

A multi-scale comparison of trait linkages to environmental and spatial variables in fish communities across a large freshwater lake

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Abstract Species present in communities are affected by the prevailing environmental conditions, and the traits that these species display may be sensitive indicators of community responses to environmental change. However, interpretation of community responses may be confounded by environmental variation at different spatial scales. Using a hierarchical approach, we assessed the spatial and temporal variation of traits in coastal fish communities in Lake Huron over a 5-year time period (2001–2005) in response to biotic and abiotic environmental factors. The association of environmental and spatial variables with trophic, life-history, and thermal traits at two spatial scales (regional

basin-scale, local site-scale) was quantified using multivariate statistics and variation partitioning. We defined these two scales (regional, local) on which to measure variation and then applied this measurement framework identically in all 5 study years. With this framework, we found that there was no change in the spatial scales of fish community traits over the course of the study, although there were small inter-annual shifts in the importance of regional basin- and local site-scale variables in determining community trait composition (e.g., life-history, trophic, and thermal). The overriding effects of regional-scale variables may be related to inter-annual variation in average summer temperature. Additionally, drivers of fish community traits were highly variable among study years, with some years dominated by environmental variation and others dominated by spatially structured variation. The influence of spatial factors on trait composition was dynamic, which suggests that spatial patterns in fish communities over large landscapes are transient. Air temperature and vegetation were significant variables in most years, underscoring the importance of future climate change and shoreline development as drivers of fish community structure. Overall, a trait-based hierarchical framework may be a useful conservation tool, as it highlights the multi-scaled interactive effect of variables over a large landscape.

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Introduction

The importance of factors acting at different spatial scales has long been acknowledged as a common theme in ecology (Wiens 1989). Broad regional-scale environmental

factors can overwhelm local inter- and intra-specific interactions (Menge and Olson 1990; Grossman et al. 1998), but the importance of factors at different spatial scales in shaping community structure may be temporally variable and linked to specific disturbances from local to regional scales (Connell et al. 1997; Edwards 2004). Furthermore, communities contain species with distinct functional traits: these species may show different responses to forces acting at different spatial scales (Hughes et al. 1999; Burrows et al. 2009). Thus, determination of the scales at which communities are structured requires the appropriate temporal and taxonomic resolution.

The presence of species with specific traits in distinct habitats is the result of a set of environmental and historical filters operating at spatial scales ranging from regional to local (Smith and Powell 1971; Keddy 1991; Poff 1997; Jackson et al. 2001). This process produces communities in which traits are organized hierarchically across spatial scales (Allen and Starr 1982), and community analyses based on this concept have been helpful in understanding the organization of a variety of systems (e.g., streams, Lamouroux et al. 2002; Hoeinghaus et al. 2007; forests, Lindenmayer et al. 2006). Despite the importance of hierarchical filters in biodiversity monitoring and conservation (Zacharias and Roff 2000), a hierarchical framework has rarely been used to describe multi-scale trait assemblages in lentic habitats, even though lakes could be subject to the same hierarchical processes as streams.

In the study reported here, we investigated how a hierarchical analysis can provide new insights into the effects of environmental variation at different spatial scales on coastal fish communities along a 300-km stretch of the Lake Huron shoreline. Lake Huron is one of the largest of the North American Great Lakes, and our analysis is based on a 5-year (2001–2005) survey of the coastal fish communities found in the Georgian Bay and North Channel basins [Electronic Supplementary Material, ESM1]. These basins of Lake Huron have different hydrological regimes (Sly and Munawar 1988): compared to Georgian Bay, the North Channel has a shorter flushing time, a larger catchment area compared to its surface area, a shallower mean depth, and less human development along its shoreline. In addition, the North Channel receives inflow directly from Lake Superior, which may substantially influence its biotic and abiotic characteristics. Thus, there are a broad range of conditions that may affect the distribution of traits in fish communities found within each region.

Although a hierarchical organization of freshwater lakes is typically considered at the scale of the landscape (Tonn et al. 1990), we expect that the same processes that drive the organization of a series of interconnected lakes on a landscape will also occur within a large freshwater lake. For example, distant locations within a large lake may be

more influenced by smaller scale differences in basin or shoreline morphology than by regionally homogeneous influences (e.g., Blukacz et al. 2009). Further, a hierarchical organization of communities is common in coastal marine systems (Menge 1992), a functional analogue of coastal systems in large freshwater lakes.

Our main objective was to test the hypotheses that the trophic, life-history, and physiological traits of species making up the fish communities in Lake Huron would be (1) predominately influenced by small local-scale variation and (2) that this pattern will be consistent over time. These hypotheses stem from results of comparable studies. For example, Edwards (2004) showed that during periods of relative environmental stability, coastal kelp beds were generally structured at the smallest spatial scales, associated with particular physical and biological factors; however, following a substantial disturbance (i.e., an El Niño event), greater amounts of variation were explained by larger spatial scales, representing climatic factors. Other studies have also documented greater variability in communities at smaller spatial scales (Karlson and Cornell 1998; Hughes et al. 1999). As coastal areas in our study were generally unaffected by broad-scale climatic disturbances (e.g., strong El Niño events) over the 5-year survey (Environment Canada: <http://www.ec.gc.ca/adsc-cmda/default.asp?lang=En&n=E0ABE4B3-1>), we predict that local-scale variation will be more important. There are, however, other broad-scale factors that may influence our predictions, such as population expansion of double-crested cormorants (*Phalacrocorax auritus*) and offshore food-web changes. Double-crested cormorants are fish-eating waterbirds that have undergone rapid expansion in the Lake Huron basin in recent decades (Ridgway et al. 2006b); however, the effects of these waterbirds on fish communities have been variable, and information on the responses of large-lake fish communities is lacking (Stapanian 2002). Additionally, substantial changes in the offshore food-web of the entire Lake Huron basin have occurred in the last decade (Warner et al. 2009), which may have consequences for coastal and nearshore fishes (Fielder et al. 2007).

