Association between biogeographical factors and boreal lake fish assemblages

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Abstract Five regions in insular Newfoundland Canada, comprising 152 lakes, were studied to identify associations between species composition (presence and absence), geographical location and environmental variables (pH, area, depth, alkalinity, secchi disc depth and shoreline development factor). Correspondence analysis and canonical variate analysis were used to distinguish regional patterns. Five biologically and environmentally distinct areas were identified. The degree of association between biological, environmental and geographical distances were contrasted using Mantel's test. Regional fish community structure was significantly correlated with large-scale geographical distance but not with environmental parameters or small scale distance. It was proposed that large scale processes such as post-glacial dispersion, climate and recent species introductions are important determinates in structuring regional fish assemblages. Differences in individual lake character were important determinates in intraregional variability in fish assemblage type. Sampling strategies for regional modelling and management are discussed.

KEYWORDS: biogeography, environmental gradients, fish assemblages, multivariate analysis, Newfoundland, regional discrimination, salmonids.

Introduction

The structure of fish assemblages in lakes is dependent on the interaction of multiple ecological processes over varying temporal and spatial scales. To explain this structure there is a need to generalise and discriminate the shaping factors (Tonn & Magnuson 1982; Jackson & Harvey 1989). In this respect, both local (habitat diversity, competition, predation) and regional (climate, dispersal, historical biogeography) factors influence the patterns observed in species assemblages (Connor & Simberlof 1983; Ricklefs 1987).

Notwithstanding, it has been recognised that studies of community organisation must acknowledge differing scales associated with these factors (Jackson & Harvey 1989), but the majority of studies have failed to do so. Results from studies on northern temperate lakes suggest that lakes are not random mixtures of a common regional species pool but rather a small number of repeatable assemblages types (e.g. Harvey

1978, 1981; Tonn & Magnuson 1982; Eadie & Keast 1984; Rahel 1984). These studies were based on single regions and focussed primarily on local factors (Robinson & Tonn 1989). More recently, attempts have been untaken to examine community organisation over wider spatial scale by making intercountry comparisons (Tonn, Magnuson, Rask & Toivonen 1990). Jackson & Harvey (1989) suggested that it is critical that comparisons of similar biotas are made from differing geographical regions, thus extending our knowledge and understanding of the relative contribution of local vs regional processes to the biogeographical patterns observed. In this context, no such studies on fish community organisation have been conducted in insular Newfoundland.

Factors that have been identified as important in structuring northern temperate fish assemblages are physiochemical factors, such as pH, alkalinity and low winter oxygen concentrations (e.g. Tonn & Magnuson 1982; Rahel 1984, 1986; Jackson & Harvey 1989;

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Persson 1997), productivity (Eadie & Keast 1984; Marshall & Ryan 1987; Gibson & Haedrich 1988), lake depth (Johnson, Leach, Minns & Oliver 1977; Harvey 1978; Jackson & Harvey 1989) and lake size (Johnson *et al.* 1977; Harvey 1978; Rahel 1986). Differential dispersal ability among species may also influence species composition (MacArthur & Wilson 1967; Tonn & Magnuson 1982; Jackson & Harvey 1989). Human alterations to aquatic systems such as habitat degradation and introduction of exotic species can also have profound effects on fish assemblages (Cowx & Gerdeaux 2004; van Zyll de Jong, Gibson & Cowx 2004).

Identifying non-random associations of fish species and the factors responsible for structuring them is essential for understanding community dynamics and predicting how external (e.g. introduction of exotics) and internal (e.g. eutrophication) mechanisms could influence that structure (Robinson & Tonn 1989). Additionally, these patterns can be used as a basis for classification, representative sampling and management of differing fish assemblages in a large number of lakes over large regional areas.

In this study the fish communities in lakes representing five areas of insular Newfoundland are examined. The objectives were: (i) to investigate if local and regional factors and processes are responsible for observed patterns in regional fish assemblages; (ii) to determine whether regional fish communities differ sufficiently to discriminate regions; (iii) to determine which environmental factors in individual lakes determine different assemblage types; and (iv) to outline a sampling strategy to collect demographic and environmental data to create a generalised regional fisheries model.

Materials and methods

Lake selection and sampling

Initially data on 673 lakes contained in the insular Newfoundland provincial lake database were examined. All lake data were examined to ensure a complete set of biological (fish presence and absence information) and environmental variables (surface area, shoreline development factor, maximum depth, pH, alkalinity, secchi disc depth, location) were available. Lakes with incomplete information were eliminated leaving a database of 255 lakes. A second round of selection was based on the following specific criteria: (i) lakes were fished with multiple gears (i.e. gill nets, small mesh fyke nets and angling); and (ii) surveys were conducted during the summer season (June to August). Of the 255 eligible lakes, only 152 met the selection criteria. The 152 lake data set provided regional coverage and a complete set of variables for analysis (environmental, geographical and biological matrices; Table 1), representing five distinct ecoregions (Damman 1983; Fig. 1).

