Fish and Benthic Invertebrates: Community Concordance and Community–Environment Relationships

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Fish and benthic invertebrates from 40 lakes in south-central Ontario showed significantly concordant patterns based on community structure. Fish communities were associated significantly with lake morphological characteristics, but were uncorrelated with water chemistry. Large, deep lakes differed from shallow lakes in their fish species, having richer faunas due to the additional cold-water species. Centrarchid species occurred more frequently in small, shallow lakes than in larger lakes. The invertebrate community was not correlated with lake morphology, but showed a significant association with water chemistry, principally lake pH. A strong contrast in the abundance of *Chaoborus* and *Holopedium* existed, but it was unclear whether this was due to a predator–prey relationship or to differences in acid tolerance. Although the lakes showed similar patterns in the composition of both communities, each community was associated with a different set of environmental factors. Biotic processes within and between communities explain this paradox in community–environment relationships. Such biotic interactions may involve direct processes such as fish predation on a particular invertebrate taxon or indirect factors, e.g., where fish limit the abundance of invertebrate predators, thereby limiting the impact of these invertebrate predators.

On observe chez les populations de poissons et d'invertébrés benthiques de 40 lacs de la partie sud-centre de l'Ontario, des caractéristiques significativement concordantes qui relèvent de la structure des communautés. Il existe une association significative entre les communautés de poissons et les caractéristiques morphologiques des lacs, mais pas avec la chimie de l'eau. Les grands lacs profonds se distinguent des lacs peu profonds par leur composition spécifique; ils ont une faune plus riche du fait de la présence d'espèces d'eau froide. On observe les centrarchidés plus souvent dans les petits lacs peu profonds que dans les grands lacs. La communauté d'invertébrés n'est pas en corrélation avec la morphologie du lac, mais il existe une association significative avec la chimie de l'eau, principalement le pH du lac. Il existe un contraste marqué entre l'abondance de *Chaoborus* et de *Holopedium*; toutefois, on ignore si cette situation est attribuable à une relation prédateur–proie ou à des différences dans la tolérance à l'acidité. Même si la composition des deux communautés s'apparente d'un lac à l'autre, chacune de celle-ci est associée à un ensemble distinct de facteurs écologiques. Les mécanismes biotiques à l'oeuvre à l'intérieur des communautés et entre elles expliquent ce paradoxe observé dans les relations entre les communautés et le milieu. Ces interactions biotiques peuvent être constituées de mécanismes directs comme la prédation exercée par des poissons sur un taxon donné d'invertébrés, ou encore par des facteurs indirects comme la présence de poissons qui limitent l'abondance de prédateurs invertébrés, ce qui se trouve à limiter l'impact de ces derniers.

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Community ecologists typically study interspecific relationships or the relationship between a group of species and their physical–chemical environment. Such studies lead researchers to greater understanding of interspecific relationships, such as predation and competition, from which ideas can be formulated and tested experimentally. As well, relationships between communities and their environment provide strong evidence of the importance that various environmental factors have in determining species' distribution and abundance. Although recognition of the importance of community-level studies is increasing (e.g., Carpenter 1988a; Cole et al. 1991 and references therein), there are remarkably few studies examining communities of very different trophic or taxonomic level from the same environment. Within aquatic environments, numerous studies have considered fish, benthic invertebrate, phytoplankton, or zooplankton communities. Such research has concentrated on (1) a single community and the abiotic environment, (2) the effects that one or a few species from one community have on another community, (3) the changes in biomass and production across different communities, and (4) the changes in diversity of different communities due to environmental conditions.

Overall, ecologists generally have not considered whether different communities show similar patterns across varied environments and whether environmental conditions affect different communities in a comparable manner. For example, there is evidence that structure of fish communities is due to characteristics of lake morphometry (Harvey 1978, 1981; Tonn and Magnuson 1982; Jackson 1988), lake water chemistry (Harvey 1975; Somers and Harvey 1984; Rahel 1986; Kelso and

Lipsit 1988), and predation (Harvey 1981; Tonn and Magnuson 1982; Jackson 1988; Jackson et al. 1992). Similarly, researchers have concluded that zooplankton and benthic invertebrate communities are structured by fish predation (e.g., Brooks and Dodson 1965; Morin 1984; Post and Cucin 1984; Butler 1989; McQueen et al. 1990; but see Thorp and Bergey 1981a, 1981b), water chemistry (e.g., pH, phosphorus; Sprules 1975; Tessier and Horowitz 1990; Kilgour and Mackie 1991), and the complexity of the environment (Lodge et al. 1988).

More recently, experimental manipulation of lakes (e.g., Carpenter et al. 1987; Vanni 1988) has been used to study and test relationships between different taxocene or trophic levels while negating criticisms regarding enclosure/exclosure studies. Given the scope of these lake-wide manipulations and interlake variability, replication amongst lakes is impossible. In addition, results from such manipulations may differ when lakes have different environmental conditions (e.g., eutrophic versus oligotrophic or acid versus circumneutral). Comparisons of different communities across many lakes differing in environmental conditions require large, survey-based studies where the variation in different environmental conditions can be examined relative to the different communities.

Given the variation in importance attributed to different environmental factors in different systems having different species, our objective is to determine the relationship of fish and benthic invertebrate communities to their chemical and morphological environments. Specifically, we test whether lake water chemistry or morphology shows a greater association with the structure of both communities and whether both communities exhibit similar relationships with these abiotic components. Additionally, we test whether both communities exhibit similar patterns of lake association (i.e., do lakes show similar relationships in both community analyses?) across the lake set.

Methods

Data Collection

Forty lakes from south-central Ontario (see Table 1) were sampled for lake water chemistry, lake morphology, and the abundance of fish and benthic invertebrates. Lakes were chosen to provide equal representation across a range of surface area (9–124 ha) and pH (5.1–6.9). Chemical concentrations of calcium, magnesium, sodium, potassium, chloride, sulphate, dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), total phosphorus, and total nitrates were determined by the Ontario Ministry of the Environment (1981). Lake pH was determined in the field. Lake area, volume, maximum depth, and total shoreline perimeter were determined. Although compound or ratio variables (e.g., lake mean depth, lake area to watershed area) are often incorporated in such studies, they were not included due to their statistical properties and confounding natures (e.g., Kenney 1982; Jackson et al. 1990; Jackson and Somers 1991).

