

Julian D. Olden · Donald A. Jackson
Pedro R. Peres-Neto

Spatial isolation and fish communities in drainage lakes

Received: 25 October 1999 / Accepted: 27 November 2000 / Published online: 22 February 2001
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Abstract Fifty-two drainage lakes, located in south-central Ontario, Canada, were examined to study the association of isolation- and environment-related factors with fish community composition. Eight quantitative measures of lake isolation were examined, each of which incorporated potential ecological “challenges” that a fish encounters when moving between lakes. A Procrustean approach was employed to assess the degree of concordance between fish assemblage structure, measures of lake isolation and environmental conditions (i.e., lake morphology and water chemistry). Our results revealed a high concordance between patterns in fish community composition and lake isolation and lake morphology at the watershed scale, suggesting that insular and habitat-related factors influence the structure of fish communities. At the scale of the individual lake, this relationship varied greatly, ranging from a strong match of community composition with both spatial and abiotic conditions to communities exhibiting weak association with these conditions. Furthermore, we showed that alternative measures of lake isolation provide additional insight into potential factors shaping patterns in fish community composition; information not provided using straight-line distances between lakes. Finally, the statistical methodology outlined in this paper provides a robust technique for assessing both the overall association between multivariate data matrices (i.e., landscape or regional scale), as well as facilitating the examination of smaller-scale relationships of individual observations (i.e., local scale).

Keywords Extinction · Colonization · Dispersal · Lake connectivity · Isolation

J.D. Olden (✉) · D.A. Jackson · P.R. Peres-Neto
Department of Zoology, University of Toronto, 25 Harbord Street,
Toronto, Ontario, M5S 3G5, Canada

Present address:

J.D. Olden, Department of Biology, Colorado State University,
Fort Collins, CO 80523-1878, USA
e-mail: olden@lamar.colostate.edu
Tel.: +1-970-4912414, Fax: +1-970-4910649

Introduction

Factors regulating the species composition of disjunct habitats (e.g., islands) have been a major focus of ecological and evolutionary studies since the work of Darwin and Wallace. Most studies have been directed at how abiotic environmental conditions or biotic interactions contribute to the maintenance of populations. MacArthur and Wilson (1967) focused attention on the role of colonization and extinction on islands, and these ideas were extended to other insular habitats (e.g., Brown 1971; Barbour and Brown 1974). Levins (1969) and Hanski (1982, 1991) showed that the movement of individuals between patches or insular habitats contributes to survival and distribution of a species. Individual species differ in their probability of colonizing patchy habitats due to differential abilities to disperse and the effects of varying distances between patches. As a result, sites exhibiting similar environmental characteristics may have dissimilar faunas because of differential chances of colonization and extinction for each species. Terrestrial ecologists have found these ideas useful for understanding systems containing highly fragmented habitats (Harrison et al. 1988; Paine 1988; Fahrig and Merriam 1994). Several studies have considered how readily individuals may move between patches and the longevity of populations in patches with various degrees of connectivity. It is believed that more isolated patches will have reduced rates of colonization, equal or more extreme extinction rates (reduced “rescue effect”; Ray and Gilpin 1991) and, as a consequence, a more depauperate community. Changes in the degree of isolation through alterations to patch connectivity may lead to changes in population viability and community composition. More recently, ecologists have applied these ideas of patch or metapopulation dynamics to issues of conservation [see Saunders et al. (1991) for a review].

Despite the substantial amount of empirical and theoretical work on patch dynamics and the role of habitat connectivity in terrestrial ecosystems, there has been limited application to aquatic ecosystems (see Jackson et

al. 2001. This lack of attention is surprising given that many aquatic ecosystems provide direct counterparts to patch habitats (e.g., stream sites and lakes) and corridors (i.e., streams, rivers). Furthermore, compared to terrestrial studies where researchers must often assume the dispersal pathway between habitat patches, aquatic organisms are confined to the interconnecting streams and rivers between water bodies. Therefore, lakes within a watershed provide a unique study system where inter-patch distances can be more readily defined and quantified. The patchy, insular nature of seepage and drainage lakes influences both the colonization and persistence of local fish populations, thereby influencing fish community composition (Tonn and Magnuson 1982; Tonn et al. 1990; Magnuson et al. 1998; Matthews and Robison 1998). Fish populations in lakes that are more isolated from other waterbodies will be more susceptible to local extinction and more limited in their recolonization rates. On the other hand, high rates of fish dispersal between lakes can result in great similarities in fish community composition (homogenization *sensu* Radomski and Goeman 1995) among connected lakes. Although seepage lakes are completely isolated from one another (except during periods of extreme flooding or due to stocking activities by humans), the degree of isolation among drainage lakes is determined primarily by the length of adjoining watercourses, and by the type and number of natural and artificial obstacles. Natural obstacles or barriers include temporary factors such as beaver dams, seasonal drying or warming of waterways, as well as permanent channel characteristics such as strong currents, riffles, cascades and waterfalls. In addition, rivers that contain a strong piscivore may have reduced movements of fishes among tributaries due to predation on potential dispersers (Townsend and Crowl 1991; Fraser et al. 1999), or may promote movement by inducing dispersal of individuals from side pools and channels (Fraser et al. 1999).

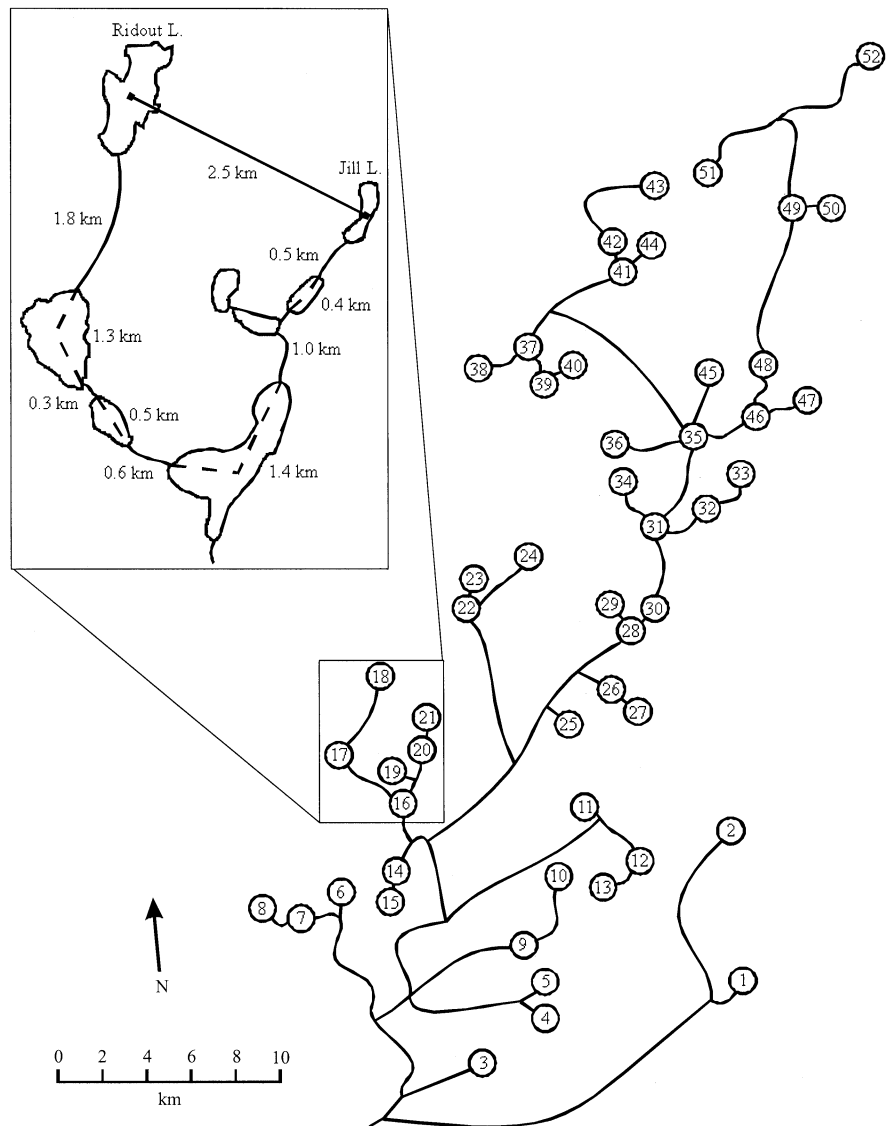
The effects of spatial isolation among habitat patches in streams, rivers and lakes may have considerable implications for understanding the main forces shaping fish population and community dynamics, and for the management and conservation of our aquatic resources. Relationships between habitat conditions and population characteristics (e.g., spatial distribution, abundance) could be confounded if lake isolation causes a reduction in the dispersal rates of fish species, thereby excluding them from potentially available habitat. In such cases, isolation-related factors could decouple associations between fish community composition and the surrounding abiotic environment (e.g., Angermeier and Schlosser 1989; Snodgrass et al. 1996; Snodgrass and Meffe 1998). Ultimately, this could affect our understanding of population and community ecology of fishes, influence our interpretation of factors controlling lake food webs (e.g., Hershey et al. 1999), and reduce or even eliminate the validity of biological assessment measures [e.g., "index of biotic integrity" (Karr 1981)]. Knowledge regarding the spatial connectedness of lakes is essential for under-

