Implications of long-term dynamics of fish and zooplankton communities for among-lake comparisons

Julian D. Olden, Olaf P. Jensen, and M. Jake Vander Zanden

Abstract: Understanding the environmental determinants of lake community composition has been a central pursuit in freshwater ecology. Previous studies have defined community composition based on temporally limited surveys, with the implicit assumption that interannual variation is negligible compared with among-lake variability. Using a long-term data set for fish and zooplankton communities in five north temperate lakes (Wisconsin, USA), we found that interannual, within-lake similarity in species composition (a measure of temporal stability in community composition) generally exceeded community similarity among lakes. Despite these differences, however, the strength of community–environment relationships were found to range widely (2%–99% explained variation) depending on the choice of single-year sample used in the analysis, a result of high temporal coherence in limnological and biological characteristics. Perhaps of greatest concern, interannual similarity in species composition showed consistent relationships with habitat variables commonly used to explain community differences among lakes. Decreasing lake area and shoreline perimeter (indicative of lower habitat heterogeneity) and seepage lakes were associated with low interannual similarity in community composition, thus confounding the ability to differentiate among lake communities according to their habitat characteristics. In light of our results, we offer a number of explicit recommendations for the selection and analysis of community data in future cross-lake studies.

Résumé : La compréhension des facteurs déterminants de la composition des communautés lacustres représente un objectif de recherche majeur de l’écologie des eaux douces. Des études antérieures ont défini la composition des communautés d’après des inventaires restreints dans le temps, en présupposant de façon implicite que la variation d’une année à l’autre est négligeable par rapport à la variation d’un lac à un autre. À l’aide d’une longue série chronologique de données sur les communautés de poissons et de zooplancton de cinq lacs de la région tempérée nord (Wisconsin, É.-U.), nous trouvons que la similarité d’une année à l’autre de la composition spécifique dans un même lac (une mesure de la stabilité dans le temps de la composition de la communauté) est généralement plus grande que la similarité entre les lacs. Malgré ces différences, cependant, la force des relations communauté-environnement varie considérablement (explication de 2 % à 99 % de la variation) selon le choix de l’échantillon d’une seule année retenu pour l’analyse; c’est le résultat d’une forte cohérence dans le temps entre les variables limnologiques et biologiques. Ce qui est plus inquiétant peut-être est que la similarité de la composition des communautés d’une année à l’autre est constamment en corrélation avec des variables de l’habitat qui sont couramment utilisées pour expliquer les différences de communauté entre les lacs. Les surfaces de lac et les périmètres de rivages plus faibles (des indicateurs d’une hétérogénéité réduite des habitats) et les lacs d’eau d’infiltration sont associés à des similarités faibles de composition de communauté d’une année à l’autre; cela réduit la possibilité de discriminer entre les communautés lacustres d’après les caractéristiques de l’habitat. À la lumière de ces résultats, nous faisons un certain nombre de recommandations explicites pour choisir et analyser les données sur les communautés dans les études futures impliquant plusieurs lacs.

[Traduit par la Rédaction]

Introduction

Lakes are convenient systems for studies in community ecology because they are well bounded and replicated across the landscape (Forbes 1887). The lake, as a result, is considered the de facto observational unit for community analysis, best illustrated by the “lakes-as-islands” analogy for fish (e.g., Barbour and Brown 1974; Browne 1981; Eadie et al. 1986), zooplankton (Arnott et al. 2006), and macrophyte communities (Keddy 1976). Motivated by the growing need

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to understand how freshwater communities respond to environmental change, a substantial body of research in aquatic ecology has focused on establishing relationships between whole-lake habitat attributes and properties of their aquatic fauna (Schindler 2001). These studies have shown that much can be inferred about community composition from lake morphology, trophic conditions, thermal and chemical characteristics, and degree of geographic isolation (e.g., fishes: Minns 1989; Magnuson et al. 1998; Olden and Jackson 2002; and zooplankton: Dodson 1992; Dodson et al. 2000; Rusak et al. 2002). Indeed, many variables have been measured and parameters devised for explaining patterns of fish and zooplankton community composition among lakes at both small and large spatial scales.

Aquatic ecologists and managers have long recognized the difficulties and challenges imposed by the inherent spatial and temporal complexity of lake ecosystems. For example, it is accepted that fish and zooplankton communities show strong within- and among-lake variability in their composition (e.g., Locke and Sprules 1994; Pinel-Alloul 1995; Brind'Amour et al. 2005). Yet surprisingly, previous attempts to quantify associations between species composition and attributes of the environment typically use fish and zooplankton survey data taken in a single year for a given lake, and data from different lakes are often collected across many different years. For example, Olden (2003) used physical and chemical characteristics of 286 north temperate lakes to develop predictive models of fish community composition using single-year fish surveys that were collected over a 20-year period. This study is by no means atypical, and the fish ecology literature is replete with similar examples (e.g., Matuszek and Beggs 1988: 15 years; Minns 1989: 29 years; Mandrak 1995: 92 years). Moreover, studies typically define a lake's fish or zooplankton community based on a single year of sampling, a practice that does not respect the long-term variability in community structure that may characterize many lakes (Magnuson et al. 2006).

Despite this widespread practice in community analyses, little is known of the role that interannual variation in community composition plays relative to the among-lake variation that is typically the focus of these investigations. This raises a number of fundamental questions. How important is within-lake, interannual community variation relative to among-lake variation? If interannual variation is substantial, is the degree of variation related to lake characteristics typically used to explain among-lake differences in species composition? Do these relationships differ among major taxonomic groups, such as fish and zooplankton? Understanding the magnitude of interannual variability in community structure is critical for interpreting the results from studies that relate spatial patterns of environmental variation to community structure, both of which continue to be treated as static entities.