Fish species were sampled using fine- and coarse-meshed trap nets, baited minnow traps, clear plastic traps (Casselman and Harvey 1973), and multimeshed gill nets. Species abundance data from each sample were tabulated. Population estimates were calculated using mark–recapture methods in several lakes (Harvey and Lee 1981). Relative abundance estimates for each species from each sampling method were evaluated relative to Petersen population estimates. Despite intensive sampling (e.g., in excess of several hundred samples for some gears in some lakes), inconsistent rankings of abundance between gears within and across lakes for different species were found (D.A. Jackson, unpublished data). As the relative abundance data proved to be an unreliable indicator of abundance, analyses were restricted to fish species' presence–absence data. For community analyses, species found in only a single lake were excluded, as they contribute very little information in across-lake comparisons.

Benthic invertebrates were sampled by SCUBA divers. Sediment cores were taken at 10 locations along each of six transects in each lake (Allison and Harvey 1981; Collins et al. 1981). Transects were stratified relative to the proportion of each substrate type and stratum area following Allison and Harvey (1981). Each set of 10 cores was preserved immediately in 10% formalin. Invertebrates were separated from the substrate using a sucrose-floatation method (Allison and Harvey 1981) and generally identified to the family or order to remain consistent with previous studies (see Table 1) (Allison and Harvey 1981, 1988). These higher taxonomic levels have been recommended for marine community studies, as they retain the major trends present in studies using more resolved taxonomic levels, but reduce the large numbers of rare taxa (Warwick 1988, 1993). However, additional research is warranted as to the importance this taxonomic resolution has in the interpretation of freshwater community–environment patterns.

Nineteen of the 40 lakes were sampled in 1979 and 1980 for determination of chemistry, fish species, and benthic invertebrate abundance (Allison and Harvey 1981; Harvey and Lee 1981). The remaining 21 lakes were sampled in 1989 for determination of benthic invertebrates and water chemistry. The data for fish in these 21 lakes are from Jackson (1988). Additional details are found in Jackson (1992).

Statistical Analysis

Water chemistry and lake morphometry variables were transformed to approximate normal distributions and linearize bivariate relationships. Square-root transformations were used with potassium, sulphate, nitrate, phosphorus, lake surface area, volume, maximum depth, and perimeter. Magnesium concentration was arcsin-transformed and the remaining chemistry variables, except pH, were log-transformed.

Benthic data were first summarized within each lake. Various transformations of the benthic abundance data were made to linearize bivariate relationships and were based on preliminary analysis using Taylor's Power Law. However, the $\log_{10}(x + 1)$ transformation was found to provide results comparable with those using Taylor's Power Law. Similar findings have been indicated by Green (1979). Lake means were calculated using the transformed data and formed the basis of subsequent multivariate analyses.

Both the fish and invertebrate data sets were analyzed using correspondence analysis (CA). These communities were compared with the lake water chemistry and morphology data sets using canonical correspondence analysis (CCA, ter Braak 1986). This multivariate method summarizes the maximum amount of variation in one of the biotic data sets while constraining it to be associated with axes based on linear composites of the environmental data. For example, relationships among the invertebrate taxa are summarized such that the community relationships and the gradients in water chemistry are maximally correlated. The method permits a multivariate direct-gradient analysis of the community and environment.

Multivariate summaries of the benthic invertebrate and fish

TABLE 1. Codes for lake, fish, and invertebrate names.

Lake code	Lake	Fish code	Fish species	Invertebrate code	Invertebrate taxa
Bass	Basshaunt	B	Burbot (*Lota lota*)	Acar	Acari
Bent	Bentshoe	BBH	Brown bullhead (*Ictalurus nebulosus*)	Bosm	Bosminidae
Bigw	Bigwind	BM	Brassy minnow (*Hybognathus hankinsoni*)	Cala	Calanoida
B_Ch	Blue Chalk	BND	Blacknose dace (*Rhinichthys atratulus*)	Cera	Ceratopogonidae
Buch	Buchanan	BNM	Bluntnose minnow (*Pimephales notatus*)	Chaob	Chaoborinae
Cind	Cinder	BNS	Blacknose shiner (*Notropis heterolepis*)	Chir	Chironomidae
Clay	Clayton	BS	Brook stickleback (*Culaea inconstans*)	Chyd	Chydoridae
Cross	Crosson	BT	Brook trout (*Salvelinus fontinalis*)	Cycl	Cyclopoida
Dickie	Dickie	C	Cisco (*Coregonus artedi*)	Daph	Daphniidae
Gull	Gullfeather	CC	Creek chub (*Semotilus atromaculatus*)	Elmi	Elmidae
Harv	Harvey	CS	Common shiner (*Notropis cornutus*)	Ephe	Ephemeroptera
Heen	Heeney	FHM	Fathead minnow (*Pimephales promelas*)	Gast	Gastropoda
L_Cl	Little Clear	FSD	Finescale dace (*Phoxinus neogaeus*)	Harp	Harpacticoida
L_Fl	Lower Fletcher	GS	Golden shiner (*Notemigonus crysoleucas*)	Holo	Holopedidae
L_Wr	Little Wren	ID	Iowa darter (*Etheostoma exile*)	Macro	Macrothricidae
McKe	McKeown	LC	Lake chub (*Couesius plumbeus*)	Misc	Miscellaneous
Plas	Plastic	LMB	Largemouth bass (*Micropterus salmoides*)	Neur	Neuroptera
Poor	Poorhouse	LT	Lake trout (*Salvelinus namaycush*)	Nemt	Nemata
Porc	Porcupine	NRD	Northern redbelly dace (*Phoxinus eos*)	Odon	Odonata
R_Ch	Red Chalk	PD	Pearl dace (*Semotilus margarita*)	Olig	Oligochaeta
Rido	Ridout	PKS	Pumpkinseed (*Lepomis gibbosus*)	Ostr	Ostracoda
Soli	Solitaire	RB	Rock bass (*Ambloplites rupestris*)	Pele	Pelecypoda
Teap	Teapot	RT	Rainbow trout (*Oncorhynchus mykiss*)	Sidi	Sididae
Thre	Three Island	SMB	Smallmouth bass (*Micropterus dolomieu*)	Talt	Taltridae
Trou	Troutspawn	SS	Slimy sculpin (*Cottus cognatus*)	Tric	Trichoptera
Walk	Walker	WS	White sucker (*Catostomus commersoni*)		
		YP	Yellow perch (*Perca flavescens*)		

communities were compared using PROTEST (Jackson 1992). PROTEST is a test of matrix concordance incorporating Procrustean matrix rotation (Gower 1971, 1975; Digby and Kempton 1987; Rohlf 1990) where translation, rotation, reflection, and dilation fit one matrix to another matrix. In this example, the method tries to match the position of each lake in a multivariate space defined by the CA of the invertebrate data to the position of the same lake in the space defined by the CA of the fish species, thereby assessing the degree to which both communities have similar interlake patterns. The method