standing and predicting the potential dispersal and colonization of introduced species within any watershed. For example, introductions of strong littoral predators (e.g., smallmouth bass, northern pike) likely result in the local extinctions of many small-bodied species (Jackson and Harvey 1989; Robinson and Tonn 1989; Jackson et al. 1992; Chapleau et al. 1997; Findlay et al. 2000; MacRae and Jackson 2001). Therefore, the fish communities of many lakes may be affected by the introduction of a single predator into a single lake via dispersal and subsequent biotic interactions with native fishes. As a result, the management and stocking of lakes must be considered in a watershed context incorporating interconnections among lakes, rather than on a lake by lake basis as decisions made regarding one system may impact significantly on neighbouring lakes within a short time frame.

Although various field and modelling approaches have been used in studying habitat isolation in terrestrial ecosystems, there are few examples involving aquatic studies. Researchers have often developed relatively simple measures of lake isolation, including straight-line distance (e.g., Magnan et al. 1994), watershed area (e.g., Tonn and Magnuson 1982), lake elevation (e.g., Magnuson et al. 1998), presence or absence of intermittent or permanent inlets and outlets (e.g., Rahel 1986; Robinson and Tonn 1989), and watercourse distance to the nearest neighbouring lake (e.g., Tonn et al. 1990). In many cases it is implied that colonization of a lake only originates from the closest, adjacent lake. However, fish could move more widely over time within a watershed, for example using a series of lakes as "stepping stones" for colonization (Magnuson 1976). Clearly, there is a need for a more formal examination of the role of lake isolation in shaping fish communities. More quantitative measures of spatial isolation, incorporating different characteristics of the watershed that contribute to the insular nature of lakes, are required. Gaining this knowledge will aid our understanding of the role that isolation plays in determining species diversity and community composition. In the present paper, we have the following objectives:

1. Examine several published and newly proposed quantitative measures of spatial isolation for drainage lakes, each of which provide large-scale or global measures of the challenges fish encounter when dispersing among lakes.
2. Assess the relationship between patterns in fish community composition and factors related to the degree of lake isolation and environmental conditions, at both the lake and watershed scale.
3. Demonstrate the use of Procrustean methods for examining these relationships between the data sets, and highlight their potential use for assessing both the overall degree of concordance between data sets and facilitating the examination of smaller-scale relationships among individual observations.

Fig. 1 Schematic map of the study lakes located in the Black and Hollow River watersheds; *inset* illustrates inter-lake distances between Jill Lake and Ridout Lake for example calculations in Materials and methods



Materials and methods

Ecological data

This study focuses on 52 drainage lakes located within the Black and Hollow River watersheds of south-central Ontario, Canada (Fig. 1). The lakes are located within a heterogeneous landscape with lake elevation ranging from 320 m to 488 m above sea level. Most lakes contain one or more inlets and a single outlet, and are connected to one another by watercourses ranging in distance from 63 m to 138 km. Each lake was surveyed to determine fish community composition, as well as quantifying lake morphological and water chemistry characteristics. Intensive sampling using fine- and coarse-meshed trap nets, baited minnow traps, seine nets, clear plastic traps, and multi-meshed gill nets (see Jackson and Harvey 1989, 1997), was conducted to estimate the presence/absence of each fish species. Sampling was conducted continuously for 3–7 days and nights using all types of sampling gear in all available habitats to maximize the number of species captured (see Jackson and Harvey 1989; Jackson et al. 1992 for details). Increased effort was used in larger lakes and some lakes were sampled repeatedly at different time periods to determine whether additional species could be captured. No additional species were found during these re-sampling periods. Species not

captured after intensive sampling were assumed to be absent or so rare as to be of minimal importance for community comparisons. From the 31 fish species captured, those found in 5% or more of the study lakes were used for the analyses (Table 1). A series of abiotic variables were also measured for each lake (Table 2). Lake morphological variables included lake area, volume, maximum depth, shoreline perimeter, and island perimeter. The water chemistry dataset consisted of pH, alkalinity, conductivity, colour, and concentrations of calcium, sodium, chloride, dissolved organic carbon, dissolved inorganic carbon, magnesium, potassium and sulphate [see Jackson (1988) for details].

Measures of lake isolation

This section describes the calculation of eight lake isolation measures. In all cases, distances were calculated from 1:50,000 topographic maps, and were recorded in kilometers. After each isolation measure is described, we provide an example of the calculation using Ridout Lake (lake no. 18) and Jill Lake (lake no. 21), illustrated in the inset of Fig. 1.

The latitudinal and longitudinal position of each lake was used to generate an inter-lake distance matrix based on SL-dis, i.e., Euclidean distance, between the center of each of the lakes. Given the limited latitudinal variation involved, no correction was made

Table 1 List of fish species, including species abbreviation (*Code*) and occurrence (%) in the 52 study lakes

Common name	Scientific name	Code	Occurrence
Blacknose dace	<i>Rhinichthys atratulus</i>	BND	10
Blacknose shiner	<i>Notropis heterolepis</i>	BNS	21
Bluntnose minnow	<i>Pimephales notatus</i>	BNM	31
Brook stickleback	<i>Culaea inconstans</i>	BS	12
Brook trout	<i>Salvelinus fontinalis</i>	BT	35
Brown bullhead	<i>Ameiurus nebulosus</i>	BB	67
Burbot	<i>Lota lota</i>	B	17
Cisco	<i>Coregonus artedii</i>	C	6
Creek chub	<i>Semotilus atromaculatus</i>	CC	75
Common shiner	<i>Luxilus cornutus</i>	CS	31
Fathead minnow	<i>Pimephales promelas</i>	FHM	17
Finescale dace	<i>Phoxinus neogaeus</i>	FSD	23
Golden shiner	<i>Notemigonus crysoleucas</i>	GS	44
Iowa darter	<i>Etheostoma exile</i>	ID	8
Lake chub	<i>Couesius plumbeus</i>	LC	6
Lake trout	<i>Salvelinus namaycush</i>	LT	15
Largemouth bass	<i>Micropterus salmoides</i>	LMB	21
Northern redbelly dace	<i>Phoxinus eos</i>	NRD	44
Pearl dace	<i>Margariscus margarita</i>	PD	25
Pumpkinseed	<i>Lepomis gibbosus</i>	PKS	88
Rock bass	<i>Ambloplites rupestris</i>	RB	6
Smallmouth bass	<i>Micropterus dolomieu</i>	SMB	31
White sucker	<i>Catostomus commersoni</i>	WS	79
Yellow perch	<i>Perca flavescens</i>	YP	85

Table 2 Distribution parameters [median, lower quartile (*LQ*), upper quartile (*UQ*), minimum (*Min.*) and maximum (*Max.*)] for lake isolation, lake morphology and water chemistry variables