In this paper, we address these questions by examining temporal patterns in fish and zooplankton community composition from five north temperate lakes in northern Wisconsin, USA, surveyed over a 24-year period as part of the North Temperate Lakes Long Term Ecological Research Program (NTLLTERP; see http://lter.limnology.wisc.edu/). Our first objective is to compare within-lake patterns of interannual similarity (a measure of temporal stability in community composition) to patterns of among-lake similarity in fish and zooplankton community structure. Through this examination, we can address the question of whether the communities of neighbouring lakes that vary considerably with respect to habitat availability and complexity, productivity, and degree of landscape connectivity (but share the same regional species pool) are distinguishable despite varying degrees of interannual variation in community similarity. Second, we examine whether the choice of certain combinations of single-year surveys can influence our ability to model community–environment relationships. This addresses the concern of whether single-year estimates of community composition are appropriate for cross-lake comparisons that use data collected from different years. Third, we relate patterns of interannual similarity in community structure to habitat descriptors that are typically used in community–environment studies to describe among-lake differences in species composition. This question explores how the predictive performance of community–environment models may be affected by interannual changes in species composition that characterize many lakes. By reconciling the knowledge gained by addressing these three objectives with known sampling effort and extent needed to characterize fish and zooplankton in lakes (Jackson and Harvey 1997; Arnott et al. 1998), we aim to improve our understanding of the suitability of using the single-year lake survey as the de facto observational unit for community analysis.