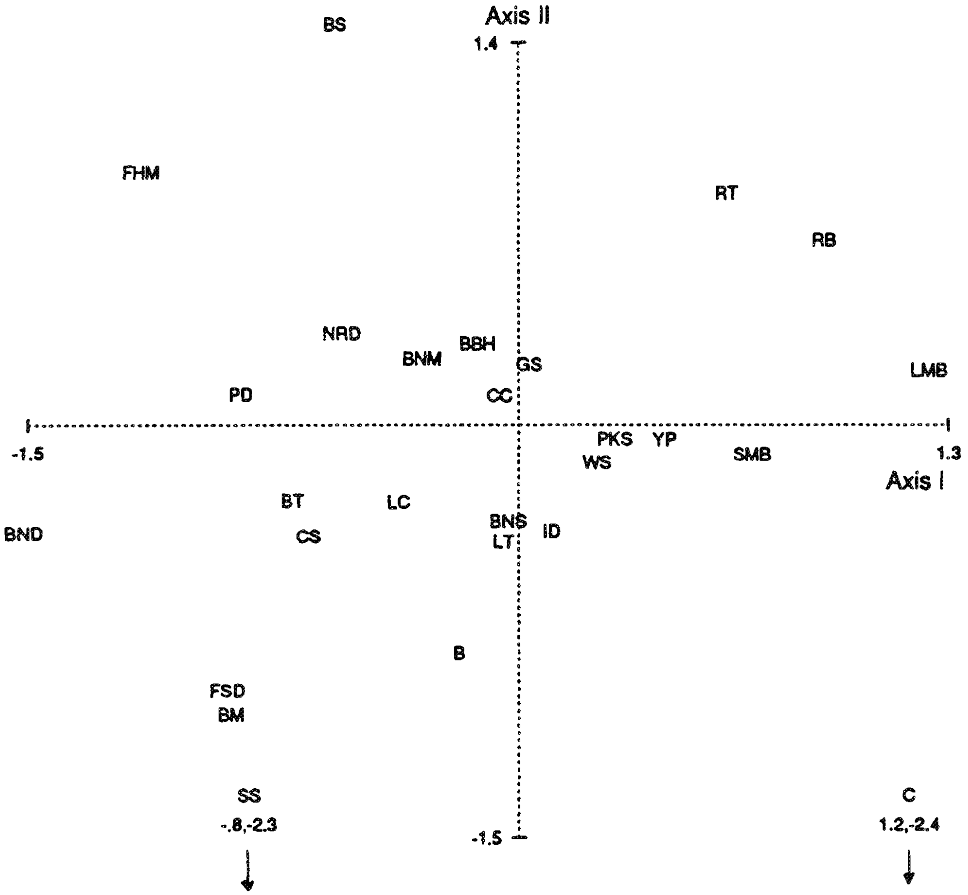

FIG. 1. Association of fish species from a CA of fish presence–absence across lakes. Species codes are defined in Table 1.

TABLE 2. Eigenvalues from principal components analysis (PCA) of lake water chemistry and morphology, CA of the benthic invertebrate and fish communities, and CCA of communities and environmental data.

	Eigenvalues				
Data set	Axis I	Axis II	Axis III	Axis IV	Total
PCA chemistry	4.879	2.396	1.497	1.153	12.00
PCA morphology	3.029	0.753	0.191	0.027	4.000
CA fish	0.272	0.217	0.181	0.179	2.032
CCA fish, chemistry	0.144	0.115	0.101	0.078	2.032
CCA fish, morphology	0.121	0.073	0.034	0.018	2.032
CA invertebrate	0.067	0.045	0.041	0.033	0.336
CCA invertebrate chemistry	0.042	0.019	0.017	0.012	0.336
CCA invertebrate, morphology	0.019	0.013	0.008	0.004	0.336

minimizes the sum-of-the-squared deviations (i.e., m^2; Gower 1975) between the pair of points representing each lake such that the greater the similarity of the multivariate configurations from the data sets, the lower the m^2 value. This measure is compared with that derived from repeatedly randomizing the configuration from one matrix and recalculating the m^2. The percentage of m^2 values equal to or less than the observed m^2 provides the significance level of the test.

Results

Fish Community–Environment Relationships

The CA of the fish community summarizes 42% of the total variance in the first four axes (Table 2). Plots of the species composition contrast small-bodied fishes, principally cyprinids, on the left side of the first axis with larger species, predominantly

