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Climate Change and Fish Communities: A Conceptual Framework

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Abstract.—Many autecological effects of temperature on fish are known, and fishery biologists have begun to incorporate this knowledge into population-level relations that can be used to assess possible effects of climatic warming on fishes and their habitats. However, the problem of extrapolating these or other relations to multispecies assemblages is not straightforward, given the complexity of community-level phenomena. I present a conceptual framework that views fish assemblages as products of a series of filters, operating at different spatial and temporal scales, through which an assemblage's component species must pass. This framework can facilitate an understanding of the processes that organize fish assemblages and suggest ways in which the complex problem can be divided into manageable pieces. I apply this framework in an examination of small-lake fish assemblages in three regions on two continents. The procedure reveals local and regional relations of richness and composition and highlights the importance of isolation, extinction, and colonization, as well as temperature, that must be considered in climate change assessments. This community-level framework can organize accumulated knowledge of fish assemblages, identify causal processes behind community-level patterns, and focus research needed for the management of fish assemblages in the face of major anticipated changes in climate.

There is increasing concern among scientists that global climate is on the verge of a major alteration due to effects of human activities on atmospheric gases. A doubling of the atmospheric concentration of CO_2 is projected for the next century, accompanied by the addition of significant amounts of other "greenhouse gases" (Ripley 1987; Ramanathan 1988). By inserting the projected increase of CO_2 into general circulation models, climatologists are predicting a global warming of 2–4°C and a generally more active hydrological cycle (e.g., Hansen et al. 1984; Washington and Meehl 1984). If these predictions are correct, the earth will experience greater changes in climate, and at a faster rate, than have occurred at least since the end of the last glaciation, 12,000 years ago. Hydrological effects of these changes should include not only higher water temperatures and longer ice-free periods (Barry 1986), but also increased seasonal fluctuations in water levels (Ripley 1987).

Fishery biologists should be especially concerned about these climatic and hydrological changes. Climatic factors are important correlates of productivity in aquatic ecosystems (Brylinsky 1980). As ectotherms, fish are directly influenced by the temperature of their environment. Temperature has major influences on many organismal processes in fish, including spawning, development, growth, and metabolic scope (Fry 1971; Hokanson 1977; Brett 1979). Because of selective pressures associated with these processes, it is not surprising that fish exhibit temperature selection in both laboratory and field, or that the "preferred temperature" is at or close to the physiologically optimum temperature for a given species (Coutant 1987). The existence of temperature preferences (and avoidances) implies that the thermal structure of a water body determines the amount of habitat that is suitable for a species—i.e., that temperature is an ecological resource (Magnuson et al. 1979).

Effects of temperature on the physiology and autecology of fish are reasonably well known, or at least amenable to direct experimentation, yet incorporating knowledge of temperature effects gained at the organismal level into problems of higher-level phenomena is not straightforward (Coutant 1987). As a result, few translations of organismal temperature effects to higher levels of organization have been successful or even attempted (Christie and Regier 1988). One successful approach was that of Shuter et al. (1980), who incorporated results of autecological studies into a deterministic model of relations between temperature and first-year survival for smallmouth bass *Micropterus dolomieui*. The model was then used to assess the implications of both short-term alterations in thermal environment, such as effects of a power plant on a local population, and long-term regional alterations, such as those produced by climate change. Christie and Regier (1988), building upon the work of Schlesinger and Regier (1983), developed measures of "optimal thermal habitat" for four commercially important fish species, and showed that these measures were strongly correlated with the species' sustained yield in 21 large lakes.

Although the success of these studies points to a measureable link between organismal and population-level responses to environmental temperature, fishery biologists recognize that single-species models are incomplete (Shuter et al. 1980). Our science must also consider indirect and higher-level phenomena, including patterns and processes operating at the level of the community or fish assemblage (Evans et al. 1987).

To begin to address potential community-level effects of an altered climate, some vegetation scientists have combined established relations between climate and vegetation (Holdridge 1947) with climatologists' projections of climate change to predict the future distribution of plant formations (Emanuel et al. 1985). Reasoning that there may be no modern analogues for future climatic conditions, others have turned to the paleoecological record, suggesting that communities extant during the Holocene climatic optimum may serve as models for the expected warming (Edlund 1986). There is only limited knowledge of past distributions of fish species (and essentially none for fish assemblages), however, and quantitative relations between climate and fish communities like those available for vegetation have not been developed.

To examine potential effects of climate change on fish assemblages and to address the role that community ecology can play in this pending environmental crisis, I begin by assessing the problems faced by community ecologists when they examine such issues. I then provide a simple conceptual framework that may offer insights into how these problems can be divided into manageable component pieces. I end by applying existing knowledge of fish assemblages in small north-temperate lakes to this framework to make initial qualitative predictions and to illustrate how a community-level approach can focus the research needed to manage fish assemblages in the face of climatic change.

Nature of Ecological Communities

As a science, ecology deals with the higher levels of the biological hierarchy, of which the community is one of the most complex (Southwood 1987). A simple definition of community ecology is the study of the "organization" of ecological communities, including the number, identity, relative abundance, and ecological attributes of the component species, the interrelationships of these species, and how all of these vary over space and time (Brown 1987). Goals of community ecology are to identify patterns of ecological communities, to determine the causal processes that underlie these patterns, and to generalize these explanations as far as possible (Wiens 1984).