Our second objective was to examine the separate roles of hierarchical environmental and spatial factors in shaping the distribution of species traits in our system, as there is evidence that fish communities can be structured by both purely spatial and purely environmental processes, where a spatial signal is indicative of dispersal limitation (Jackson et al. 2001; Olden et al. 2001; Beisner et al. 2006; Bertolo and Magnan 2006). Understanding spatial patterns in communities is a necessity for effectively predicting responses of taxa to environmental change: species may be absent from a suitable habitat because of mechanisms of isolation, thereby reducing the efficacy of predictions

related to species–environment associations (Olden et al. 2001). Additionally, spatial patterns of trait distributions may be particularly informative, as they can allow inference of the processes that are responsible for the observed pattern. For example, taxa with life-history strategies associated with movement to periodically favorable habitats for spawning (Winemiller and Rose 1992) will likely exhibit greater spatial variation compared to less migratory taxa. However, these mechanisms of isolation may be absent from large open systems, such as Lake Huron; therefore, we predict that spatial variation in traits that is independent of environmental gradients will be minimal. A series of analytical steps was used to test our hypotheses.

Materials and methods

Study design and sampling

In order to capture the hierarchical structure of freshwater fish communities, we used a hierarchical sampling design. Seven sampling sites located within each of seven frames ($n = 49$) were sampled in Georgian Bay and the North Channel from 2001 to 2005 (ESM1). The frames were 20 km in length and located about 20 km from each other. Sites were located roughly <5 km apart and were chosen to represent the prevalent habitat within each frame, but also to have all habitat types represented within a frame. Sampling took place from mid-August to mid-September each year. Quantitative electrofishing techniques were used to assess coastal fish community composition at the sampling sites following the methods of Casselman and Grant (1998). A boat-mounted electrofishing unit was powered by a 7,000-W AC generator. The output was converted to DC voltage that was pulsed, half-wave rectified, and set at a constant 240 V with a current flow between 5 and 7 A (amps). The current flow was adjusted to immobilize the fish on the bottom and in the water column in a transect of fixed width (1.5 m) and length (200 m) parallel to the shore that was sampled during the daytime at each site. Fish were dip-netted and enumerated behind the anode array of six stainless-steel dropper rods that were mounted from a common boom on each side of the front of the boat, generating densities for each species of fish. The same transect was sampled each year, using GPS to locate the sites. Sample depths ranged from 0.3 to 3.5 m (average 1.3 ± 0.66 m), and there was inter-annual variation in sample depths attributable to changes in water levels (coefficient of variation at same site across study years 42%). The sampling rate varied slightly among frames (0.22 ± 0.02 to 0.25 ± 0.02 m s⁻¹), as did amperage (5.89 ± 0.43 to 6.71 ± 0.45 A); however, these differences were minor and likely did not influence our results.

Sites with no fish present were excluded from further analysis. For more sampling details, see Ridgway et al. (2006a).

Abiotic environmental and spatial variables

Watershed usage was determined by comparing Ontario land-use classification maps (Ontario Ministry of Natural Resources 2002) with sub-drainage basin boundaries (Natural Resources Canada 2007) in ArcGIS ver. 9.2. Watershed development was the sum of land used for agriculture, mining activities, and settlements, whereas the amount of water in the watershed was the sum of wetlands, marshes, and waterbodies. We derived air temperature data from the Canadian National Climate Data Archive (<http://climate.weatheroffice.ec.gc.ca>) for nearby stations. Mean daily air temperature for each year was averaged from ice-off to the end of August.

We estimated the degree of wave exposure of sites by determining the fetch (i.e., distance of the sampling sites to land) from eight compass points and calculating effective fetch using the Scheffer et al. (1992) formula, which accounts for the direction of prevailing winds. Wetland area was calculated using the Great Lakes Coastal Wetland Inventory map in ArcGIS 9.2 (<http://www.glc.org/wetlands/inventory.html>). Wetlands were grouped according to the primary hydrogeomorphic classification (Albert et al. 2005) and were summed within a 10-km radius of sampling sites, as this distance reflects the maximum range of movement experienced by most fishes (Minns et al. 1996). Different habitat categories were characterized visually, and temperature and conductivity were measured at every sampling site annually (Table 1).

To assess the contribution of spatial variation in structuring traits, we used the eigenvector-mapping method of Dray et al. (2006). This method creates synthetic variables (i.e., eigenvectors) that are generated from a matrix of distances (d_{ij}) between sites. The matrix is truncated by a threshold value, t , which we chose to be 10 km, as this value likely reflects the maximum range of movement experienced by most fishes (Minns et al. 1996). The remaining connected sites are weighted by a function of their proximity to each other: $1 - [d_{ij}/\max(d_{ij})]$. Eigenvectors are then computed from the centered connectivity matrix in the R libraries *spdep* and *spacemakeR* (R Development Core Team 2010). Typically, this method generates some eigenvectors with eigenvalues near zero (i.e., no explained variation); these eigenvectors were dropped from subsequent analyses. The eigenvectors with the largest eigenvalues typically represent broad-scale spatial patterns, whereas those with small eigenvalues represent small local-scale spatial patterns (Dray et al. 2006, see ESM2 for examples). Eigenvectors with positive eigenvalues are

Table 1 Environmental and spatial variables within each level of the hierarchy

Scale	Variables	Code	Type	Range	Mean
Regional basin	Watershed developed	Developed	Percentage	2.7–44.0	23.2
	Watershed water/wetlands/marshes	Water	Percentage	26.9–52.3	39.9
	Surface area (km ²)	Surface area	Quantitative	3,950–15,111	8,733
	Air temperature (°C)	Air temp	Quantitative	13.6–18.1	16.2
	<i>ev1-6</i>	<i>ev1-6</i>	Positive autocorrelation eigenvector map	Regional scale	n/a
	<i>ev38-49</i>	<i>ev38-49</i>	Negative autocorrelation eigenvector map	Regional scale	n/a
Local site	Barrier wetlands (km ²)	Barrier	Quantitative	0–83.2	4.8
	Lacustrine wetlands (km ²)	Lacustrine	Quantitative	0–51.1	4.6
	Riverine wetlands (km ²)	Riverine	Quantitative	0–74.9	2.9
	Aerial cormorant surveys	Cormorants	Quantitative	6–1,944	230
	Effective fetch (m)	Eff fetch	Quantitative	7–22,842	3,666
	Conductivity (μS cm ⁻¹)	Conductivity	Quantitative	56.2–186.7	166.0
	Temperature (°C)	Water temp	Quantitative	7–27.5	19.9
	Bedrock	Bedrock	Percentage	0–75	9
	Boulder	Boulder	Percentage	0–75	12
	Rock rubble	Rock-rubble	Percentage	0–100	41
	Sand and gravel	Sand-gravel	Percentage	0–50	7
	Silt and clay	Silt-clay	Percentage	0–90	8
	Vegetation	Vegetation	Percentage	0–100	23
	<i>ev7-12</i>	<i>ev7-12</i>	Positive autocorrelation eigenvector map	Local scale	n/a
	<i>ev15-37</i>	<i>ev15-37</i>	Negative autocorrelation eigenvector map	Local scale	n/a