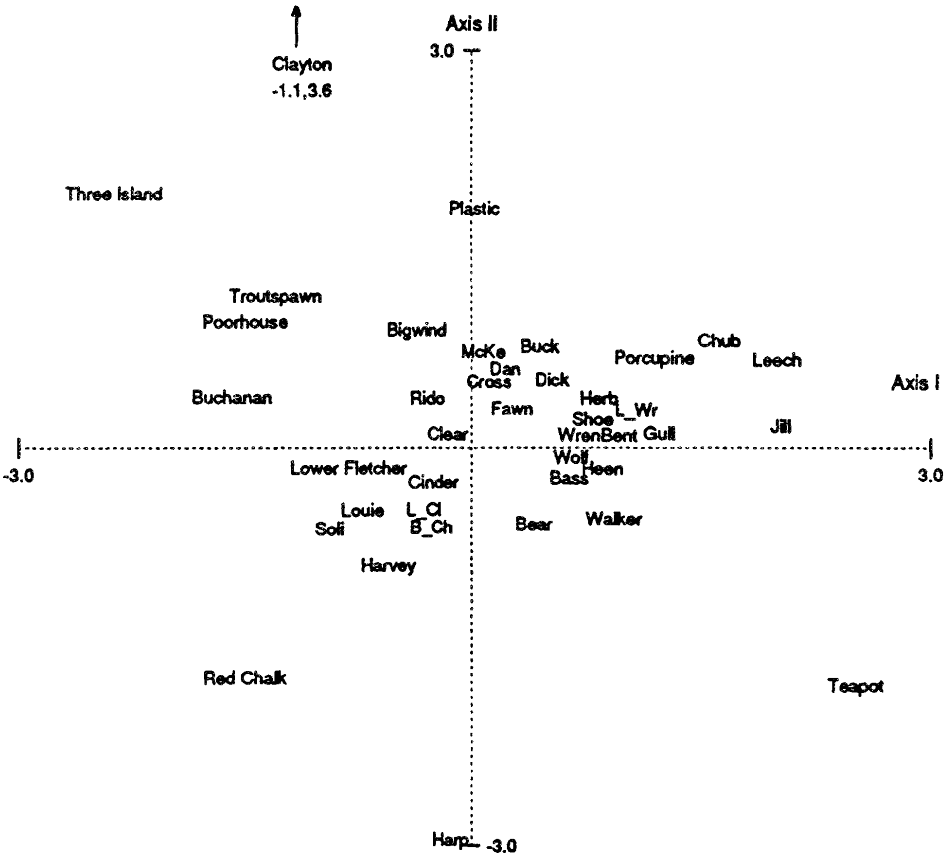

FIG. 2. Association of lakes based on a CA of fish species presence–absence.

centrarchids, which are positioned on the right (Fig. 1). No discernible pattern in composition was interpreted from the second axis. On the graph, a species is positioned at the centroid of the coordinates from the corresponding plot of lakes (i.e., Fig. 2) that contain the species. For example, fathead minnow occurs in Three Island, Troutspawn, Poorhouse, Solitaire, Bigwind, Buchanan, and Poorhouse lakes. Therefore, it is plotted at the centroid of the CA coordinates for these lakes. If one considers a line passing through the origin, then species located at the same end of the line are found together frequently whereas species located at opposite ends are found together rarely, if at all. Similarly, lakes positioned at opposite ends contain distinctly different fauna. For example, opposite the fathead minnow is the cisco which occurs in Teapot and Harp lakes. Fathead minnow and cisco do not co-occur in this lake set, and the lakes containing fathead minnow have a different fish fauna from those lakes containing cisco. Rarely occurring species (e.g., cisco, slimy sculpin) are positioned farther away from the graph origin, as are the lakes containing these rare species (e.g., Teapot and Harp).

The first axis from the CCA of the fish community and water chemistry was nonsignificant ($P = 0.50$). Therefore, no additional examination of this relationship is presented here, but additional details are found in Jackson (1992).

A CCA of fish species and lake morphometry shows a strong relationship between species such as lake trout, rainbow trout, cisco, burbot, and slimy sculpin and large, deep lakes (Fig. 3). Smaller, shallower lakes tended to include largemouth bass, rock bass, and brown bullhead. Several species, including smallmouth bass, golden shiner, pumpkinseed, yellow perch, white sucker, creek chub, northern redbelly dace, and Iowa darter, exhibit equal tendencies to occur in small and shallow or large and deep lakes.

Most lakes are easily categorized along the axis of depth and lake size (Fig. 4). Red Chalk, Harp, Blue Chalk, Clear, Bigwind, and Louie lakes are the larger, deeper lakes. Cinder and Bear lakes are somewhat atypical in that they are large, deep lakes, but they have extremely long lake perimeters relative to other lakes. The small, shallow, polymictic lakes include Leech, Jill, Dickie, and Fawn. Due to their relative shallow depths, these lakes typically do not stratify and have isothermal profiles during the late summer. Plastic Lake is positioned with this group but is deep enough to stratify thermally. Many lakes (e.g., Herb and Solitaire) are positioned orthogonal to the general lake size and depth axis and do not show similar trends in lake morphometry and fish species composition. The first two canonical axes account for 49 and 30% of the explained joint variance in fish species and lake morphometry. A significant relationship ($P = 0.03$) existed between the canonical axes of fish species composition and lake morphometry.

Invertebrate Community–Environment Relationships

The first four axes from a CA of benthic invertebrate abundance accounted for 55% of the total variance (Table 2). The first axis (20%) is dominated by the separation of *Chaoborus* from the remaining taxa. *Chaoborus* is positioned to the extreme right whereas several species (e.g., *Holopedium*) are located at the left end (Fig. 5). Increased occurrence and abundance of *Chaoborus* are associated with decreased occurrence and abundance of *Holopedium*, Pelecypoda, and Daphniidae. As *Chaoborus* and Bosminidae are positioned at right angles to one

