INTERCONTINENTAL COMPARISON OF SMALL-LAKE FISH ASSEMBLAGES: THE BALANCE BETWEEN LOCAL AND REGIONAL PROCESSES

WILLIAM M. TONN, JOHN J. MAGNUSON, MARTTI RASK, AND JORMA TOIVONEN

Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; Center for
Limnology and Department of Zoology, University of Wisconsin–Madison, Madison,
Wisconsin 53706; Lammi Biological Station, University of Helsinki, SF-16900 Lammi,
Finland; Finnish Game and Fisheries Research Institute, Central Fish Culture Station
for Eastern Finland, SF-58175 Enonkoski, Finland

The idea that local and contemporary processes (e.g., interspecific interactions), combined with such regional and historical processes as immigration and extinction, should produce predictable patterns of community organization rekindled interest in questions concerning community similarity and convergence (MacArthur and Wilson 1967; MacArthur 1972). Can knowledge of the structure and function of one community be used to predict the organization of a second, environmentally similar but geographically distant community composed of unrelated species? This question probes the generality of our understanding of community organization and the extent to which community ecology can become a predictive science (A. Johnson 1973; Orians and Paine 1983; Westoby 1988).

Arriving at an answer, however, has not been easy (Orians 1987). Several studies have found high degrees of similarity in various community properties (e.g., Pianka 1973; Cody 1974; Fuentes 1976; Schluter 1986), but others have not (e.g., Ricklefs and Travis 1980; Lawton 1984; Mahon 1984). Two geographically distant communities in similar local environments may or may not have similar characteristics because of regional or historical factors. For example, Mahon (1984) found that fish assemblages in streams and rivers of Poland and Ontario differ in species richness and that species from the two regions differ in distribution patterns, life-history traits, and morphological adaptations. These results reflect differences in size and isolation of glacial refuges and the presence and importance, in Ontario, of entire families of lake-dwelling specialists. In contrast, similar characteristics exist between assemblages of European and western North American stream fishes, in part because of greater similarity of Pleistocene and post-Pleistocene events in these regions (Moyle and Herbold 1987).

Recognizing the importance of large-scale phenomena, Ricklefs (1987) challenged community ecologists to expand the geographical and historical scopes of their concepts and investigations. Because community-level characteristics may

be differentially influenced by small- versus large-scale processes, these investigations must incorporate phenomena from several scales. Manipulative studies are frequently inappropriate or impractical for such questions, but comparative studies and natural experiments, incorporating multivariate analyses of large-scale pattern, can often provide appropriate tests of large-scale hypotheses (Diamond 1986; Ricklefs 1987; Brown and Maurer 1989).

The value of such large-scale comparisons depends on how well the local environments are matched (Orians 1987). Small forest lakes in glaciated regions of the Holarctic are similarly aged ecosystems containing repeatable suites of environmental conditions. Common forms of environmental severity, such as winter hypoxia and dystrophy (stained, acidic waters), can profoundly influence fish assemblages (Rahel 1984). Distinct patterns of fish-species composition and richness have been observed within a number of regions (see, e.g., Zhakov 1974; Robinson and Tonn 1989). Given the insular nature of lakes (Magnuson 1976), their isolation, as well as their area and habitat diversity, may have important effects on fish-assemblage composition and richness (Barbour and Brown 1974; Tonn and Magnuson 1982; Eadie and Keast 1984; Rahel 1986).

These common characteristics and overall structural simplicity, combined with inevitable differences in species composition and regional history, make small Holarctic lakes good ecological systems for intercontinental comparisons and the investigation of the relative roles of local and regional processes. In this study, we explore the concept of community similarity with fish assemblages in small forest lakes of Finland and Wisconsin. We addressed the following questions. Do similar patterns of fish-species richness exist in small lakes of Finland and Wisconsin? To what extent are any community-level patterns in each region influenced by local abiotic characteristics or by the presence of dominant predators or competitors? Are assemblage structures of the two regions associated in similar ways with the local environment, such that the relations between assemblage structures and the environment for one region can be used to predict fish-assemblage patterns in another region? How do regional or historical influences affect intercontinental comparisons?