The simplicity of these goals belies the complexity faced by community ecologists, which in turn has led to considerable recent controversy (Schoener 1987). During the 1960s and early 1970s, theoretical ecologists attempted to uncover generalities of community organization, relying primarily on deterministic, equilibrium models of interspecific competition. Increasingly, however, it is appreciated that community patterns may be influenced by a host of additional or alternative processes, as well as by the complicated interplay of these processes (Harvey et al. 1983). The relative importance of these processes depends on such factors as their timing, frequency, and intensity, on physiological, ecological, and life history characteristics of component species, on the regional and historical setting of the community, and even on the spatial and temporal scale at which patterns and processes are observed. Thus, some communities will appear to be "organism-driven" whereas others are "environment-driven" (Southwood 1987), some are in an equilibrium state but others are not (Wiens 1984), some are deterministic whereas others are stochastic (Grossman et al. 1982), and most communities are somewhere in between these endpoints.

This "kaleidescope of possibilities" (May 1986) has led community ecologists to wonder whether or not ecological communities are so complex, variable, and unique that useful community theory is not possible (Colwell 1984). Lack of a general theoretical framework may have contributed to the recent controversies, but ecologists are coming to recognize that "there are no grand generalizations . . . no naive dichotomies" (May 1986); indeed, "a theory explaining global patterns in community ecology is doomed to failure" (Price 1984).

A Conceptual Framework

Given that the conceptual basis of community ecology is in a state of flux, that a unified theory explaining global patterns is not on the horizon, and that we already have problems making predictions for relatively small, local changes such as habitat alterations, exploitation, or species introductions, will community ecologists be able to predict the effects of global climate change on fish assemblages? (See, e.g., Magnuson 1976; Hickley

1986; Moyle 1986.) To prepare even a qualitative scenario for climatic change and fish assemblages, the processes influencing communities should be arranged into a unified framework that encompasses appropriate spatial and temporal scales; we might then be able to assess the relative importance of these factors under future conditions and to identify major structuring mechanisms that are likely to operate in an altered climate.

The framework presented here is based on the view that ecological communities are open systems; patterns and processes observed in local assemblages are determined not only by local, contemporary mechanisms acting within assemblages, but also result from processes operating at larger spatial and temporal scales (O'Neill 1989; Roughgarden 1989). Properties of a local fish assemblage, including the number, identity, and relative abundance of the component species, can be viewed as the product of a series of screens, or filters (Figure 1). Each filter may be identified with particular spatial and temporal scales (Table 1), although these scales (and therefore the filters themselves) form a continuum (Addicott et al. 1987). Large-scale phenomena generally act as "upstream" filters; only a portion of possible species pass through them and influence lower levels (Simpson 1953; Smith and Powell 1971; Holmes 1986, in press; Blondel 1987). The usefulness of this model for an understanding of community-level effects of climatic change is that we may be able to focus our efforts on properties of fish assemblages most vulnerable to alteration of climate if we can identify which filters will likely be affected by the disturbance. The keys, of course, are that we understand the nature of these filters and that we identify the species that will pass through a particular filter to a lower level and those that will not.

Continental Filters

In studies of impending climatic change, the time scale usually ranges from 10^1 to 10^2 years; however, the spatial scale can be global. When one examines ecological patterns at an intercontinental scale, it is essential that the evolutionary and geological contexts of the fauna and its landscape be known (Coope 1987). Selective speciation and extinction during Pleistocene and earlier disturbances, combined with distinct refuges and routes for dispersal, shaped continental patterns of richness and composition and the morphological, physiological, and life history traits of species in contemporary faunas (Smith 1981; Mahon 1984).

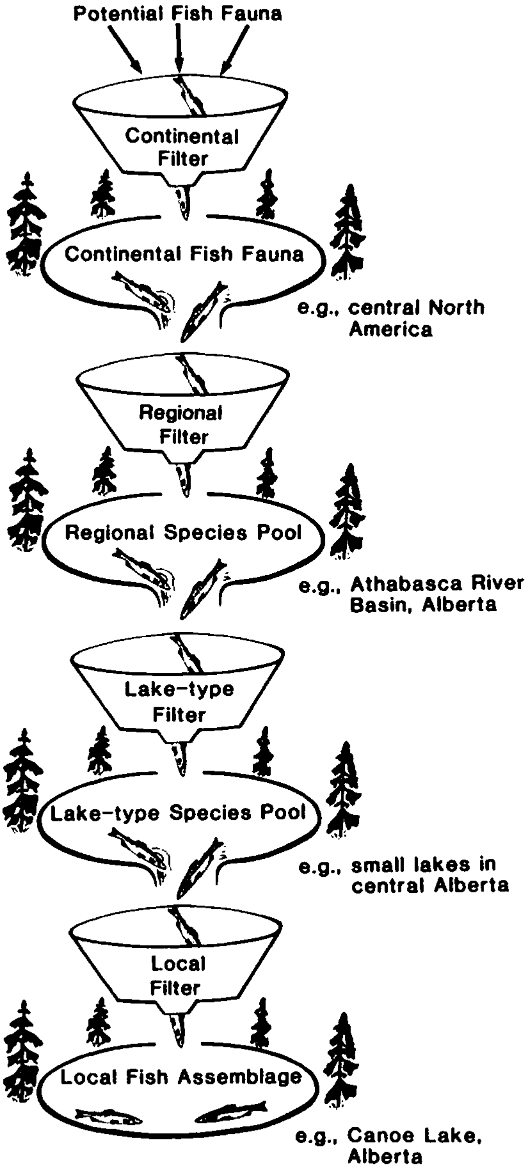

FIGURE 1.—Graphic representation of a conceptual framework in which a series of factors, events, and processes operate as filters at several spatial and temporal scales to structure and organize local fish assemblages in small lakes.