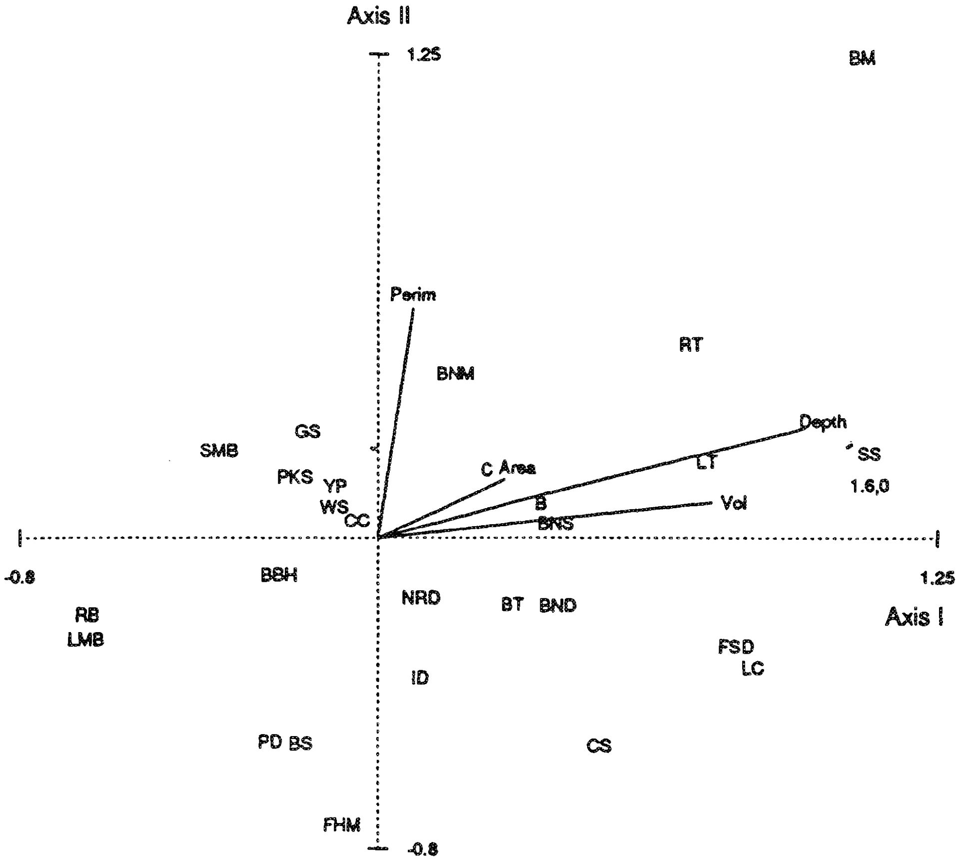

FIG. 3. Association of fish species and lake morphometry from a CCA of fish and lake morphometry across lakes.

another, the occurrence and abundance of these two taxa appear to vary independently of one another. In general, the second axis (13.5%) contrasts Bosminidae with the remaining taxa, particularly the Odonata, Macrothricidae, and Taltridae.

The plot of the lake ordination (Fig. 6) shows Fawn Lake at the extreme right end, followed by Dan, Poorhouse, and McKeown lakes. Overall, the only distinguishing trend along this axis is an increasing predominance of dystrophic lakes as one moves from left to right along the first axis. There are no apparent trends in the relative positioning of lakes along the second axis.

The chemistry-constrained ordination of the invertebrates led to a representation of the taxa similar to that found in the ordination of the invertebrates alone (Fig. 7). The first axis retains the contrast between *Chaoborus* and *Holopedium* whereas the second axis shows extremes of Bosminidae to Odonata. The first axis approximates a gradient of pH, calcium, and DOC, with the position of *Chaoborus* indicating a greater abundance at lower pH and lower calcium concentrations but higher DOC. The second axis shows a weak gradient associated with phosphorus and nitrates positively associated with Bosminidae and negatively with Ephemeroptera, Neuroptera, and Trichoptera.

The lake ordination has Fawn and Cinder lakes distinct from the remainder of the lakes (Fig. 8). Most lakes are clustered together in the central portion of the graph. When lake water chemistry is considered with the invertebrates, a pH gradient is found to extend from high-pH lakes (e.g., Blue Chalk and Red Chalk) to lakes of lower pH (e.g., Fawn and McKeown). The canonical axis, dominated by the pH gradient, is associated significantly ($P < 0.01$) with the first axis from the benthic invertebrates. This axis explains 34% of the joint variation in the invertebrate and chemistry data, indicating close correspondence between the invertebrate biota and their chemical environment.

The first axis from the CCA of the invertebrate community and lake morphology was nonsignificant ($P = 0.17$). Therefore, no additional examination of this relationship is presented here, but additional information can be found in Jackson (1992).

Comparison of Fish–Invertebrate Communities

Four CA axes from each of the fish and invertebrate ordinations were used in the PROTEST analysis. These axes were derived as weighted mean species scores so that the scaling represented an Euclidean distance plot. The test showed a significant concordance between the two matrices ($P = 0.02$), indicating that the arrangements of lakes in each ordination space are more similar than expected due to random chance. The inclusion of additional CA axes resulted in similar conclusions, but fewer axes yielded probabilities greater than 0.10.

Discussion

The fact that the lakes exhibit similar patterns based on their fish and benthic invertebrate communities may not be surprising. Considerable research has shown that fish can alter both the benthic and nektonic communities. Many studies have been based on enclosures where fish are held or exclosures where fish

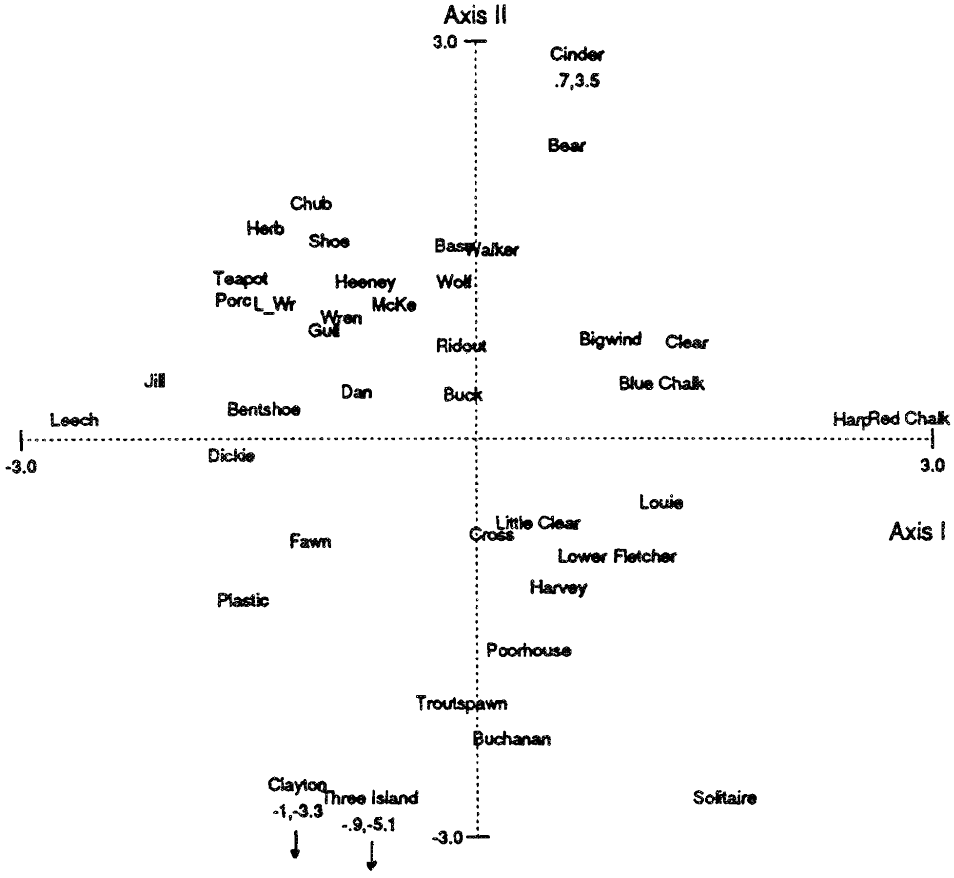

FIG. 4. Association of lakes based on a CCA of fish species and lake morphometry.