Data analysis

Regional discrimination Correspondence analysis (CA) was used to convert species composition (presence and absence) data into continuous variables. Lake ordination scores from CA were then used in univariate analysis of variance (ANOVA) and multivariate analysis of variance (MANOVA) to determine whether lakes were regionally distinct. The CA scores were normally distributed and were used untransformed in subsequent canonical variate analysis (CVA) to examine relationships between regions. Differences between regions with respect to environmental variables were examined using ANOVA and MANOVA. All environmental variables were log-transformed with the exception of pH. CVA was used to examine the relationship between the regions with respect to environmental variables.

Mahalanobis distance was used as a generalised distance between regional centroids in the space defined by CVA (Legendre & Legendre 1998). Correspondence analysis scores of the species presence and absence data were used to calculate Mahalanobis distance among the centroids in CVA. This provided a measure of the biological distance among the regions

Table 1. Mean and ranges for number of species per lake, lake surface area, shoreline development factor, maximum depth, pH, alkalinity, secchi disc depth for the five regions surveyed

| Region	No. of lakes	No. of species	Surface area (ha)	Shoreline development factor	Maximum depth (m)	Secchi depth (m)	pH	Alkalinity (ppm)
Northern	24	4 (1–7)	234 (3–3263)	2.4 (1.2–5.6)	16.5 (1.1–52)	3.5 (1.1–7.0)	7.5 (6.5–8.2)	73.8 (6.8–119)
Western	33	3 (1–8)	228 (1–2278)	1.6 (0.31–3.1)	33.02 (1–130)	4.07 (0.75–9.2)	6.86 (5.2–8.0)	24.4 (0.7–132)
Eastern	20	5 (3–7)	551 (1–1968)	1.8 (1.1–2.8)	17.04 (4.9–60)	4.25 (2.5–7.5)	6.2 (5.6–6.8)	4.2 (1.2–12)
Terra Nova	25	2 (1–7)	117 (0.7–973)	1.9 (0.78–6.5)	8.7 (1–22.6)	3.12 (1.2–4.5)	6.7 (6.1–7.1)	8.2 (1.4–52)
Avalon	50	4 (1–6)	175 (3.2–496)	2.5 (1.2–6.4)	12.0 (2.2–32.6)	3.7 (2.0–4.9)	6.2 (4.7–7.0)	4.9 (0.8–11.9)
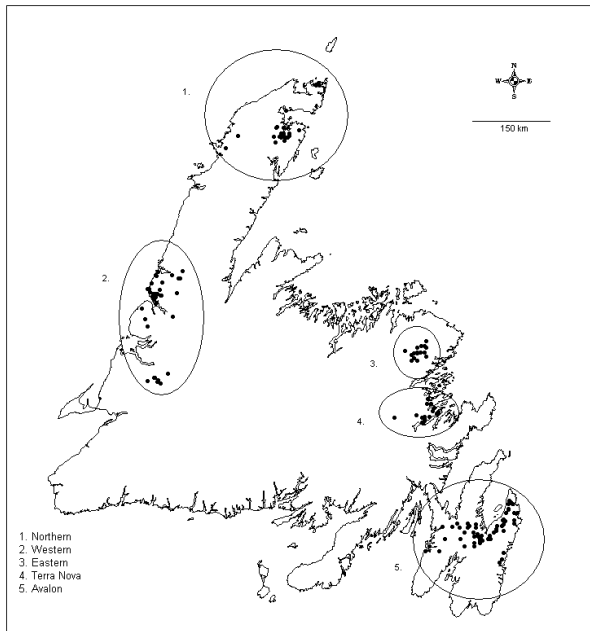
Figure 1. Newfoundland and Labrador, lakes and geographical regions sampled.

(Jackson & Harvey 1989). Regional environmental distance was also described as Mahalanobis distances from the combined set of environmental parameters. Geographical centroids were identified by longitude and latitude of the midpoint of the region (Jackson & Harvey 1989). The distance between each region was then calculated using Euclidean distance (Sneath & Sokal 1973) between regional centroids. The inverse of geographical distance was also used to examine whether distance was a significant factor between adjacent regions (Jackson & Harvey 1989). Inverse distance measures provide a greater weighting of smaller distances and are recommended for testing of local patterns (Mantel 1967; Mathews 1987; Jackson & Harvey 1989).

Correspondence among biological, environmental and geographical distances Mantel's test was used to determine whether non-random inter-regional associations exist for distance matrices based on CA scores, environmental variables and geographical centroids (Jackson & Harvey 1989). Mantel's test is a randomisation test that calculates the probability that two distance matrices are more similar than expected by chance alone (see Douglas & Endler 1982; Jackson & Harvey 1989; Jackson & Somers 1989). The relative importance of large, medium and small-scale processes was determined with Mantel's test with distances between region

centroids or inverse distances respectively (see Jackson & Harvey 1989). Each Mantel's test used 10 000 permutations.