ev Eigenvector, *n/a* data not available

representative of positive spatial autocorrelation, whereas those with negative eigenvalues represent negative spatial autocorrelation. Here, we will distinguish between positive and negative autocorrelation, as these signals may represent different processes. For example, seed dispersal in terrestrial plants may be positively autocorrelated at short distances, whereas negative autocorrelation may be an indicator of competition. It is important to note that significance of spatial variables in subsequent analyses may represent a number of different factors. For example, eigenvector 3 (*ev3*) in the ESM2 may represent a dispersal barrier between Georgian Bay and the North Channel; however, it may also represent covariation with broad-scale thermal patterns (air temperature) or other unmeasured spatially distinct signals (e.g., productivity).

Biotic environmental variables

Double-crested cormorants were censused using yearly aerial surveys from July to September. In the aerial surveys, ten line transects within each sampling frame were broken into eight 2.5-km sections, and cormorants within each section were counted approximately biweekly

(Ridgway et al. 2006a). We summed cormorant abundance at sites located within 20 km of electrofishing sites, as there is evidence that cormorant feeding typically occurs within roughly 20 km of colonies (Stapanian et al. 2002).

Increased abundances of some nearshore fish species have been linked to significant changes in the offshore food-web of Lake Huron from 2001 to 2004 (Fielder et al. 2007). In particular, alewife (*Alosa pseudoharengus*) is a non-native pelagic fish known to suppress the recruitment of species like walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*). We did not detect increased abundance of either walleye or yellow perch in our study (A. Strecker, unpublished), which suggests that offshore and coastal habitats may be acting in isolation of each other. Therefore, we did not consider offshore food-web changes further in our analyses.

Community traits

Life-history traits of fish species were characterized using the classification of Winemiller and Rose (1992), where species fall into a triangular continuum that is bounded by three distinct life-history strategies: equilibrium, periodic,

and opportunistic (Table 2). Species at each endpoint of the continuum tend to inhabit areas where these tradeoffs are favored: equilibrium species are found in more stable environments, periodic species occur in seasonally or periodically suitable habitats, and opportunistic species occupy disturbed and unstable habitats.

To classify the fish species in our study into this life-history framework, we collected data on length at maturity (a proxy for age at maturity), mean fecundity, and investment per progeny (a surrogate of juvenile survivorship; ESM3), from the Ontario Freshwater Fishes Life History Database (Eakins 2008) and FishBase (Froese and Pauly 2009). Attributes were plotted in three-dimensional space, standardized to z scores, and Euclidean distance was calculated to each life-history endpoint (Olden and Kennard 2010). Species were then assigned to equilibrium, periodic, or opportunistic strategies ('hard assignment') based on the distance to the closest endpoint (definitions in Table 2; assignments in ESM3). Concurrent analyses conducted with the values for the distance to each endpoint ('soft assignment') yielded qualitatively similar results, although the life-history traits were located much closer to the centroid, indicating a weaker signal. Fish were also categorized into trophic and thermal guilds with the Ontario Freshwater Fishes Life History Database (Eakins 2008) and Coker et al. (2001) (Table 2). In total, there were nine traits, with three in each category (life-history, trophic, and thermal). Although there are many other traits that would be useful in characterizing fish trait niches, the traits chosen here are responsive to environmental variation across large geographic distances (Irz et al. 2007; Erős et al. 2009) and, thus, are suitable for the purposes of our study.

Finally, we constructed a site \times trait matrix. This was done by multiplying a species \times trait matrix by a site \times species matrix. The species \times trait matrix is filled with binary presence/absence values (e.g., 1 if a species displays a trait, 0 if not), and the site \times species matrix is

filled with species relative abundances. Separate matrices were constructed for each study year, and traits were standardized prior to matrix construction.

Statistical analysis

Our first step was to qualitatively describe the relationship between fish species and traits. We performed a principal coordinates analysis (PCoA) (Legendre and Legendre 1998) on a species \times trait matrix using the Phi similarity coefficient (S), which was converted to a distance measure by $(1 - S)^{1/2}$ (Jackson et al. 1989). The Phi coefficient is a measure of association that is not influenced by the frequency of occurrence of traits, as are most other similarity coefficients (Jackson et al. 1989). As categorical traits become correlated when they are converted to binary traits, we also used Gower's dissimilarity coefficient, which can accept qualitative variables (Gower 1971). As there was no difference between PCoA performed using the Phi coefficient or Gower's coefficient, the values from the Phi coefficient are reported here for simplicity.

To test our prediction that spatial patterns in fish communities would be consistent over time, we used the methodology of Legendre et al. (2010) to examine space–time interactions in the absence of replication. Briefly, it is of general interest to ecologists to understand whether spatial structures change over time or whether communities change over time in different ways across space; however, long-term studies typically have unreplicated study units, leading to insufficient degrees of freedom to test interactions. Following Legendre et al. (2010), we used a two-way analysis of variance (ANOVA) model with a coding structure for space and time that allows us to test for significant main effects as well as a space–time interaction. As the presence of a significant interaction would confound the interpretation of subsequent analyses, we report here that there was no significant space–time interaction in the

Table 2 Traits of fish species observed in Georgian Bay and the North Channel. Life-history endpoints are defined following Olden and Kennard (2010)

Category	Trait	Type	Description
Trophic	Piscivore	Binary	Consumes fish
	Insectivore	Binary	Consumes insects or other invertebrates
	Omnivore	Binary	Consumes both plant and animal matter
Life-history	Opportunistic	Binary	Small size at maturation, produce small clutches, small-bodied, low survivorship of juveniles
	Periodic	Binary	Large size at maturation, seasonal spawners, produce large clutches, are large-bodied, low survivorship of juveniles
	Equilibrium	Binary	Large size at maturation, small to medium-sized, produce moderate-sized clutches, and have high survivorship of juveniles
Thermal	Cold	Binary	<19°C
	Cool	Binary	Approx. 19–25°C
	Warm	Binary	>25°C

fish community structure (999 permutations; $F = 0.95$, $P = 0.67$), indicating that the spatial structure of the community did not change over the course of our study.