are excluded, but the treatment is assumed to have no direct affect on the benthic community. Several of these cage and whole-lake studies have documented changes in the composition of the invertebrates (Zaret and Paine 1973; Mills and Schiavone 1982; Magnan 1988; Butler 1989), reductions in the average size of the invertebrates (Morin 1984; Post and Cucin 1984), or reductions in the standing biomass but increased production of invertebrates (Post and Cucin 1984). There are other studies demonstrating a lack of effect (e.g., Thorp and Bergey 1981a). Results from enclosure/exclosure studies have been questioned regarding methodological problems (e.g., biofouling; Thorp and Bergey 1981a). As well, the spatial and temporal scale of these studies has been criticized, as ecological processes may differ at larger scales due to environmental heterogeneity and prey refuge, and seasonal effects may differ from those found in short-term enclosure experiments (Carpenter 1988b; Stein et al. 1988; Wellborn and Robinson 1991).

Rather paradoxically, our study shows similar structure between the fish and benthic invertebrate communities across the lakes, but different relationships for each taxonomic community and the lake environmental conditions. Fish communities appear to be structured more by the morphological characteristics of the lakes whereas the invertebrate results indicate that the chemical environment is more critical. The importance of lake morphology, particularly depth, to fish communities is well recognized (Johnson et al. 1977; Harvey 1978; Tonn and Magnuson 1982; Jackson 1988). Many species require cold-water refuges during summer; unless lakes are sufficiently deep and productivity too low to cause anaerobic conditions below the epilimnion, these species are excluded from the community. At the latitude and elevation of the lakes in this study, summer epilimnial temperatures may exceed the upper lethal temperatures of cold-water species (trout, char, and ciscoes) and approach those of cool-water species (e.g., white sucker).

During winter, low oxygen levels may develop under the ice cover of shallow lakes especially. Fish species differ in their tolerance to, and ability to find refuges from, such low-oxygen conditions. Species such as centrarchids and esocids show limited tolerance relative to cyprinid and ictalurid species. Thus, there may be community-wide selection of species based on their oxygen requirements (Jackson and Harvey 1989). In this study, the centrarchids were found to be associated with the smaller, shallower lakes (Fig. 7). In general, centrarchids are intolerant of low oxygen levels. Therefore, it can be inferred that winter oxygen conditions do not appear to be of major importance across all the lakes, but low levels may be important in specific lakes, e.g., Three Island (Jackson 1988). The environmental condition contributing the most to fish community structure is likely lake depth and the associated thermal stratification permitting survival of cold-water species such as lake trout, rainbow trout, and cisco during the summer. Thus, depth and the related temperatures and oxygen levels provide selective forces acting on the community throughout much of the year (Jackson et al. 1992).

The effect of water chemistry was inferred with the benthic invertebrate communities where a significant relationship was found between community composition and a pH-dominated environmental gradient. Several studies have shown a reduction

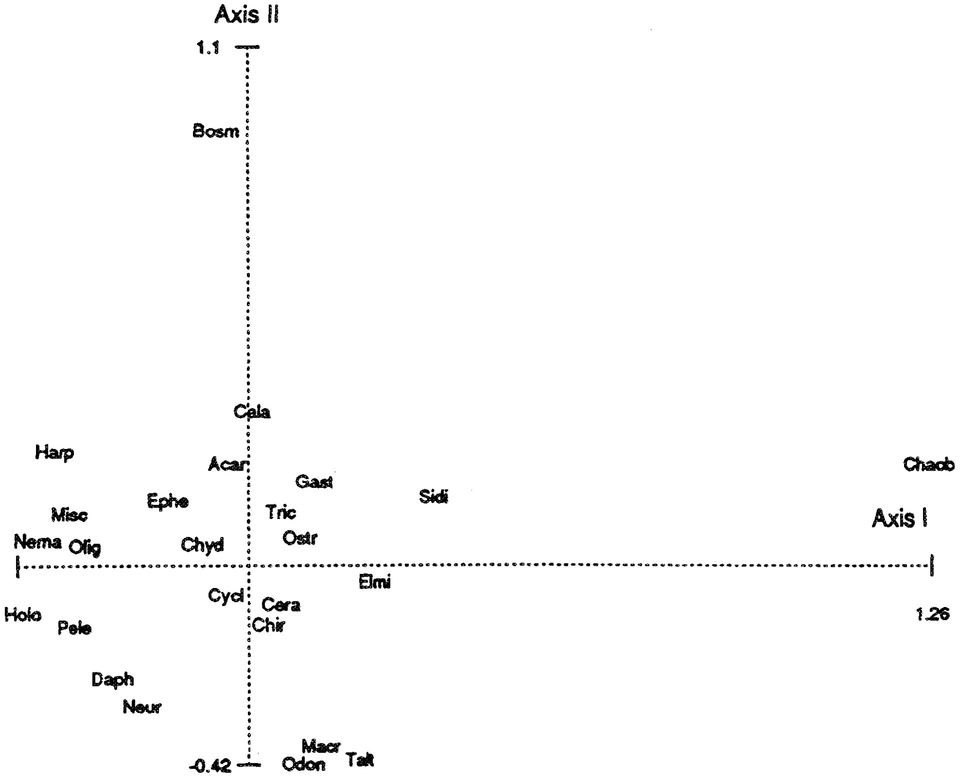

FIG. 5. Association of benthic invertebrates from a CA of invertebrate abundance across lakes.