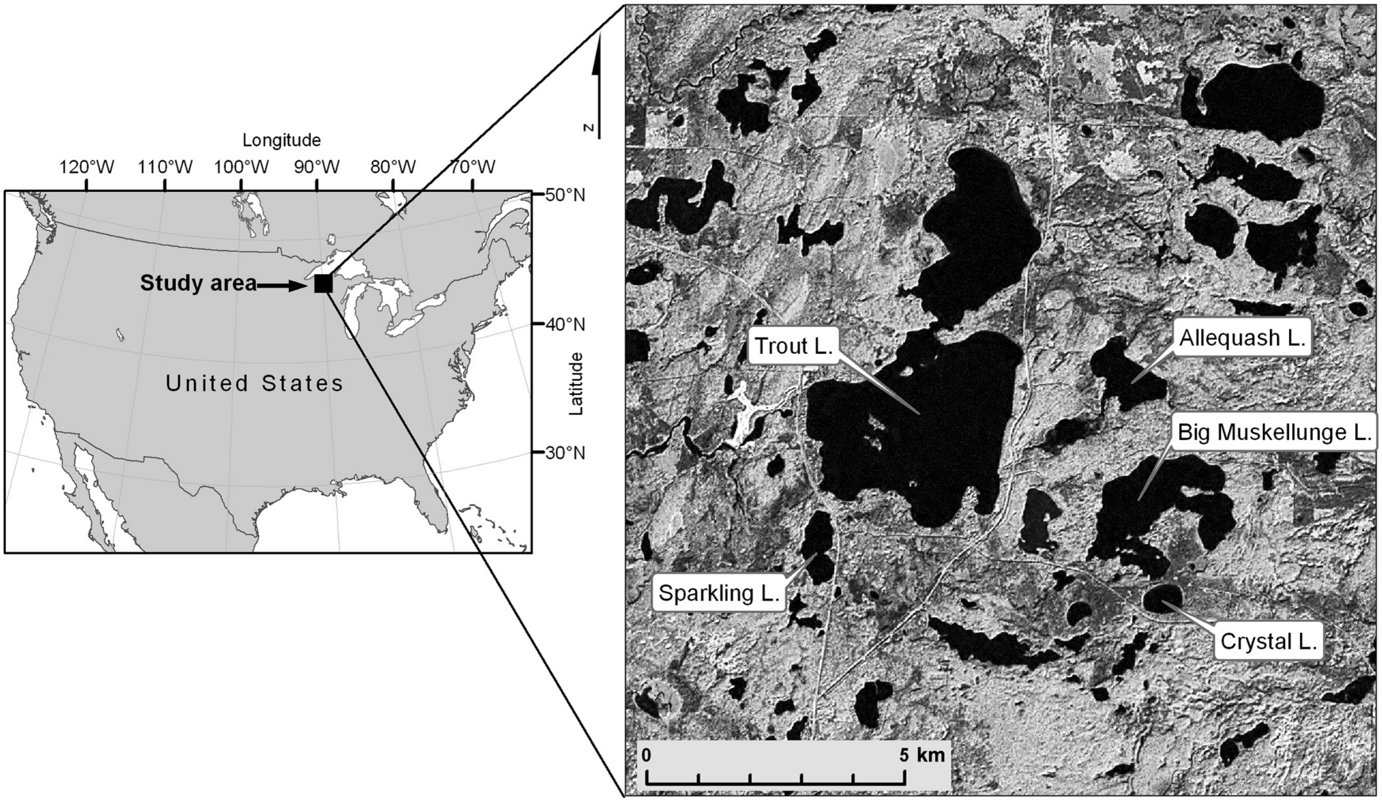
Materials and methods

Study sites

Our study uses fish and zooplankton community data for a group of north temperate lakes surveyed extensively over a 24-year period (1981–2004) as part of the Long-Term Ecological Research Program (Magnuson et al. 2006). Data are collected from nine primary lakes and two bogs in Wisconsin, and here we use five lakes located in the Northern Highland Lake District (NHLD), Vilas County, Wisconsin (46°01′N, 89°41′W): Allequash Lake, Big Muskellunge Lake, Crystal Lake, Sparkling Lake, and Trout Lake (Fig. 1; Table 1). We restricted our analysis to these neighbouring lakes to avoid the confounding patterns of spatial and temporal variability caused by gross differences in landscape position, regional species pools, and climate drivers (Rusak et al. 2002). NHLD is within the mixed forest ecoregion of northern Wisconsin, USA, to the south and east of Lake Superior (Martin 1965). The climate of the NHLD is heavily influenced by its proximity to Lake Superior, leading to cool summers and cold winters, and precipitation occurs year-round. The ice-free season typically extends from late April until November, and the frost-free season is from early June until mid-September.

The consistency and intensity of sampling protocols provides the opportunity to investigate interannual differences in fish and zooplankton community structure without the confounding effects of sampling effort and different methods (see Weaver et al. 1993; Jackson and Harvey 1997; although we recognize that field personnel have changed over time). The NHLD has been the recipient of species invasions over the past century, including rusty crayfish (*Orconectes rusticus*) that may influence fish population dynamics but is unlikely to result in the lake-wide extirpation of fish species, and

Fig. 1. Location of the five study lakes in the Northern Highland State Forest Region, Wisconsin, USA. Photo courtesy of The Environmental Remote Sensing Center, The Nelson Institute, University of Wisconsin – Madison, Madison, Wisconsin.



rainbow smelt (*Osmerus mordax*) that is thought to have contributed to the extirpation of cisco (*Coregonus artedi*) from Sparkling Lake in 1990 (Hrabik et al. 1998). Our analysis was based on a species-by-site matrix containing records of species' presence or absence for a total pool of 51 fish species and 85 zooplankton taxa (NTLLTERP 2004*a*) collected over a 24-year period in the five study lakes. The lake is commonly used as an operational unit in community analysis, and in this study we refer to a fish or zooplankton community as those species recorded present in a single lake in a single year.

Fish and zooplankton community data

The study lakes were intensively sampled every year using five types of fishing gear (beach seines, trammel nets, fyke nets, gill nets, and boat electroshocking) to determine fish species occurrence. Field protocols are standardized and are described elsewhere (NTLLTERP 2004*b*). The same sampling sites were visited each year, with all surveys conducted between late July and early September. Sampling locations were selected at random in the first year and have remained fixed since then. Three beach seine hauls (each measuring 12.2 m long by 1.2 m deep, with 6.4 mm stretched mesh nylon on the wings and 3.2 mm stretched mesh in the bag) were conducted at night at each of six locations per lake. A 30.5 m long by 1.1 m deep trammel net with an inner panel of 51 mm stretched mesh nylon was deployed for 24 h at two sites per lake. Fyke nets constructed of 7 mm stretched mesh nylon measuring 12 m in length with an 8 m long by 1.25 m deep lead were deployed for 24 h at six sites per lake. Two consecutive 24 h vertical gill net sets (each containing seven panels measuring 4 m wide and 33 m long with stretched mesh sizes of 19, 25, 32, 38, 51, 64, and 89 mm, respectively) were conducted at the deepest point in each lake. Lastly, a boom-style boat electroshocker using pulsed 240 volt, 3–5 amp DC current was used to sample 30 min transects in each lake. For all sampling methods, all fish captured were identified to species and counted. Fish community composition was defined by presence or absence of individual species from the entire data set (i.e., all gears combined).

Zooplankton samples were collected biweekly from June to September at the deepest part of each lake to determine zooplankton presence or absence. Field protocols are standardized and are described in greater detail elsewhere (NTLLTERP 2004*c*). A 45 L Schindler–Patalas trap with 53 μm mesh was used to collect samples at 2 m depth intervals from the surface to the bottom. Samples were preserved in ethanol, hypsometrically pooled (i.e., a subsample was taken from each depth interval in proportion to the volume represented by that depth interval), and two replicate 1 mL subsamples were taken. For this study, we pooled data from the two subsamples. All macrozooplankton were identified to species where possible, and otherwise to genus.

Statistical analyses

We compared fish and zooplankton community composition among lakes across the 24 years by conducting separate analyses of similarity (ANOSIM) and nonmetric multidimensional scaling (NMDS) (PRIMER software, v. 5.2.9,

Table 1. Characteristics of the five north temperate lakes examined in our study.

	Lake				
Characteristic	Crystal	Sparkling	Allequash	Big Muskellunge	Trout
Location					
Latitude (°N)	46°00′	46°00′	46°02′	46°01′	46°01′
Longitude (°W)	89°37′	89°42′	89°37′	89°37′	89°40′
Morphology					
Area (ha)	36.7	64.0	168.4	396.3	1607.9
Mean depth (m)	10.4	10.9	2.9	7.5	14.6
Maximum depth (m)	20.4	20.0	8.0	21.3	35.7
Shoreline length (km)	2.3	4.3	9.5	16.1	25.9
Landscape position	High	Moderate	Low	Moderate	Low
Connectivity	Seepage	Seepage	Drainage*	Drainage*	Drainage*
Chemistry[†]					
pH	6.0	7.3	7.5	7.3	7.6
ANC (μequiv.·L^{-1})	16	612	795	366	829
Conductivity (μS)	14	80	88	49	93
Total P (μg·L^{-1})	8.6	15.2	29.3	22.5	16.9
Total N (μg·L^{-1})	207	375	364	489	235
SiO_2 (μg·L^{-1})	20	3582	6486	145	4311
Productivity[‡]					
Secchi depth (m)	7.3	6.1	3.1	6.7	4.6
Chlorophyll (μg·L^{-1})	1.8	2.2	8.3	3.0	3.3
Fish richness (no. of species)	6–12	9–17	17–24	14–22	19–26
Zooplankton richness (no. of taxa)	16–27	18–29	24–32	16–33	16–38

Note: Reported values are 24-year means for chemistry and the range of fish and zooplankton taxonomic richness over the 24-year study period. ANC, acid-neutralizing capacity.

