

What controls who is where in freshwater fish communities — the roles of biotic, abiotic, and spatial factors¹

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

Abstract: We examine evidence for the structuring of fish communities from stream and lake systems and the roles of biotic, abiotic, and spatial factors in determining the species composition. Piscivory by fish is a dominant factor in both stream and lake systems whereas evidence for the importance of competition appears less convincing. Within small streams or lakes, the impact of predation may exclude other species, thereby leading to mutually exclusive distributions and strong differences in community composition. Within a geographic region, abiotic effects frequently dictate the relative importance of piscivory, thereby indirectly influencing the composition of prey species present. The spatial scale of studies influences our perceived importance of biotic versus abiotic factors, with small-scale studies indicating a greater importance of competition and large-scale studies emphasizing abiotic controls. The scale of the individual sites considered is critical because smaller systems have higher variability and wider extremes of conditions than larger lakes and rivers. The stability of physical systems and degree of spatial connectivity contribute to increased diversity in both larger stream and larger lake systems. We identify challenges and needs that must be addressed both to advance the field of fish community ecology and to face the problems associated with human-induced changes.

Résumé : Nous avons étudié la structuration des communautés de poissons dans les cours d'eau et les lacs, ainsi que le rôle des facteurs abiotiques, biotiques et spatiaux dans la détermination de la composition spécifique. La piscivorie par les poissons s'avère être un facteur dominant, tant dans les cours d'eau que dans les lacs; en revanche, le rôle de la compétition est établi de façon moins convaincante. Dans les petits cours d'eau et lacs, la prédation peut exclure des espèces, ce qui résulte en des répartitions mutuellement exclusives et de fortes différences dans la composition des communautés. Dans une même région géographique, les facteurs abiotiques contrôlent souvent l'importance relative de la piscivorie, influençant ainsi la composition spécifique des proies présentes. L'échelle spatiale à laquelle les études sont conduites affecte la perception que l'on peut avoir de l'importance relative des facteurs biotiques par rapport aux facteurs abiotiques; les études à petite échelle révèlent une plus grande importance de la compétition, alors que celles à grande échelle mettent de l'avant les facteurs de contrôle abiotiques. L'échelle spatiale des sites individuels choisis revêt une importance critique, parce que les systèmes plus petits sont plus variables et présentent un plus grand éventail de conditions extrêmes que les grands lacs et les rivières. La stabilité des systèmes physiques et le degré de connectivité spatiale entraînent un accroissement de la diversité, tant dans les rivières que les lacs de grande taille. Nous identifions, en terminant, des défis à rencontrer et des besoins à combler pour faire progresser l'écologie des communautés de poissons et pour pouvoir faire face aux problèmes causés par les changements anthropiques.

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Introduction

Ecological communities and the study of their structuring factors have a long, rich history. Studies focused on terrestrial systems stimulated some of the initial and heated debates about whether or not communities contain discrete and nonrandom assemblages (e.g., Connor and Simberloff 1979) and whether species, and therefore communities, are regulated by biotic or abiotic factors (e.g., Andrewartha and Birch 1954). In many of these cases, aquatic community

ecologists have joined into these debates subsequently, yet have not initiated the research and theory. However, other topics have demonstrated the leadership of aquatic ecologists. For example, in general, aquatic ecologists have accepted the view of ecosystem-level factors in determining species composition for a longer period of time. Because shoreline boundaries of lakes and rivers were perceived as limiting the potential for movements and dispersal by aquatic organisms, early ecologists focused on the factors operating within each individual system in a more holistic

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D.A. Jackson,² P.R. Peres-Neto, and J.D. Olden.³ Department of Zoology, University of Toronto, Toronto, ON M5S 3G5, Canada.

¹Invited perspective for this 100th Anniversary Issue.

²Corresponding author (e-mail: jackson@zoo.utoronto.ca).

³Present address: Department of Biology, Colorado State University, Fort Collins, CO 80532-1878, U.S.A.

manner than terrestrial ecologists, who placed more emphasis on dispersal and colonization to influence species abundance and composition. During the last two decades, we have seen a convergence of these ideas, with terrestrial ecologists placing greater emphasis on ecosystem-level processes than in the past and aquatic ecologists viewing these boundaries as being less discrete. Studies of movements of aquatic organisms (fish, zooplankton, mollusks), whether accidental introductions of exotics, the stocking of fish to new locations, or the natural movements of such species between systems, have shown that the scale at which much of our research has been conducted may need to be expanded. A great deal of the aquatic research has focused on freshwater fish communities, our topic as well, undoubtedly due to their economical and societal importance.

Our first goal in this paper is to provide a snapshot of important findings and generalizations regarding the role of biotic and abiotic factors in regulating fish communities of stream and lake systems. We summarize the field's progression and our current understanding, ideas, and research approaches. We limit ourselves to particular sets of factors that have been identified as important in multiple studies or that we view as particularly promising. Space limitations require us to focus on major sets of factors and omit others that we consider to be less important across studies, although they may be important in specific cases. We attempt to remedy this limitation by directing the reader to associated studies that provide more detail on these topics (e.g., Matthews 1998). However, prior to this summary, we must address the ways of classifying fish communities and whether communities represent anything other than random sets of species sampled at particular locations and times. If they do not, then further analysis may be a fruitless exercise. Our second goal is to examine how spatial arrangements of systems affect fish community composition and how the perceived importance of various biotic and abiotic conditions depends on the spatial scale considered. Finally, we single out what we believe are promising avenues of research or needs for research that can provide major advances in our field. In contrast with most other studies which focus on either lake or stream communities, we seek to identify similarities or differences between the two types of systems, as these should aid in stimulating additional research avenues.

Fish communities: do they really exist, and if so, how do we classify them?

Fish communities are described or classified in various ways reflecting the goals of the study, attributes to be emphasized, and the degree of quantitative analysis employed. In some cases, communities or species assemblages have been named on the basis of ecological and numerical dominance of a particular species or group of species that are of economic value (e.g., Ryder and Kerr 1978). This approach is particularly convenient for resource managers, as the identified species are generally those of management interest. Lake fish assemblages have been designated using this approach or in a more quantitative manner (e.g., Johnson et al. 1977). Similar approaches exist within stream fish community analysis (e.g., Echelle et al. 1972).

Another approach to community analysis has been to classify species into guilds, i.e., species sharing attributes, gen-

erally based on feeding or reproduction. This approach is convenient and useful due to its functional nature, as it focuses on specific ecological attributes of the species. Feeding or trophic guilds classify species based on their diet or manner of feeding (e.g., Keenleyside 1979). For species with restricted and consistent diets, this works well. However, many fishes vary their diets as a consequence of ontogeny or opportunity, and a feeding-guild classification needs to be flexible to accommodate the fact that a species may switch between guilds as it grows from a fry to an adult. Individual species may need to be classified into several guilds, thereby complicating the desired use of a simple guild-based approach. However, the explicit recognition of ecological attributes and level of data reduction provided by the guild approach has some appeal.

An additional approach to community classification is through the use of multivariate statistical methods. Although the use of multivariate methods to summarize community patterns began in the early 1900s, their application to fish community analysis is more recent. Some of the first applications to fishes were those by Smith and Powell (1971) and Harvey (1975). Researchers were motivated by the idea that multivariate approaches provided an objective approach in identifying patterns in species assemblages and their relationships with environmental conditions. Since the initial use of multivariate approaches with fish communities, we have advanced in developing and applying methods to predict the assemblages (e.g., Magnuson et al. 1998), to test the association between communities and environmental conditions in lakes (e.g., Jackson and Harvey 1993) and rivers (e.g., Taylor et al. 1993), to measure and remove the role of spatial autocorrelation (e.g., Mandrak 1995), and to assess the importance of isolation (e.g., Olden et al. 2001).

When studying fish communities, researchers make the implicit assumption that the associations of species arise from either biotic or abiotic factors or some combination of the two. However, if the communities are indeed random (i.e., local fauna are composed of random sets of species from the regional pool), then there is little point in studying them in detail because derived patterns may be meaningless. So what evidence exists supporting the hypothesis that fish communities are actually nonrandom in their structure (see Evans et al. (1987) for additional discussion)? One would like to assume that relationships from analyses of communities or community-environment relationships indicate that communities are nonrandom, but this is not necessarily the case because such "interpretable patterns" can be derived from random data too (Jackson 1997). Consequently, we need to consider evidence from studies that specifically test whether or not communities show nonrandom patterns in time and (or) space. The assessment of whether stream fish communities are random or structured (alternatively, stochastic or deterministic) was the focus of a series of papers in the 1980s (Grossman et al. 1982; Yant et al. 1984). This exchange of papers suggested that numerically dominant species often showed consistent patterns over time but that rare species varied greatly, and patterns of rank abundance were also complicated due to seasonal species movements. These findings provided evidence that the timing and extent of sampling may be important factors affecting our perception of stream fish community structure. The spatial and

temporal scales involved may be important given that variability in species composition and environmental conditions may have different scales (Ross et al. 1985). Finally, the resolution or scale of the data used in such analyses may also influence our conclusions. Rahel (1990) showed that differences in our interpretation may occur depending on whether species relative abundance, rank abundance, or presence–absence data (a quantitative scale issue) are used as the measure of community composition.