To account for the hierarchical nature of our environmental variables, we ran preliminary partial ordination analyses in which we tested the significance of local-scale variables on the abundance of species traits (trait \times site matrix) while controlling for the effects of regional-scale variables (Legendre and Legendre 1998). Partial ordinations are analogous to partial multiple regressions, where all variables but the variable of interest are held constant, allowing for significance testing of the variable of interest without the confounding effects of covariables. For local-scale variables that were significant in partial ordinations at $P < 0.05$, we removed the effect of the regional-scale variables by performing a multiple regression and retaining the residuals from the model, which were then used for further analysis.

Redundancy analyses (RDA) were used to describe the relationship between trait abundances (trait \times site matrix) and environmental and spatial variables (Legendre and Legendre 1998). RDA was chosen as communities generally showed a limited range in their gradient, determined with a detrended correspondence analysis. Environmental variables were standardized as z scores, and colinear variables were discarded if variance–inflation factors exceeded 10.

As numerous studies have demonstrated that environmental and spatial factors can covary with each other, we used a series of statistical analyses designed to assess the independent and shared contributions of these variables. As the usage of the eigenvector mapping method generates a large number of spatial variables (number of sites $- 1$), we first filtered these variables by running a RDA on each spatial variable in every year, only retaining variables that explained significant variation in traits ($P < 0.05$). Partial RDAs (“all-variable partial RDAs”) were used to assess the independent contributions of environmental variables (controlling for spatial covariation ES) and spatial variables (controlling for environmental covariation SE). Spatial variables were further broken down into positive autocorrelation ($+SE$) and negative autocorrelation ($-SE$) as outlined in the [Abiotic environmental and spatial variables](#) section. Both environmental and spatial partial RDAs indicated that there was a substantial amount of variation contained in the covariable set, thus we assessed the shared covariation between environmental and spatial variables (SNE) with variation partitioning (Peres-Neto et al. 2006). Additionally, we assessed the relative contributions of regional- and local-scale variables in shaping fish species traits with variation partitioning. The significance of independent fractions was assessed with permutation tests

(Legendre and Legendre 1998). Permutations of this nature may have inflated type I error rates (Dray and Legendre 2008); however, Anderson and Legendre (1999) demonstrated that this method produces more consistent results compared to other permutational procedures.

Finally, for several variables that were significant in our analyses, we also assessed the correlations of traits with these variables by running a partial RDA with the single significant variable (“single-variable partial RDA”) while holding all other significant variables constant. The loading of traits on the first constrained axis was indicative of the correlation of the trait with the chosen variable. This was only performed on variables that were identified as significant in “all-variable partial RDAs.” As the amount of variation explained in multivariate ordinations was influenced by the number of variables included in the model (Peres-Neto et al. 2006), we corrected for this bias using the scripts provided in the R library *vegan* and report the adjusted R^2 (R^2_{adj}) values for variation partitioning results. All analyses were performed in R ver. 2.10 (R Development Core Team 2010).

Results

Distribution of traits across species and space

The fish species found in Georgian Bay and the North Channel could be categorized by a combination of trophic, life-history, and thermal traits (Fig. 1). The first principal coordinate axis explained 30% of the variation in traits (PCoA1; $\lambda_1 = 5.65$) and was positively associated with warm-water and equilibrium strategists and negatively associated with cool-water thermal strategists (Fig. 1). The second principal coordinate axis explained 24% of the trait variation (PCoA2; $\lambda_2 = 4.40$) and separated insectivores, opportunistic, equilibrium, and cold-water taxa from omnivores, piscivores, and periodic strategists (Fig. 1). All traits were found within all sampling frames; however, there were differences in the relative distribution of traits (Table 3). Piscivores and warm-water fishes tended to be more common at Georgian Bay sites compared to North Channel sites, which had greater abundances of insectivores and cold-water taxa (Table 3). However, we found a tendency for considerable variation of each trait within the set of sites from Georgian Bay and from the North Channel. Bluntnose minnow (*Pimephales notatus*), sculpin (*Cottus* spp.), lake chub (*Couesius plumbeus*), smallmouth bass (*Micropterus dolomieu*), and rock bass (*Ambloplites rupestris*) were the most abundant species, and bluntnose minnow, smallmouth bass, carp (*Cyprinus carpio*), sculpin, and bowfin (*Amia calva*) had the highest biomass.

Fig. 1 Principal coordinate analysis (PCoA) of the association of traits with fish species in Georgian Bay and the North Channel of Lake Huron. Species scientific names are given in Electronic Supplementary Material S3 and trait definitions are provided in Table 2