Regional patterns in fish assemblage type To discriminate regional differences in lake types, the fish assemblage types were defined by the presence or absence of seven major fish species, i.e. brook trout, *Salvelinus fontinalis* (Mitchill), rainbow trout, *Oncorhynchus mykiss* (Walbaum), brown trout (Salmo trutta L.), Atlantic salmon, *Salmo salar* L., Arctic charr, *Salvelinus alpinus* L., American eel, *Anguilla rostrata* (L.) and rainbow smelt, *Osmerus mordax* (L.). Correspondence analysis was used to investigate regional patterns in fish assemblage type. Lake ordination scores from CA of fish assemblage types were tested with chi-square to determine whether lakes were regionally distinct. Difference in individual lakes was examined using MANOVA.

Distribution patterns in individual species to specific lake features To investigate how individual species responded to specific lake characteristics, distribution patterns of the seven most frequently occurring species were analysed by the occurrence sequence method (Schoener & Schoener 1983). Lakes were ranked along sequences of increasing value for each environmental factor. The pattern of occurrence of individual species distributions was then tested using Mann–Whitney *U*-tests. If presence or absence of a species was related to any of the environmental factors, then the species distribution would concentrate at one end of the sequence: if there was no relationship then the occurrence distribution should not reveal a pattern relative to the sequence. This analysis determines the precision of any distributional threshold along an environmental gradient without making an assumption about the exact location of such a threshold (Schoener & Schoener 1983; Robinson & Tonn 1989). All statistical and numerical procedures were completed using SYSTAT and NT-SYS. For all tests, significance was determined at $\alpha = 0.05$.

Results

Biological similarity

The five regions were distinct along the CA axis (MANOVA, Wilk's Lamdba, $F = 7.09$, $P < 0.0001$). Canonical variate analysis confirmed the MANOVA output and illustrated the biological differences among the regions (Fig. 2), while the Malahanobis distances (listed in Table 2) discern the inter-regional associa-
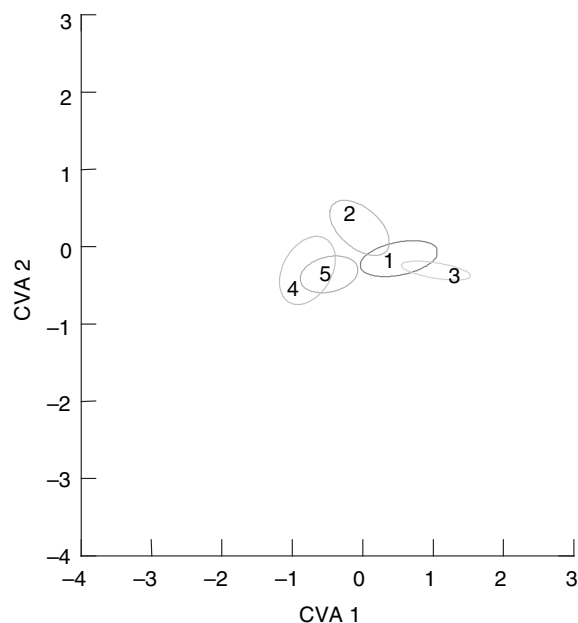
Figure 2. Axis I and II from the canonical variates analysis showing separation of regional centroids based on fish presence and absence with 95% confidence ellipses. Regions: 1, Northern; 2, Western; 3, Eastern; 4, Terra Nova, 5, Avalon.

tions. All regional centroids were significantly ($P < 0.01$) different from one another with the exception of the Terra Nova and Western regions ($P > 0.05$). Jackknife classification in the CVA indicated a moderate regional fidelity (correct classification) ranging from 9 to 72%. Only two of the five regions had fidelities over 50% and one at 25% and the remaining two <25% (Table 3). Eastern region and Terra Nova regions classified 55% ($n = 11$) and 72% ($n = 18$), respectively. The remaining three regions showed little fidelity, the Northern, Western and Avalon regions exhibited 25, 9 and 18% fidelity respectively. In total, of the 152 lakes used in the analysis only 30% or 46 lakes were correctly classified. Regional patterns in CVA (Fig. 2) separated the

Table 2. Mahalanobis distances between regional centroids of correspondence analysis (CA) scores for presence and absence data (lower left triangle) and Mahalanobis distances for environmental characteristics (upper right triangle)

Region	Northern	Western	Eastern	Terra Nova	Avalon
Northern	0	5.5	6.7	12.1	29.9
Western	5.8	0	8.9	6.5	22.9
Eastern	1.8	12.4	0	10.9	29.2
Terra Nova	11.5	**1.6**	18.4	0	14.3
Avalon	3.8	**2.8**	11.4	7.9	0

$P < 0.05$ unless otherwise indicated in bold $P > 0.05$.