Jackson et al. (1992), in a comparison of null models, showed that the fish communities in lakes from each of five different regions were all structured nonrandomly in space. Several studies have recently examined the question of whether fish communities demonstrate concordance with other ecological communities. If two or more communities based on different taxonomic groups show concordant patterns across a range of sites, one can be more confident that the patterns are nonrandom. Example studies have used fish and benthic invertebrate communities from lakes (Jackson and Harvey 1993) and streams (Kilgour and Barton 1999) to show the concordance in these communities across the various locations. These findings support the idea that various fish communities show nonrandom patterns in composition over time and (or) space. We do not know whether this is a general finding for lakes and streams due to the limited number of published studies; however, the studies available do suggest that fish communities are highly structured. In addition, the fact that many studies show similar relationships between particular assemblages and their surrounding environment (e.g., stream flow, lake winter oxygen) provides additional evidence for nonrandom structuring of fish communities.

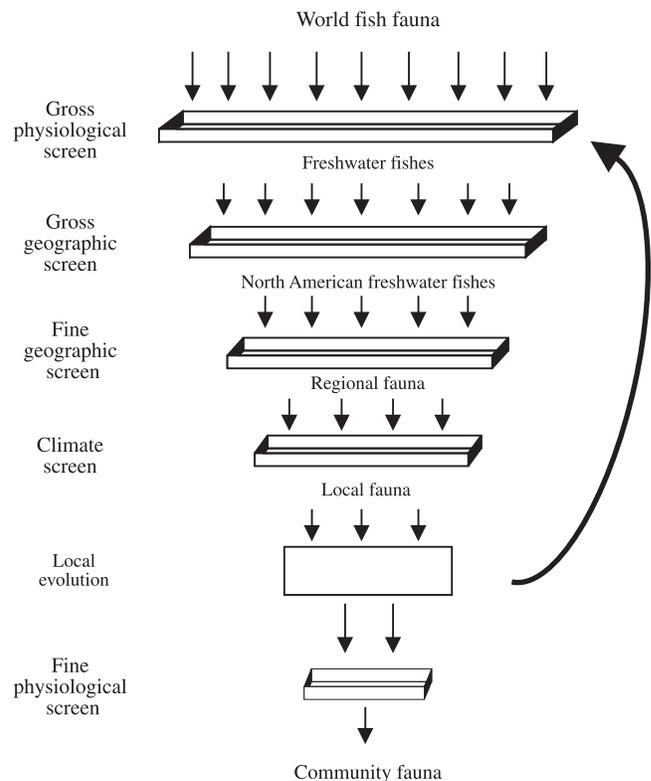
The interaction between issues of scale and the roles of biotic and abiotic factors in structuring fish communities is recognized. Smith and Powell (1971) proposed that the local fish community is the result of a series of selective pressures ranging from geographical effects (e.g., vicariant events) to physiological effects. They proposed a series of screens or filters removing species from the global fauna until only the species found at a particular site remained (Fig. 1). They favored an autecological structuring of the local community that was consistent with the importance that they attributed to abiotic conditions. Jackson and Harvey (1989) and Tonn (1990) proposed similar views regarding this hierarchical nature of factors and scale but placed increased emphasis on the role of biotic interactions, specifically predation, in addition to abiotic factors. We stress that although we structure our paper into sections examining each of these components, there are strong interactions among these three components, and recognition of these interactions is critical in examining virtually any freshwater fish community.

Biotic factors structuring fish communities

Predation

Predation has been shown to have very strong effects on fish communities via direct and indirect mechanisms. Various studies of lake communities have shown the strong and rapid effects imposed by predators, with much of the evidence coming from studies related to species introductions (e.g., Li and Moyle 1981). While the changes in a few lakes

Fig. 1. Selective filtering of the global fish fauna into the set of species comprising the local community within a lake or stream. This is an adaptation redrawn from the hierarchical screening provided by Smith and Powell (1971).



have been followed over time, e.g., the Nile perch (*Lates niloticus*) impact on the Lake Victoria cichlid fauna, other evidence demonstrates the impact of predatory species on communities. Studies by Jackson et al. (1992), Chapleau et al. (1997), and others have shown that many species of small-bodied fishes do not coexist in small temperate lakes where piscivorous species, such as northern pike (*Esox lucius*) or bass (smallmouth (*Micropterus dolomieu*), largemouth (*Micropterus salmoides*)), are present. Cyprinid assemblages show strong negative associations with these predators, and one generally finds either predatory species or the prey assemblage in these small lakes but not both groups. Habitat complexity has been shown to strongly influence the viability of prey populations under predation risk (e.g., Everett and Ruiz 1993), whereas other studies have shown that some species remain vulnerable regardless of the habitat available in small lakes (e.g., MacRae and Jackson 2001). Without these refugia, the prey species may become extinct locally. However, as the size of the lake considered exceeds 150–200 ha in surface area, there is a general trend for both groups to coexist in lakes (D.A. Jackson, unpublished data), likely due to increased habitat heterogeneity and inherent spatial components in the population dynamics of the various species that are not found in the smaller lakes.

Stream-based studies have shown strong predation effects (see Gilliam and Fraser 2001 and references therein). Power et al. (1985) and numerous other studies have shown that predators can affect the choice of habitat by prey species within streams. This may lead to different assemblages be-

ing present in particular pools or riffles because prey species move to sites providing less risk of predation (e.g., Gilliam and Fraser 2001). Prey species may move to areas where predators have difficulty in accessing them (e.g., Schlosser and Angermeier 1990), and these may be habitats different from those selected when predators are not present (e.g., piranha's (*Pygocentrus notatus*) effect on other species; Winemiller 1989). Gorman (1988) suggested that some of the structure attributed to stream fish assemblages is due to prey species' common avoidance of predators, i.e., species collectively congregating in habitats affording greater protection from predation.

While direct predation effects are often expressed strongly and quickly by the elimination of one or more prey species in the lake or stream system, there are additional, but less obvious, indirect effects by which predators may structure fish communities. When prey species alter their choice of habitat and foraging to reduce predation risk, they may experience corresponding changes in life history and fitness reduction. Slower growth generally means that the individual and species remain vulnerable to predation for a longer time. Fecundity may be reduced if individuals mature at a smaller size, and individuals in poorer condition may experience increased mortality during environmentally stressful periods. For example, Shuter et al. (1980) showed size-selective mortality in the overwinter survival of smallmouth bass. Therefore, predator avoidance may contribute to reduced growth that may be sufficient to prevent successful survival through the winter, thereby preventing the successful long-term survival of the species within such systems. Although the direct effect of smallmouth bass on cyprinids has been discussed, predation can lead to indirect biotic effects through competition. Vander Zanden et al. (1999) showed changes in the diet of lake trout (*Salvelinus namaycush*) as a consequence of bass being introduced into lakes. The bass reduced the availability of the littoral forage base, leading to a reduction in the quality of the trout diets, potentially with life history consequences. Differences in the efficiencies of predators can contribute to changes in the communities (Matthews et al. 1994), particularly when more effective predators are introduced into either lake or stream systems. An example is where a particular assemblage of cyprinids may coexist with salmonid predators, but the diversity of cyprinids is reduced following the introduction of bass into the lakes (MacRae and Jackson 2001). The difference in the cyprinid assemblage response is because the salmonid species are less effective littoral predators than the bass in these lakes.

Predation effects can arise through reduced or enhanced changes in the rates of movements of species between habitat patches. Emigration will hasten the reduction of the population size of prey species by adding to the losses due to direct predation on individuals. Enhanced emigration due to the presence of predators has been shown in lakes (He and Kitchell 1990). However, this is not always the case, as other studies have shown both increased and decreased rates of movements (e.g., Gilliam and Fraser 2001 and studies cited therein). Changes in rates of movement can alter the meta-population dynamics of fish communities within watersheds encompassing various tributaries or sets of lakes, with the consequences dependent on the spatial arrangements of the water bodies and their connectivity (discussed below).

Experimental studies confirm that the impact by predators is swift and considerable (He and Kitchell 1990). Prey species move into shallow waters, frequent complex habitats, or leave the site to avoid predators (He and Kitchell 1990). Size-selective predation (Wahl and Stein 1989) has been shown to have a strong influence on which individuals and species survive, thereby leading to potentially different communities depending on the presence of particular predators, i.e., those selecting only small-bodied prey species versus those feeding on all species. An important feature identified by Matthews (1998) is that despite the large number of potential predator-prey combinations (e.g., about 900 species of fish in North America), most studies have been limited to examining only a few predators (e.g., largemouth bass, smallmouth bass, creek chub (*Semotilus atromaculatus*)) and prey (e.g., small creek chub, fathead minnow (*Pimephales promelas*), northern redbelly dace (*Phoxinus eos*)). Consequently, the current ideas and theories related to fish predator-prey relationships are based on a limited range of potential species combinations, and comparisons incorporating other groups of species will be helpful.