Regional Filters

A region can be defined broadly as an area of relatively uniform climate that has experienced a generally similar geologic history; its fauna has also experienced a similar evolutionary history. Because of its divided and heterogeneous nature,

TABLE 1.—Sample of processes and features associated with four general types of biogeographical filters. Also listed are ranges of spatial and temporal scales over which these filters operate and examples of biological patterns that result. Overlapping scales indicate that the processes and features operate along a continuum; thus, the borders of adjacent filters are not distinct.

		Approximate scale		
Type of filter	Associated processes and features	Spatial	Temporal	Pattern
Continental (inter and intra)	Continental drift Dispersal and speciation Orographic events Glaciation: selective extinction, refugia, dispersal barriers	10^4–10^7 km^2	10^3–10^7 years	Holarctic distributions Endemic taxa Biogeographic patterns of body size and life history Refugial faunas Disjunct distributions
Regional (subcontinental, provincial)	Climatic differences Dispersal barriers: watershed boundaries, geomorphic changes Edaphic differences: shield versus sedimentary Landscape differences: lake districts, permanent versus intermittent streams	10^3–10^5 km^2	10^1–10^3 years	Physiological and life history adaptations Latitudinal and longitudinal gradients in richness and composition Regional differences in productivity Distribution and abundance of lake types
Lake-type	Hydrarch succession Abiotic conditions: stratification, seasonality, disturbance frequency, severity Resource distribution and abundance	Patchy within regions	10^0–10^2 years	Physiological and life history adaptations Richness and composition of assemblage types Assemblage patterns of morphology and resource use
Local (individual lake, lake basin)	Isolation Morphometry: area, depth, structural complexity Biotic interactions	10^{-2}–10^2 km^2	10^{-2}–10^1 years	Local richness and composition Population structure Production Assemblage stability

the aquatic landscape is not easily delineated; a major watershed (e.g., the Laurentian Great Lakes), a major landform (the Fennoscandian Peninsula), or even a political unit (state or province) might all operationally define an aquatic region. Features acting as regional filters include past and present dispersal barriers, climatic differences, and geomorphic or edaphic limits (Legendre and Legendre 1984; Table 1).

A regional examination can help identify biological requirements that limit a particular species' distribution and abundance. Occurrence in a region can be limited by climatic factors for those species lacking physiological, life history, or autecological traits needed for the maintenance of viable populations under prevailing conditions. Meisner et al. (1987) provided a list of Ontario species whose distributions seem to be governed by temperature—whose northern boundaries, for example, match certain July isotherms. Climatic gradients expressed as isolines of summer temperature, dates of lake freeze-up, and lengths of growing season also correspond to boundaries of "homogeneous icthyogeographic regions" within Québec (Legendre and Legendre 1984). As a result of these filters, certain species are barred from more northerly regions even in the absence of physical barriers; this process undoubtedly contributes to the observed latitudinal gradient of fish species richness (McAllister et al. 1986).

Lake-Type Filters

Within a region, spatial variation and patchiness occur among lakes because of their discrete, bounded nature and variation in their limnological conditions. Although no two lakes are identical, correlations among limnological conditions exist (Wetzel 1975) and, as a result, the lakes of a region can usually be classified into several groups or "lake types." Due to limitations caused by the age and temporal stability of a water body, by abiotic conditions, by abundances and distributions of resources, by a lake's isolation from sources of colonization, and by interactions with the local biota (Table 1), not all species in a regional species pool are capable of persisting in each lake type. Studies of fish assemblages in lakes of a single region have also shown relatively discrete and repeatable fish assemblage types that are associated with discrete and repeatable lake types (see "An Example," below). These assemblage types are characterized by their repeatable patterns of richness and species composition among assemblages, and by assemblage-level patterns of physiological, life history, morphological, and resource use traits. The biological traits encompassed by members of a regional pool of species, including the degree of specialization of individual species, influences the proportion of a regional pool found in each lake type.

Local Filters

Most studies at the level of individual fish assemblages or groups of similar assemblages have focused on local influences on community structure and function. As a result, we have some understanding of ways local assemblages are affected by area and habitat diversity (Eadie and Keast 1984); winterkill, floods, and other disturbances (Kushlan 1976; Magnuson et al. 1985); pH, alkalinity, and other water chemistry traits (Rago and Wiener 1986; Rahel 1986); and competition, predation, and other biotic interactions (Tonn and Paszkowski 1986; Colby et al. 1987). Temperature has occasionally been assigned a direct role (Inskip and Magnuson 1983), but can also have indirect effects by, for example, influencing resource partitioning (MacLean and Magnuson 1977; Crowder and Magnuson 1982) and feeding relations (Persson 1986; Bergmann 1987). Limited spatial extent and an insular, patchy nature are other important features of lakes and other freshwater habitats. Small lakes are like islands; like species assemblages of true islands, local richness in small lakes is typically correlated with surface area and measures of isolation (Barbour and Brown 1974; Magnuson 1976; Browne 1981; Eadie et al. 1986). Theoretical and empirical studies of assemblages in patchy habitats have revealed the importance of colonization and dispersal to regional and local coexistence (Atkinson and Shorrocks 1981; Hanski and Ranta 1983; Chesson and Case 1986). The importance of isolation and the role of dispersal from neighboring habitats in maintaining or altering richness and composition of local fish assemblages have not been investigated systematically; only rarely have these factors been addressed (Magnuson et al. 1985).

Local assemblages are not structured solely by local factors, as we have seen, but are controlled to some degree by regional and historical processes (Ricklefs 1987). Quantification of the extent of regional (and other larger-scale) influences has not been common, but is becoming an important area of community ecology (Giller and Gee 1987; Roughgarden 1989). If we can establish local–regional relations for fish assemblages of a given region or lake type, such relations may provide us with important tools for predicting the effects of enrichment or impoverishment brought about by climatic change.