Table 3. Canonical variates analysis classification table for 152 lakes surveyed for CA from fish species presence and absence data and environmental characteristics. Numbers correspond to numbers and percentages of lakes classified in each region

Region	Northern	Western	Eastern	Terra Nova	Avalon	% correctly classified
CA from fish species presence and absence data						
Northern	6	2	10	4	2	25
Western	6	3	3	18	3	9
Eastern	5	4	11	0	0	55
Terra Nova	2	2	1	18	2	72
Avalon	21	8	5	8	8	16
Total	40	19	30	48	15	30
Environmental characteristics						
Northern	20	2	0	1	1	83
Western	6	13	5	4	4	41
Eastern	0	1	16	3	0	80
Terra Nova	1	4	3	16	1	64
Avalon	1	2	2	9	30	68
Total	28	22	26	33	36	66

regions on the first axis (CV 1) accounting for 82.6% of the intergroup variability. The second axis distinguished the northern and western regions, but also separated the Avalon region from all other regions. The second axis accounted for 17.4% of the intergroup variation.

Environmental similarity

Individual environmental variables separated the regions (surface area, $P < 0.0001$; pH, $P < 0.0001$; shoreline development factor, $P < 0.0001$; maximum depth, $P < 0.005$; alkalinity, $P < 0.0001$) with the exception of secchi disc depth ($P > 0.05$). In addition, a MANOVA using the same environmental variables was also significant (Wilk's Lambda $F = 12.53$, $P = < 0.0001$; Fig. 3). Malahanobis distances (listed in Table 2) highlighted inter-regional associations, with all regional centroids being significantly different from one another ($P < 0.001$). Lakes exhibited a high degree of fidelity with respect to environmental variables (Table 3). A jackknife classification of the lakes revealed 66% or 100 of the 152 lakes were correctly classified. The Northern and Eastern regions exhibited a high degree of fidelity, with 83% ($n = 20$) and 80% ($n = 16$) of the lakes being correctly classified, respectively. A moderate level of fidelity was found for the Terra Nova and Avalon regions, at 64% ($n = 16$) and 68% ($n = 30$), respectively. The lowest fidelity was found for the Western region, with only 41% ($n = 13$) correctly classified. Regional patterns in CVA (Fig. 3) showed separation of the all regions on the first axis (CV 1), accounting for 67% of the
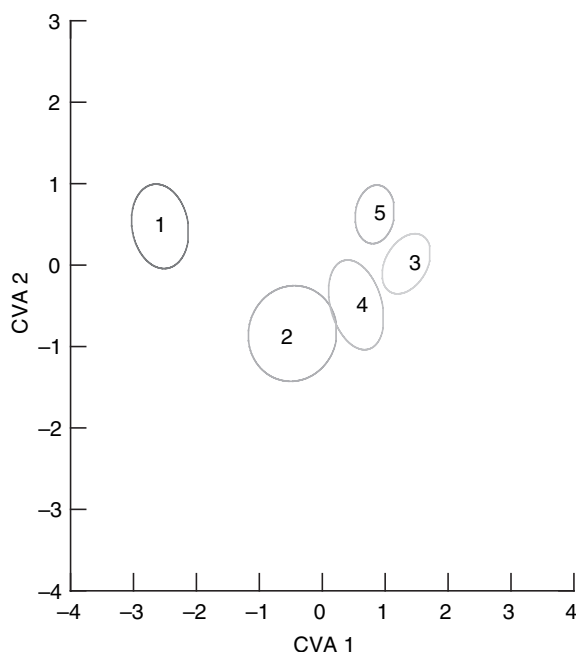
Figure 3. Axes I and II from canonical variates analysis showing separation of regional centroids based on environmental distance with 95% confidence ellipses. Region: 1, Northern; 2, Western; 3, Eastern; 4, Terra Nova; 5, Avalon.

intergroup variability. The second and third axis accounted for 14% of the variability. The CVA provides clear separation of the regions with respect to environmental character.

Correspondence between the biological, environmental and geographical matrices

Mantel's test found that biological similarity among regions was significantly associated with geographical separation ($P = 0.032$). Biological similarity among the regions was not significantly associated with inverse distance ($P = 0.083$) and environmental distances ($P = 0.19$). Environmental distance among regions was significantly associated with geographical separation ($P = 0.048$) but not inverse distance ($P = 0.12$).

Regional patterns in fish assemblage type

Regional patterns in CA showed separation of all regions (Fig. 5). The number of different fish assemblages by region are indicated in Fig 4. The Northern, Avalon and Terra Nova regions supported all five defined assemblages, the Western region had four and the Eastern region supported only three of the assemblage types. The predominate fish assemblages

among all regions comprised American eel, Atlantic salmon and brook trout, representing 38% of all lakes; the next most prominent assemblages were brook trout lakes at 18%, brook trout and American eel at 17% and brook trout and Atlantic salmon at 14%.