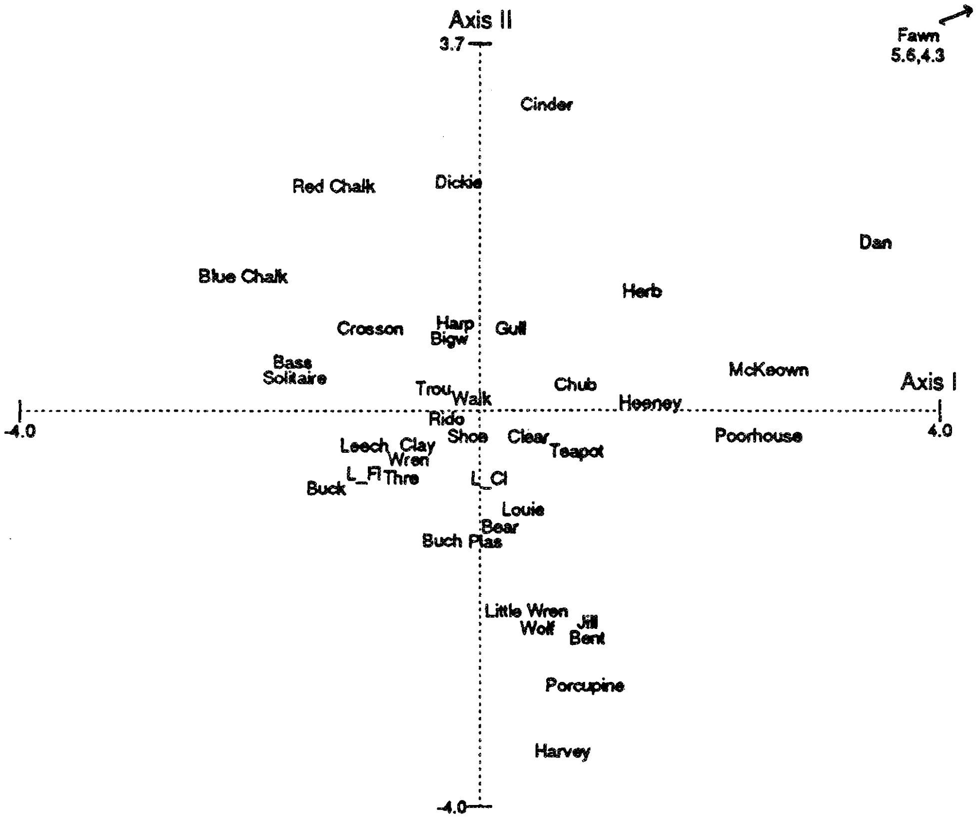

FIG. 6. Association of lakes based on a CA of benthic invertebrate abundance.

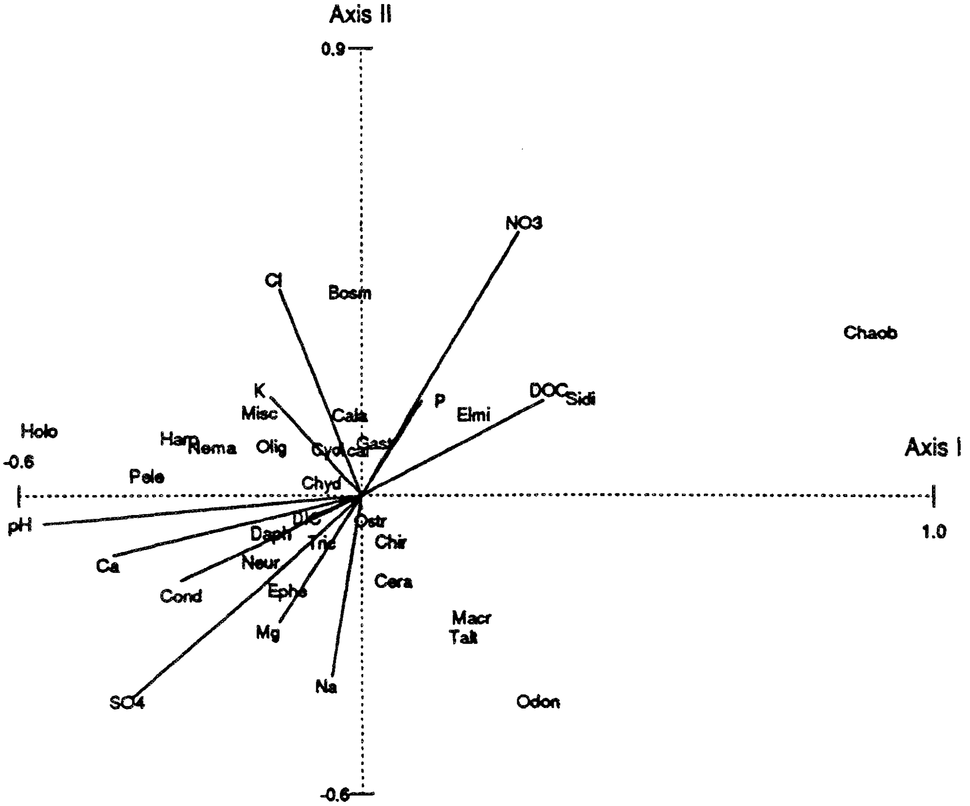

FIG. 7. Association of benthic invertebrates and water chemistry from a CCA of invertebrate abundance and water chemistry across lakes.