An Example

To illustrate how this conceptual framework can be applied to actual fish assemblages, I compare and interpret community patterns in small lakes of three regions on two continents: northern Wisconsin (Tonn and Magnuson 1982; Rahel 1984), central Alberta (Robinson and Tonn 1989), and central and southern Finland (Tonn et al., in press). The Appendix contains the common and scientific names of species occurring in these studies.

Climate and limnological characteristics of small lakes in Finland and northern Wisconsin display many similarities. Lake waters of the two regions are generally dilute and acidic, and meso-oligotrophic and dystrophic lakes are common in both regions. However, historical and zoogeographic differences between Wisconsin and Finland have resulted in distinct regional faunas. Alberta's fish fauna is, to a large extent, a subset of Wisconsin's; however, there are important edaphic and climatic differences between Alberta on the one hand, and Wisconsin and Finland on the other. Lake water in central Alberta tends to be alkaline with considerable amounts of nutrients and other dissolved ions; most lakes are meso-eutrophic or eutrophic. Local relief is low, as is annual precipitation, and drainage patterns are often not well developed; most small lakes have only intermittent outlets, if any. Because of the similarities and differences in fish faunas and lake characteristics among the three regions (Table 2), an understanding of the different filters operating to produce the observed patterns should be valuable when we try to predict effects of climatic changes.

Continental Filters

North America and Europe were connected as a single land mass from the Triassic until the Paleocene, and a Bering connection between North America and Asia existed from the late Cretaceous through most of the Tertiary; this latter connection appeared again in the Pleistocene when sea levels dropped (Briggs 1986). These past connections permitted dispersal of freshwater fishes between North America and the Old World; as a result, many families are Holarctic in their geographical distribution (e.g., Cyprinidae, Esocidae, Percidae). Compositional similarities among the

TABLE 2.—Examples of patterns for the fishes of northern Wisconsin, central Alberta, and central and southern Finland resulting from the operation of continental, regional, lake-type, and local filters. Patterns were initially described by Tonn and Magnuson (1982), Rahel (1984), Robinson and Tonn (1989), and Tonn et al. (in press).

Type of filter	Pattern		
	Wisconsin	Alberta	Finland
Continental	Relatively species-rich North American fauna	Same as Wisconsin	Relatively species-poor European fauna
	Holarctic and North American taxa	Same as Wisconsin	Holarctic and Eurasian taxa
	Many small, short-lived, nonmigratory species	Same as Wisconsin	Many large, long-lived, migratory species
Regional	Relatively species-rich fauna	Relatively species-poor fauna	Same as for continental
	Species from the Mississippian glacial refugium	Species from the Mississippian–Missourian and Columbian glacial refugia	
Lake-type	Lower percentage of regional fauna in small lakes	Same as Wisconsin	Higher percentage of regional fauna in small lakes
	Pike, mudminnow, bass assemblage types	Pike, stickleback assemblage types	Roach, crucian carp, perch assemblage types
	Size-limited predation important in structuring assemblages	Same as Wisconsin	Size-limited predation relatively unimportant
Local	Relatively species-rich assemblages	Relatively species-poor assemblages	Same as Wisconsin
	Isolation, winter hypoxia, area, pH are important abiotic features	Similar to Wisconsin; pH less important	Same as Wisconsin

regional fish faunas of Wisconsin, Alberta, and Finland are moderately high at the familial level (Table 3).

However, because continental connections were severed for millions of years, lineages evolved independently. Thus, within Holarctic families, only a portion of the genera and even fewer species are Holarctic. For example, the family Percidae, although probably of European origin, is now Holarctic, as are the genera *Perca* and *Stizostedion* (Collette and Bănărescu 1977). However, since the disappearance of a North Atlantic dispersal route, endemic forms have evolved on each side, such as the North American tribe Etheostomatini (darters) and the European genus *Romanichthys*. Within the Mississippi basin, extensive speciation occurred among fishes of several families, resulting in a diverse fauna of species with small body size, limited mobility, and relatively specialized ecological niches: for example, *Etheostoma* (Smith 1981; Mahon 1984).

TABLE 3.—Pairwise compositional similarities (Czekanowski's coefficient; Pielou 1984) among the freshwater fish fauna of Finland (SF), northern Wisconsin (Forest, Iron, Oneida, and Vilas counties; WI) and the Athabasca River basin of Alberta (AB). Coefficients above the diagonal of 1.0 are for families of fishes; coefficients below the diagonal are for species. Czekanowski's coefficient can range from 0.0, when no taxa are in common, to 1.0, when two faunas are identical.

Region	SF	WI	AB
SF	1.0	0.62	0.67
WI	0.04	1.0	0.64
AB	0.09	0.44	1.0

The Pleistocene Epoch was probably more stressful for freshwater fishes in northern Europe than in central North America. In Europe, direct north–south migration routes were blocked by mountains that ran east–west, as well as by other dispersal barriers (Bănărescu 1975). Reaching and returning from glacial refugia in the areas of the Black and Caspian seas was likely as difficult as it was indirect. Widespread selective extinction occurred; conditions favored large, long-lived, and migratory species that could persist through several years of adversity without successful reproduction and recruitment (Bănărescu 1975; Mahon 1984; Table 2). In contrast, the great Mississippi–Missouri river system provided a nearby, intact refuge for fishes of central North America; with few major barriers to dispersal from the north, it is unlikely that extinction was significant.