Competition

Although there is no consensus regarding the role of inter-specific competition in structuring stream and lake fish communities, the ample literature associated with resource partitioning among fishes suggests that competition may play an important role in the local organization of communities (see Ross 1986). Most studies are based on field observations, and many suggest that niche segregation rather than competitive exclusion is the predominant outcome resulting from competitive interactions. Although there are few studies that compare the importance of different resource axes in separating species, habitat segregation appears to be the most prevalent resource-partitioning mechanism identified for lake and stream fishes (Grossman et al. 1998). However, most observational studies do not test directly whether competition is the most plausible mechanism responsible for the patterns observed or whether other uncontrolled factors could give rise to similar results. For example, allopatric speciation with posterior contact (Wiley and Mayden 1985) can generate patterns equivalent to the competition hypothesis because of differential adaptation to distinct habitats.

In lake systems, the strongest evidence for competition comes from a combination of observational and experimental studies conducted on centrarchid assemblages that demonstrated that competition caused shifts in habitat use, thereby facilitating exploitation of different food sources (Werner 1984). In a review of the literature involving numerous assemblages, Robinson and Wilson (1994) found that habitat diversification appears to be the mechanism allowing coexistence of lake fishes. In addition, they showed that evolutionary responses to competition, such as character displacement promoting morphological differences, especially between benthic and pelagic forms, are much more common than previously considered. Recognizing that habitat is an important component of the niche for a variety of lake species highlights an important evolutionary consideration. Given that similar habitats occur in lakes in very different parts of the world, it is not surprising that comparable habitat segregation occurs in many areas. Although the species composi-

tion may be quite different, ecological equivalents are represented in these different regions. This convergence of ecotypes from disparate regions implies that habitat differentiation is very important because habitats are relatively more stable over evolutionary times than other resource parameters such as food quality and availability. In fact, Jackson et al. (1992) suggested that habitat-related differences and predation effects, rather than competition, structure lake fish communities.

In contrast with that for lake fish communities, the knowledge of competitive interactions in structuring stream fish communities remains somewhat superficial (Resetařits 1997). There are several studies showing the presence of competition among stream fishes (e.g., Resetařits 1997). However, due to the environmental variability in stream systems, ecologists continuously debate whether behavioral, morphological, and physiological adaptations play a more important role than interactions such as competition (Grossman et al. 1998). The net increase of species richness along gradients of high to low environmental variability (Gilliam et al. 1993) and the fact that average population densities are often far below the maximum have been used to argue that competition is less important in shaping stream community structure. Populations in variable environments could be stable but at densities below where competition becomes important. Streams simultaneously may have both "harsh conditions" where disturbance might play an important role and "benign environments" where interactions could be significant due to environmental stability (Townsend 1989). There are dissenting views (Lóbon-Cerviá 1996; Rodríguez and Lewis 1997) regarding the importance of spates and droughts as population controls in streams given the associated stress and potential for population decline during such events. Much of the controversy regarding the importance of competitive interactions in structuring stream fish communities may arise from different scales being used in different studies (Taylor et al. 1993). The importance of the range in habitat conditions and spatial scale is critical in whether competition is viewed as an important factor or not.

Most freshwater fish ecologists now accept the idea that combinations of local biotic and abiotic factors with associated regional factors are responsible for structuring local communities (e.g., Angermeier and Winston 1998). However, the accumulation and interpretation of evidence from numerous isolated small-scale studies does not provide a suitable basis for interpreting large-scale patterns (Underwood and Petraitis 1993). We need to determine whether competition can influence community structure at scales that are larger than the "garden experiments" that are commonly used in resource limitation experiments.

Only recently have stream fish ecologists started to interpret evidence of competition from empirical observation or natural experiments over large spatial scales, where other processes that could have led to equivalent patterns are partitioned out in the design and analysis. Winston (1995) presented a compelling case in which null models rather than controlled experiments were used to investigate whether interspecific competition was a more parsimonious explanation for patterns of species co-occurrence relative to other alternative hypotheses such as history (see Douglas and Matthews 1992). Natural experiments not only accommodate

larger numbers of species, geographic and time scales, treatment levels, and their combinations, but they can also be used to control for confounding effects that could mimic the results of competition, such as different habitat optimums (e.g., Taylor 1996). Natural experiments have contributed substantially to our insight regarding the importance of competition in structuring stream fish communities, and additional insight can be obtained provided that more adequate sampling and statistical designs and sophisticated analytical tools are applied. Some competitive effects, such as exclusion over large scales, can be best detected through natural experiments. Such resulting patterns can indicate (i) at which spatial scales local interactions have an important effect, (ii) the resources that appear limiting and therefore under competition, and (iii) which species are most likely to be affected, thereby providing the initial evidence for competitive interactions. Where appropriate, additional experiments can help define the specific mechanisms (e.g., density or size compensation, types of resource) through which competition influences population trajectories.

Abiotic factors structuring fish communities

Biotic factors, whether predation or competition, show comparable effects on the fish communities in both lake and stream/river systems. However, the abiotic influences in lakes and streams are quite different in their relative importance in determining the fish community composition. Many of the factors in lakes show variation principally in a vertical orientation whereas stream systems exhibit them in longitudinal arrangements, often semireplicated within pool-riffle pairings along the length of each stream. In general, the abiotic components of both systems can be divided into physical and chemical factors.

Physical

Climatic conditions control the potential range that any given species can occupy. Whether or not species occupy the various sites within this potential range is due to a combination of historic/biogeographic conditions defining the regional species pools (e.g., previous opportunities to colonize the area or in situ speciation) and contemporary factors at a smaller scale (e.g., predation, environmental gradients). This nesting of selective pressures yields the realized set of species at a site, i.e., the community, relative to the regional pool of species defined by the climatic and historical conditions. Smith and Powell (1971) first formalized this relationship such that the local fish community was the product of selection on the global fish fauna by various environmental, biogeographical, and evolutionary factors that were portrayed graphically as a series of screens or filters (Fig. 1). Tonn (1990) presented a similar framework of nested filters removing components of the fauna resulting in the realized local fish community.

Climatic factors can be divided into those related to temperature and those related to precipitation. Temperature has been long recognized to limit the range of species both in a broad geographic scale (e.g., Shuter et al. 1980) and at finer scales within particular lakes or streams (e.g., Grossman and Freeman 1987). High temperatures may produce high physiological demands and stress while also reducing the oxygen

saturation levels of water. So the combination of increased metabolic demand and decreased oxygen availability can prove limiting or lethal. Aquatic systems may have thermal refugia if they stratify and the hypolimnion remains sufficiently oxygenated (see below). Stream systems often have comparable refugia where deeper pools having groundwater inflows provide refuge from the daily heating during summer periods (e.g., Matthews and Berg 1997).

Low temperatures may limit the distribution of species and affect community composition (Magnuson et al. 1979). Shuter et al. (1980) showed that average July temperatures below 15°C prevented young-of-the-year smallmouth bass from growing to a sufficient size to overwinter successfully, therefore precluding long-term viability of the population. We discussed earlier the impact that this predator has on other species of fish. Therefore, in areas near the northern limits of the range of smallmouth bass, temperature plays a major role in determining the composition of these communities. Winter temperature is important in affecting the mixing regime of lakes and the duration of ice cover for temperate or boreal/alpine lakes. In turn, the mixing regime affects the availability of oxygen in deeper waters of dimictic lakes and the availability of oxygen in monomictic systems, particularly those in warmer climates. Within stream systems, low temperatures can have direct impacts by determining the duration, form, and depth of ice formation. Ice may provide a surface cover, thereby limiting oxygen exchange, or ice may thicken, potentially freezing to the bottom, thereby killing fish directly. Spring thaws can provide severe ice scouring, effectively removing the fish and much of the habitat from the streams (Scrimgeour et al. 1994). Such effects tend to be greater in headwaters of alpine systems or temperate/boreal streams than in the lower reaches. The ability to survive during freezing or scouring conditions differs among species due to behavioral, physiological, and morphological adaptations. Therefore, community composition differs in systems experiencing different levels of the stresses. However, limited research has been directed at studying fish communities during winter months in cold regions. The difficulty in working in adverse conditions has limited our knowledge, and additional work is required given that these periods may represent a substantial proportion of each year and may be the critical periods of the year for some communities.

Lake or stream morphology affects the consequences of local temperature conditions and other abiotic factors (e.g., oxygen). The surface area of lakes is strongly related to species diversity in lakes (e.g., Barbour and Brown 1974). Increased fetch contributes to increased wave action that may lead to the formation and maintenance of coarse, rocky littoral habitats that may not exist in smaller lakes. These habitats may enhance community diversity because these new spawning, nursery, or feeding habitats may not be present in smaller lakes. Area and fetch of lakes influence the temperature of the surface waters, the depth to which mixing occurs, and the associated hypolimnetic volume. The morphology of lakes also influences the proportion of the euphotic or productive zone relative to the hypolimnion. Lakes having proportionately smaller hypolimnetic volumes are more prone to experiencing temperature and oxygen stress, thereby potentially limiting the viability of cold-water species during summer. For a given level of production and respiration, a

shallow lake will experience a proportionately greater depletion of oxygen during the winter. Given the taxonomic variation in sensitivity to oxygen stress (see below), morphometric differences among lakes can lead to very different fish communities.