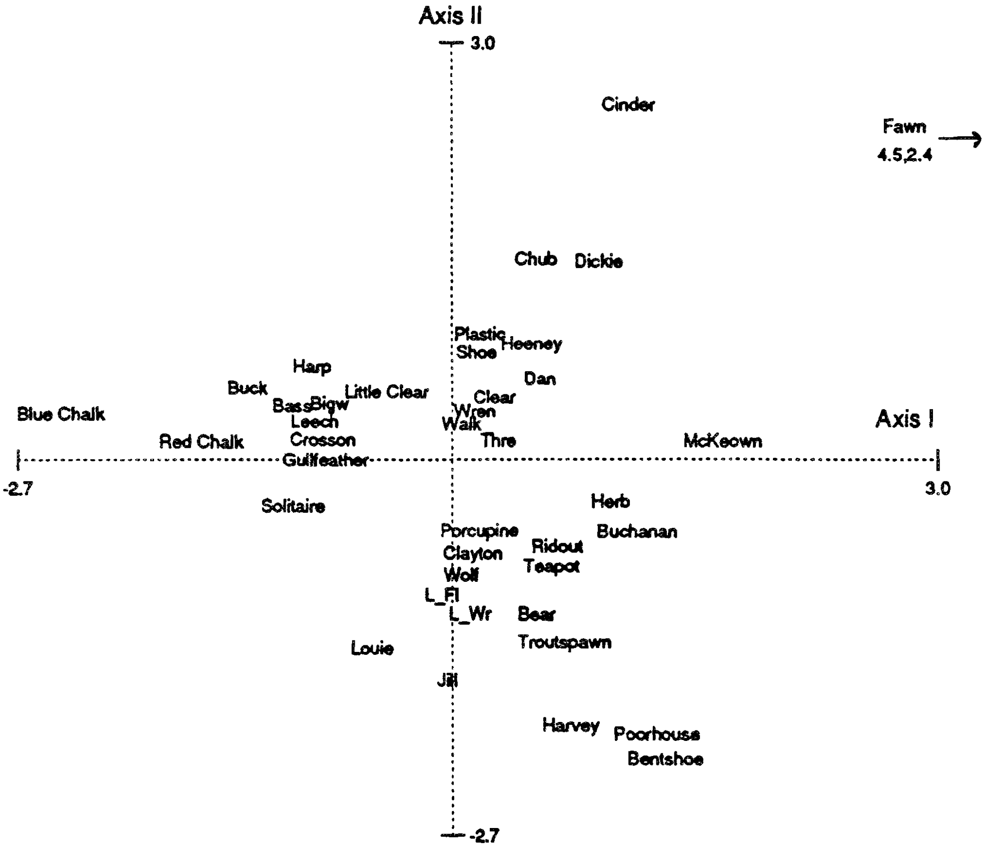

FIG. 8. Association of lakes based on a CCA of invertebrate species and lake water chemistry.

in taxonomic richness in acidified lakes (e.g., gastropods and pelecypods (Hagen and Langeland 1973; Roff and Kwiatkowski 1977; Collins et al. 1981; Harvey and McArdle 1986), macrothricids (Økland 1969; Harvey and McArdle 1986), *Mysis relicta* (Nero and Schindler 1983), and decapods (France 1984)). Reductions in the biomass or density of ephemeropterans, odonates, trichopterans, neuropterans, and plecopterans have all been found in acid-stressed lakes (Hagen and Langeland 1973; Grahn et al. 1974; Hendrey et al. 1976), although Harvey and McArdle (1986) found no reductions in these taxa.

Given the considerable variation and conflicting results among studies, the relationships between invertebrates and pH are unclear. Some of this variability may be attributed to the concentration and bioavailability of toxic metals, most especially aluminum (Stokes et al. 1989). Simultaneous changes occurring at different trophic levels within the lakes may also confound the relationship. Taxa such as fish and crayfish may limit the abundance of various benthic organisms through predation. As fish, crayfish, and additional predators are often intolerant of acid conditions, these species may be reduced or eliminated, thereby reducing predation pressure on more acid-tolerant taxa, and their numbers of prey may increase. This indirect effect of lake acidification has the potential to alter considerably the dynamics of ecosystems. Reductions in fish predation may lead to increased predation by *Chaoborus*, thereby altering the cladocerans and, subsequently, additional zooplankton and phytoplankton species via competition. Clearly, the complexity of these interactions complicates any direct assessment of the relationship between pH and the benthic community. Although the literature generally agrees that changes in the benthos occur, it is likely that some of the changes may be indirect rather than strictly due to the toxicity of the hydrogen ion per se.

Chaoborus abundance was associated with more acid lakes, but negatively correlated with *Holopedium*. Yan et al. (1985) found that *Chaoborus* abundance was greatest in acid lakes. Yan et al. (1988) showed a negative relationship between *Daphnia* spp. and *Holopedium*, but they could not determine whether differential predation or pH tolerance was more important in the negative correlation between the abundances of these taxa. Results show both the latter taxa to have similar occurrences and both are correlated negatively with *Chaoborus* abundance. Whether this pattern depends on a lesser tolerance to acid by Daphniidae and *Holopedium* relative to *Chaoborus* or a direct predator–prey effect between these taxa is unclear. The results show that lakes with circumneutral pH had increased abundances of *Holopedium*, Pelecypoda, Ephemeroptera, Neuroptera, Harpacticoida, and Nemata. Lakes with lower pH and higher DOC conditions had greater concentrations of *Chaoborus*, Sididae, and Elmidae relative to higher pH lakes. The most abundant taxon was Chironomidae which was ubiquitous and showed no trend in abundance or occurrence relative to lake acidity. Similar results were found by Harvey and McArdle (1986).

The paradox of a concordance between the fish and invertebrate communities but different relationships between the communities and the environment is due likely to an interaction between the biotic and abiotic environments. The fish community is structured primarily on the basis of the physical environment of the lake. Conditions necessary for spawning, e.g., shoals, as well as cold-water refuges for various species, may only be present in larger lakes. Within a general lake morphotype, chemical conditions such as pH and dissolved oxygen are likely important in determining the viability of certain species (e.g., fathead minnow and smallmouth bass). These particular factors contribute to determining the fish species that can survive within a lake. In addition to these factors, the abundance of fishes will be influenced by lake productivity via invertebrate productivity.

The invertebrate community is structured by the chemical portion of the abiotic environment. In conjunction with the influence of chemistry, the invertebrates are impacted by the fish community. The interactions between the fish and invertebrates are likely complex due to a variety of direct and indirect effects (sensu Kerfoot and Sih 1987). Some invertebrate taxa may be limited in abundance due to direct predation by fish or show increased abundance due to reduced invertebrate predation mediated by fish. Given the network of possible interactions between these two communities, it is difficult to predict the responses of many invertebrate taxa to changes in their chemical environment. The relationship of some invertebrate taxa (e.g. cladocerans) with different fish communities is predictable, and similar patterns result from surveys across lakes or from experimental manipulations. However, the response of many benthic taxa may be species specific as shown by changes in size structure of invertebrate communities (Post and Cucin 1984). A general shift to smaller taxa, reduced biomass, and increased rates of production is to be expected with increased predation by fish, but our understanding remains insufficient to permit more detailed predictions about benthic-community structure in response to changes in the fish community.

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