishless lakes. Instead, we found negligible differences between bird assemblages on fishless and small-fish lakes. Coincidentally, these two lake types were indistinguishable in morphometry and water chemistry (C. Paszkowski, unpublished data). The main discernible effect of fish on birds was actually positive, providing food resources for piscivores, especially on lakes with pike-dominated assemblages.

In north-central Alberta, the morphometric features of lakes are the major determinants of community structure for birds and fish. In contrast, studies in northern Europe and eastern North America have shown lake water chemistry, especially nutrient concentrations and pH, to be a stronger predictor of patterns of both fish and bird assemblages (e.g. Tonn *et al.*, 1990; Blancher *et al.*, 1992; Kauppinen & Väisänen, 1993; Suter, 1994). However, our study lakes were all mesotrophic to eutrophic, eliminating the possibility of finding distinctive assemblages in oligotrophic or dystrophic habitats, as exist elsewhere. Furthermore, all lakes were circumneutral to alkaline, so no fish species were excluded owing to low pH conditions. Instead, winter hypoxia acts as the major filter for fish communities; species are selectively eliminated and fishless lakes exist when isolated lakes are too shallow to provide sufficient oxygen or unfrozen water to support fish during the winter.

Our study demonstrated that a relatively small number of environmental characteristics broadly dictate habitat quality within the lakes of north-central Alberta such that these few factors are capable of shaping taxonomically divergent assemblages, resulting in patterns of community concordance. Since explicit, quantitative studies of community concordance are still in their infancy, the generality of our results is unknown. Although a previous study also found significant community concordance (Jackson & Harvey, 1993), no clear, over-riding environmental signal was observed, and complex or indirect interactions between the two communities (fish and invertebrates) were evoked to explain concordance.

Spatially based studies of community concordance may learn from temporally based studies of coherence: simple but strong signals offer the greatest explanatory power (Kratz *et al.*, 1998). Although concordance between assemblages can invite proposals of co-evolution or cause-and-effect relationships (e.g. fish-eating raptors are present on a suite of lakes

because yellow perch are present as a food source), concordance is only a starting point for the identification of mechanisms behind patterns. The possible roles of coarse-filter abiotic factors must be evaluated, as well as the influence of fine-filter biotic interactions (Tonn *et al.*, 1990). General patterns do exist across lake ecosystems and the analysis of community concordance is a powerful approach for detecting them, but ecologists must then adopt appropriate scales and perspectives to understand the processes behind these patterns.

Acknowledgments

We gratefully acknowledge field and technical assistance from B. Gingras, R. Vandenbos, M. Janowicz, S. Boss, O. Stephen, C. Martynuik and K. Westcott. Field work was conducted from the University of Alberta Meanook Biological Research Station, and was supported by NSERC research grants to C.A.P. and W.M.T., and grants to C.A.P. from the University of Alberta and the North American Loon Fund. We are grateful to D. Jackson and P. Peres-Neto for providing the PROTEST program, to T. Kratz, P. Soranno and S. Baines (North-Temperate Lakes LTER) for inviting us to participate in the Organization of Lake Districts workshop, and to T. Kratz, J. Magnuson and T. Frost for hosting us during manuscript preparation while on sabbatical leave at University of Wisconsin Trout Lake Station. Thanks also to two anonymous reviewers and D. Jackson for commenting on earlier versions of this manuscript.