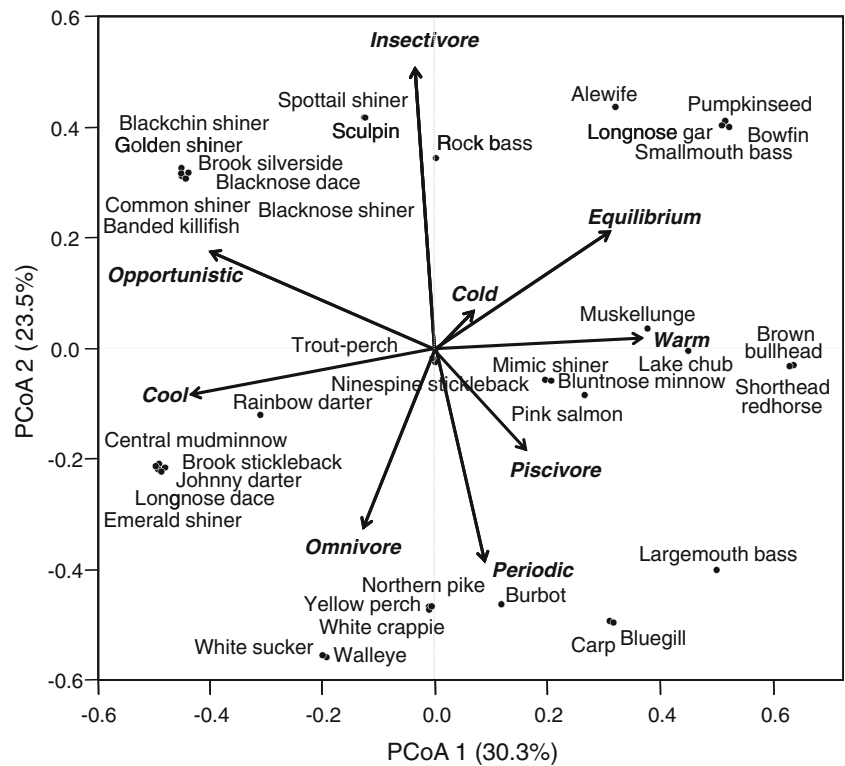


Table 3 Average relative abundance (%) of trophic, life-history, and thermal traits across frames (1–7) located in Georgian Bay and the North Channel over all study years

Traits	Georgian Bay			North Channel			
	1	2	3	4	5	6	7
Trophic							
Piscivore	27.0	16.9	31.0	4.7	15.4	23.2	11.3
Insectivore	5.0	10.3	9.9	25.1	24.5	42.0	47.8
Omnivore	68.0	72.9	59.1	70.2	60.1	34.9	40.9
Life-history							
Opportunistic	67.5	80.0	62.3	70.9	79.0	61.4	67.9
Periodic	5.0	8.4	10.0	8.1	8.1	16.9	10.5
Equilibrium	27.5	11.6	27.7	21.0	12.9	21.7	21.6
Thermal							
Cold	1.9	2.4	2.4	42.2	19.6	48.6	54.3
Cool	17.4	21.9	40.3	10.0	21.4	24.9	24.3
Warm	80.7	75.7	57.3	47.8	59.0	26.5	21.4

See ESM1 for the location of the frames

Linkages between abundance of traits and environmental/spatial variables

Overall, we found that there were significant effects of time and space on coastal fish assemblages, but there was no significant space–time interaction. Communities changed significantly over the course of the 5-year study (999

permutations; $F = 1.56$, $P = 0.04$) and were spatially distinct (999 permutations; $F = 4.59$, $P < 0.01$). To elucidate these results, we used redundancy analyses to assess the relative contributions of environmental and spatial variables in explaining community composition in each year from 2001 to 2005. There were significant differences among years in the amount of variation in fish traits explained by environmental and spatial variables as well as spatial–environmental covariation (Fig. 2). Total variation described by spatial and environmental variables ranged from $R^2_{adj} = 0.28–0.53$, with each year showing distinct differences in the relative importance of variables. Environmental variables explained more variation in trait abundance than spatial variables in 2001 and 2003 (Fig. 2). In contrast, spatial and spatially structured environmental factors explained more variation in 2002, 2004, and 2005 (Fig. 2). In 2002 and 2005, the independent contributions of environmental variables were generally minor in comparison to spatial and spatially structured environmental gradients (Fig. 2). Positive spatial autocorrelation (+SIE) explained some variation in traits in all years, but negative spatial autocorrelation (–SIE) was less influential (Fig. 2). All spatial and environmental fractions were significant at $P < 0.05$, with the exception of environment ($P = 0.47$) and positive autocorrelation ($P = 0.06$) in 2002, and positive ($P = 0.07$) and negative ($P = 0.07$) autocorrelation in 2005 (note that the shared spatial–environmental fraction cannot be tested).

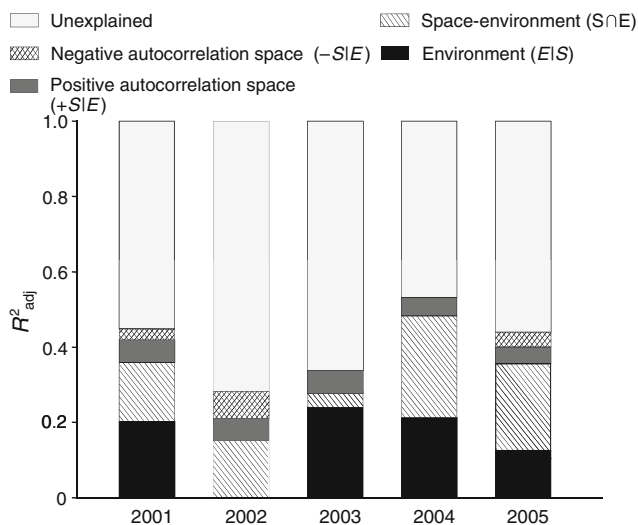


Fig. 2 Proportion of variation (R^2_{adj}) in trait abundance attributed to environmental variables ($E|S$), shared covariation between environmental and spatial variables ($S\cap E$), positively autocorrelated spatial variables ($+S|E$), negatively autocorrelated spatial variables ($-S|E$) or unexplained, from 2001 to 2005. The shared fraction is indicative of a spatially structured environmental gradient. All spatial and environmental fractions were significant at $P < 0.05$, with the exception of environment ($P = 0.47$) and positive autocorrelation ($P = 0.06$) in 2002, and positive autocorrelation ($P = 0.07$) and negative autocorrelation ($P = 0.07$) in 2005

We also identified the relative importance of variation at different hierarchical spatial scales. In 2002, 2004, and 2005, regional basin-scale variables were generally the most important, whereas local site-scale variables were more significant in structuring fish community traits in 2001 and 2003 (Figs. 3, 4). Both regional and local fractions of variation were significant in all years ($P < 0.05$).