	Median	LQ	UQ	Min.	Max.
Lake isolation					
Watercourse distance (km)	30.8	19.3	51.4	0.06	138.1
Elevation (m)	350	335	387	320	488
Lake morphology					
Area (ha)	35.7	16.8	62.8	5.5	2821.0
Maximum depth (m)	13.4	8.1	23.7	3.0	73.2
Shoreline perimeter (km)	3.8	2.5	6.0	1	104.7
Volume ($\times 10^4$ m ³)	23.3	6.8	52.0	1.9	6150.0
Water chemistry					
Alkalinity (Eq L ⁻¹)	27.5	15.5	48.5	0.00	122.0
Calcium (mg L ⁻¹)	2.58	2.35	2.87	2.05	3.68
Chloride (mg L ⁻¹)	0.30	0.20	0.40	0.05	7.50
Colour (platinum units)	13.50	9.00	22.88	1.00	230.0
Conductivity (mhos/cm)	29.00	24.88	31.00	9.00	49.50
Dissolved organic carbon (mg L ⁻¹)	3.95	3.30	5.20	1.20	18.0
Dissolved inorganic carbon (mg L ⁻¹)	0.80	0.40	1.10	0.20	2.00
Magnesium (mg L ⁻¹)	0.69	0.60	0.84	0.43	1.97
pH	6.00	5.74	6.40	4.79	6.90
Potassium (mg L ⁻¹)	0.40	0.34	0.45	0.21	5.62
Sodium (mg L ⁻¹)	0.69	0.54	0.85	0.41	4.60
Sulphate (mg L ⁻¹)	6.17	5.51	6.89	2.69	34.00

to account for convergence of longitudinal lines. Commonly, the straight-line distance (SL-dis) between sampling sites is used as a measure describing the spatial arrangement of habitats within the landscape (e.g., Magnan et al. 1994; Sjögren Gulve 1994; Little et al. 1997). For this reason, we chose to use this spatial measure. The SL-dis between Ridout Lake and Jill Lake is 2.5 km.

Watercourse distance (WC-dis) between each study lake was calculated as the shortest distance between two lakes following the connecting waterways. The WC-dis between Ridout Lake and Jill Lake is 7.8 km. In addition, the location of lakes along the watercourse can be considered as a series of stepping stones (sensu MacArthur and Wilson 1967), such that fish could colonize lakes in steps, thus aiding the movement of individuals between distant

lakes. Arguably, two lakes in a chain with a third lake between them may be less isolated than two lakes lacking such an intermediate lake (Magnuson 1976). For this reason, the WC-dis excluding the distance traveled through other intermediate lakes might more accurately represent the distance between a set of lakes (WC-body). The WC-body connecting Ridout Lake and Jill Lake is 4.2 km (equal to 7.8 km minus 3.6 km).

For fish moving between lakes, movement downstream may represent a more passive dispersal, whereas movement upstream requires energetic expenditures. To incorporate the fact that upstream lakes are potentially more difficult to colonize, we developed two measures that represent the distance between lakes that involves only upstream movement. Since the upstream distance

from lake A to B is not necessarily equal to the upstream distance from lake B to A, an asymmetric distance matrix was constructed. This matrix was subsequently decomposed into two components. The first matrix was the symmetrical component (US-sym), which was the average of the upstream distances between two lakes (i.e., the average of A to B and B to A). The upstream distance from Ridout Lake to Jill Lake is 1.9 km, and the upstream distance from Jill Lake to Ridout Lake is 4.5 km, resulting in an US-sym of 3.2 km (average of 4.5 km and 1.9 km). The second matrix was the skew component (US-skew), which was calculated as the difference between the average upstream distance between these lakes (US-sym) and the upstream distance between lake A and B. The US-skew between Jill Lake and Ridout Lake equals 1.3 km, which is calculated as 4.5 km (US-sym) minus 3.2 km (the upstream distance from Jill Lake to Ridout Lake). Similarly, the US-skew between Ridout Lake and Jill Lake is -1.3 km (equal to 1.9 km minus 3.2 km). The magnitude of US-skew is the same between the lakes (1.3 km), therefore, only the positive US-skew value was retained. The decomposition of the original asymmetric upstream distance matrix into two components was required to ensure that we accounted for all of the information regarding the upstream distance between the lakes. The symmetric portion (US-sym) represents the average upstream distance between lakes and the US-skew provides a measure of the distance between a pair of lakes in terms of their relative upstream components. Both US-sym and US-skew describe the potential difficulties a fish faces when traveling upstream, such as the general constriction of the watercourse closer to headwaters, greater probability of encountering obstacles (i.e., riffle areas or waterfalls), and traveling against the flow of water.

To explore patterns of lake connectivity within the watershed, we constructed a hydrographic tree (Magnan et al. 1994). At each bifurcation in the tree, a node number was assigned. A lake-by-node matrix was constructed by indicating each node (assigning a value of 1) that connects the lake to the origin or "root" of the tree, and 0 to all the remaining nodes. This procedure results in each lake being classified by a row vector of binary values (0 or 1). An inter-lake Euclidean distance matrix (hydrographic tree; HG-tree) was constructed based on the lake-by-node matrix. Hydrographic trees provide a quantitative measure of the number of different streams changes that a fish encounters when dispersing from one lake to another and therefore, represent increasing isolation between any two lakes [see Magnan et al. (1994) for more details]. Although this approach provides a relative measure of the order of differences between pairs of lakes, it loses all information related to the magnitude of the scale of distances between lakes.

The last two measures of spatial isolation incorporated WC-dis and difference in elevation between the study lakes. Two distance matrices were constructed where the first represented the WC-dis and the second was based on the difference in elevation between lakes. Both of these 52-by-52 distance matrices (i.e., 52 lakes) were used to produce two isolation measures in the following manner. Both distance matrices were unfolded from a triangular form into a continuous vector [see Legendre and Legendre (1998), p 560]. A matrix of size 1,378 by 2 (i.e., the $(52 \times 51)/2 + 52$ rows and two columns) was created by combining the two vectors. A principal component analysis (PCA) (the equivalent of a model II regression) was employed using these two variables. The first axis summarized the general allometric relationship between inter-lake WC-dis and elevation difference. This set of 1,378 observations from the first axis was then converted back into a triangular matrix of inter-lake distances. This matrix (D-elev1) provides a generalized measure of the overall distance, both by water and elevation, between any two lakes. The second axis (i.e., PCA axis II) provides a measure uncorrelated with the information on axis I and represents the relative change in elevation compared to distance by water (i.e., stream gradient measure). In a similar fashion, the 1,378 observations from axis II were converted back into a triangular distance matrix (D-elev2). These two measures of spatial isolation incorporated the notion that fish may have greater difficulty gaining access to higher elevation lakes within a watershed because of the energetic costs associated with swimming against

the water current and increased probability of encountering barriers.

In summary, each of the measures of lake isolation described above were represented using lake-by-lake distance matrices that described the degree of lake isolation based on ecological considerations of dispersal. Each of these measures quantified potential "challenges" a fish may encounter when moving between lakes, incorporating the idea that the characteristics of the interconnecting streams and rivers could contribute to the insular nature of many lakes.