*These lakes are located in the same watershed.

[†] pH, ANC, and conductivity were calculated from the average of spring and fall mixis sampling; total P, total N, and SiO_2 were calculated from spring mixis sampling.

[‡] Secchi disk depth was measured between 1 June and 31 August of each year; chlorophyll (surface) was taken from open water season.

Primer-E Ltd, Plymouth, UK). ANOSIM based on Bray–Curtis similarity coefficient (Bray and Curtis 1957) was used to test the null hypothesis of no difference in fish–zooplankton community composition between lakes across years. ANOSIM is a nonparametric, multivariate procedure broadly analogous to analysis of variance (ANOVA) that has been widely used for testing whether or not groups of sites are statistically different in respect to their relative similarities in community composition (Clarke 1993). ANOSIM tests priori-defined groups (i.e., lakes) against random groups in ordination space by calculating the average of all rank similarities among years within lakes (r_w) and the average of rank similarities among years between lakes (r_b). A test statistic, R, is then calculated as $(\bar{r}_b - \bar{r}_w) / 0.5M$, where $M = [n(n-1)]/2$ and n is the total number of samples (Clarke 1993). The value of R lies between –1 and +1. A value of 1 indicates that all years within lakes are more similar to one another than any years from different lakes; a value of 0 indicates that there is no difference among lakes (i.e., representing the null hypothesis); and a value of –1 indicates that all years within lakes are less similar to one another than any years from different lakes (Clarke and Gorley 2001). We conducted 9999 random permutations to assess the statistical significance of R. ANOSIM is particularly suited for this analysis, as we can explicitly test for differences in fish and zooplankton community composition between lakes and among years and compare an interpretable statistic that measures how separate lakes are, on a scale of –1 (indistinguishable) to 1 (all similarities within lakes across years are less than any similarity between lakes).

NMDS is an ordination method that preserves the rank-ordered distances between sample points in ordination space and for our purposes provides a useful approach for visualizing differences in fish and zooplankton community composition across lakes and over time. NMDS uses an iterative approach that rearranges samples in ordination space to minimize a measure of disagreement (referred to as stress) between the compositional dissimilarities and the distance between the points in the ordination diagram (Kruskal 1964). A distance matrix based on the Bray–Curtis (dis)similarity coefficient was then used to ordinate the sample sites in two dimensions using 10 random starts (a comparison of stress versus dimensionality supported the interpretation of two dimensions). Lake–year combinations with similar community compositions are located closer together in multidimensional space, whereas lake–year combinations with dissimilar communities are positioned farther apart (Kruskal and Wish 1978).

We used regression analysis to assess the relationship between within-lake interannual similarity in fish and zooplankton community composition and habitat descriptors of the lakes that are typically used to explain between-lake differences in communities. These descriptors include surface area, maximum depth, shoreline perimeter, Secchi disk depth, landscape position related to elevation (low, moderate,

Table 2. Results from the analysis of similarity (ANOSIM) illustrating the results from pairwise lake comparisons of zooplankton (upper-right diagonal) and fish community composition (lower-left diagonal).

	Crystal	Sparkling	Allequash	Big Muskellunge	Trout
Crystal	—	0.54	0.89	0.88	0.72
Sparkling	0.67	—	0.74	0.52	0.50
Allequash	0.92	0.93	—	0.59	0.65
Big Muskellunge	0.88	0.67	0.92	—	0.33
Trout	0.94	0.84	0.96	0.92	—

Note: A value of 1 indicates that all years within one lake are more similar to one another than any years from the other lake; a value of 0 indicates that there is no difference among lakes (i.e., representing the null hypothesis); and a value of –1 indicates that all years within one lake are less similar to one another than any years from the other lake. All values were statistically significant at $P < 0.001$.

or high), and connectivity (seepage lake with no stream connections or drainage lakes with stream connections).

We performed a Monte Carlo experiment to address whether the choice of certain combinations of single-year surveys influences the statistical analysis of among-lake differences in fish and zooplankton communities. For each lake, we randomly selected a single year of community data from s consecutive years of records, where $s = 1$ (2004), 2 (2003–2004), 3 (2002–2004), …, 24 (1981–2004). Using this data, we performed separate regression analyses between fish and zooplankton richness and lake surface area, in addition to conducting canonical correspondence analyses (ter Braak 1986) relating fish and zooplankton community composition to three commonly used descriptors of lake habitat: surface area, maximum depth, and Secchi disk depth. The entire process (i.e., random selection of community data and statistical analyses) was repeated 10 000 times. This analysis mimics the common situation in the literature where data spanning a range of years are used in community analyses. A Mantel test was performed to assess the correlation between two distance matrices representing the interlake dissimilarities according to their fish and zooplankton communities.