References

- Baines S.B., Webster K.E., Kratz T.K., Carpenter S.R. & Magnuson J.J. (2000) Synchronous behaviour of temperature, calcium, and chlorophyll in lakes of northern Wisconsin. *Ecology*, in press.
- Blancher P.J., McNicol D.K., Ross R.K., Wedeles C.H.R. & Morrison P. (1992) Towards a model of acidification effects on waterfowl in eastern Canada. *Environmental Pollution*, **78**, 57–63.
- Borcard D., Legendre P. & Drapeau P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.
- ter Braak C.J.F. (1987) Ordination. *Data Analysis in Community and Landscape Ecology* (eds R.H.G. Jongman, C.J.F. ter Braak and O.F.R. van Tongeren), pp. 91–169. Pudoc, Wageningen.
- ter Braak C.J.F. (1991) *Canoco*, Version 3.12. Agricultural Mathematics Group, Wageningen.
- Brown M. & Dinsmore J.J. (1986) Implications of marsh size and isolation for marsh bird management. *Journal of Wildlife Management*, **50**, 392–397.
- Carpenter S.R., Kitchell J.F. & Hodgson J.R. (1985) Cascading trophic interactions and lake productivity. *Bioscience*, **35**, 634–639.
- Cox R.R., Jr, Hanson M.A., Roy C.C., Euliss N.H., Jr, Johnson D.H. & Butler M.G. (1998) Mallard duckling growth and survival in relation to aquatic invertebrates. *Journal of Wildlife Management*, **62**, 124–133.
- Craig R.J. & Beal K.G. (1992) The influence of habitat variables on marsh bird communities of the Connecticut River estuary. *Wilson Bulletin*, **104**, 295–311.
- Dufrène M. & Legendre P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.
- Eadie J.McA. & Keast A. (1982) Do goldeneye and perch compete for food? *Oecologia*, **55**, 225–230.
- Elmberg J., Nummi P., Pöysä H. & Sjöberg K. (1993) Factors affecting species number and density of dabbling duck guilds in North Europe. *Ecography*, **16**, 251–260.
- Elmberg J., Nummi P., Pöysä H. & Sjöberg K. (1994) Relationships between species number, lake size and resource diversity in assemblages of breeding waterfowl. *Journal of Biogeography*, **21**, 75–84.
- Eriksson M.O.G. (1979) Competition between freshwater fish and goldeneyes (*Bucephala clangula*) for common prey. *Oecologia*, **41**, 99–107.
- Eriksson M.O.G. (1985) Prey detectability for fish-eating birds in relation to fish density and water transparency. *Ornis Scandinavica*, **16**, 1–7.
- Gauch H.G. (1982) *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.
- Gibbs J.P., Longcore J.R., McAuley D.G. & Ringelman J.K. (1991) *Use of wetland habitats by selected nongame water birds in Maine*. Fish and Wildlife Research 9, U.S. Fish and Wildlife Service, Washington DC.
- Giles N. (1990) Effects of increasing larval chironomid densities on the underwater feeding success of downy tufted ducklings *Aythya fuligula*. *Waterfowl*, **40**, 74–79.
- Gingras B.A. & Paszkowski C.A. (1999) Breeding patterns of common loons on lakes with three different fish assemblages in north-central Alberta. *Canadian Journal of Zoology*, **77**, 600–609.
- Hanson M.A. & Riggs M.R. (1995) Potential effects of fish predation on wetland invertebrates: a comparison of wetlands with and without fathead minnows. *Wetlands*, **15**, 167–175.
- Hargeby A., Andersson G., Blindow I. & Johansson S. (1994) Trophic web structure in a shallow eutrophic