Following the Wisconsinan glaciation in central North America, geological and hydrological events shaped watersheds and provided or blocked specific pathways for the recolonization of glaciated areas. Large volumes of meltwater were produced, forming periglacial lakes whose overflow created new stream channels that connected these lakes to river systems in the south (Robison 1986). In central North America, this allowed rapid and widespread movement of many fishes out of the Mississippian and Missourian refugia. Dispersal pathways existed to drainages currently in the Hudson Bay, Laurentian Great Lakes, Atlantic, and Mackenzie River systems (Paetz and Nelson 1970; Bailey and Smith 1981; Burr and Page 1986; Crossman and McAllister 1986; Lindsey and McPhail 1986). However, because of the temporary nature of these various pathways, some species failed to make some of these transfers (Paetz and Nelson 1970), contributing to a reduction of species richness in regions more peripheral to the central Mississippian–Missourian refugia.

Because of existing dispersal barriers among continents, the modern fish faunas in North America and Europe still reflect the operation of these Pleistocene filters. Total faunal richness in central North America is considerably greater than in Europe, despite general climatic similarities (Briggs 1986). Pairwise similarities between the regional faunas are low at the species level for Wisconsin versus Finland and Alberta versus Finland (Table 3; Appendix). Stream fishes of the two continents differ substantially from each other in ecomorphology, life history, and degree of habitat specialization, in the general directions described earlier (Mahon 1984; Moyle and Herbold 1987; Table 2); it seems likely that comparable differences occur also among fishes of small lakes.

Regional Filters

As much or more freshwater habitat is found in Finland (totaling 10% of its area) as in other European countries. However, Finland's fish fauna is depauperate (Table 4), even relative to other regions in Europe; for example, Romania has only 71% of Finland's surface area but twice as many fish species (Bănărescu 1964). Finland's distance from Black–Caspian sea refugia, the lack of direct dispersal routes to and from those refugia, and the region's northern climate all are likely reasons for the low species richness.

Despite their present access to the Beaufort Sea, most fish species in Alberta's Athabasca River basin came from the same Mississippi–Missouri river system that provided Pleistocene refuge to the Wisconsin fish fauna (Crossman and McAllister 1986; Lindsey and McPhail 1986). Not surprisingly, compositional similarity with the regional fauna of northern Wisconsin is much greater at the species level for the Athabasca fauna than for the fishes of Finland (Table 3; Appendix). However, the cooler and drier climate in Alberta, in combination with temporally limited access and unsuitable habitats for specialists along postglacial dispersal routes (Paetz and Nelson 1970), have acted as effective regional filters for many of the species currently found to the south and east. These filters have been taxonomically selective; for example, the Athabasca basin contains no centrarchids and ictalurids, and only one darter (Paetz and Nelson 1970). Because of these regional filters, the Athabasca basin and Finland contain a similar number of species, about half of the number found in the study area in northern Wisconsin (Table 4).

TABLE 4.—Species richness of freshwater fishes in three regions at three scales. Regional species pool is the total number of species present in the study area; small-lake species pool is the total number of species found in each set of study lakes (a small lake is defined as being ≤ 100 hectares); local species richness is the number of species occurring within individual study lakes. Data from Finland and Wisconsin are from Tonn et al. (in press); data from Alberta are from Robinson and Tonn (1989).

Statistic	Finland	Wisconsin[a]	Alberta[b]
Regional species pool	37	65	31
Small-lake species pool	20	23	11
Percent of regional pool in small lakes	54%	35%	35%
Mean local species richness (range)	3.7 (1–10)	4.4 (1–11)	2.4 (1–5)
Number of study lakes	113	51	36

[a] Forest, Iron, Oneida, and Vilas counties.
[b] Athabasca River basin.

Lake-Type Filters

As indicated earlier, several characteristics of individual lakes may be involved as "lake-type filters" (Table 1). The variable used initially in the studies contributing to this example was surface area: only lakes of 100 hectares or less were considered. Based on the conclusions of Mahon (1984) concerning the habitat generality of European fishes, one would expect that many European species could be found in a variety of habitat types, including small and large lakes, streams, and rivers. Consistent with these expectations, a much higher proportion of the total regional species pool occurs in small lakes in Finland than in Wisconsin (Table 4). Although Wisconsin has more species than Finland overall, a relatively porous small-lake filter in Finland paired with a less permeable small-lake filter in Wisconsin has resulted in similar total numbers of small-lake species (the small-lake species pool) in Finland and Wisconsin (Table 4; Appendix). The proportion of the Athabasca River basin's fauna that occurs in small lakes is identical to the proportion for northern Wisconsin, suggesting a similar permeability of small-lake filters. Because of a smaller regional fauna, however, Alberta has only half as many total species in its small lakes as does Wisconsin.

Within this general set of small forest lakes, studies from each region have consistently shown that species composition differs in regular ways among fish assemblages within a region; assemblages can be classified into groups of related "assemblage types" because of shared species composition, environmental characteristics, and (often by inference) ecological processes. In northern Wisconsin, Tonn et al. (1983) classified the small-lake assemblages into three types, which they referred to as "mudminnow," "bass," and "pike" after the characteristic or dominant species (central mudminnow, largemouth bass, and northern pike). In a finer-scale analysis of a portion of these lakes, Rahel (1984) subdivided the "mudminnow" assemblage type in two, "*Umbra–Perca*" and "cyprinid."