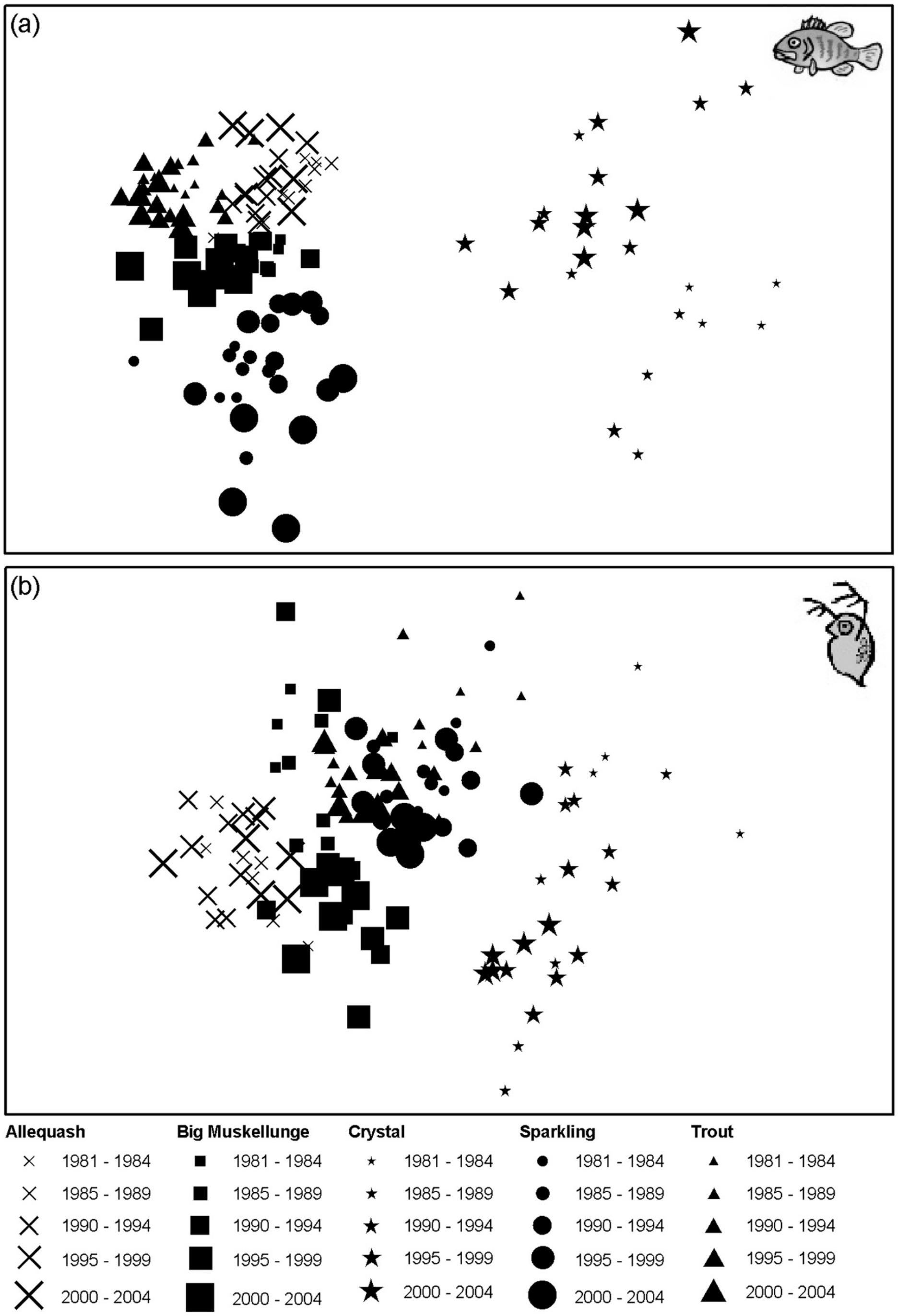
Results

We found significant among-lake differences in fish community composition (global $R_{\text{ANOSIM}} = 0.75$, $P < 0.001$) and zooplankton community composition (global $R_{\text{ANOSIM}} = 0.60$, $P < 0.001$), indicating that within-lake similarity across years exceeded among-lake similarity in community composition. Post hoc ANOSIM comparisons revealed that all lakes were statistically distinguishable from each other with respect to both fish and zooplankton community structure (Table 2). The smallest and largest lakes, Crystal and Trout, were the most distinctive in their fish fauna ($\bar{R}_{\text{ANOSIM}} = 0.93$ and 0.92, respectively), followed by Sparkling Lake ($\bar{R}_{\text{ANOSIM}} = 0.85$), Allequash Lake ($\bar{R}_{\text{ANOSIM}} = 0.85$), and Big Muskellunge Lake ($\bar{R}_{\text{ANOSIM}} = 0.78$). In contrast, Allequash Lake and Crystal Lake showed the greatest distinction in their zooplankton fauna ($\bar{R}_{\text{ANOSIM}} = 0.76$ and 0.72, respectively), followed by Big Muskellunge Lake ($\bar{R}_{\text{ANOSIM}} = 0.58$), Sparkling Lake ($\bar{R}_{\text{ANOSIM}} = 0.58$), and Trout Lake ($\bar{R}_{\text{ANOSIM}} = 0.55$). For all comparisons, lakes showed greater interannual similarity in their fish community composition (Table 2), and there was little concordance in patterns of among-lake similarity between the two taxonomic groups (Mantel standardized $R = 0.33$, $P = 0.35$).