Specific associations between traits and environmental/spatial variables

Warm-water taxa, piscivores, and opportunistic strategists generally clustered together in ordination space and tended to be positively associated with air temperature and watershed development and negatively correlated with vegetation (Fig. 4). Opportunistic life-history strategies tended to occupy different regions of ordination space from those of equilibrium and periodic strategists, whereas omnivores and insectivores clustered together in most years of the study (Fig. 4). Not surprisingly, insectivores and omnivores tended to be negatively correlated with piscivores, and cold-water species were negatively correlated with air temperature (Fig. 4). Silt-clay habitat was significant in 3 years and was associated with cool-water and periodic strategists (Fig. 4). Cormorant abundance was significant in 2003 and was negatively correlated with periodic, insectivorous, and cool-water fishes (Fig. 4c).

Cormorant abundance was negatively correlated with vegetation, suggesting that cormorants may forage in low vegetation habitats (Fig. 4c).

By examining the independent effects of variables while controlling for confounding covariates (“single-variable partial RDAs”), we can directly assess relationships between variables and traits. We chose to test vegetation, which was clearly a dominant variable in the study, as well as all significant spatial variables, as we were interested in the scales to which different traits responded. Vegetation was a significant variable in all years but 2002, influencing piscivores, opportunistic, cold- and warm-water taxa (negative), and insectivores, periodic, and cool-water fish abundance (positive) (Table 4). Interestingly, the direction of the effect of vegetation reversed for a number of trait categories in 2004, the coldest year of the study (Table 4). No single spatial variable was significant in >1 year (independent of environmental variation) (Table 4). Most traits seem to be influenced at multiple spatial scales (e.g., piscivores, opportunistic), and, with the exception of omnivores, most traits were moderately to highly spatially structured (Table 4).

Discussion

Trait composition within communities can reflect the role of functional groups in the ecosystem and the prevailing environmental conditions (Poff 1997). The use of traits in biomonitoring and ecological studies has proven an effective way to reduce some of the complexity of communities and allow comparison of communities across regions (Lamouroux et al. 2002). Using a hierarchical approach designed to assess the independent effects of local-scale variables, we observed significant temporal variability in some responses of traits to environmental and spatial variables in coastal fish communities, as well as shifts in the importance of regional-basin versus local-site scale variables. These results have implications for the conservation of species and habitats, as well as our understanding of the hierarchical filters that structure communities (Allen and Starr 1982).

We observed significant inter-annual variability in the responses of fish community traits to environmental and spatial variables, as well as significant spatial structuring of traits (Figs. 2, 4). We had hypothesized that fish community traits would respond to spatial scales consistently across years; this prediction was met, as we did not observe a significant change in the spatial scales of trait distributions over time using the space-time interaction methodology of Legendre et al. (2010). Our analysis indicated that traits are structured at multiple spatial scales, with no clear dominance of one scale over the other (Fig. 3), contrary to

Table 4 Correlation of traits with axis 1 of single-variable partial redundancy analyses for vegetation and significant spatial variables (e.g., *ev1*)

Traits	Environmental				Spatial					
					Regional scale		Local scale			
	Vegetation				<i>ev1</i>	<i>ev41</i>	<i>ev7</i>	<i>ev8</i>	<i>ev12</i>	<i>ev22</i>
	2001	2003	2004	2005	2005	2001	2002	2004	2001	2002
Trophic										
Piscivore	-0.20	-0.16	0.02	-0.28	0.33	-0.40	0.16	0.23	-0.38	-0.17
Insectivore	0.08	0.16	-0.01	0.27	-0.23	0.39	0.25	-0.26	0.33	0.16
Omnivore	0.12	-0.01	-0.01	-0.01	-0.09	-0.01	-0.44	0.04	0.02	0.01
Life-history										
Opportunistic	-0.29	-0.31	0.28	-0.45	0.26	-0.01	0.34	0.09	-0.41	0.32
Periodic	0.16	0.40	-0.28	0.13	0.00	-0.19	-0.45	-0.06	0.12	-0.24
Equilibrium	0.18	-0.04	-0.04	0.38	-0.30	0.21	0.06	-0.05	0.35	-0.12
Thermal										
Cold	-0.39	-0.08	0.34	-0.40	-0.12	0.31	0.29	-0.04	0.01	-0.36
Cool	0.34	0.45	-0.49	0.42	-0.24	-0.22	-0.36	-0.32	0.43	-0.08
Warm	-0.03	-0.42	0.23	-0.10	0.37	-0.04	0.14	0.38	-0.48	0.41

Note: the response of traits to spatial variables should be assessed only within each column (e.g., piscivores and insectivores exhibit opposing responses to spatial variable *ev1*)