Mudminnow assemblages occurred in small, shallow, isolated lakes that were typically acidic and generally had low concentrations of dissolved oxygen during winter. In addition to central mudminnows, these assemblages often included populations of stunted yellow perch and one or more cyprinid species. Lakes with bass assemblages were similarly small, isolated and acidic, but were deeper and had fewer winter oxygen problems. Frequently occurring species included largemouth bass, yellow perch, and one or two *Lepomis* species. Lakes containing pike assemblages, like mudminnow lakes, were shallow and had low winter oxygen levels, but pike lakes were considerably larger, circumneutral, and connected to other watersheds via outlet streams. Tonn and Magnuson (1982), Tonn et al. (1983), and Rahel (1984) suggested that predation by largemouth bass and northern pike often excluded small-bodied, soft-rayed fishes from bass and pike assemblages, but that such species could survive in the harsh, isolated environments of the mudminnow lake-type, from which both the piscivores and the larger-bodied, spiney-rayed fishes that coexisted with them were excluded.

Small lakes in central Alberta are missing more than half of the species found in Wisconsin, including central mudminnow and largemouth bass. However, Robinson and Tonn (1989) did find that small-lake assemblages in the Athabasca River basin could be classified into two main types ("pike" and "stickleback–fathead"), which were basically depauperate versions of the pike and cyprinid assemblages of Wisconsin. Furthermore, their study suggested that the same ecological factors—piscivory and winterkill (and to a lesser extent their interaction through lake isolation), were again primary determinants of assemblage type. It appears that lake-type filters are similar in these two regions of north-temperate North America, both of whose faunas took refuge in the Mississippi–Missouri system during Pleistocene glaciation.

Using analyses similar to those used in Wisconsin and Alberta, Tonn et al. (in press) were unable to identify discrete fish assemblage types in small Finnish lakes based on species composition (presence–absence). They concluded that size-limited predation, one of the major lake-type filters operating in the central North American regions, does not exclude species from Finnish assemblages because most Finnish species can exceed the maximum body size that is vulnerable to piscivores. However, Tonn et al. (in press) did distinguish three assemblage types ("crucian carp," "perch," and "roach") by including data on the relative abundances of species and were able to show that the limnological characteristics used to distinguish lake types in Wisconsin (size, depth, isolation, acidity) could similarly distinguish lake types in Finland. Crucian carp, perch, and roach assemblages occurred in Finnish lakes that were limnologically similar to Wisconsin lakes with mudminnow, bass, and pike assemblages, respectively. Abiotic features of small lakes on the two continents may operate similarly as lake-type filters, reflecting inherently important characteristics of the discrete, insular, and structurally simple nature of small, north temperate lakes throughout the Holarctic. However, because different continental filters have led to distinct regional faunas, these abiotic features interact with different biological mechanisms to produce fish assemblage types.

Local Assemblages

How do these larger-scale filters affect individual small-lake fish assemblages? Consistent with the total numbers of species occurring in small lakes of each region (lake-type richness), the average number of species per lake is similar in Wisconsin and Finnish lakes but is significantly lower in Alberta (Table 4). Consequently, in each of the three regions, mean local richness represents about 20% of the total number of species found in small lakes. Thus, a single relation between total lake-type richness and mean local richness holds for all three regions (Figure 2, lower). As noted previously, a single relation between local and regional richness is also shared by Wisconsin and Alberta (Figure 2, upper). In Finland, local richness is considerably higher than expected given the low regional richness.

What are the effects of local factors on local assemblages? Several empirical and functional relations have been identified between community-level properties and physicochemical and morphometric properties of the lakes in which they occur. Detailed examination of these relations has not been undertaken in all three regions considered here. However, the species–area relations for the study lakes of Wisconsin and Finland are statistically indistinguishable (Tonn et al., in press). In addition, fish species richness in Finnish lakes having outlet streams is significantly greater than it is in lakes without outlets. Few such relations are significant in Alberta, at least in part because of the limited range of local richness observed (0–5 species; Robinson and Tonn 1989).

Finally, biotic interactions, including competition, predation, and parasitism, can act as local filters and affect patterns of relative abundance, density, production, and resource use within local assemblages (Table 1). A detailed presentation of such effects is beyond the scope of this paper (for examples, see Svärdson 1976 and Werner 1986), but they must be integrated as local filters into studies of the organization of fish assemblages.

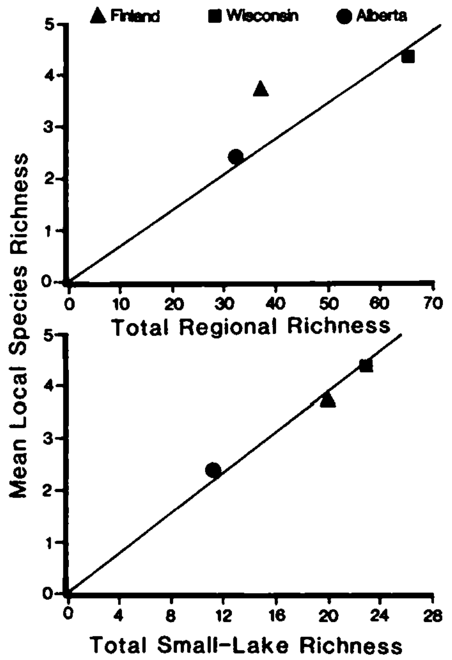

FIGURE 2.—Relations between local and regional richness (upper) and local and small-lake richness (lower) for fish assemblages in small lakes of Finland, northern Wisconsin (Forest, Iron, Oneida, and Vilas counties), and central Alberta (Athabasca River basin). Mean local species richness is the average number of species occurring within individual lakes, total regional richness is the total number of fish species present within the designated areas, and total small-lake richness is the total number of species occurring in each set of study lakes, all of which have areas of 100 hectares or less (see Table 4). Also included are regression lines passing through the origin for Wisconsin and Alberta (upper) and all three regions (lower).