Results from the NMDS corroborate the compositional differences among lakes, but also show that the magnitude of interannual similarity in both fish and zooplankton community composition can be high and can differ greatly among lakes (Fig. 2). For example, although Crystal Lake was the most distinct from the other lakes, it exhibited the lowest temporal similarity in fish and zooplankton community structure (average Bray–Curtis similarity = 64.9% and 62.9%, respectively). In contrast, the fish community of Big Muskellunge Lake was the least distinct from the other lakes, yet showed among the highest interannual similarity (average Bray–Curtis similarity = 83.5%). Not surprisingly, there was a large range in estimates of fish and zooplankton richness among study years (Table 1). Taken together, the ANOSIM and NMDS results indicated that despite low interannual similarity in community composition, among-lake differences in fish and zooplankton faunas were still larger and distinguish the lakes from each other.

Predictor variables that are commonly used in lake community-environment studies (habitat availability, productivity, and degree of isolation) showed varying associations with mean interannual similarity in fish and zooplankton community composition across the study lakes. Despite our limited statistical power associated with small sample sizes, our analysis revealed a number of interesting trends (Fig. 3). Interannual similarity in fish community structure showed a positive, logarithmic association with both lake surface area ($R^2 = 0.52$, $F_{[1,3]} = 3.29$, $P = 0.17$; Fig. 3*a*) and shoreline perimeter ($R^2 = 0.72$, $F_{[1,3]} = 8.02$, $P = 0.06$; Fig. 3*b*), a negative linear correlation with Secchi disk depth ($R^2 = 0.45$, $F_{[1,3]} = 2.48$, $P = 0.21$; Fig. 3*c*), and no relationship with maximum depth ($R^2 = 0.03$, $F_{[1,3]} = 0.01$, $P = 0.94$). Similar, but statistically weaker, trends were observed for zooplankton communities. Interannual similarity in community structure showed a negative linear association with Secchi disk depth ($R^2 = 0.48$, $F_{[1,3]} = 2.73$, $P = 0.19$; Fig. 3*c*), a weak logarithmic relationship with shoreline perimeter ($R^2 = 0.16$, $F_{[1,3]} = 0.61$, $P = 0.49$; Fig. 3*b*), and no trends with lake surface area ($R^2 = 0.20$, $F_{[1,3]} = 0.07$, $P = 0.83$; Fig. 3*a*) and maximum depth ($R^2 = 0.03$, $F_{[1,3]} = 0.10$, $P = 0.78$). Finally, the magnitude of within-lake similarity in both fish and zooplankton community composition increased along a gradient of increasing lake connectivity (Fig. 3*d*). Isolated lakes with no stream connections (i.e., seepage) and positioned in moderate and high elevations of the landscape (i.e., Crystal Lale and Sparkling Lake) exhibited low interannual similarity in community composition compared with those lakes with

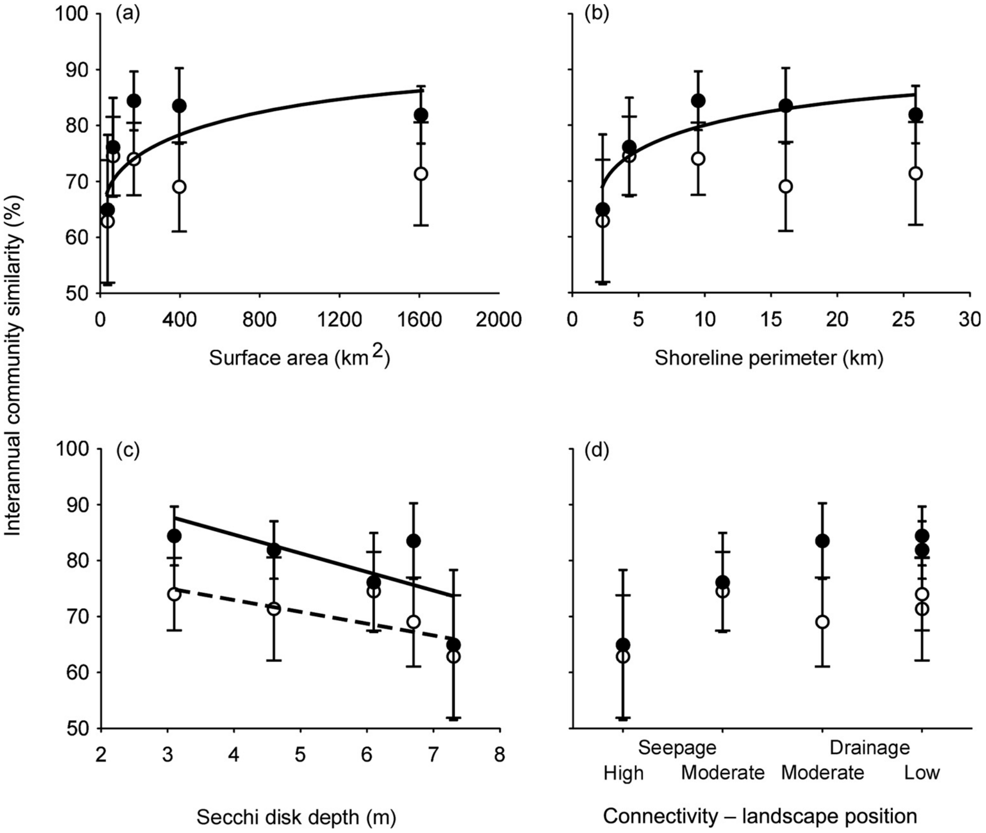
Fig. 2. Spatial and temporal patterns in fish (*a*) and zooplankton (*b*) community composition in the five study lakes sampled from 1981 to 2004, with different symbols for each lake, according to the nonmetric multidimensional scaling based on Bray–Curtis dissimilarity. Stress values were 0.14 for fish and 0.23 for zooplankton. Note that zooplankton data are not available for Allequash Lake in 1981.



stream connections (i.e., drainage) located at lower elevations. However, given the intercorrelations among lake characteristics (e.g., isolated lakes exhibit small surface areas: Table 1), the interpretation of these relationships should be done with care.