Correlations >0.1 are given in bold

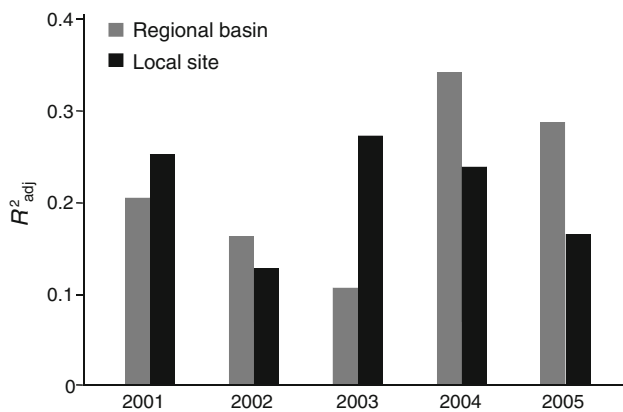


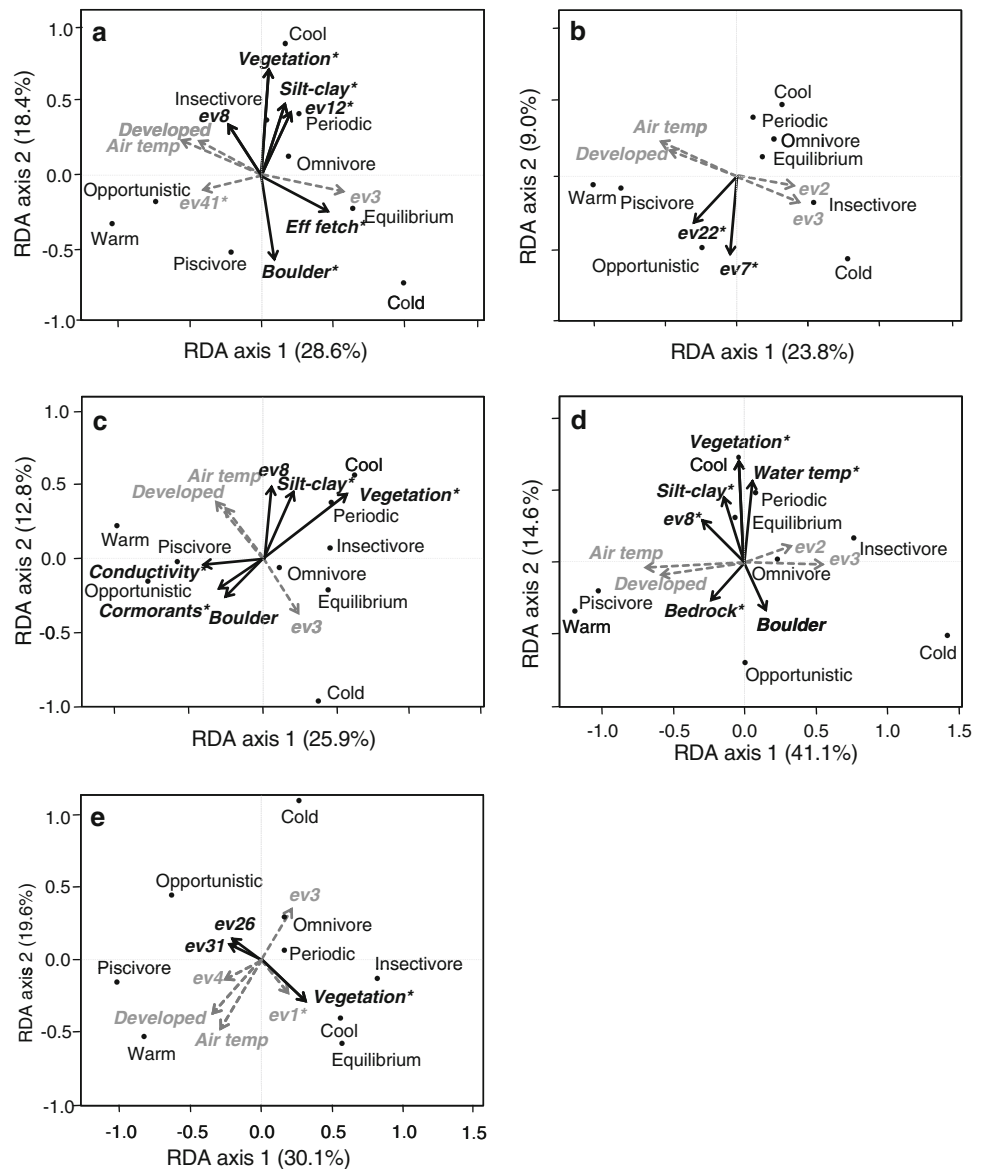
Fig. 3 Proportion of variation (R^2_{adj}) in trait abundance attributed to regional basin and local site-scale variables from 2001 to 2005. All fractions are significant at $P < 0.001$

our prediction that local site-scale variables would be most important in all years of our study (Karlson and Cornell 1998; Hughes et al. 1999; Edwards 2004). However, there were some inter-annual differences in the relative importance of variables at local versus regional scales (Fig. 3). For example, local variables were more important than regional variables in 2 years, namely, 2001 and 2003. These inter-annual differences may reflect broad-scale processes masking the influence of smaller scale variation (Brazner and Beals 1997; Grossman et al. 1998; Edwards 2004). Although there were no extreme weather events during our study, such as a strong El Niño, the importance

of regional basin-scale variation in fish traits in 2002, 2004, and 2005 may be related to shorter term (i.e., seasonal) temperature events. In our survey, summer air temperatures were the coldest and warmest in 2004 and 2005, respectively (National Oceanic and Atmospheric Administration: <http://tidesandcurrents.noaa.gov/nwlon.html>). Additionally, there was a moderate El Niño event in 2002 (Environment Canada: <http://www.ec.gc.ca/adsc-cmda/default.asp?lang=En&n=E0ABE4B3-1>). Warmer air temperatures have been linked to changes in the timing of large-lake thermal stratification, resulting in shifts in phytoplankton blooms and a mismatch in the timing of crustacean zooplankton populations with phytoplankton biomass, with possible consequences for higher trophic levels (Winder and Schindler 2004). These deviations in temperature may override the effects of environmental variables at smaller scales. Indeed, temperature is largely considered to be a master variable for fishes (Magnuson et al. 1979), controlling growth rates, reproduction, and development (Shuter and Post 1990), and may thus have an influence on the distribution of traits in fish communities at both warm and cold extremes (Casselman 2002).

Other factors may also have influenced the inter-annual differences observed in the relative importance of different spatial scales to fish community trait abundance. Rudstam et al. (2004) showed that double-crested cormorants can significantly affect fish communities; however, we detected significant effects of cormorants on trait composition in only 1 study year. We cannot rule out the possibility that

Fig. 4 Redundancy analyses (RDA) of trait abundance in 2001 (a), 2002 (b), 2003 (c), 2004 (d), and 2005 (e). Dashed gray and solid black vectors represent significant regional and local variables, respectively, and circles represent trait categories. Asterisks represent variables that were significant in partial RDAs ($P < 0.05$) and therefore represent significant independent contributions. All ordinations were significant using Monte Carlo permutation testing ($P < 0.05$). Abbreviations as in Table 1



these fish-eating birds may be affecting coastal fish communities, but it may be that cormorants are generalist feeders, which would likely prevent us from detecting effects with the trait-based framework that we have used. Additionally, we failed to observe noticeable effects of offshore food-web changes on coastal fish communities. Thus, we can rule out several of the major factors that were occurring at the entire lake scale as explanations for inter-annual variation in the importance of regional versus local scales. It is clear that coastal fish communities in Lake Huron are highly temporally and spatially dynamic; therefore, to fully understand these complex assemblages, sampling strategies must reflect the scales identified here.