Fish Assemblages and Climate Change

From the conceptual model described above and the framework it provides for understanding how fish assemblages are put together, what kinds of insights can be gained concerning potential community-level effects of climate change? Considering continental-scale filters and the general patterns of richness, life history, and body size associated with them, can we make any general predictions regarding the relative effects of expected climate changes on the central North American versus the European ichthyofaunas? Because the fishes of Europe already represent the survivors of a strong filter operating during the Pleistocene Epoch, an initial expectation might be that the composition of this fauna will show fewer changes than that of central North America. Is this expectation justified?

Perhaps the most important large-scale effect of climate warming on ichthyofaunas would be shifts in geographic distributions resulting from local extinctions of southerly populations and invasions of species into areas farther north than their current distributional limits. The literature on biological invasions tentatively suggests (i) that invasion success is negatively correlated with the richness of the "receiving" fauna (Diamond and Case 1986b), (ii) that the probability of establishment increases for mobile species with a low mortality rate, a high carrying capacity, low level of population fluctuations, and larger body size (Wilcox and Murphy 1985; Crawley 1986; Lawton and

Brown 1986), and (iii) that generalist invaders typically do better than specialists (Holdgate 1986). Traits associated with (ii) and (iii), along with longer life spans, should reduce rates of local extinction as the environment is altered (Pimm et al. 1988), or at least increase population persistence in a deteriorating environment until emigration routes open. Most of these traits have been attributed to the European, rather than to the central North American, ichthyofauna (Mahon 1984). Similarly, a region full of lake-type generalists may not be especially vulnerable because these species are likely to tolerate a wider range of environmental conditions than specialists. Conversely, a region with a high proportion of specialists may be particularly vulnerable to climate changes if those changes adversely alter environmental conditions, resources, or the isolation of habitats on which the species specialize.

An important feature of the conceptual model presented here is its explicit recognition of the influence that larger-scale phenomena have on local assemblages. An initial attempt to quantify some of these influences is represented by the examination of relations between the mean species richness of local assemblages and the richness of larger-scale species pools (Figure 2). Perhaps these relations can be used in a predictive manner to generate expectations for local assemblages should a region's species pool increase or decrease in response to climate change. For example, based on the upper relation in Figure 2, the richness of an average small-lake fish assemblage in central North America might increase or decrease by one species for every increase or decrease of 13–15 species in the regional pool. Of course, this relation is only preliminary. Still, these or other general relations could offer regional "rules of thumb" to fishery biologists anticipating the magnitude of potential effects caused by an altered climate.

Will local factors that operate as filters be altered by climate change? If so, how will this alter the organization of local assemblages? Although increased water temperature is the most obvious, and perhaps most important, of the alterations expected from climate warming, two other influential features of small lakes that may be altered are lake isolation and environmental adversity not directly related to increased temperatures. If these local influences are altered, forces that maintained a particular assemblage organization will likely be weakened. Environmental adversity such as winterkill can eliminate predators or competitors and provide a local refuge for the vulnerable or subordinant species that composed mudminnow, stickleback, and crucian carp assemblage types. If this adversity is reduced by shorter, milder winters, the refuge could be eliminated, as could the assemblage type dependent upon it. A similar loss of refuge could occur if altered surface discharge patterns opened dispersal routes to previously isolated habitats. In both cases, the "patchiness" of a region will be reduced, the potential effect being the reduction in regional coexistence of species that are unable to coexist locally (Atkinson and Shorrocks 1981; Hanski and Ranta 1983; Kareiva 1986).

Individual species will also be favored or harmed by altered environmental conditions, depending on their autecological responses to different conditions. For example, in the Wisconsin and Finnish study lakes, yellow perch and Eurasian perch, respectively, are the most ubiquitous species in small lakes, occurring in a variety of environmental conditions and assemblage types. Within the small lakes of Alberta, however, yellow perch is restricted to larger, deeper lakes, which likely have lower probabilities of winterkill. Because of the generally high productivity of Alberta lakes, and oxygen depletion rates that are strongly correlated with measures of production (Babin and Prepas 1985), Robinson and Tonn (1989) speculated that Alberta lakes may be subjected to more frequent and severe winterkills. Combined with the greater isolation of Alberta lakes, which generally lack permanent surface drainage, this may result in higher extinction rates and lower colonization rates for Alberta populations, and thus a lower frequency of occurrence of yellow perch than in Wisconsin. Although other conditions affecting yellow perch could improve with climate change, the importance of local isolation, extinction, and colonization should not be overlooked when potential effects of climate change are considered. Increased productivity and altered surface discharge are expected in many regions because of climate changes, so patterns of increased extinction and decreased colonization probabilities may emerge for other fish species. Therefore, effects of hydrological alterations should demand as much attention as effects of temperature.

Discussion

Can a community-level conceptual model contribute to fishery biologists' efforts to understand and prepare for climate change? In contrast to earlier theoretical mathematical models, conceptual models can play important roles in fields such as community ecology that are "rich in descriptive detail but poor in generally accepted theory" (Giller and Gee 1987). Such models can provide a framework for organizing the accumulated "details" of a field; the most successful models are also able to identify causal processes and thus offer the potential for both explanatory interpretation and testable predictions.

The central theme of the conceptual model presented here is that ecological systems should be viewed from a series of spatial and temporal scales. Ecological communities are open systems; their structure and organization result not only from local processes, but from processes and events (i.e., filters) that operate at other, external scales (Figure 1). The diversity of influences on the responses of fish assemblages to complex environmental change requires an examination of all these different filters. Purely reductionist attempts to understand community organization in terms of individuals and single-species populations will reduce our abilities to identify larger-scale patterns and thus to fully understand the structure and function of communities. To paraphrase Maynard Smith (1986): although community and higher-level phenomena may eventually be interpreted by autecologists in their own terms, it is unlikely that autecologists will actually discover such phenomena.