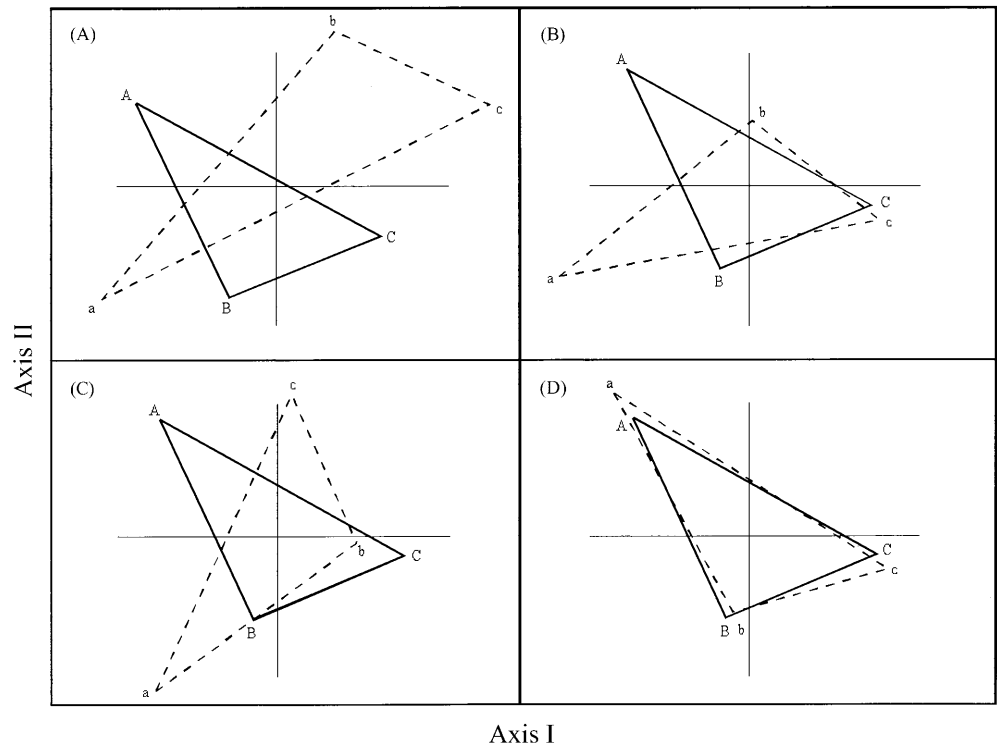
Statistical analyses

To summarize compositional patterns in fish community assembly, correspondence analysis (CA) was conducted on the species presence/absence data matrix. CA was chosen because it is not affected as adversely by data that contains numerous zero values (Gauch 1982) as are many other ordination methods. To summarize patterns in environmental conditions among the lakes, PCA of the correlation matrices was employed to ordinate the lakes separately on the basis of water chemistry and lake morphology. All environmental variables (except pH) were $\log(x+1)$ transformed prior to PCA to linearize bivariate relationships. Principal coordinate analysis (PCoA) was performed on each isolation-distance matrix to reduce the number of dimensions and summarize the majority of the variation in the original data into a subset of axes. PCoA was used because of its ability to analyse a wide range of distance (association) matrices, which was essential due to the nature of our isolation measures. To facilitate interpretation of the results in all cases only the first two dimensions were retained since they explained the majority of the variation in the original data.

Concordance between lake ordination scores from the two-dimensional multivariate summaries of the fish communities, isolation measures, lake morphology, and lake water chemistry were compared using a Procrustean approach. Procrustes analysis is a superimposition method which in the simplest case, compares a pair of ordinations by using a rotational-fit algorithm that finds the optimal match between corresponding observations of the ordinations (see Gauch 1982; Digby and Kempton 1987; Jackson 1995; Legendre and Legendre 1998). Figure 2 illustrates the steps of Procrustes analysis, using two configurations each containing three data points (e.g., three lakes: A, B, and C). The most commonly used Procrustes fitting method is based on the least-squares criterion, which superimposes the coordinates of observations from one ordination onto those of another ordination so as to minimize the total squared distances between corresponding points (m^2 statistic; Gower 1975; Rohlf 1990; Rohlf and Slice 1990). A disadvantage of the least-squares approach is that the superimposition of two ordinations can often result in a general lack of fit for most points when one or more atypical observations are present. A single atypical data point can exert a great influence due to the least-squares criterion resulting in all other points being "pulled" away from their corresponding data points in the other ordination. This effect tends to average the error across all points rather than the single atypical one, potentially masking the true underlying relationship. The result can be to make atypical points appear acceptable or represent typical observations as potential outliers, and as a consequence make the direct interpretation of residuals misleading (Siegel and Benson 1982; Rohlf and Slice 1990). Such situations are well recognized in methods such as regression analysis (Chen et al. 1994).

To account for the potential shortcomings of the least-squares method, Siegel and Benson (1982) described a resistant-fit approach for optimal superimposition of data configurations or ordinations in Procrustes analysis. Resistant-fit techniques are similar to the nonparametric analogs of least-squares regression analysis, and minimize the potentially strong influence of unusual observations. With this fitting technique, the influence of a few atypical points is negligible and the interpretation of residuals is appropriate. A number of resistant-fit algorithms exist for Procrustes analysis and in this analysis we used the repeated-medians algorithm.

Fig. 2A–D Operations involved in comparing two configurations using Procrustes analysis. **A** Original configurations or ordinations where the apices of the triangles are analogous to lake positions in an ordination, **B** ordinations after translation and standardization (configurations share a common centroid and scale), **C** ordinations after reflection, **D** ordinations after rotation and dilation. *Lower case letters* represent the rotated ordination (i.e., fish community), and *upper case letters* represent the target ordination (i.e., lake isolation, lake morphology or water chemistry). Reflection, rotation and dilation of the rotated ordination are performed to minimize the sum of the squared distance (m^2) between corresponding observations (i.e., lakes) of the two ordinations



Other robust and resistant methods might be used, but these methods generally have lower breakdown values than repeated medians (Siegel and Benson 1982). The breakdown value describes the proportion of the data that can be changed without greatly influencing the estimated value, i.e., a measure having a low breakdown point may be affected even if only a few atypical points are present (e.g., Chen et al. 1994). Siegel (1982) showed that the repeated median algorithm has a breakdown point at nearly 50%, which is higher than least-squares (0%) or alternative techniques such as the single median method (29%). Therefore we employed resistant-fit Procrustes analysis using the repeated medians algorithm.

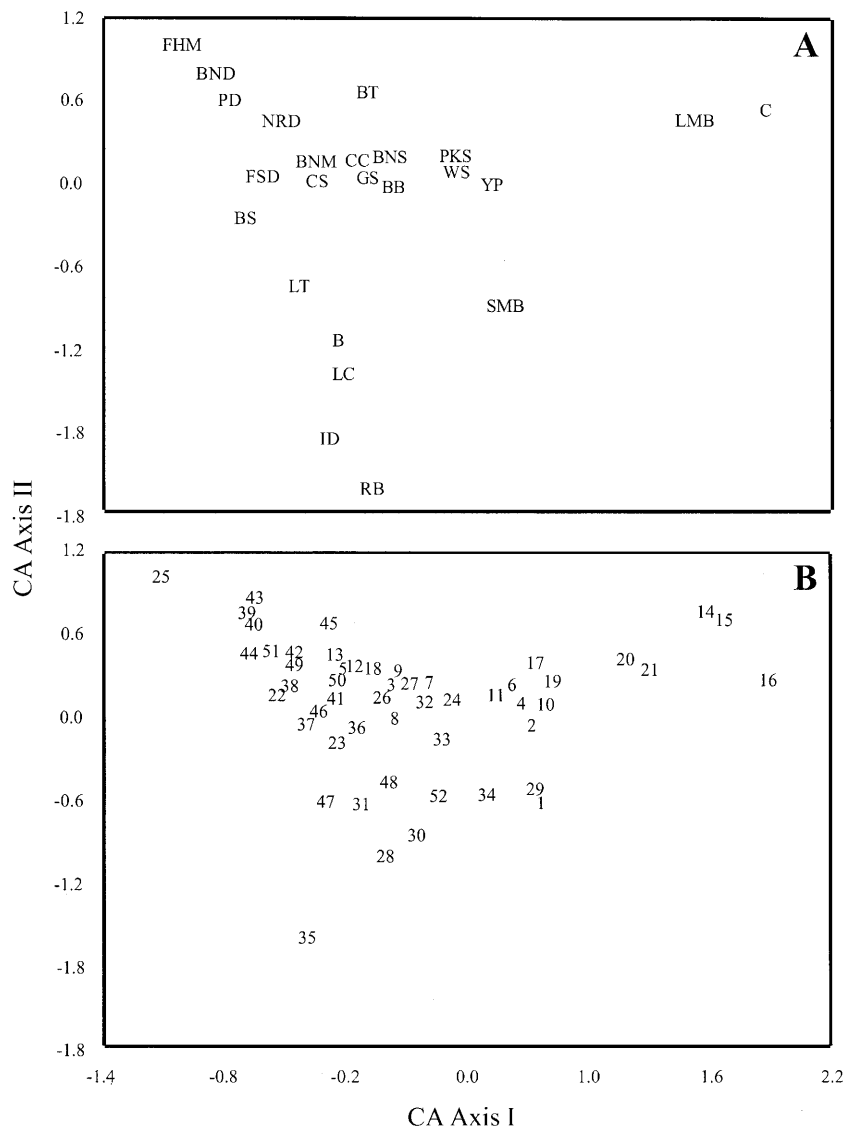
To statistically test the degree of concordance between fish community composition, lake isolation measures, lake morphology, and lake water chemistry, a Procrustean randomization test [PROTEST: Jackson and Harvey (1993); Jackson (1995); Legendre and Legendre (1998)] was used. PROTEST estimates the significance of an observed m^2 statistic with the underlying null hypothesis being a random association between the two datasets (e.g., fish community and lake morphology ordinations). This procedure randomly permutes the original observations of one matrix in a way that each lake can be assigned to any of the possible values attributed to other lakes (Jackson 1995). This results in one matrix being unchanged, and the second matrix being randomly permuted, but maintaining its within-matrix covariance structure. After each permutation, the m^2 statistic between the two matrices is recalculated. The proportion of calculated m^2 statistics, including the observed m^2 , that is smaller than or equal to the observed m^2 statistic provides the significance level of the test. In this study, 9,999 random permutations of the data were employed in order to ensure the stability of the probability estimates (Jackson and Somers 1989). In each comparison, the lake ordination scores defined by fish community composition was the rotated ordination (e.g., Fig. 2a–c), whereas the lake morphology, water chemistry and lake isolation ordinations were considered the target and therefore were fixed (e.g., Fig. 2A–C). The analysis was performed in this manner because the isolation, morphology, and chemistry matrices were considered to be the independent variables, and the species composition to be dependent on the degree of connectivity with other lakes in the watershed and habitat conditions. Procrustes analysis was conducted using the GRF-ND software (Slice 1994).