The predominant assemblages varied by region. The Northern region comprised 25% ($n = 6$) brook trout, Atlantic salmon and eel lakes, and 21% ($n = 5$) brook trout lakes (Fig. 4). In the Western region both brook trout lakes and brook trout–eel lakes contributed 30% ($n = 10$) of lakes surveyed (Fig. 4). The Eastern region comprised 45% ($n = 9$) Atlantic salmon and brook trout and 35% ($n = 7$) Atlantic salmon, brook trout and eel lakes. Terra Nova has the highest proportion of brook trout lakes with 44% ($n = 11$) (Fig. 4). The Avalon region has a wide array of fish assemblages, with 42% ($n = 21$) being Atlantic salmon, brook trout and eel lakes. The highest percentage of other assemblages occurred in the Avalon region, with 30% of the lakes surveyed consisting brown trout–other species (20%, $n = 10$), rainbow trout lakes (6%, $n = 3$) and Arctic charr–other species (4%, $n = 2$) lakes. The Northern (17%, $n = 4$), Western (27%, $n = 9$) and Eastern (20% $n = 4$) region's other assemblages were predominantly Arctic charr–other species lakes. The Terra Nova region's other assemblages were rainbow trout–brown trout lakes (8%, $n = 2$) and Arctic charr–other species lakes (8%, $n = 2$).

Distribution patterns in individual species to specific lake features

Occurrence sequence analysis indicated that Atlantic salmon ($P = 0.01$), American eel ($P = 0.008$) and rainbow smelt ($P = 0.002$) were found more often in larger surface area lakes (Table 5). American eel additionally occurred more often in complex shorelines ($P = 0.024$) and less acidic lake environments ($P = 0.013$). Arctic charr occur in deep ($P = 0.009$) and clear lakes ($P = 0.0001$). Rainbow trout occurrence can be defined by complex shorelines ($P = 0.005$) and high alkalinity ($P = 0.02$) (Table 5). The remainder of the species were uniform in their distribution across environmental conditions.

Discussion

Regional discrimination

Although the regional discrimination of presence and absence of fish species was statistically significant, in
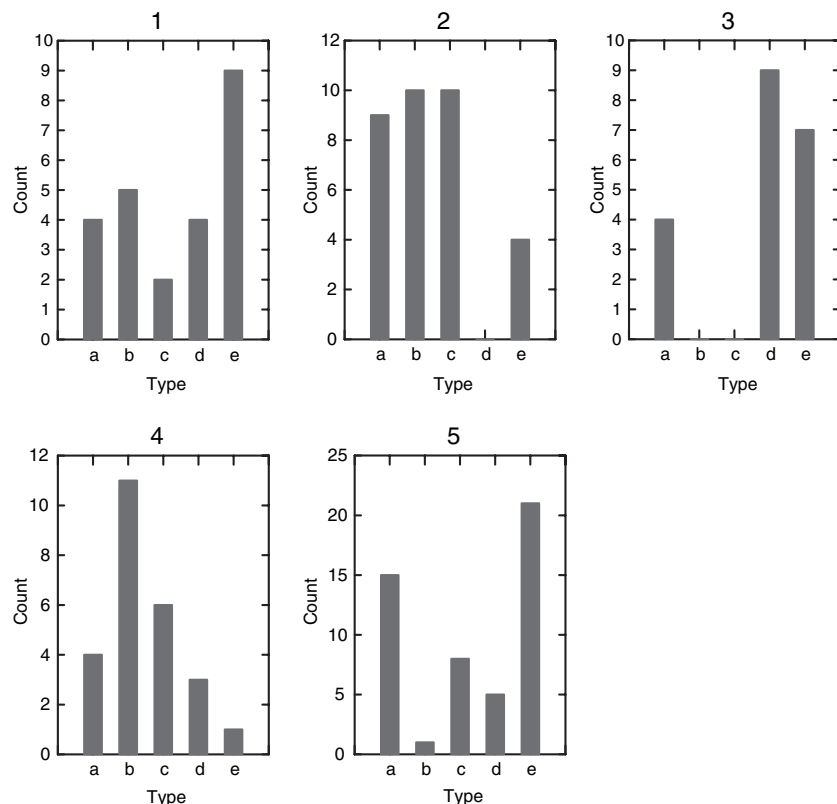
Figure 4. Fish assemblage in five regions of insular Newfoundland. Regions: 1, Northern; 2, Western; 3, Eastern; 4, Terra Nova; 5, Avalon. Assemblages: a, other; b, brook trout; c, brook trout and eel; d, Atlantic salmon and brook trout, and e, Atlantic salmon, brook trout and eel.
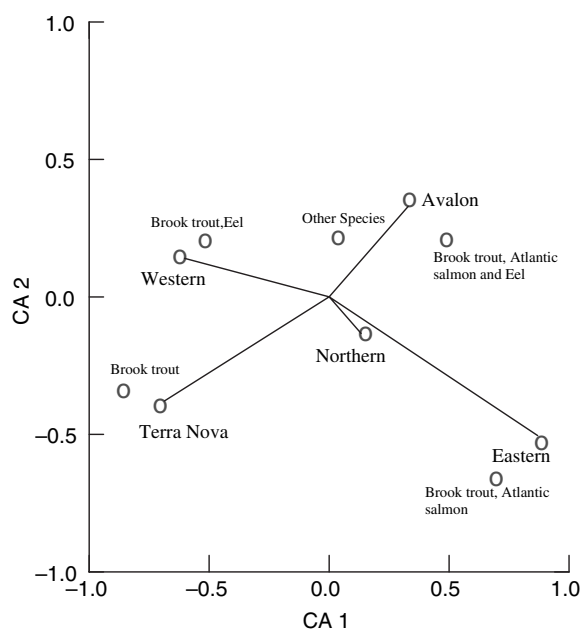