Results from the Monte Carlo experiment showed that our ability to explain cross-lake patterns in fish and zooplankton community composition is greatly affected by the choice of survey year. By randomly selecting single-year community data from increasingly longer periods of collection (i.e., 2004, 2003–2004, etc.), we found that the strength of the relationship between lake area and taxonomic richness progressively decreased and became more variable for both fish (Fig. 4*a*) and zooplankton (Fig. 4*b*). We observed similar decreases in the explanatory power of the canonical correlation analysis (CCA) models for fish and zooplankton community structure with increasing periods of collection (fish: 72%–69%; zooplankton: 80%–75%). In summary, a selection of single-year survey data from the entire 24-year period resulted in highly variable area–richness relationships for both fish

Fig. 3. Mean interannual similarity (Bray–Curtis similarity coefficient) of fish (solid circles) and zooplankton (open circles) community composition versus (*a*) lake surface area, (*b*) shoreline perimeter, (*c*) Secchi disk depth, and (*d*) connectivity–landscape position. Bars represent ±1 standard deviation. Fitted regression lines (fish, solid; zooplankton, broken) are shown for all relationships for which $R^2 > 0.4$. These include for fish ($y = 3.9 \ln(x) + 57.7$, $R^2 = 0.52$) in panel *a*; for fish ($y = 7.1 \ln(x) + 63.3$, $R^2 = 0.72$) in panel *b*; and for both fish ($y = -3.2 \ln(x) + 95.9$, $R^2 = 0.45$) and zooplankton ($y = -1.9 \ln(x) + 81.0$, $R^2 = 0.48$) in panel *c*.



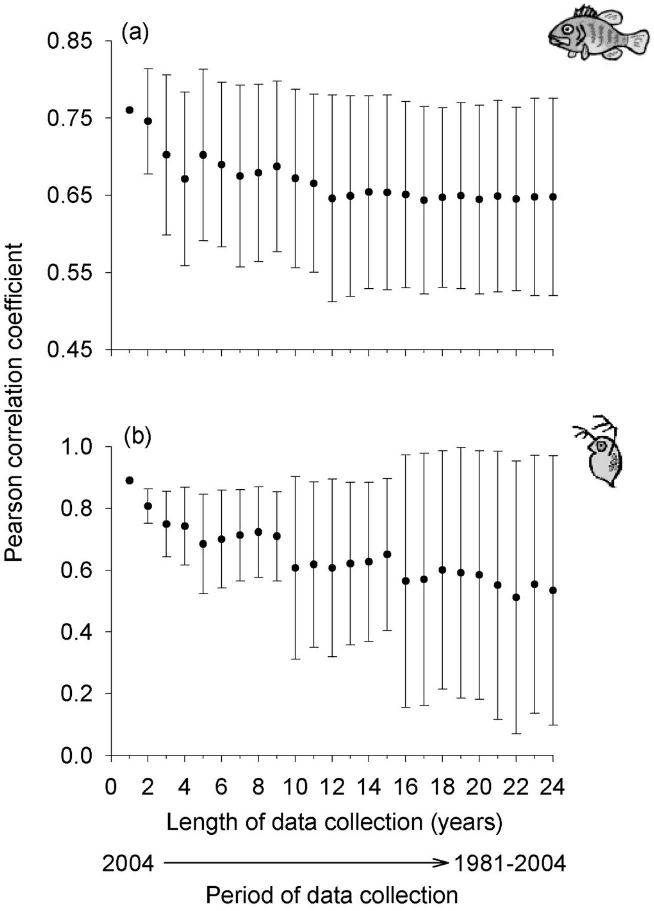
($R^2 = 0.05$–0.86) and zooplankton ($R^2 = 0.02$–0.99), as well as substantial variation in the portion of community variation explained by the CCA models for fish (49.6%–87.5%) and zooplankton (58.3%–89.1%). When repeating this analysis using data collected in the same year ($n = 24$), we observed decreased explained variability in species richness (fish: $R^2 = 0.49$–0.85; zooplankton: $R^2 = 0.49$–0.90) and community composition (fish: 56.0%–80.3%; zooplankton: 68.4%–84.0%).

Discussion

Aquatic ecologists are well aware that lakes exhibit heterogeneity on a broad range of spatial and temporal scales (Hinch 1991; Jackson et al. 2001). In fact, analyses of fish and zooplankton community structure depend on the existence of spatial variability in species composition. While cross-lake studies of community composition have received considerable attention, the extent to which temporal variation in lake community structure, and ultimately the selection of survey data, may influence these modeling endeavours remains unknown. Two common practices in freshwater ecology highlight this concern. First, community composition of a lake is defined according to fish and zooplankton sampling conducted in a single year; second, community–environment analyses are typically based on data sets composed of multiple lakes collectively surveyed over a long time period. Our examination of fish and zooplankton communities in neighbouring north temperate lakes over a 24-year period revealed that change in community similarity among years is both prevalent and differs among lakes. Temporal variation in community composition is likely a result of rare species that may be opportunistic and only periodically exist in certain years; alternatively, these species may be always present but are undetectable using typical sampling techniques during times of low population numbers.