Although alternative approaches, such as the Mantel test or canonical correspondence analysis (CCA), allow us to compare two or more matrices, the Procrustean approach has advantages over them given our specific goals. First, the Mantel test is simply a correlation between distance matrices and provides no insight into which observations show a good match between their fish community composition relative to lake isolation and environment, and which ones do not. Similarly, CCA tests for overall relationships between data sets, but does not show the degree of concordance for each observation. Given that we are interested in determining how closely each lake matches in its community composition and isolation/environment conditions, the Procrustean method is ideal. In addition, we wish to examine whether principal patterns of variation in the community match with principal patterns in lake isolation measures and environmental conditions, which is not assessed using CCA.

Results

CA of the species presence/absence dataset provided a two-dimensional summary of dominant patterns in fish assemblage structure among the study lakes. The results show that as you progress positively from left to right along axis I and from top to bottom along axis II (Fig. 3A), the species composition shifts from communities containing primarily small-bodied fishes (mainly cyprinids) to communities containing large-bodied fishes (e.g., *Micropterus* spp.). Lakes located in the top-left corner of Fig. 3B contain relatively greater numbers of smaller-bodied species compared to lakes located at the bottom and right of Fig. 3B which contain proportionally greater numbers of large-bodied species. Furthermore, lakes clustered close together in Fig. 3B share similar fish community compositions, whereas lakes positioned

Fig. 3 Association of **A** fish and **B** lakes based on correspondence analysis of fish species presence-absence. Letters in **A** refer to species codes in Table 1, and numbers in **B** refer to lakes depicted in Fig. 1



at opposite ends of the plot contain distinctly different fauna.

At the scale of the watershed (i.e., the complete set of study lakes), Procrustes analysis assesses the overall degree of concordance between patterns in community composition, lake isolation and habitat-related conditions. The results from the Procrustes analyses indicated that the fish community ordination was significantly associated with SL-dis ($m^2=0.752$, $P=0.001$), HG-tree ($m^2=0.810$, $P=0.001$), WC-dis ($m^2=0.780$, $P=0.012$), WC-body ($m^2=0.843$, $P=0.007$), D-elev1 ($m^2=0.736$, $P=0.001$), US-sym ($m^2=0.772$, $P=0.010$), US-skew ($m^2=0.776$, $P=0.028$) and marginally non-significant with D-elev2 ($m^2=0.884$, $P=0.068$). The fish community ordination was also significantly correlated with the ordination of the lakes based on morphological characteristics ($m^2=0.839$, $P=0.001$), but not with water chemistry ($m^2=0.971$, $P=0.998$). To ensure that relationships between these ordinations were not confounded due to inter-correlations between the lake isolation and morpholo-

gy data sets we compared these ordinations and found that lake morphology and all measures of isolation were not significantly concordant ($m^2=0.937$ to 0.969 , $P=0.209$ to 0.980). This shows that the morphological characteristics of the lakes were not spatially autocorrelated and suggests that isolation-related and lake morphology factors are contributing independently to the observed patterns in fish assemblages found in these lakes.

In addition to assessing overall relationships between data sets, Procrustes analysis also facilitates a more detailed examination of the superimposition of the ordinations upon each other. That is, similarities and differences in the position of each of the individual lakes between the ordinations can be examined. Deviation in the position of a particular lake on two superimposed ordinations is represented by a line segment called a vector residual. The length of the vector residual represents the magnitude of the residual or lack of fit. Studying these deviations provides a useful diagnostic tool because a small vector residual indicates a close match and a large

Table 3 Ranked vector residuals for a subset of lakes from the comparison of fish community ordination and ordinations based on measures of lake isolation (*SL-dis*, *HG-tree*, *WC-dis*, *WC-body*, *D-elev1*, *D-elev2*, *US-sym*, *US-skew*), lake morphology (*Morph*) and water chemistry (*Chem*). Ranks range from 1 for the largest vector residual, indicating a weak match between the position of

the lake defined by the two ordinations, to 52 for the smallest vector residual, indicating a strong match between the position of the lake defined by the two ordinations. *Numbers in parentheses* represent study lakes depicted in Fig. 1. Lakes are grouped together in the table according to shared patterns in vector residual ranks for all ordination comparisons.

Lake	Ranked vector residual									
	SL-dis	HG-tree	WC-dis	WC-body	D-elev1	D-elev2	US-sym	US-skew	Morph	Chem
McDonald L. (12)	15	10	7	8	24	7	8	12	5	1
South McDonald L. (13)	9	8	4	6	17	5	4	10	14	5
Big Orillia L. (14)	13	14	8	19	23	3	9	13	1	6
Little Orillia L. (15)	17	14	11	20	25	4	12	11	11	3
Teapot L. (16)	8	17	9	18	12	9	10	4	13	4
Poker L. (5)	5	3	6	7	7	10	6	3	49	2
Wrist L. (8)	1	2	10	4	14	11	7	8	52	12
Big East L. (3)	3	1	3	3	4	12	3	1	8	24
Cinder L. (9)	14	11	14	9	16	21	15	7	17	45
Jill L. (21)	29	23	22	35	35	17	21	20	46	8
Herb L. (33)	44	32	47	31	33	49	46	49	47	11
Poorhouse L. (44)	35	44	41	48	15	50	41	43	35	7
Little Wren L. (30)	22	51	28	39	49	33	28	25	2	47
Ernest L. (32)	42	31	52	32	36	52	52	51	6	20
Sunken L. (34)	49	29	40	26	32	51	37	36	3	39
Kawagama L. (35)	20	19	17	15	39	18	16	16	9	40
Crosson L. (7)	2	9	13	5	19	16	11	5	33	42
Red Chalk L. (22)	6	7	12	11	5	8	5	9	42	48