Stream morphology affects flow dynamics, both temporally and spatially. Geomorphology, soil development, and vegetative cover all affect the rates at which precipitation or snowmelt reaches the principal channel. The result is that systems behave very differently depending on the relative contributions of groundwater versus surface flow in combination with the precipitation regime. The degree of variability associated with velocity selects for species capable of surviving within these flow regimes (see Statzner et al. 1988) or those able to recolonize quickly. Some studies show minimal effects on the adults in fish communities even after major floods (e.g., Matthews et al. 1994). The morphology of the streams varies such that some streams have well-developed pool-riffle patterns due to the underlying geology whereas other systems may have geologies that do not readily develop such patterns (e.g., recently glaciated PreCambrian bedrock in north-temperate regions or alpine systems). Morphological features, such as depth, are often strongly related to community composition. Depth of streams is negatively correlated with the probability of winter freezing and oxygen depletion and with high water temperatures during summer periods (Schlosser 1987). Shallow streams are more variable with greater extremes in the range of conditions experienced by the associated communities in much the same way that shallow lakes experience greater extremes annually.

Structural complexity of the environment interacts with other characteristics of the abiotic and biotic environment and contributes to the community diversity. Substrate surface irregularities, such as rocks or woody material (i.e., necromass), alter the stream flow and deepen some regions through hydraulic scouring (Shetter et al. 1946) with fish being attracted to the area because it is energetically less demanding than maintaining a position in the open water. Areas in both streams and lakes with more complex habitat characteristics have been identified as providing both enhanced foraging and enhanced refuge from predation, thereby contributing to increased diversity (Flebbe and Dolloff 1995). In a similar way that hard surfaces enhance diversity, different assemblages may be found depending on the level of macrophyte cover provided, although this is not strictly an abiotic factor.

Chemical

The principal chemical factors affecting community composition identified repeatedly in studies of lake and stream fish communities are dissolved oxygen levels (e.g., Zalewski and Naiman 1984) and the acidity of the system (e.g., Harvey 1975). We indicated the importance of oxygen and its relationship with water temperature (e.g., the capacity of water to hold oxygen decreases as temperature increases while metabolic demand typically increases). In deeper temperate lakes, the fish assemblages become spatially segregated during summer, since species requiring colder, oxygen-rich waters are restricted to deeper waters whereas many of the small-bodied species (e.g., cyprinids) occupy shallow, littoral areas. This reduces some predatory and competitive interac-

tions within lakes because the species are spatially segregated for a significant portion of the year. In contrast, the principal littoral predators in temperate North American lakes (e.g., bass, pike) occupy similar habitats with these smaller species, and their concentration together in the epilimnion during summers may contribute to patterns of mutual exclusion (Jackson et al. 1992). In shallower lakes, the cold-water assemblages are absent generally due to a combination of both thermal stress and oxygen depletion in the deeper waters. Large predatory species generally require higher levels of oxygen, and many smaller species have behavioral and physiological adaptations that allow them to survive even at low oxygen levels (Magnuson et al. 1985). Therefore, periodic reductions in dissolved oxygen levels contribute to the loss of predatory species such as pike and bass whereas prey species may be relatively unaffected (e.g., Harvey 1981). Small differences in the development of winter anoxia result in very different community composition in adjacent lakes. Streams also exhibit variation in the level of oxygen present, perhaps without the availability of oxygen-rich counterparts (e.g., hypolimnetic waters) being available as a refuge. Shallow, slow-moving sections of streams are prone to temperature elevation and decreased oxygen levels due to high decomposition and respiration rates, thereby stressing fish present or favoring different species. The combination of temperature and oxygen stress may eliminate intolerant species, such as salmonids, from stream systems. Tropical systems having low flow rates, or flood-plain ponds, frequently develop low oxygen levels due to high ambient temperatures and high respiration and decomposition rates. Tropical fishes exhibit a greater degree of air breathing relative to temperate fishes (Kramer 1983), likely reflecting this selective pressure imposed on these communities due to anoxia.

Acidity of lakes and streams has a strong effect on fish communities. Species richness in lakes declines as waters acidify (e.g., Somers and Harvey 1984). Anthropogenic acidification in temperate North America and northern Europe has contributed to the loss of many populations and changes to the fish communities, as many of the small-bodied species are more vulnerable (Rahel and Magnuson 1983) than the larger species, in contrast with the relationship for dissolved oxygen. The potential for acidification is influenced by geology and by the lakes' position within the landscape. Lakes positioned on carbonate-based bedrock and with deeper soils generally show less impact of acidification than lakes located on granitic rocks, assuming that other factors are equal. Therefore, there can be substantial differences in the water chemistry and the associated fish communities among lakes at relatively small scales (e.g., kilometres; Somers and Harvey 1984) as well as differences between regional faunas and communities at larger scales (e.g., tens to hundreds of kilometres; Jackson and Harvey 1989). Location in the watershed also contributes (Kratz et al. 1997) because headwater lakes generally acidify more quickly than downstream lakes as lake surface area represents a greater proportion of the total catchment area; therefore, it provides less potential to buffer the precipitation. These headwater lakes experience a loss in species diversity even though they generally begin with a more depauperate fauna because species richness is correlated with lake size (Magnuson 1976). Some regions contain naturally occurring acid lakes or streams due to the

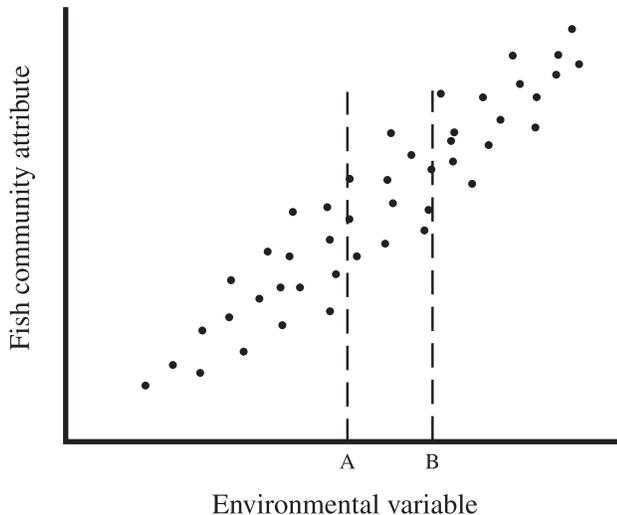
presence of high concentrations of organic acids originating from adjacent wetlands. The fish communities of these areas have undergone long-term selection for such conditions whereas anthropogenic acidification has been mainly restricted to the past two to four decades, generally not providing sufficient time for selection or for colonization by tolerant species.

Scale and spatial aspects of fish communities

The aspects of scale and space are somewhat interrelated given that large-scale studies involve greater spatial areas than small-scale studies or, alternatively, incorporate greater periods of time. Although we consider scale separately from the biotic and abiotic components, such distinctions are rather artificial, since these three sets of factors are generally interrelated and their interactions confound attempts to separate out specific main effects. The perceived importance of various abiotic or biotic factors is generally dependent on the scale at which the study is carried out. Moreover, biotic interactions and population dynamics are clearly related to variation in abiotic components (Power et al. 1988).

Within terrestrial and aquatic systems, one finds that habitat and environmental heterogeneity increases with the spatial or temporal scale (Zalewski and Naiman 1984). Studies examining the relationship between habitat and fishes tend to focus at one of two scales (Hinch 1991). Lake studies either compare in detail the fish assemblages and habitat use at different sites within a lake, often through time, or operate at a larger scale, examining the compositional patterns among lakes using each lake as an observational unit (e.g., Johnson et al. 1977) with less accurate or precise estimates of the abundance of species. Many of the studies at the large scale simply use species presence-absence as the level of data resolution due to the difficulties in obtaining reliable estimates of relative or rank abundance (see Jackson and Harvey 1997). Similarly for stream studies, researchers focus on obtaining detailed data at very small spatial scales or less detailed data for larger comparative studies (Lamouroux et al. 1999). In the case of small-scale studies in lakes or streams, researchers often study aspects related to fine-scale habitat use or habitat partitioning and address questions related to direct interactions between species (e.g., competition). The detailed information required at such fine scales prevents comparable studies from being conducted at larger spatial scales (Hinch 1991), at least without considerable cost. Large-scale studies often focus on the degree to which major environmental conditions (e.g., pH, maximum or minimum temperature, oxygen conditions) are related to community composition and typically find stronger relationships between these patterns than do fine-scale studies. One factor contributing to this scale-related difference in the importance of abiotic factors is the degree of variation found in the sites sampled. Small-scale studies are usually more limited in the range of these environmental variables (e.g., range of *A* to *B* in Fig. 2) whereas the range in the variation is emphasized in the large-scale comparisons. This difference in the range of variation associated with variables makes it difficult to detect significant effects of these environmental conditions. In contrast, the large-scale studies may lack the data resolution to

Fig. 2. Importance of the range considered for any environmental variable in whether it shows a strong relationship to a community attribute. We see a strong relationship between the variables if the entire range of the environmental variable is included. However, if we restrict the range of this variable (e.g., A to B), we lose the ability to detect the significant association. This effect occurs when we choose studies encompassing a large scale with many locations versus the small spatial scale, but intensively studied sites common in studies of biotic interactions. The large-scale studies typically find significant associations with the abiotic factors whereas the small-scale studies do not find the same relationships.



detect effects due to some small-scale environmental conditions and biotic effects such as competition, particularly given that the large-scale studies may not encompass the same species across the sites, thereby preventing direct observations between these species across the sites. So there has been a trade-off in the level of information collected depending on (i) whether the researcher's hypothesis is directed towards competitive interactions (e.g., Werner 1984) or major abiotic constraints (e.g., Magnuson et al. 1998) or (ii) whether a researcher has the resources to carry out the large-scale versus small-scale studies, which may affect which hypotheses is examined.