Figure 5. Axes from correspondence analysis of fish assemblage type vs. region.

reality it is more difficult to draw definitive conclusions. The low species diversity characteristic of insular Newfoundland (Scott & Crossman 1964) is reflected in simple communities that vary in frequency occurrence and species richness. Unlike temperate freshwater fisheries, which may have greater than 50 species (e.g. Pires, Cowx & Coelho 1999) in a regional species pool, northern boreal systems have generally less than 13 species (e.g. Robinson & Tonn 1989). Consequently, one must decide whether the variation observed is sufficiently large to warrant the discrimination of regions and lake types based on different fish species composition.

Lake ordination scores from the CA suggested that regions were distinctive with respect to species presence and absence. The extent to which the regions differed along the CA axes is a relative measure of biological separation (Jackson & Harvey 1989). Lakes in the Eastern region were most distinct. The eastern region had the least variability in fish assemblage type but had the highest complexity (Fig. 4; Table 4). This region exhibited a high degree of regional fidelity in both biological and environmental properties of lakes in the CVA. The greatest cause of variation in the environ-

Table 4. Occurrence of fish species in the five regions expressed as a percentage of lakes, community complexity and total number of fish assemblage types by region

Species and community types		Regions and percentage occurrence				
Common name	Scientific name	Northern	Western	Eastern	Terra Nova	Avalon
Brook trout	*Salvelinus fontinalis*	100.00	97.00	100.00	100.00	86.00
Arctic char	*Salvelinus alpinus*	17.00	24.00	20.00	8.00	4.00
Brown trout	*Salmo trutta*	0.00	0.00	0.00	8.00	20.00
Atlantic salmon	*Salmo salar*	71.00	30.00	100.00	32.00	70.00
Rainbow trout	*Onchorhnychus mykiss*	0.00	3.00	0.00	8.00	6.00
American eel	*Anguilla rostrata*	54.00	64.00	55.00	44.00	72.00
Rainbow smelt	*Osmerus mordax*	67.00	15.00	80.00	12.00	30.00
Banded killifish	*Fundulus diaphanus*	0.00	0.00	15.00	0.00	0.00
Two-spined stickleback	*Gasteroteus wheatlandi*	8.00	6.00	0.00	0.00	2.00
Three-spined stickleback	*Gasteroteus auleatus*	75.00	39.00	95.00	24.00	70.00
Four-spined stickleback	*Apeltes quadracus*	4.00	6.00	0.00	0.00	2.00
Nine-spined stickleback	*Pungitius pungitius*	13.00	9.00	0.00	0.00	2.00
Community complexity		0.95	0.59	1.00	0.30	0.92
Number of community types		7.00	8.00	3.00	6.00	14.00

Table 5. Results of occurrence sequence analysis for the seven most common fish species along a gradient of six environmental variables

	Species Distribution						
Environmental variable	Atlantic salmon	Brook trout	Arctic char	Brown trout	American eel	Rainbow trout	Rainbow smelt
Surface area	HIGH	U	U	U	HIGH	U	HIGH
Shoreline development	U	U	U	U	**HIGH**	HIGH	U
PH	U	U	U	U	**HIGH**	U	U
Secchi disc	U	U	*HIGH*	U	U	U	U
Maximum depth	U	U	*HIGH*	U	U	U	U
Alkalinity	U	U	U	U	U	HIGH	U

Species are classified as being on the low or high end of the distribution or having a uniform distribution throughout the gradient. All tests were Mann–Whitney U-tests of the patterns of species presence and absence. Significance at the $P < 0.05$ level is indicated in bold and at $P < 0.01$ is in italics.

ment of the area is the result of climatic differences (Damman 1983).

The Western and Terra Nova regions were also biologically distinct. These regions support simple communities with an intermediate number of fish assemblages (Fig. 4; Table 4). The two regions were difficult to distinguish in the CVA. Species encountered were common to both regions, with brook trout and eel predominating. Atlantic salmon, rainbow smelt and three-spined stickleback occurred less frequently compared with other regions. In the Western region, the lower occurrence of these species may be the result of differential dispersal ability of different fish species linked to large elevation changes during post-glacial colonisation. Terra Nova lakes were characterised by the lowest surface areas, shallower depth range and lower maximum secchi disc depth range. These smaller, shallow lake environments (morphometric

constraints) also have lower species richness (Tonn & Magnuson 1982; Jackson & Harvey 1989). Additionally, shallower lakes in the Terra Nova region may limit species because of little availability of overwintering habitat and high over-winter mortality (Tonn & Magnuson 1982).