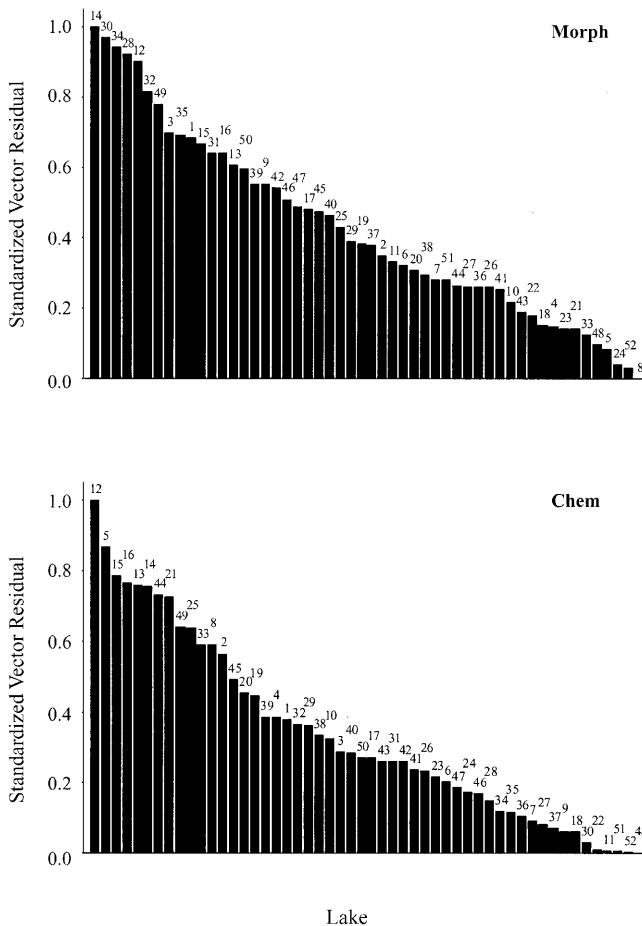
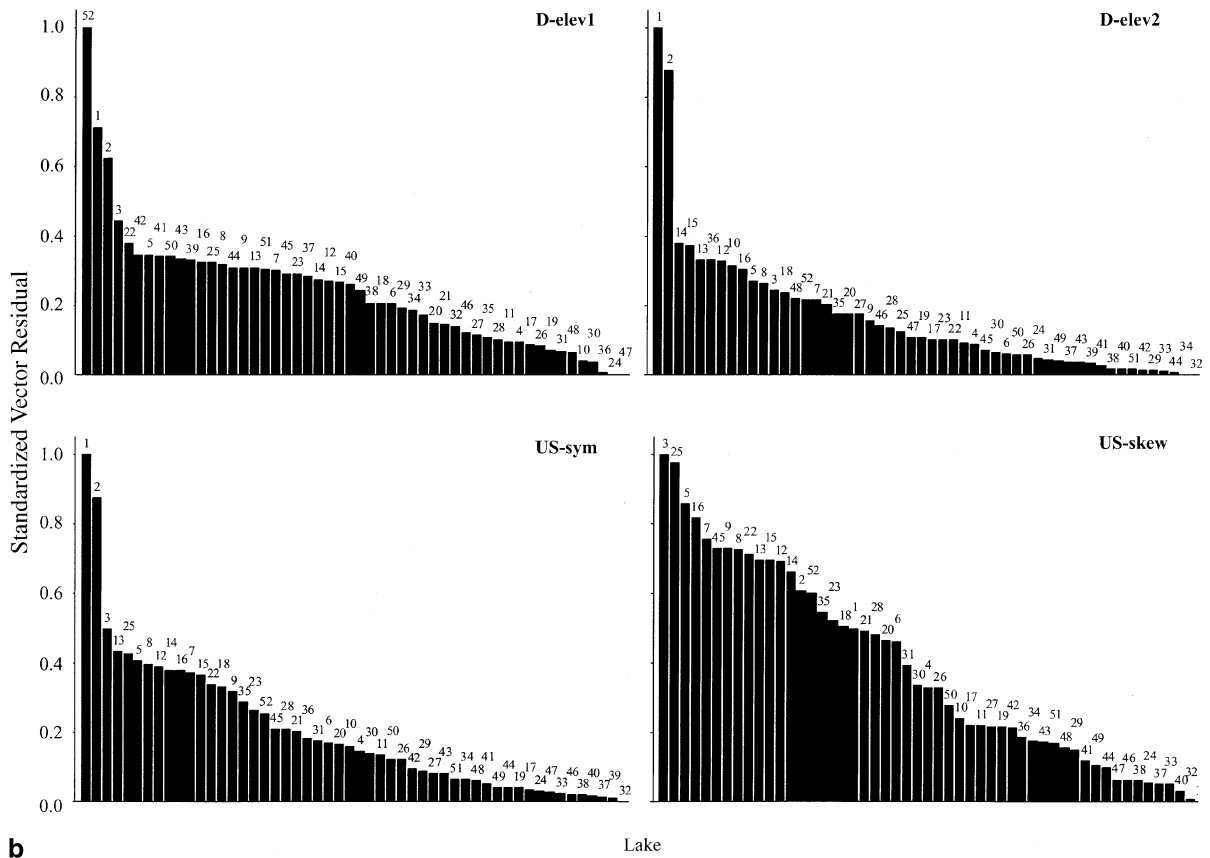
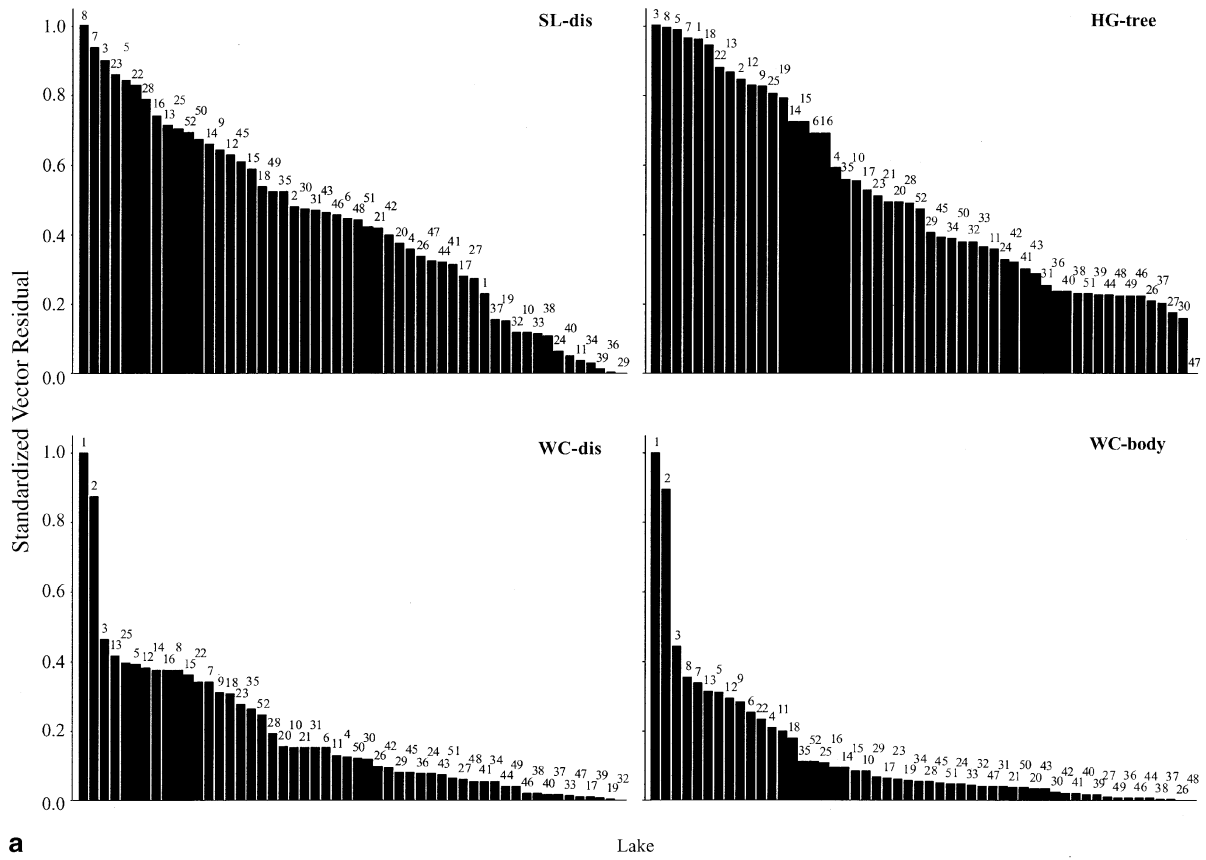


Fig. 4 Standardized vector residuals from the comparison of fish community composition with lake morphology (*Morph*) and water chemistry (*Chem*). *Numbers above bars* represent study lakes depicted in Fig. 1

vector residual indicates weak association for a particular lake between the two ordinations being compared. In this case, the vector residuals are represented by a line joining the best-fit position of a given lake (observed fish community composition) and the target position of that lake (lake isolation, lake morphology or water chemistry ordination). Therefore, the magnitude of the vector residual reveals which lakes contain fish assemblages that agree with expectations based on lake isolation or habitat conditions (small vector residual) and which lakes deviate from these expectations (large vector residual). For clarity we do not present the vector residual plots illustrating the superimposition of each pair of ordinations, but rather present the standardized values of the vector residuals for each lake (Figs. 4 and 5). Residuals were standardized to range between 0 and 1 to make the results scale independent, and lakes were ordered (in decreasing order) based on their standardized vector residual to facilitate comparisons among results. Ranks ranged from 1 to 52 (i.e., number of lakes) where a rank of 1 indicates the lake having the poorest match between fish community composition and isolation/environment conditions and a rank of 52 indicates the strongest match compared to other lakes in the watershed. Figs. 4 and 5 show the standardized vector residuals for lake morphology and water chemistry, and lake isolation, respectively. The vector residuals show that the degree of fit between community, environment and isolation ordinations varied greatly across lakes, despite the fact that community composition was highly correlated to patterns in lake isolation and morphology, and uncorrelated with water chemistry at the watershed scale.