Some characteristics of aquatic systems are likely to make spatial scale a more important determinant of community structure than in terrestrial systems. Stream systems incorporate a strong longitudinal pattern given their long length relative to width. There are few, if any, terrestrial ecosystems that show such consistent longitudinal patterns throughout the world. This corridor-like formation leads to many attributes unique to stream systems. Studies at small scales identify differences in the microhabitat available and the types of fish assemblages found therein (Grossman and Freeman 1987). Such differences relate to characteristics associated with substrate, flow, and structure providing cover and often are identified at scales within a few metres that encompass either a pool or a riffle habitat (Cooper et al. 1998). However, increasing the level of spatial scale includes greater differences among the habitats, since pools and riffles may be contrasted within the same study. The differences in sub-

strate, depth, flow, and oxygen are now greater when pool-riffle contrasts are included. Increasing the scale further often does not provide a comparable jump in the range of habitats considered because stream systems incorporate semireplicated patterns of pools-riffles along the length of the stream. However, increasing the scale to include the entire length of the stream or multiple streams often leads to a substantial increase in the range of habitat conditions because there are major differences in environments from headwater to stream mouth locations (e.g., Vannote et al. 1980 and references therein). There may be considerable differences between watersheds where historical or biogeographic factors provide constraints on the communities by defining the regional pool of species from which the species can be drawn (e.g., Matthews and Robinson 1998). At smaller scales, local environmental gradients constrain the set of potential species from the regional pool with biotic interactions (predation, competition), leading to the realized communities at a local scale (Fig. 1). Much of our understanding about the importance of environmental gradients in organizing stream fish communities has been from studies at intermediate and small scales along longitudinal gradients within streams (Rahel and Hubert 1991), along pool-riffle sequences (Angermeier and Schlosser 1991), and in microhabitat use (Grossman et al. 1998). Local-scale factors are usually easier to measure, identify, and correlate with fish distributions than large-scale processes (Lamouroux et al. 1999) but are also more variable temporally. If local processes persist over intermediate (e.g., streams from different watersheds) and large scales (different watersheds), they can contribute dramatically to our understanding of community organization (Levins 1992).

Some important generalizations have arisen about the role of abiotic factors in structuring stream fish communities along longitudinal stream gradients. The main patterns of longitudinal succession of fishes in streams are the addition and substitution of species along gradients (Gilliam et al. 1993). Additions of species are usually related to environmental gradients having relatively smooth transitions of abiotic factors along longitudinal stream profiles (Vannote et al. 1980) and will contribute to more nested patterns of community composition (i.e., sites having fewer species are simply subsets of more speciose sites; e.g., Taylor 1997) whereas species substitutions correspond to abrupt discontinuities in stream geomorphology or abiotic conditions (e.g., temperature), promoting isolation of the site and species (Balon and Stewart 1983). The continual addition of species from small headwater streams to larger rivers is a consistent pattern in most temperate and tropical stream fish communities (Matthews 1986). This pattern is attributed mainly to the increased habitat diversity and stability downstream along watershed gradients (Meffe and Minkley 1987), with these components of the physical environment being positively associated with the variability of stream flow (Statzner et al. 1988). Lower-order streams support low diversity and less-structured assemblages due to a relatively high variability in their environment. Recolonization dynamics, temporal variation in reproductive success, and the ability to find suitable refugia during harsh conditions appear to be more important than biological interactions as determinants of community organization in such streams (e.g., Schlosser and Kallemejn 2000).

Physical disturbance reduces the densities of populations with the result that biotic interactions may not appear as important as abiotic conditions in determining community structure (Jackson et al. 1992). Temporal heterogeneity associated with stream habitat characteristics provides an important factor influencing fish communities. The major form of environmental variability (e.g., frequency, magnitude) in stream ecosystems is fluctuation in stream flow. Changes in these characteristics alter the physical habitat of streams and rivers, thereby influencing the composition and stability of fish communities (e.g., Grossman et al. 1998), primarily due to increased mortality and a reduction in recruitment. Response of fish assemblages depends on the degree of change relative to the flow regime and how various geomorphic and ecological processes respond to this relative change (Poff and Ward 1990). Furthermore, longitudinal and lateral variation in stream discharge can lead to complex spatial and temporal dynamics of fish populations and communities (see Schlosser (1991) for examples). In higher-order streams, where the catchment area is larger and thus hydraulic variation is lower, habitat characteristics are more stable and communities are able to persist for relatively longer periods of time. Maximum diversity is likely to occur in sites where the habitat diversity is enhanced and strong interspecific interactions are mediated by intermediate environmental disturbance (Resh et al. 1988). Zalewski and Naiman (1984) proposed a conceptual model where there is a gradual shift from abiotic to biotic regulation of stream fish communities as stream order increases.

Research on associations between environmental characteristics and the distribution and abundance of fish species across space has contributed greatly to our understanding of the relative importance of local abiotic and biotic factors (or combinations of them) in determining community structure (e.g., Taylor et al. 1993), whether species–environment relationships persist over intermediate and large spatial scales (e.g., Lohr and Fausch 1997), and whether environmental variables remain associated with fish assemblages at different levels of spatial scales (low- versus high-order streams, riffles versus pools; e.g., Grossman et al. 1998).

Although we have focused on stream systems in examining the role of scale and the interplay between abiotic and biotic components, similar results are found from studies of lake fish communities. Small-scale studies incorporate more limited contrasts of environmental conditions and tend to emphasize the importance of competitive interactions and habitat partitioning (e.g., Werner 1984). In very small lakes, there is a much greater temporal variation in environmental conditions (i.e., greater variability in temperature and oxygen), but less spatial variation, than in larger lakes. This increased variability likely contributes to annual or periodic reductions in species abundances due to thermal or oxygen stress, thereby reducing the potential for competitive interactions because resources may not become limiting (Jackson et al. 1992). With larger lakes, the environmental variability is dampened through thermal inertia, and stratification provides cold-water habitat throughout the year. Larger lakes also have greater habitat diversity and generally greater species richness (Magnuson 1976). This parallels the species addition effect found in streams. Studies incorporating multiple lakes tend to include lakes differing in size, thereby having systems exhibiting different degrees of environmental vari-

ability. This range in variability over time and space emphasizes the importance of abiotic factors in structuring lake communities at large scales, in contrast with small-scale comparisons emphasizing competitive interactions (Fig. 2). In contrast with competition being most evident in small-scale studies, both large- and small-scale studies identify predation effects, thereby indicating its importance in structuring fish communities within and across scales.

Spatial dynamics

Although the role of space in habitat heterogeneity is widely recognized, the importance attributed to spatial aspects in population and community dynamics has increased recently (Hanski 1999 and references therein). Many of these terrestrial and theoretical studies show the importance of spatially structured populations (e.g., metapopulations) in the maintenance of species diversity and community composition. The movement of individuals between habitats can reduce the rates of local extinction as well as permit recolonization following local extinctions. The rates of interpatch movement have important implications ranging from population genetics to community composition. To date, there has been limited recognition of the role of spatial isolation and metapopulation dynamics within aquatic systems. Some early studies identified the similarity of lakes (Barbour and Brown 1974) and rivers (Eadie et al. 1986) to islands or insular habitats. A few studies have attempted to quantify the degree to which lakes are isolated from one another (e.g., Magnuson et al. 1998) based on measures of the connections between lakes. The degree of habitat insularity in streams and lakes depends on a number of natural and anthropogenic conditions. Seepage lakes show complete isolation from other aquatic habitats (Magnuson 1976), except during periods of extreme flooding or human stocking activities. Isolation among drainage lakes is a function of the number, length, and suitability of connecting watercourses (Olden et al. 2001). Suitability of a watercourse for fish movement depends on the number and magnitude of artificial (e.g., water regulation dams) and natural barriers (e.g., beaver dams, waterfalls), stream morphology such as the number of stream confluences, the prevalence of seasonal drying or warming of streams, and channel characteristics such as depth. Within-stream connectivity is determined by these systems factors, but the role of beaver dams has been identified as providing a temporally varying barrier or facilitator to dispersal, both because the dams have limited life spans and because different species may benefit from the creation of standing water habitat (Snodgrass and Meffe 1998). Beaver dams and ponds are direct barriers to upstream dispersal and may provide unsuitable habitat because other species (e.g., predators) may predominate in the ponds, or alternatively, the ponds serving as “stepping stones” aid in the dispersal of species throughout a stream system. Piscivory influences the degree of isolation among habitats by imposing a risk of predation on potential dispersers. Increased density of piscivores may have conflicting effects in reducing the rate of movement by killing and (or) blocking prey as well as increasing movement by inducing prey to disperse from side pools or climb cascades to escape predators (see Gilliam and Fraser 2001).