Extinction and recolonization dynamics play a significant role in shaping freshwater fish community structure (Tonn et al. 1990; Magnuson et al. 1998). These dynamics

are influenced by the degree of spatial isolation of systems, as fish movement is restricted to water courses; thus, the inclusion of spatial predictors into models of fish distributions can greatly improve understanding of linkages between environmental conditions and species (Olden et al. 2001). In our study, the addition of multi-scale spatial predictors increased variation explained in trait composition by 25%, on average, with a high of 32% in 2004 ($SE + SNE$; Fig. 2). In general, the fraction of variation explained by spatial variables, independent of environmental factors, was small (average 8%, range 5–13%); however, these values are on par with values obtained for fish communities in smaller groups of lakes (11%, Beisner et al. 2006; 6%, Erős et al. 2009). Interestingly, variables representing positive spatial autocorrelation appeared to be more important predictors of fish traits than were variables

representing negative autocorrelation, suggesting that the trait distribution of fish communities tends to be more structured by processes that generate patchiness or clumping. Although it is possible that spatial predictors are representative of unmeasured environmental factors, we quantified a number of variables known to be important to freshwater fishes, including temperature, habitat, predators, and conductivity. Our results suggest that coastal fish communities in large lakes may be structured in functionally similar ways to drainage lakes. This may be due to the nature of our coastal sampling sites: many of these shallow nearshore areas would freeze over in winter and be less accessible, thus promoting an annual recolonization of sites. Also, some coastal fishes show high nest fidelity and can have substantial genetic divergence within the same lake, despite the absence of geographic barriers (Stepien et al. 2007), which implies that dispersal may be limiting for some coastal species. Although we might expect that small-bodied species are possibly more dispersal limited because of a lower mobility and smaller home range size, the ratio of abundance of small-bodied to large-bodied fishes was not related to the amount of independent spatial variation explained ($R^2 = 0.10$). This lack of an association implies that dispersal limitation might be species specific: for example, omnivores appear to be less spatially structured compared to other trait characterizations, suggesting that these species are not limited by dispersal and are prevalent in most sites (Table 4). Further study is necessary to elucidate the mechanistic basis of the spatial patterns that we have observed here.

In general, we were able to describe moderate amounts of variation in fish community traits in Lake Huron. This is not uncommon in ecological studies: both taxonomic and trait-based approaches for fish communities in lakes and rivers tend to yield results similar to those of our study (20–60% of variation explained: Beisner et al. 2006; Hoeninghaus et al. 2007; Mehner et al. 2007; Erős et al. 2009). That we observed such a range of variation (28–53%) within the same lake over a period of 5 years likely reflects a combination of both process and sampling error. Fish utilize coastal areas at different parts of their life cycle (Stephenson 1990), generating both seasonal and diurnal variation in habitat selection that likely influences the probability of detection with electrofishing techniques. Diekmann et al. (2005) revealed that although species richness and diversity were highest in littoral zones sampled by electrofishing, about 21% of fish species were missed by electrofishing (compared to gill nets), whereas 12% of species were only found with electrofishing. In our study, 11 species were only found in a single location on a single date. Thus, some of the unexplained variability in our study is likely related to the detection of rare species. However, the use of a trait-based classification should

reduce the influence of rare species. It is of interest that fish from all trait categories were found in all sampling frames in our study, despite the possibility of exceeding physiological tolerances. For example, cold-water species were found in low abundance in Georgian Bay (Table 3) despite water temperatures that often exceeded 22°C. Indeed, water temperatures taken concurrent with fish community sampling were generally not significantly correlated with fish thermal traits (Fig. 4). This result suggests that fish species may periodically venture into unsuitable habitats, confounding our ability to link environmental preferences with the presence of specific traits (e.g., cold-water lake trout in warm-water habitats, Morbey et al. 2006) and possibly in part underlying the sometimes weak explanatory power of the variables used in this study. Additionally, although our analysis included a number of variables that are important to fish communities, the inclusion of other important factors, such as competitive interactions (Jackson et al. 2001), may have increased the amount of variability explained. Despite the large continuous nature of Lake Huron, there was significant variability in environmental factors (Table 1) and fish assemblages: average compositional similarity of fish communities between lake basins was 0.41 (Phi coefficient). These factors suggest that there were detectable differences in communities and environmental conditions with the analyses used herein.

Traits provide an important template to understand the factors that influence communities, including associated tradeoffs and relationships with environmental and spatial variability (e.g., life history, Winemiller and Rose 1992; Olden et al. 2006). For example, we observed multi-year correlations between vegetation and life-history traits, especially for opportunistic (negative) and periodic (positive) taxa (Table 4). This outcome was expected, as periodic strategists have adopted life-history traits that succeed in periodically suitable habitats, such as coastal waters and wetlands (i.e., vegetated areas), which are utilized by many fishes at some point in their life span (Stephenson 1990). It also seems likely that these life-history traits are correlated with other trait categories, such as trophic level: several periodic life-history taxa are classified as omnivores or piscivores and thus may have been foraging in vegetated habitats for smaller-bodied opportunistic prey (Fig. 1). However, omnivores were strongly correlated with vegetation in only 1 year (Table 4); thus, it seems likely that vegetation is having some significant effects on life-history trait abundance. Additionally, some traits appeared to be insensitive to spatial scales, suggesting that taxa with flexible or intermediate characteristics are more broadly distributed than species with more specialized traits, such as insectivores and warm-water fishes. Assessments of specific associations of traits and environmental and spatial factors in fish communities may provide insight into

mechanisms structuring communities that are not reflected in species distributions. Some of the species that adopt different life-history strategies belong to the same family; consequently, traditional taxonomic approaches may have failed to detect significant associations and prevented meaningful patterns from being uncovered (e.g., Olden et al. 2006).

In conclusion, our hierarchical analysis provided new insights into the factors structuring coastal fish communities in Lake Huron. Studies that document the interaction between environmental and spatial factors on freshwater fish communities have been largely conducted in small drainage lakes (Beisner et al. 2006; Bertolo and Magnan 2006), hence our study provides important evidence that many of the same factors influence large lake fish assemblages as well. From a conservation standpoint, our demonstration that traits are sensitive to air temperature and vegetation highlights the importance of climate change and shoreline development as drivers of changes in fish community structure. From an ecological standpoint, our demonstration of consistent spatial scales in trait distribution over the course of our study suggests that there is a general stability in the scales at which community traits are structured, but that there may be dynamic inter-annual shifts between local versus regional forces over time.

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