Despite the low interannual similarity within lakes, our results show that the communities of the study lakes were distinguishable from each other. This is an encouraging finding because the lakes examined in this study vary considerably with respect to habitat availability and complexity, productivity, and degree of landscape connectivity (but share the same regional species pool) and therefore are expected to be characterized by different communities. These findings are corroborated by recent studies emphasizing the importance of spatial over temporal variation for differentiating among zooplankton communities in this region (Kratz et al. 1987; Rusak et al. 2002). By extension, our results also suggest that with increasing environmental resemblance of lakes, any differences in community composition among lakes may be dwarfed by high interannual dissimilarity within lakes. Therefore, the suitability of using single-year survey data in

Fig. 4. Pearson's correlation coefficient for the relationship between fish (*a*) and zooplankton (*b*) taxonomic richness and lake surface area according to the random selection of single-year survey data for each lake from increasingly longer lengths of data collection. Circles represent the mean and bars represent ±1 standard deviation from 10 000 Monte Carlo simulations. The single point for 2004 (or 1 year) represents the correlation coefficient using data collected only in 2004, whereas the last point represents the correlation coefficient for using single-year data randomly selected from a 24-year period (1981–2004).



studies of lake community ecology may depend on the degree of between-lake environmental similarity.

Despite overall differences in taxonomic composition among the study lakes, the strength of community–environment relationships for both fish and zooplankton were found to range widely, depending on the length of time over which the lakes included in the analysis were surveyed. Our results suggest that the choice of certain combinations of single-year samples can influence our ability to model community–environment relationships and even affect the familiar species – lake area relationship reported for fish and zooplankton. When community analyses are based on a collection of lakes surveyed over increasingly longer time periods, the strength of the relationship between lake area and richness weakens and becomes more variable. This result is caused by temporal coherence in limnological and biological characteristics among north temperate lakes that are driven by large-scale processes such as climate (Magnuson et al. 1990; Rusak et al. 1999; Willis 2003). As a result, by conducting community analyses with lakes whose communities are characterized using data collected in different years, we are likely to decrease our ability to model between-lake differences in community composition by introducing temporal variability into the analysis (this explains the reduced range of explained variation for analyses conducted with data collected on the same year). This may put into question previous attempts to model community–environment associations using data from lakes surveyed at different points in time. On the other hand, survey data spanning shorter time periods such as collections typically made during a field-based research project may be successfully combined with minimal consequences for community analyses.

Perhaps of greatest concern was our finding that interannual similarity in fish and zooplankton composition showed consistent relationships with habitat variables commonly used to explain community differences among lakes. Decreasing lake area and shoreline perimeter — indicative of lower habitat availability and heterogeneity — was associated with decreasing interannual similarity in community composition. Drainage lakes located at low elevations in the watershed exhibited higher interannual similarity compared with high elevation seepage lakes, suggesting that biotic exchange via stream–lake connections may help temper annual variability in species occurrence resulting from the influence of extrinsic environmental factors (Olden et al. 2001; Havel and Shurin 2004). Though interesting patterns, the sample size of five lakes provides little statistical power, and intercorrelations between environmental variables make it difficult to interpret these relationships. However, focusing on these lakes provides a unique opportunity to address our study objective because of the intensive and consistent sampling of fish and zooplankton communities over 20+ years. Moreover, we are fortunate to have long-term data for lakes located in close geographic proximity to eliminate the confounding effects of temporal differences in community composition caused by regional environmental drivers (Rusak et al. 2002).

The consideration of temporal and spatial variability in aquatic systems is essential for understanding the ecology of freshwater biota (Schindler 2001), but only recently has data become available to address such topics. We offer the following recommendations to ecologists using the lake as an observational unit in community analyses. First, caution should be exercised when using single-year estimates of community structure in cross-lake studies. We found low interannual similarity in fish and zooplankton community composition, which affected our ability to model community–environment relationships. Ecologists who are interested in modeling lake communities without the confounding influence of regional-scale processes such as temporal coherence in climate should pay special attention to the timing of the surveys and focus on analyzing data collected in short time intervals. This approach should enhance our ability to elucidate among-lake differences in community composition driven by lake-specific environmental factors.

Second, because interannual similarity within lakes exceeded among-lake similarity in community composition, single-year estimates of community composition collected over different years may be adequate when studying lakes across a broad environmental gradient. However, as the environmental gradient shortens and lakes become more similar in their habitat characteristics, we expect that interannual, within-lake variability will play an increasing role in influencing our ability to model differences among lakes.

Third, our results suggest that the magnitude of interannual community similarity is correlated with environmental variables that ecologists typically use to model between-lake differences in community composition. Future studies can account for temporal variation in community structure by characterizing the species membership of each lake based on data from multiyear surveys. The specific number of samples and years needed to do this are informed by studies such as Arnott et al. (1998), who provided compelling evidence that single-year surveys of zooplankton communities are highly variable and inadequate for characterizing species richness. Similar results were shown for fish communities by Magnuson et al. (1994).

In conclusion, our results generally support the use of single-year surveys in cross-lake studies in freshwater community ecology, but illustrate that understanding the environmental factors driving differences in community structure among lakes is likely to be complicated by among-year differences in species composition within lakes. Future investigations aimed at elucidating the mechanisms underlying these relationships are likely to provide important insight into the resilience of communities to environmental change and ultimately influence how we sample and analyze lake community data.

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