Two points should be noted concerning Figure 1. First, the model does not explicitly incorporate human activities. Although phenomena such as exploitation or habitat alteration can be included at lower levels among biotic interactions, abiotic conditions, or resource distribution and abundance, interventions such as stocking or accidental introductions can circumvent dispersal barriers and therefore bypass several filters. If and when such interventions do occur, their effects on both the local assemblage and larger region must be considered.

The second point is that the filters do not always operate in the unidirectional manner depicted in Figure 1. As suggested above, human introductions can bypass all but the local filter, after which dispersal will be controlled by "higher" filters in reverse order. Another such example is offered by the one species of sculpin (*Cottus cognatus*) and one sucker (*Catostomus catostomus*) whose ranges are predominantly North American but also extend into northeastern Siberia. The ranges of these species expanded into Siberia during the Pleistocene when they occurred in the Beringian refugium (Lindsey and McPhail 1986). Presumably, other species of North American sculpins and suckers could have similarly dispersed into Asia, thus passing through a continental filter, if the opportunity had been available. However, based on their modern distributions, it appears that "lower-level" (e.g., regional) filters, prevented other sculpins and suckers from first reaching Alaska, thus making the Beringian route unavailable.

My detailed example, presenting the model "at work," should have made clear two other points. The patterns and processes I described by no means characterize completely the organization of small-lake fish assemblages. Additional empirical studies are required, at various scales, in different regions, on different phenomena, to describe additional patterns behind this organization and provide a more complete understanding of these systems. Second, although I am confident that the basic framework of the model is widely applicable (e.g., Simpson 1953; Smith and Powell 1971; Holmes 1986, in press; Blondel 1987), the "descriptive details" of small lakes and their fishes will certainly differ from those of other systems. Progress in understanding natural systems requires not a blind mistrust of general models, but an interplay between the particular and the general (Colwell 1984).

Once patterns of fish assemblage organization have been identified, we can then ask, What filters have operated to create these particular patterns and how will these filters be affected by climate change? When examined in this framework, the rather daunting proposition of predicting effects of global climate change on fish communities can be divided into a set of at least potentially answerable questions. It is unlikely, with a general conceptual model, that we will attain the resolution necessary to answer specific questions regarding individual local assemblages; no model can simultaneously emphasize realism, generality, and precision (Levins 1966; Colwell 1984). However, "far better an approximate answer to the *right* question, which is often vague, than an exact answer to the *wrong* question, which can always be made precise" (J. Tukey, in Lewin 1983). I believe that by providing insights into the types of data and types of research that are needed to predict and understand how fish communities are put together, the development and use of a conceptual framework such as the one presented here will help fishery biologists ask the full set of right questions regarding climate change and fish communities.

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Appendix: Fish Communities in Study Regions

TABLE A.1.—Common and scientific names of fish species occurring in the sets of study lakes in Finland, northern Wisconsin, and central Alberta (AB) that were used in community analyses by Tonn and Magnuson (1982), Rahel (1984), Robinson and Tonn (1989), and Tonn et al. (in press).

Family and species	Common name	Present in region (×)		
		Finland	Northern Wisconson	Central Alberta
Salmonidae				
Coregonus albula	Vendace	×		
Coregonus lavaretus	Whitefish	×		
Oncorhynchus mykiss	Rainbow trout			×
Osmeridae				
Osmerus eperlanus	Smelt	×		
Umbridae				
Umbra limi	Central mudminnow		×	
Esocidae				
Esox lucius	Northern pike	×	×	×
Cyprinidae				
Abramis brama	Bream	×		
Alburnus alburnus	Bleak	×		
Blicca bjoerkna	White bream	×		
Carassius carassius	Crucian carp	×		
Leuciscus idus	Ide	×		
Leuciscus leuciscus	Dace	×		
Phoxinus phoxinus	Minnow	×		
Rutilus rutilus	Roach	×		
Scardinius erythrophthalmus	Rudd	×		
Tinca tinca	Tench	×		
Notemigonus crysoleucas	Golden shiner		×	
Notropis cornutus	Common shiner		×	
Notropis heterolepis	Blacknose shiner		×	
Phoxinus eos	Northern redbelly dace		×	×
Phoxinus neogaeus	Finescale dace		×	×
Pimephales notatus	Bluntnose minnow		×	
Pimephales promelas	Fathead minnow		×	×
Semotilus margarita	Pearl dace		×	×
Catostomidae				
Catostomus commersoni	White sucker		×	×
Moxostoma sp.	Redhorse		×	
Ictaluridae				
Ictalurus melas	Black bullhead		×	
Ictalurus natalis	Yellow bullhead		×	
Gadidae				
Lota lota	Burbot	×		×
Gasterosteidae				
Pungitius pungitius	Ninespine stickleback	×		
Culaea inconstans	Brook stickleback		×	×
Centrarchidae				
Ambloplites rupestris	Rock bass		×	
Lepomis gibbosus	Pumpkinseed		×	
Lepomis macrochirus	Bluegill		×	
Micropterus dolomieui	Smallmouth bass		×	
Micropterus salmoides	Largemouth bass		×	
Poxomis nigromaculatus	Black crappie		×	
Percidae				
Gymnocephalus cernuus	Ruffe	×		
Perca fluviatilis	Eurasian perch	×		
Stizostedion lucioperca	Zander	×		
Etheostoma exile	Iowa darter		×	×
Perca flavescens	Yellow perch		×	×
Cottidae				
Cottus gobio	Miller's thumb	×		