To demonstrate the interpretation of Procrustean results, we present a set of lakes that exhibit similar trends



in their ranked residual vectors. Table 3 shows that the fish communities of some lakes exhibited a strong association with some measures of lake isolation (lakes 12–16; hereafter referring to the numbering of the lakes on Fig. 1), some with lake morphology (lakes 5,8), some with chemistry (lakes 3,9), some with lake morphology and isolation (lakes 21, 33, 44), others with water chemistry and isolation (lakes 30, 32, 34, 35), and still others match with lake morphology and chemistry (lakes 7, 22). There were also a number of differences among the isolation measures. For example, Big Orillia Lake (lake 14) and Little Orillia Lake (lake 15) demonstrated a strong association with WC-body and D-elev1 and Teapot Lake (lake 16) exhibited good concordance with HG-tree and WC-body (Table 3, Fig. 5), showing that these measures were more successful in explaining patterns in species composition in these particular lakes compared to the other isolation measures. A number of lakes (e.g., lakes 3, 12–15) exhibited contrasting fits based on D-elev1 compared to D-elev2 (Table 3). This was interesting since both of these measures incorporate differences in WC-dis and elevation among the lakes, but each describe different aspects of this relationship. Finally, a number of lakes showed poor agreement with SL-dis, whereas they showed close agreement with other measures of lake isolation (e.g., lakes 8,13,16,23,28; Fig. 5).

Discussion

Watershed patterns in fish communities, lake isolation and environmental factors

Communities are rarely structured by a single factor; rather, they are usually determined by an array of factors acting simultaneously. In temperate North America, variables describing biotic, abiotic and lake isolation conditions have been frequently identified as important factors shaping fish species richness and community composition (e.g., Johnson et al. 1977; Harvey 1975, 1978, 1981; Tonn and Magnuson 1982; Eadie et al. 1986; Jackson and Harvey 1989, 1993; Jackson et al. 1992; Matthews and Robison 1998). The results from our study indicate a strong association between fish community composition and factors related to lake morphology, but not water chemistry, for all study lakes. This suggests that whole-lake attributes of lakes are important determinants of fish community composition. Lake morphological factors include surface area, volume and shoreline and island perimeter which are correlated with habitat diversity (Eadie and Keast 1984), and maximum depth which is negatively correlated with winter dissolved-oxygen concentra-

tions and related to thermal stratification (Tonn and Magnuson 1982; Jackson and Harvey 1989).

In addition to lake morphology, the results suggest that the spatial configuration and degree of interconnectedness of the lakes within the watershed play important roles in structuring patterns in community structure. Similar to the role of the environment, isolation-related factors have also been shown to be important determinants shaping temperate fish assemblages (Barbour and Brown 1974; Magnuson 1976; Eadie et al. 1986; Jackson 1988; Tonn et al. 1990; Magnuson et al. 1998). The fact that alternative measures of lake isolation were highly concordant with patterns in fish community composition emphasizes the fact that developing and testing isolation measures other than straight-line distance is an important exercise and can provide important additional insight into the role of isolation in shaping fish communities. Alternative measures of lake isolation incorporated the idea that fish movement between lakes (and within/between rivers) occurs predominantly via corridors of aquatic habitat, and therefore colonization rates among lakes will depend primarily on the number, length and suitability of these corridors. Watercourses with unsuitable characteristics could limit, or even preclude, the movement of fish from one lake to another. Factors might include the number of stream changes or confluences, and stream-habitat characteristics of the connecting waterways (e.g., channel width, depth), which vary from pools to swift-flowing riffles to waterfalls and dams. These conditions may represent an increasing series of obstacles to fish moving between lakes, but present a greater obstacle for species moving upstream compared to downstream. Therefore, assuming a suitable habitat is present, species could colonize more readily downstream and species richness should be greater, on average, downstream. Depending on each species' size, swimming speed, and thermal tolerances, such stream conditions may represent species-selective filters or barriers. Small-bodied and poor-swimming species may be incapable of moving upstream past riffles, minor cascades or waterfalls, whereas larger and fast-swimming species may pass with varying degrees of success. Cool- and cold-water species may be restricted in their movement to colder periods of the year or prevented entirely due to low water levels and ice during the winter. As a consequence, upstream colonizing species may pass through species-selective "filters", which, in combination with lake morphology and chemistry, determine the resultant fish community (Smith and Powell 1971; Tonn 1990; Poff 1997; Hershey et al. 1999; Jackson et al. 2001).

As an aside, we advocate caution when interpreting community relationships with lake isolation because a lake's relative position in the landscape can also influence lake morphometry (i.e., size and shape) and a variety of limnological characteristics, such as the concentration of major ions and the vertical distribution of primary production (D'Arcy and Carignan 1997; Kratz et al. 1997; Riera et al. 2000). The lack of correlation between all measures of lake isolation and lake morpholo-

◀ **Fig. 5** Standardized vector residuals from the comparison of ordinations based on fish community composition with lake isolation ordinations. Numbers above bars represent study lakes depicted in Fig. 1. *SL-dis* Straight-line distances; *HG-tree* hydrographic tree; *WC-dis*, *WC-body*, *D-elev1*, *D-elev2*, *US-sym* and *US-skew* see Methods and materials for description of isolation measures

gy and water chemistry suggests that our results are not confounded by this interaction, and thus we are more confident in interpreting relationships between lake isolation and fish community structure among our study lakes.

Lake patterns in fish communities, lake isolation and environmental factors

Our results show that the spatial arrangement of the lakes, characteristics of the interconnecting streams and lake morphology correspond strongly to patterns in fish community composition. However, at the scale of individual lakes, local fish communities were found to exhibit varying levels of correlation with lake isolation and environmental conditions. In many cases, our results showed that patterns in community structure were better explained by isolation-related factors compared to lake morphology and water chemistry. This supports the hypothesis that the insular nature of many lakes could mask associations between fish community composition and the lake habitat conditions. Angermeier and Schlosser (1989) suggested that when extinction and colonization processes are important, there should be a lack of relationship between assemblage structure and habitat characteristics. Snodgrass et al. (1996) employed the same argument when they suggested that the lack of relationship between wetland size and community richness in isolated wetlands of the Upper Coastal Plain (USA) could result from the dependence between fish community structure and differences in immigration rates between species. Our results support this perspective. For example, Big Orillia Lake (lake 14), Little Orillia Lake (lake 15) and Teapot Lake (lake 16) contain unusual fish communities for their small area and shallow size, including the presence of two cool- or cold-water species, brook trout and cisco. Consequently, it is not surprising that these lakes exhibited poor agreement with expectations based on lake morphology and water chemistry; however, they were shown to have high concordance with three isolation measures: HG-tree; watercourse distance among lakes excluding intermediate water bodies (WC-body); and stream gradient (D-elev1). Although environment conditions may not be optimal for such species in these communities, the fact that the lakes are well connected to other water bodies (in terms of WC-dis and elevation) facilitates the persistence of the species. In this situation, these lakes possibly act primarily as recipients of immigrating species (i.e., sinks) from adjacent systems (i.e., sources). The notion of source-sink populations in aquatic communities has been suggested for coral reef fishes (Sale 1978, 1979) and stream fishes (Osborne and Wiley 1992; Schlosser 1995; Fraser et al. 1999), with each of these studies providing evidence supporting the importance of immigration from source areas for shaping species richness and fish community structure in potential sink habitats. We believe that source-sink dynamics or true metapopulations can exist

in these study lakes (and drainage lakes in general), which perhaps exhibit sub-optimal biotic and environmental conditions but are highly connected to other lakes with suitable conditions. However, to establish whether such lakes contain true metapopulations (Pulliam 1988; Watkinson and Sutherland 1995) would require detailed measurements of birth, death, immigration and emigration rates, which would be challenging to assess with fish communities. Nevertheless, our results indicate candidate lakes where the study of such relationships may be informative.