Despite the fact that aquatic systems seem to be ideal models of habitat patches and connecting corridors, there is

limited evidence indicating whether fish communities show metapopulation characteristics (e.g., Gotelli and Taylor 1999), and few studies document limited rates of movement of species. Hill and Grossman (1987) showed that stream fish movements were small, on the order of metres, over extended periods of time. This contrasts with other findings (D.A. Jackson, unpublished data) showing high rates of movements of some species between lakes (25% of recaptured white sucker (*Catostomus commersoni*) and 5% of small-mouth bass were recaptured in lakes other than where they were tagged). Given the frequency with which some shallow lakes experience lethal environmental conditions during the winter or summer, it is likely that recolonization is an essential factor in the maintenance of lake fish communities. Fish species differ in their abilities to move through these connecting waterways. Different streams vary in their characteristics, either facilitating or preventing the movements of various species (providing selective filters based on the temperature and flow characteristics of the streams). The interaction of the species and stream characteristics contributes to differences between communities, even in lakes with similar environmental conditions. Increased rates of transfer of particular species (i.e., sport fishes) between water bodies due to human activities are leading to more consistent or homogenized fish communities (Rahel 2000). Given the noted effects that many of these introduced species have as dominant littoral predators, their strong impacts on the indigenous fish community contribute to a loss of biodiversity, particularly among-lake diversity.

Spatial dynamics and habitat heterogeneity are also of concern in the maintenance of biodiversity within lakes frequented by humans. Many lakes undergoing development by humans actually have reduced habitat heterogeneity, thereby reducing the potential for habitat segregation and refuge from predation. Cottagers modify existing habitats by removing macrophytes and woody structures in favor of sandy beaches or shore with retaining walls. The net effect is the opposite of habitat fragmentation in that many of these lakes are actually experiencing habitat homogenization as the lakes become increasingly developed and lacking in spatial complexity.

Advances and challenges in fish community ecology

This section identifies problems that seem to be limiting our current understanding of fish community ecology and highlights those promising areas of research or areas that we believe represent priorities for future research. We chose such areas due to either technological advances or theoretical and empirical advances from other fields (e.g., terrestrial ecology) that indicate areas of promise or, alternatively, because of the potential implications of ignoring areas.

The spatial dynamics of populations and communities are an important topic that is being virtually ignored within the context of aquatic systems, in particular by resource managers. Although terrestrial and theoretical ecologists have carried out extensive work related to spatial dynamics of single species or communities (see Hanski 1999), there is limited work examining lakes (e.g., Olden et al. 2001) and streams (Schlosser and Kallemeyn 2000). Whether this reflects a

general lack of interest or the associated costs of monitoring movements of fishes in aquatic systems is uncertain. Having this information would help integrate the roles of biotic and abiotic factors across varying spatial scales by determining more precisely how individual fish are using space to minimize biotic and abiotic stress. Human activities are modifying habitats in stream systems and groups of lakes to varying degrees. Changes in the connectivity due to damming or alterations to flow patterns, coupled with habitat modification, may threaten the long-term viability of existing populations and communities. We have a severely limited knowledge base from which to predict outcomes or identify risk. Spatial dynamics are important for understanding the basic ecology but also need to be recognized by resource managers. For example, typically the management of a lake sport fish population is carried out without considering that populations in nearby lakes may be directly linked and that management decisions (e.g., stocking of bass) may have direct implications for the communities in the nearby lakes. Planning for stocking programs generally assumes that there is limited, if any, exchange of individuals between systems. This current paradigm of viewing lakes and streams is outdated. It fosters mismanagement of the resources and fails to recognize the mechanisms by which introduced pathogens and exotics can quickly impact an entire regional fauna. In contrast with this "isolation" paradigm, restoration projects often assume implicitly that such movements between water bodies will occur and provide the seeds for a recovery of the community, but we do not know how realistic such assumptions may be. We need an information base about the degree of fish movement within and between lakes and streams to better understand the mechanisms necessary for the maintenance of fish communities.

The application of advancing technologies, such as radio-telemetry and stable isotope methods, is promising. Telemetry methods provide a better definition of a species' spatial occupancy and the movements of individuals and their use of particular habitats. Telemetry can provide insight into the linkages between specific habitat features and the members of a fish community, particularly given that the use of such features may vary depending on time (day versus night or seasonally) and due to ontogenetic changes in the fishes. To date, much of our knowledge has been gained by netting or trapping of fish that integrates long periods of time. The dynamic nature of individuals and their interactions with other species is lost in such coarse levels of detail. In contrast, the real-time information obtained from telemetry approaches can provide a wealth of information about community dynamics not available previously. Determining the relative importance and timing of use of various habitat types both provides a fundamental understanding of the use these features by the various community constituents and provides managers with an improved array of methods to minimize potential impacts during development or resource exploitation. Such technology provides the basis to determine detailed information about physiological processes, small-scale environmental conditions, and larger-scale use of lakes or streams over time. Stable isotope and hard tissue chemical analysis can provide information related to the individual dates of movements between freshwater and saltwater systems, alterations to energy flow as a result of changes to adjacent

terrestrial habitats, and historical measures of ecosystem impacts due to species introductions (e.g., Vander Zanden et al. 1999). Such techniques provide sophisticated approaches to recreate historical conditions and timing of events, similar to the goals of paleolimnologists.

Another area where additional effort would be particularly valuable is extended temporal data sets. The limited nature of long-term monitoring of fish communities in lakes and streams (e.g., Long Term Ecological Research Areas (LTER)) is highly constraining. The number of sites involved and the range of communities and environmental conditions currently studied are very limited. This scarcity of long-term data sets necessitates that spatial comparisons be used to study the mechanisms regulating communities whereas temporal comparisons may provide better information for specific hypotheses. The "space-for-time" substitution is often used but may not be appropriate in some or perhaps many cases. Currently, we do not know whether the substitution is appropriate. It is these long-term programs, employing consistent sampling approaches, that provide us with an understanding of the temporal dynamics of fish communities. These studies can provide estimates on natural rates of colonization and extinction and direct linkages connecting changes in habitat and responses by species and communities. Such temporal information is critical (Lester et al. 1996) in detecting the impacts of large-scale environmental changes (e.g., acidification, climate change) as well as providing our basic ecological understanding of fish community regulation. Currently, there is considerable concern related to potential changes in abiotic conditions within streams and lakes due to climatic warming. Given that species generally have limited rates of dispersal between watersheds (unless moved by humans), major shifts in environmental conditions will likely prove adverse for fish communities, given the lack of time to compensate or disperse. However, despite these concerns, given our lack of current LTER programs, we will likely not be in a position to determine if such changes do occur unless additional programs are established and their data made widely available.

We need to develop new approaches to assess the relative importance of environmental conditions and species interactions in the structuring of fish communities. Although the organization of fish communities has been credited to a balance between abiotic factors and biotic interactions, studies usually emphasize one over the other. It is important to note that both components are not only complementary and interactive, but their effects can have similar roles in organizing communities, thereby complicating our advancement in understanding community processes. Therefore, studies including different components and using both experimental and observational approaches are necessary to disentangle biotic and abiotic effects and measure their relative magnitudes. Experimental studies usually emphasize the importance of interactions with or species-specific responses to particular abiotic variables (e.g., swimming speed) whereas field studies frequently establish the importance of abiotic variables by establishing correlations between species distribution and environmental gradients. Differences in methodological approaches to studying the roles of biotic versus abiotic structuring have limited our understanding of various issues, such as the role of disturbance in organizing fish

communities and whether species that are environmental generalists are more or less sensitive to biotic interactions. Unless we develop studies to determine whether findings from a fine scale hold at larger scales (e.g., Angermeier and Winston 1998), we will be hampered in our abilities to understand the regulation of fish communities. Therefore, there is a great need for studies employing such multiscale approaches that incorporate both experimental and correlative approaches.

Fish community ecologists have not capitalized on many advances in analytical approaches from other fields (e.g., engineering, medicine). We have a large body of literature related to various fish species and whole communities and their association with various biotic and abiotic factors. However, we appear to be ignoring the opportunities that these present, and there has been little attempt to capitalize on this information base. The use of meta-analysis (e.g., see Englund et al. (1999) for a recent application) could serve to help partition out some of the factors summarized in our paper. The ability to separate the effects of various factors and their strengths has the potential to partition the relative roles of biotic, abiotic, and spatial components in shaping fish communities. With the extensive information at hand, a means of evaluating our understanding and predictive power is to determine the degree to which we can correctly identify the various members of communities based on the associated environmental conditions. Being able to correctly identify the communities at a series of sites provides an excellent test of our understanding, provided such tests are implemented correctly (e.g., using appropriate methods to test and validate our models; see Olden and Jackson 2000). Although some studies have developed predictive models based on single species or assemblage types (e.g., Magnuson et al. 1998), we should be trying to develop models that can predict whole communities. Such tests of the entire membership of communities will provide a measure of the state of our knowledge and identify where we are lacking. Advanced analytical tools commonly found in other disciplines, such as artificial neural networks, genetic algorithms, and classification trees, and various multivariate approaches provide the opportunity to test our hypotheses regarding the structuring of communities and provide predictive models. In many cases, one can make strong arguments for improved and more detailed analysis of existing data to address questions, but it is often easier to convince funding agencies of the need for additional data collection rather than more extensive examination of information in hand.