The Avalon is also distinct along the CA axis, exhibiting the greatest variety of fish assemblages. All other fish assemblages are mainly composed of combinations which include two alien fishes, the brown trout and rainbow trout, as well as the rainbow smelt, the distribution range of which has expanded through introductions (Scott & Crossman 1964). The Avalon also has the highest degree of stress from urban development, pollution and angling exploitation.

The Northern region is the least distinct, falling somewhere in the middle of the groups. The region had high richness and an intermediate number of fish

assemblages (Table 4; Fig. 4), and exhibited a broad range in both environmental and biological characteristics. The northern-most portion of the Northern region is climatically and geographically distinct (Damman 1983).

Correspondence between biological, environmental and geographical distance

At the centre of this investigation is the debate between deterministic and stochastic processes and non-random community structure. Jackson, Somers & Harvey (1992) suggested that if there is no significant pattern of association between fish community and regional/local environmental processes one can speculate that communities are just random subsets from a common species pool. In this study, Mantel's test indicated that fish populations are non-randomly structured. Thus, biological similarity among regions was significantly correlated with geographical separation but not significantly correlated with inverse distance. This suggests that larger scale processes may be more important in structuring assemblages. Biological similarity was not correlated with environmental distance. It can be concluded that faunal similarity is more dependent on larger scale processes such as post-glacial dispersal and climate, than on medium or small scale processes. Environmental distance was significantly correlated with Euclidean distance, suggesting that as the distance between two regions increased the more environmentally distinct they became. At the lake-specific level it is believed that habitat features can affect individual species distributions. This is an example of interaction between biogeographical patterns and habitat-related features of fish species distribution possibly resulting from interactions between biogeography and available habitats (Eadie & Keast 1984; Jackson & Harvey 1989).

Regional pattern in fish assemblage type

The average species richness in Newfoundland lakes is low at 3.6, compared with mainland northern temperate lakes with an average richness well over 10 (Harvey 1981; Rahel 1986). The absence of most piscine competitors and predators found on the mainland has resulted in a salmonid-dominated island (Gibson & Haedrich 1988). This was expected because of the exclusion of non-anadromous fishes that were unable to disperse across the marine environment. Although a low diversity was found, regional differences in fish assemblage structure were observed.

These regional differences in fish assemblages are related to large scale phenomena such as historical biogeographical events (post-glacial dispersal) and climatic factors. The degree of variability within regions is influenced by small scale factors in individual lake character (e.g. surface area, depth). These regional and local processes act as filters. Tonn *et al.* (1990) described the composition of local fish assemblages observed in small forest lakes as a product of a series of filters that operate, along unique or unpredictable events, on several spatial and temporal scales (Fig. 6; also see Tonn *et al.* 1990).

Distribution patterns in individual species to specific lake features

The matrix outlined in Table 5 can be used to suggest that differences in the environmental parameters can account for patterns of species presence and absence.
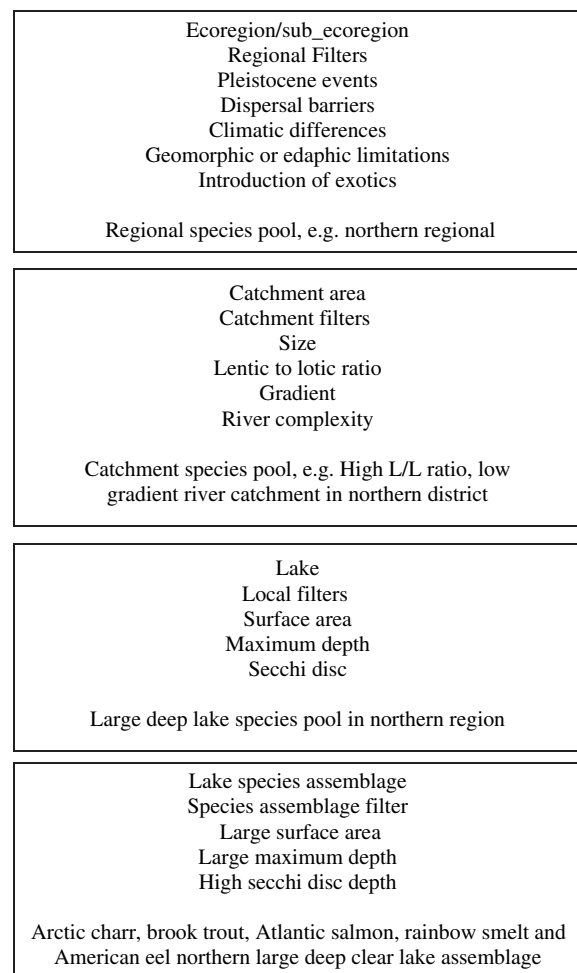

Ecoregion/sub_ecoregion
Regional Filters
Pleistocene events
Dispersal barriers
Climatic differences
Geomorphic or edaphic limitations
Introduction of exotics

Regional species pool, e.g. northern regional

Catchment area
Catchment filters
Size
Lentic to lotic ratio
Gradient
River complexity

Catchment species pool, e.g. High L/L ratio, low gradient river catchment in northern district

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Lake
Local filters
Surface area
Maximum depth
Secchi disc

Large deep lake species pool in northern region

Lake species assemblage
Species assemblage filter
Large surface area
Large maximum depth
High secchi disc depth

Arctic charr, brook trout, Atlantic salmon, rainbow smelt and American eel northern large deep clear lake assemblage

Figure 6. A conceptual model which can be used to sample a fish assemblage in a spatial and temporal context. Each filter is associated with qualitative or quantitative predictive model (modified from Tonn *et al.* 1990).