- lake during a dominance shift from phytoplankton to submerged macrophytes. *Aquatic Birds in the Trophic Webs of Lakes* (Ed. J.J. Kerekes), pp. 83–90. Kluwer Academic Publishers, Dordrecht.
- Harvey H.H. (1981) Fish communities of the lakes of the Bruce Peninsula. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **21**, 1222–1230.
- Horne A.J. & Goldman C.R. (1994) *Limnology*. McGraw-Hill, Inc., New York, NY.
- Hoyer M.V. & Canfield D.E., Jr (1994) Bird abundance and species richness of Florida lakes: influence of trophic status, lake morphology, and aquatic macrophytes. *Aquatic Birds in the Trophic Webs of Lakes* (ed. J.J. Kerekes), pp. 107–119. Kluwer Academic Publishers, Dordrecht.
- Jackson D.A. (1995) PROTEST: a PROcrustean randomization TEST of community environment concordance. *Ecoscience*, **2**, 297–303.
- Jackson D.A. & Harvey H.H. (1993) Fish and benthic invertebrates: community concordance and community-environment relationships. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2641–2651.
- Johnson R.K. & Wiederholm T. (1989) Classification and ordination of profundal macroinvertebrate communities in nutrient poor, oligo-mesohumic lakes in relation to environmental data. *Freshwater Biology*, **21**, 375–386.
- Kauppinen J. (1993) Densities and habitat distribution of breeding waterfowl in boreal lakes in Finland. *Finnish Game Research*, **48**, 24–45.
- Kauppinen J. & Väisänen R.A. (1993) Ordination and classification of waterfowl communities in south boreal lakes. *Finnish Game Research*, **48**, 3–23.
- Kerekes J.J. (1994) Preface. *Aquatic Birds in the Trophic Webs of Lakes* (Ed. J.J. Kerekes), p. viii. Kluwer Academic Publishers, Dordrecht.
- Kratz T.K., Soranno P.A., Baines S.B., Benson B.J., Magnuson J.J., Frost T.M. & Lathrop R.C. (1998) Interannual synchronous dynamics in north temperate lakes in Wisconsin, USA. *Management of Lakes and Reservoirs During Global Climate Change* (Eds G.D. George, G.J. Jones, P. Puncochar, C.S. Reynolds and D.W. Sutcliffe), pp. 273–287. Kluwer Academic Publishers, Dordrecht.
- Magnan P., Rodríguez M.A., Legendre P. & Lacasse S. (1994) Dietary variation in a freshwater fish species: relative contributions of biotic interactions, abiotic factors and spatial structure. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2856–2865.
- Magnuson J.J., Benson B.J. & Kratz T.K. (1990) Temporal coherence in the limnology of a suite of lakes in Wisconsin, U.S.A. *Freshwater Biology*, **23**, 145–159.
- Mallory M.L., Weatherhead P.J., McNicol D.K. & Wayland M.E. (1993) Nest site selection by common goldeneyes in response to habitat features influenced by acid precipitation. *Ornis Scandinavica*, **24**, 59–64.
- Mantel N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research*, **27**, 209–220.
- McCune B. & Mefford M.J. (1997) *PC-ORD. Multivariate Analysis of Ecological Data*, Version 2.0. MjM Software Design, Gleneden Beach, OR.
- McNicol D.K. & Wayland M.E. (1992) Distribution of waterfowl broods in Sudbury area lakes in relation to fish, macroinvertebrates and water chemistry. *Canadian Journal of Fisheries and Aquatic Sciences*, **49** (Suppl. 1), 81–89.
- McQueen J., Post J.R. & Mills E.L. (1986) Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1571–1581.
- Mills E.L. & Schiavone A., Jr (1982) Evaluation of fish communities through assessment of zooplankton populations and measures of lake productivity. *North American Journal of Fisheries Management*, **2**, 14–27.
- Mitchell P.A. & Prepas E.E. (1990) *Atlas of Alberta Lakes*. University of Alberta Press, Edmonton.
- Nelson J.S. & Paetz M.J. (1992) *The Fishes of Alberta*. University of Alberta Press and University of Calgary Press, Edmonton.
- Nilsson S.G. & Nilsson I.N. (1978). Breeding bird community densities and species richness in lakes. *Oikos*, **31**, 214–221.
- Paine R.T. (1980) Food webs: linkage, interaction strength and community infrastructure. *Ecology*, **49**, 667–685.
- Pinel-Aloul B., Niyonsenga T. & Legendre P. (1995) Spatial and environmental components of freshwater zooplankton structure. *Ecoscience*, **2**, 1–19.
- Prepas E.E., Dunnigan M.E. & Trimbee A.M. (1988) Comparisons of *in situ* estimates of chlorophyll a obtained with Whatman GF/F and GF/C glass-fiber filters in mesotrophic and hypereutrophic lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 910–914.
- Robinson C.L.K. & Tonn W.M. (1989) Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 81–89.
- Rodríguez M.A., Magnan P. & Lacasse S. (1993) Fish species composition and lake abiotic variables in relation to the abundance and size structure of cladoceran zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 638–647.
- Rowe J.F. (1972) *Forest regions of Canada*. Canadian Forestry Service, 1300, Department of Environment, Ottawa.

- Semenchuk G.P. (1992) *The Atlas of Breeding Birds of Alberta*. Federation of Alberta Naturalists, Edmonton.
- Sillen B. & Solbreck C. (1977) Effects of area and habitat diversity on bird species richness in lakes. *Ornis Scandinavica*, **8**, 185–192.
- Suter W. (1994) Overwintering waterfowl on Swiss lakes. *How Are Abundance and Species Richness Influenced by Trophic Status and Lake Morphology? Aquatic Birds in the Trophic Webs of Lakes* (Ed. J.J. Kerekes), pp. 1–14. Kluwer Academic Publishers, Dordrecht.
- Toivonen H. & Huttunen P. (1995) Aquatic macrophytes and ecological gradients in 57 small lakes in southern Finland. *Aquatic Botany*, **51**, 197–221.
- Tonn W.M. & Magnuson J.J. (1982) Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology*, **63**, 1149–1166.
- Tonn W.M., Magnuson J.J., Rask M. & Toivonen J. (1990) Intercontinental comparisons of small-lake fish assemblages: the balance between local and regional processes. *American Naturalist*, **136**, 345–375.
- Tonn W.M., Vandenbos R.E. & Paszkowski C.A. (1995) Habitat on a broad scale: relative importance of immigration and extinction for small lake fish assemblages. *Bulletin Français de la Pêche et de la Pisciculture*, **337/338/339**, 47–61.
- Wagner B.M.A. (1997) Influence of fish on the breeding of the red-necked grebe *Podiceps grisegena* (Boddaert, 1783). *Hydrobiologia*, **344**, 57–63.
- Webster K.E., Kratz T.K., Bowser C.J., Magnuson J.J. & Rose W.J. (1996) The influence of landscape position on lake chemical response to drought in northern Wisconsin, USA. *Limnology and Oceanography*, **41**, 977–984.

(Manuscript accepted June 1999)