Clearly, there has been no common consensus in the literature regarding the importance of various factors in determining the communities of species associated with various sites. The scale of the study interacts with the biotic and abiotic variables such that the relative importance of biotic and abiotic factors changes across spatial scales. Small streams and lakes are more variable in their abiotic environments than are larger ones. The associated extremes in the environments may affect the larger species, frequently predators, to a greater degree than the small-bodied species, often leading to their local extinction. The loss of these predatory species then contributes to a more diverse community of small-bodied species. The degree to which environmental disturbance keeps the abundances of these species well below carrying capaci-

ties likely determines whether competition becomes important in structuring the communities. Obviously, we present a generalization, as many exceptions exist to this conceptual model, and similarly, we provide a selectively limited review of the state of knowledge. We have set out to identify the progress made over the past century in understanding the factors regulating fish communities, and we hope that our paper will stimulate discussion and new ideas and contribute to formal model development in both theoretical and statistical contexts.

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References

- Andrewartha, H.G., and Birch, L.C. 1954. The Distribution and abundance of animals. University of Chicago Press, Chicago, Ill.
- Angermeier, P.L., and Schlosser, I.J. 1991. Species-area relationships in stream fishes. *Ecology*, **70**: 1450–1462.
- Angermeier, P.L., and Winston, M.R. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology*, **79**: 911–927.
- Balon, E.K., and Stewart, D.J. 1983. Fish assemblages in a river with unusual gradient (Luongo, Africa-Zaire system), reflections on river zonation, and description of another new species. *Environ. Biol. Fishes*, **9**: 225–252.
- Barbour, C.D., and Brown, J.H. 1974. Fish species diversity in lakes. *Am. Nat.* **108**: 473–489.
- Chapleau, F., Findlay, C.S., and Szenasy, E. 1997. Impact of piscivorous fish introductions on fish species richness of small lakes in Gatineau Park, Quebec. *Écoscience*, **4**: 259–268.
- Connor, E.F., and Simberloff, D. 1979. The assembly of species communities: chance or competition? *Ecology*, **60**: 1132–1140.
- Cooper, S.D., Diehl, S., Kratz, K., and Sarnelle, O. 1998. Implications of scale for patterns and processes in stream ecology. *Aust. J. Ecol.* **23**: 27–40.
- Douglas, M.E., and Matthews, W.J. 1992. Does morphology predict ecology? Hypothesis testing within a freshwater fish assemblage. *Oikos*, **65**: 213–224.
- Eadie, J.McA., Hurly, T.A., Montgomerie, R.D., and Teather, K.L. 1986. Lakes and rivers as islands: species-area relationships in the fish faunas of Ontario. *Environ. Biol. Fishes*, **15**: 81–89.
- Echelle, A.A., Echelle, A.F., and Hill, L.G. 1972. Interspecific interactions and limiting factors of abundance and distribution. I. The Red River pupfish, *Cyprinodon rubrofluviatilis*. *Am. Midl. Nat.* **88**: 109–130.
- Englund, G., Sarnelle, O., and Cooper, S.D. 1999. The importance of data-selection criteria: meta-analyses of stream predation experiments. *Ecology*, **80**: 1132–1141.
- Evans, D.O., Henderson, B.A., Bax, N.J., Marshall, T.R., Oglesby, R.T., and Christie, W.J. 1987. Concepts and methods of community ecology applied to freshwater fisheries management. *Can. J. Fish. Aquat. Sci.* **44**(Suppl. 2): 448–470.
- Everett, R.A., and Ruiz, G.M. 1993. Coarse woody debris as a refuge from predation in aquatic communities — an experimental test. *Oecologia*, **93**: 475–486.
- Flebbe, P.A., and Dolloff, C.A. 1995. Trout use of woody debris and habitat in Appalachian wilderness streams of North Carolina. *N. Am. J. Fish. Manage.* **15**: 579–590.
- Gilliam, J.F., and Fraser, D.F. 2001. Movement in corridors: enhancement by predation threat, disturbance and habitat structure. *Ecology*, **82**. In press.
- Gilliam, J.F., Fraser, D.F., and Alkins-Koo, M. 1993. Structure of a tropical stream fish community: a role for biotic interactions. *Ecology*, **74**: 1856–1870.
- Gorman, O.T. 1988. The dynamics of habitat use in a guild of Ozark minnows. *Ecol. Monogr.* **58**: 1–18.
- Gotelli, N.J., and Taylor, C.M. 1999. Testing metapopulation models with stream-fish assemblages. *Evol. Ecol. Res.* **1**: 835–845.
- Grossman, G.D., and Freeman, M.C. 1987. Microhabitat use in a stream fish assemblage. *J. Zool. (Lond.)*, **212**: 151–176.
- Grossman, G.D., Moyle, P.B., and Whitaker, J.O., Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *Am. Nat.* **120**: 423–454.
- Grossman, G.D., Ratjczak, R.E., Jr., Crawford, M., and Freeman, M.C. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecol. Monogr.* **68**: 396–420.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford Press, New York.
- Harvey, H.H. 1975. Fish populations in a large group of acid-stressed lakes. *Ver. Theor. Angew. Limnol.* **19**: 2406–2417.
- Harvey, H.H. 1981. Fish communities of the lakes of the Bruce Peninsula. *Ver. Theor. Angew. Limnol.* **21**: 1222–1230.
- He, X., and Kitchell, J.F. 1990. Direct and indirect effects of predation on a fish community: a whole-lake experiment. *Trans. Am. Fish. Soc.* **119**: 825–835.
- Hill, J., and Grossman, G.D. 1987. Home range estimates for three North American stream fishes. *Copeia*, **1987**: 376–380.
- Hinch, S.G. 1991. Small- and large-scale studies in fisheries ecology: the need for cooperation among researchers. *Fisheries (Bethesda)*, **16**: 22–27.
- Jackson, D.A. 1997. Compositional data in community ecology: the paradigm or peril of proportions. *Ecology*, **78**: 929–940.
- Jackson, D.A., and Harvey, H.H. 1989. Biogeographic associations in fish assemblages: local vs. regional processes. *Ecology*, **70**: 1472–1485.
- Jackson, D.A., and Harvey, H.H. 1993. Fish and benthic invertebrates: community concordance and community-environment relationships. *Can. J. Fish. Aquat. Sci.* **50**: 2641–2651.
- Jackson, D.A., and Harvey, H.H. 1997. Qualitative and quantitative sampling of lake fish communities. *Can. J. Fish. Aquat. Sci.* **54**: 2807–2813.
- Jackson, D.A., Somers, K.M., and Harvey, H.H. 1992. Null models and fish communities: evidence of nonrandom patterns. *Am. Nat.* **139**: 930–943.
- Johnson, M.G., Leach, J.H., Minns, C.K., and Olver, C.H. 1977. Limnological characteristics of Ontario lakes in relation to associations of walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), lake trout (*Salvelinus namaycush*), and small-mouth bass (*Micropterus dolomieu*). *J. Fish. Res. Board Can.* **34**: 1592–1601.
- Keenleyside, M.H.A. 1979. *Diversity and adaptation in fish behavior*. Springer-Verlag, Berlin.
- Kilgour, B.W., and Barton, D.R. 1999. Associations between stream fish and benthos across environmental gradients in southern Ontario, Canada. *Freshwater Biol.* **41**: 553–566.
- Kramer, D.L. 1983. The evolutionary ecology of respiratory mode in fishes: an analysis based on the cost of breathing. *Environ. Biol. Fishes*, **9**: 145–158.