Similar to the above example, the fish community composition of Sunken Lake (lake 34) illustrated poor agreement based on its morphological characteristics, but showed good agreement based on its degree of isolation and water chemistry. Sunken Lake has an unusual fish assemblage, containing a depauperate community with the presence of only yellow perch, brown bullhead and smallmouth bass. The lack of smaller-bodied species (e.g., cyprinids) in this lake is noticeable, since its habitat conditions appear to be suitable for another community given the large residuals between habitat and fish community ordinations. The lack of agreement between community composition and habitat may arise from strong predation pressure by smallmouth bass and/or due to the steep stream gradient restricting or even blocking the immigration of small-bodied species. Previously existing populations of small-bodied fishes could have been eliminated when bass colonized the lake (likely as a result of unauthorized stocking), and have not been "rescued" by re-colonization from surrounding water bodies (Ray and Gilpin 1991). Interestingly, a possible source population [i.e., Raven Lake (lake 31)] contains 13 species (a large number of which are cyprinids) and is located immediate downstream from Sunken Lake (3.2 km and 16 m in elevational difference). This example provides a good illustration of the potential inter-play between insular and habitat-related forces shaping the composition of fish communities. A number of experimental studies have examined interactions between isolation and habitat suitability (e.g., Meffe and Sheldon 1990; Peterson and Bayley 1993; Sheldon and Meffe 1994). Recently, Lonzarich et al. (1998) removed fish from pools in two Arkansas streams and showed that four measures of pool isolation (riffle length, riffle depth, position in drainage basin and distance to large pools) were related to the numerical recovery of the communities. For example, the recovery of an assemblage separated from neighbouring pools by short riffles occurred in 30 days whereas more isolated pools had not reached 70% recovery after 40 days. In addition, numerical recovery was more rapid in downstream pools and in pools that were closer to large source pools. Therefore, our study supports the idea of Lonzarich et al. (1998) that although habitat might be appropriate for the persistence of particular fish species, the degree of habitat isolation is a major factor structuring the composition of fish communities.

For a number of lakes, fish community composition showed either good agreement with expectations based

on lake isolation and morphology (e.g., Jill Lake, Herb Lake, Poorhouse Lake) or with expectations based on lake isolation and water chemistry (e.g., Little Wren Lake, Ernest Lake, Kawagama Lake), but not with both lake morphology and water chemistry. Given the observed and extensive movements of tagged fish between many of the study lakes (Jackson, unpublished data), we believe that colonization and extinction rates are interconnected in such cases. This makes intuitive sense because both isolation and habitat-related factors will influence the potential for species re-establishment following an environmental or ecological perturbation, and therefore influence the probability of local extinction (Magnuson et al. 1998). For example, the influx of individuals from adjacent lakes could provide a rescue effect for populations containing few individuals. This may prevent numbers from dropping so low as to lead to local extinction. In situations where movements are very frequent, a local population may be lost due to extreme environmental fluctuations (e.g., winterkill due to low dissolved oxygen) but individuals could re-colonize before periodic sampling detects the loss of the species.

As the crow flies or as the fish swims?

Frequently used isolation measures such as the straight-line distance between lakes provides a simple measure of the relative location of the lakes in the watershed. However, this measure will be misleading in convoluted systems where lakes close to each other in the straight-line sense are quite far apart as measured by in-water distance (e.g., Little et al. 1997). Consequently, straight-line distance will often not provide insight regarding the biologically relevant distances required for dispersal, whereas the other measures we present do. The inadequacy of straight-line distance is not only conceptually obvious, but it is also evident for a number of the study lakes. For instance, the fish communities of Blue Chalk Lake (lake 23) and Wren Lake (lake 28) showed good agreement with all measures of lake isolation except SL-dis. In this case, using such a simple measure of lake isolation would be quite misleading since one might conclude that local patterns in community composition are not influenced by the lakes' degree of isolation from other lakes in the watershed. Another example includes South McDonald Lake (lake 13) and Teapot Lake (lake 16) whose fish communities show strong concordance with expectations based on D-elev1, and WC-body and HG-tree, respectively, but both show weak concordance with all other measures of isolation, lake morphology and water chemistry. Again, measures incorporating other factors, such as the WC-dis and changes in elevation enhance the detection of isolation processes shaping species composition. Finally, an interesting finding is that the fish assemblage of Big East Lake (lake 3) showed a stronger association with D-elev2, a measure describing the relative magnitude of the stream elevational gradient between the lakes, but do not match with D-elev1, a

measure of the absolute WC-dis and change in elevation between the lakes. Apparently, the total differences in WC-dis and elevation to surrounding lakes are not important isolating factors for this lake; however, in combination as a measure of the elevational gradient, the relationship between these two factors represents a potential isolating mechanism. Since each isolation measure explained different local patterns in fish assemblage structure, we advocate the examination of various alternate measures of lake interconnectedness. This is advantageous because different aspects of the landscape can influence the ability of species to disperse, and ultimately can provide insight into determinants influencing community similarity among lakes. Optimally, alternative measures should describe watercourse- and elevation-related aspects of the landscape separating the lakes, such as US-sym, WC-dis and D-elev2.

Conclusion

Both isolation and environment-related factors can be important and should be examined for their effects in structuring fish communities. Identifying the degree of spatial isolation among lakes is important for distinguishing biogeographical factors that are potentially responsible for differences in species composition across watersheds. Our paper outlined various means of calculating the spatial connectivity between lakes, emphasizing different mechanisms that could potentially promote or prohibit the movement of fish. Inter-lake distances defined "as the fish swims" provide greater insight in species-isolation relationships compared to distances defined "as the crow flies". Although patch or metapopulation dynamics of fish assemblages have not been studied to any great extent, the potential role of fish movement in contributing to homogeneity or heterogeneity in species community composition must be considered. Isolation measures incorporating the difficulties fish encounter when traveling between water bodies will aid in identifying potentially insular drainage lakes within a watershed, as well as aid in understanding the role of isolation-related factors in shaping the composition of fish communities. An objective of our study was not to advocate the use of one "best" isolation measure for fish community studies as this may vary depending on the data set considered (e.g., relative variation in distances and elevational changes among lakes). Rather, we hope to illustrate that alternative methodologies for quantifying lake isolation should be examined when assessing the influence of spatial isolation on the structuring of fish communities. Furthermore, depending on the topographic characteristics of the landscape, researchers could use a subset of these lake isolation measures emphasizing different attributes in their data. For instance, for lakes located in a landscape of intermediate or high topographic relief, measures incorporating stream slope (i.e., D-elev1, D-elev2) and upstream distance (i.e., US-sym, US-skew) would be recommended, whereas in highly convoluted systems having limited elevational differences, water-

course distance (i.e., WC-dis, WC-body) could be optimal. Finally, the Procrustean methodology presented here provides a means of assessing the degree of overall concordance between biological and spatial multivariate data matrices as well as providing a more detailed interpretation of the relative concordance of different data sets for individual observations. This statistical methodology is a promising quantitative tool not only for aquatic studies, but also terrestrial studies. In the present study, Procrustes analysis provided a robust assessment of the importance of isolation- and habitat-related factors at the landscape scale, and also facilitated the identification of factors influencing local fish community composition. Recognizing that controlling mechanisms can vary within a spatial framework may help ecologists study the way in which physical and biological processes interact in the regulation of lake fish communities.

Acknowledgements We would like to thank John Magnuson, Brian Shuter, Keith Somers, Bill Tonn and two anonymous reviewers for their comments on early drafts. Also, we thank Pierre Legendre for his helpful remarks regarding skew-symmetric matrices. Funding for this project was provided by a Natural Sciences and Engineering Council of Canada (NSERC) Graduate Scholarship and University of Toronto scholarships to J.D.O., an NSERC Research Grant to D. A. J. and a Brazilian CNPq scholarship to P. R. P.-N. PROTEST software is available at <http://www.200.utoronto.ca/jackson/>.

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