This supports the hypothesis that intraregional variability is related to small-scale in-lake attributes. The occurrence sequence analysis suggests that more complex communities are found in lakes with larger surface areas and greater depths and clarity. For example, as the surface area of the lakes increases Atlantic salmon, American eel and rainbow smelt are potential members of the species community in that particular lake. By contrast, as maximum depth and secchi disc depth lessens Arctic char would become absent. These lake-specific filters are, however, mediated at larger regional scales by biogeographical and climatic factors. The combination of species-specific filters and larger scale factors are responsible for current assemblages.

Sampling strategies

The five regions surveyed were distinct both biologically and environmentally. The regional processes or large-scale factors that may have lead to biological distinctiveness are: (i) post-glacial dispersion; (ii) extrinsic environmental factors such as climate; (iii) the dispersal of exotic species; and (iv) range expansion of native species through translocations. It is believed that the lack of significance between faunal similarity and environmental character at the regional scale may be lack of sufficient data both in terms of refinement of the data (population dynamics information), the actual number of lakes used in the analyses and the representativeness of the lakes included. An important outcome of this study is to provide insights to aid formulation of an effective and representative sampling scheme to define further regional and local differences, and secondly, to suggest what type of existing geographical models may provide useful frameworks for scientific investigation and management.

Sampling strategies focused on regional variation in environment and community demographics are required for future modelling approaches. Selection of sampling units should be based on regional scale differences in fish communities with environment (van Zyll de Jong, Cowx & Scruton 2000). It is believed that the established ecoregion scheme for the island of Newfoundland (Damman 1983) is a suitable regional geographical model to structure future sampling. Regional differences in both environmental and biological similarity were found as a function of geographical separation. The regional centroids used in Mantel's test confirmed the Damman ecoregion locations. Consequently, it can be assumed that the Damman model is a suitable strategy for larger scale sampling.

The next logical sampling unit within each ecoregion is catchment area. Arguments supporting the use of catchment area for sampling have been made by several authors (e.g. Lester & Dunlop 2003). Catchment areas can be defined as clusters of lakes that have been structured by the same regional and local factors. These natural clusters of lakes can be expected to be exposed to the same type and levels of stress. Differences are greater between different catchments than lakes within catchments. This is a critical assumption if one is to compare fisheries between systems. The sampling regime should incorporate a comparative approach to the study of lake clusters (Fig. 6). This approach is based on two major assumptions: (i) that ecological structures and processes observed in one lake will be governed by similar processes in other similar lakes; and (ii) that comparisons of lakes and their biotic communities over space and time and over a wide range of physical, chemical and climatic conditions, will provide a much broader insight than studies at a single point in time (Evans, Henderson, Bax, Marshall, Oglesby & Christie 1987). This study provided data on the structural and functional responses of fish communities and populations over a wide range of temporal and spatial scales.

The next level of investigation is at the individual lake level within a catchment. Local processes responsible for differences in localised community structure can be used as selection criteria. What do the data suggest in terms of a quantitative sampling regime? Easily measurable properties of lakes can be used to select sites for sampling within catchments (Fig. 6). Surface area, maximum depth and secchi disc depth levels could be used for selection. In the current example, sampling levels could be established based on the ranges of observed values (5–95%; Table 1; Fig. 6). The probability of a particular species inhabiting a lake in a particular region could be predicted first by the regional species pool (what is present and absent) and then with the occurrence matrix at the lake-specific level.

The sampling strategy proposed attempts to account for the variation observed between regions and lakes. The strategy embeds these relationships in a landscape hierarchy that serves as a template for sampling (Fig. 6). This approach has attempted to set the scene for the development of regional predictive models. The next step is to select a number of catchments and begin to collect more refined data on population dynamics, importance of lake-habitat features and fisheries exploitation.

The comparative multiscale approach used in this study illustrates the importance of looking at biological processes over varying spatial scales. Multivariate

investigations of biological and environmental parameters illustrated the extent of regional differences. By relating the regional picture to individual variation in lakes it is possible to conceptualise a model that lays the foundation for direct experimentation and model building. This approach will allow questioning at the appropriate temporal and spatial scales. Beyond the direct application of a model to sampling a specific problem, it also allows the identification of critical filters in the structuring of species assemblages.

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