- Kratz, T.K., Webster, K.E., Bowser, C.J., and Benson, B.J. 1997. Influence of landscape position on lakes in northern Wisconsin. *Freshwater Biol.* **37**: 209–217.
- Lamouroux, N., Olivier, J.-M., Persat, H., Pouilly, M., Souchon, Y., and Statzner, B. 1999. Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. *Freshwater Biol.* **42**: 275–299.
- Lester, N.P., Dunlop, W.I., and Cox, C.C. 1996. Detecting changes in the nearshore fish community. *Can. J. Fish. Aquat. Sci.* **53**(Suppl. 1): 391–402.
- Levins, S.A. 1992. The problem of pattern and scale in ecology. *Ecology*, **73**: 1943–1967.
- Li, H.W., and Moyle, P.B. 1981. Ecological analysis of species introductions into aquatic systems. *Trans. Am. Fish. Soc.* **110**: 772–782.
- Lóbon-Cerviá, J. 1996. Response of a stream fish assemblage to a severe spate in northern Spain. *Trans. Am. Fish. Soc.* **125**: 913–919.
- Lohr, S.C., and Fausch, K.D. 1997. Multiscale analysis in natural variability in stream fish assemblages of a Western Great Plains watershed. *Copeia*, **1997**: 706–724.
- MacRae, P.S.D., and Jackson, D.A. 2001. The influence of predation and habitat complexity on the structure of littoral-zone fish assemblages. *Can. J. Fish. Aquat. Sci.* **58**. In press.
- Magnuson, J.J. 1976. Managing with exotics — a game of chance. *Trans. Am. Fish. Soc.* **105**: 1–9.
- Magnuson, J.J., Crowder, L.B., and Medvick, P.A. 1979. Temperature as an ecological resource. *Am. Zool.* **19**: 331–343.
- Magnuson, J.J., Beckel, A.L., Mills, E., and Brandt, S.B. 1985. Surviving winter hypoxia: behavioral adaptations of fishes in a northern Wisconsin winterkill lake. *Environ. Biol. Fishes*, **14**: 241–250.
- Magnuson, J.J., Tonn, W.M., Banerjee, A., Toivonen, J., Sanchez, O., and Rask, M. 1998. Isolation vs. extinction in the assembly of fishes in small northern lakes. *Ecology*, **79**: 2941–2956.
- Mandrak, N.E. 1995. Biogeographic patterns of fish species richness in Ontario lakes in relation to historical and environmental factors. *Can. J. Fish. Aquat. Sci.* **52**: 1462–1474.
- Matthews, K.R., and Berg, N.H. 1997. Rainbow trout responses to water temperature and dissolved oxygen in two southern California stream pools. *J. Fish Biol.* **50**: 50–67.
- Matthews, W.J. 1986. Fish faunal “breaks” and stream order in the eastern and central United States. *Environ. Biol. Fishes*, **17**: 81–92.
- Matthews, W.J. 1998. Patterns in freshwater fish ecology. Chapman and Hall, Norwell, Mass.
- Matthews, W.J., and Robinson, H.W. 1998. Influence of drainage connectivity, drainage area and regional species richness on fishes of the interior highlands of Arkansas. *Am. Midl. Nat.* **139**: 1–19.
- Matthews, W.J., Harvey, B.C., and Power, M.E. 1994. Spatial and temporal patterns in the fish assemblages of individual pools in a midwestern stream (USA). *Environ. Biol. Fishes*, **39**: 381–397.
- Meffe, G.K., and Minkley, W.L. 1987. Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. *Am. Midl. Nat.* **117**: 177–191.
- Olden, J.D., and Jackson, D.A. 2000. Torturing data for the sake of generality: how valid are our regression models? *Écoscience*, **7**. In press.
- Olden, J.D., Jackson, D.A., and Peres-Neto, P.R. 2001. Spatial isolation and fish communities in drainage lakes. *Oecologia*. In press.
- Poff, N.L., and Ward, J.V. 1990. The physical habitat template of lotic systems: recovery in the context of historical pattern of spatial-temporal heterogeneity. *Environ. Manage.* **14**: 629–646.
- Power, M.E., Matthews, W.J., and Stewart, A.J. 1985. Grazing minnows, piscivorous bass and stream algae: dynamics of a strong interaction. *Ecology*, **66**: 1448–1456.
- Power, M.E., Stewart, A.J., and Matthews, W.J. 1988. Grazer control of algae in an Ozark mountain stream: effects of short-term exclusion. *Ecology*, **69**: 1894–1898.
- Rahel, F.J. 1990. The hierarchical nature of community persistence: a problem of scale. *Am. Nat.* **136**: 328–344.
- Rahel, F.J. 2000. Homogenization of fish faunas across the United States. *Science* (Washington, D.C.), **288**: 854–856.
- Rahel, F.J., and Hubert, W.A. 1991. Fish assemblages and habitat gradients in a Rocky Mountain – Great Plains stream: biotic zonation and additive patterns of community change. *Trans. Am. Fish. Soc.* **120**: 319–332.
- Rahel, F.J., and Magnuson, J.J. 1983. Low pH and the absence of fish species in naturally acidic Wisconsin lakes: inferences for cultural acidification. *Can. J. Fish. Aquat. Sci.* **40**: 3–9.
- Resetarits, W.J., Jr. 1997. Interspecific competition and qualitative competitive asymmetry between two benthic stream fishes. *Oikos*, **78**: 428–439.
- Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., and Wissmar, R. 1988. The role of disturbance in stream ecology. *J. North Am. Benthol. Soc.* **7**: 433–455.
- Robinson, B.W., and Wilson, D.S. 1994. Character release and displacement in fishes: a neglected literature. *Am. Nat.* **144**: 596–627.
- Rodriguez, M.A., and Lewis, W.M., Jr. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecol. Monogr.* **67**: 109–128.
- Ross, S.T. 1986. Resource partitioning in fish assemblages: a review on field studies. *Copeia*, **1986**: 352–388.
- Ross, S.T., Matthews, W.J., and Echelle, A.A. 1985. Persistence of stream fish assemblages: effects of environmental change. *Am. Nat.* **126**: 24–40.
- Ryder, R.A., and Kerr, S.R. 1978. The adult walleye in the percid community — a niche definition on feeding behavior and food specificity. *In Selected coolwater fishes of North America. Edited by R. Kendall. Am. Fish. Soc. Spec. Publ.* **11**: 39–51.
- Schlosser, I.J. 1987. A conceptual framework for fish communities in small warmwater streams. *In Community and evolutionary ecology of North American stream fishes. Edited by W.J. Matthews and D.C. Heins. Oklahoma University Press, Norman, Okla.* pp. 17–24.
- Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. *BioScience*, **41**: 704–712.
- Schlosser, I.J., and Angermeier, P.L. 1990. The influence of environmental variability, resource abundance, and predation on juvenile cyprinid and centrarchid fishes. *Pol. Arch. Hydrobiol.* **37**: 265–284.
- Schlosser, I.J., and Kallemeyn, L.W. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology*, **81**: 1371–1382.
- Scrimgeour, G.J., Prowse, T.D., Culp, J.M., and Chamber, P.A. 1994. Ecological effects of river ice break-up: a review and perspective. *Freshwater Biol.* **32**: 261–275.
- Shetter, D.S., Clark, O.H., and Hazzard, A.S. 1946. The effects of deflectors in a section of Michigan trout stream. *Trans. Am. Fish. Soc.* **76**: 249–273.
- Shuter, B.J., MacLean, J.A., Fry, F.E.J., and Regier, H.A. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. *Trans. Am. Fish. Soc.* **109**: 1–34.
- Smith, C.L., and Powell, C.R. 1971. The summer fish communities of Brier Creek, Marshall County, Oklahoma. *Am. Mus. Novit.* **2458**: 1–30.

- Snodgrass, J.W., and Meffe, G.K. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. *Ecology*, **79**: 928–942.
- Somers, K.M., and Harvey, H.H. 1984. Alteration of lake fish communities in response to acid precipitation and heavy-metal loading near Wawa, Ontario. *Can. J. Fish. Aquat. Sci.* **41**: 20–29.
- Statzner, B., Gore, J.A., and Resh, V.H. 1988. Hydraulic stream ecology: observed patterns and potential applications. *J. North Am. Benthol. Soc.* **7**: 307–360.
- Taylor, C.M. 1996. Abundance and distribution within a guild of benthic stream fishes: local processes and regional patterns. *Freshwater Biol.* **36**: 385–396.
- Taylor, C.M. 1997. Fish species richness and incidence of patterns in isolated and connected stream pools: effects of pool volume and spatial isolation. *Oecologia*, **110**: 560–566.
- Taylor, C.M., Winston, M.R., and Matthews, W.J. 1993. Fish species – environment and abundance relationships in a Great Plains river system. *Ecography*, **16**: 16–23.
- Tonn, W.M. 1990. Climate change and fish communities: a conceptual framework. *Trans. Am. Fish. Soc.* **119**: 337–352.
- Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. *J. North Am. Benthol. Soc.* **8**: 36–50.
- Underwood, A.J., and Petraitis, P.S. 1993. Structure of intertidal assemblages in different locations: how can local processes be compared? *In Species diversity in ecological communities: historical and geographical perspectives. Edited by R.E. Ricklefs and D. Schluter.* University of Chicago Press, Chicago, Ill. pp. 39–51.
- Vander Zanden, M.J., Casselman, J.M., and Rasmussen, J.B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature (Lond.)*, **401**: 464–467.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Seddel, J.R., and Cushing, C.E. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **37**: 130–137.
- Wahl, D.H., and Stein, R.A. 1989. Comparative vulnerability of three esocids to largemouth bass *Micropterus salmoides* predation. *Can. J. Fish. Aquat. Sci.* **46**: 2095–2103.
- Werner, E.E. 1984. The mechanisms of species interactions and community organization in fish. *In Ecological communities: conceptual issues and evidence. Edited by D.R. Strong Jr., D. Simberloff, L.G. Abele, and A.B. Thistle.* Princeton University Press, Princeton, N.J. pp. 360–382.
- Wiley, E.O., and Mayden, R.L. 1985. Species and speciation in phylogenetic systematics, with examples from North American fish fauna. *Ann. Mo. Bot. Gard.* **72**: 596–635.
- Winemiller, K.O. 1989. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan ilianos. *Environ. Biol. Fishes*, **26**: 177–199.
- Winston, M.R. 1995. Co-occurrence of morphologically similar species of stream fishes. *Am. Nat.* **145**: 527–545.
- Yant, P.R., Karr, J.R., and Angermeier, P.L. 1984. Stochasticity in stream fish communities: an alternative interpretation. *Am. Nat.* **124**: 573–582.
- Zalewski, M., and Naiman, R.J. 1984. The regulation of riverine fish communities by a continuum of abiotic–biotic factors. *In Habitat modification and freshwater fisheries. Edited by J.S. Alabaster.* Batterworth Scientific Ltd., London, U.K. pp. 3–9.