METHODS

Study Areas

Southern Finland and northern Wisconsin contain lake districts with thousands of small forest lakes of glacial origin (Hutchinson 1957; Svärdsón 1970; Attig 1984). In both regions, lakes lie atop a granitic bedrock or granitic till, resulting in low levels of dissolved minerals (Juday et al. 1938; Toivonen 1972). Dystrophy is common in both regions. Although Finland is farther north than Wisconsin, overall climates are similar owing to the ameliorating influence of the Gulf Stream in northwestern Europe. Mean monthly air temperatures at Jyväskylä, Finland (62°16′ N, 25°50′ E), range from $-9.4°C$ in January to $16.6°C$ in July (Meteorological Institute of Finland 1984); analogous temperatures range from $-12.4°C$ (January) to $19.4°C$ (July) at Park Falls, Wisconsin (45°56′ N, 90°27′ W; U.S. Department of Commerce 1984).

In contrast to their environmental similarities, fish faunas of the two regions are compositionally dissimilar. Because of Cenozoic connections and subsequent dispersal between North America and Eurasia, several families of fishes found in Finland and northern Wisconsin are Holarctic (Briggs 1986). Since those interchanges, however, faunas have diverged considerably. Percent similarity of the two regions at the familial level is 62%, but this drops to 25% and 4% at generic and specific levels, respectively.

Data Sets

We compiled data sets for fish assemblages and environmental characteristics for 113 Finnish and 51 Wisconsin lakes containing fish. Findings of several studies were combined to cover the range of small forest lakes in both regions. (A complete set of tabular data may be purchased from the Depository of Unpublished Data, Canadian Institute for Scientific and Technical Information, National Research Council Canada, Ottawa K1A 0S2, Canada.)

Finland.—Data on 50 lakes from southern and central Finland were obtained from a study involving whole-lake sampling with rotenone followed by additional systematic collection by scuba divers (Toivonen et al. 1964; Tuunainen 1970; Sumari 1971). For one or more years from 1961 to 1969, 46 other lakes were sampled intensively with variable-mesh gill nets; we used mean relative abundances (by biomass) of the 1961 and 1962 samplings (Anonymous 1961, 1963). Mark-and-recapture studies were carried out on 5 lakes in the Evo area (Rask 1983, 1984; Rask and Arvola 1985; Rask et al. 1985). Five other lakes from the Evo Fisheries Research Station were sampled with gill nets (M. Pursiainen, personal communication), as were 3 lakes in North Karelia (J. Aho, personal communication). Finally, 4 ponds, also in North Karelia, were sampled intensively with 5-mm mesh traps and gill nets or with rotenone (Holopainen and Pitkänen 1985; I. J. Holopainen, personal communication).

As passive sampling gear, gill nets can involve some selectivity by size or species; however, the use of nets with multiple mesh sizes reduces selectivity (Hubert 1983). Indeed, 18 of 20 species found over the entire 113 lakes were caught with gill nets. The exceptions, ninespine stickleback and Miller's thumb (see App. A for scientific names), were each found in only one of the 50 lakes treated with rotenone, indicating that these species occurred infrequently in small forest lakes. Intensive sampling with experimental gill nets also provided relative-abundance data comparable to those obtained from whole-lake rotenone/scuba sampling. Eighteen lakes had been sampled with gill nets before rotenone treatment (Toivonen et al. 1964); mean percent similarity between gill-net catches and rotenone samples was 86%.

Our data sources provided measures of pH, surface area, conductivity, and maximum depth for all 113 lakes, collected by standard limnological methods. To evaluate insularity, we devised an index of lake isolation (App. B) and calculated its value for each lake using data obtained from topographical maps.

Wisconsin.—Two studies (Tonn and Magnuson 1982; Rahel 1984), using combinations of minnow traps, fyke nets, and trammel nets, provided data on species composition (presence or absence) for fish assemblages in northern Wisconsin.

Percent similarities for multiple samplings of seven lakes, ranging in richness from 1 to 11 species, averaged 99% (Tonn 1980, and unpublished data). Limnological data came from the same published sources; we also calculated our index of isolation for each Wisconsin lake using measurements from topographical maps.

Analyses

Species richness.—When comparing species richness between two areas, a number of different scales must be considered (Whittaker 1972). Lists of species composing regional faunas (Whittaker's gamma richness) were compiled from distribution maps and accounts by Becker (1983) and Koli (1984). Region was operationally defined as the geographical area bounded by lakes within our data sets. A regional but ecologically based fauna would include only species from regional faunas that are able to maintain populations in small forest lakes; we defined this fauna as species naturally reproducing within the lakes of our data sets. Proportions of regional faunas that composed these small-lake faunas were used as an indirect, regional measure of habitat specialization by fishes; these proportions were compared between regions via the z-test (R. Johnson 1973).

Because the data set from Finland included twice as many lakes as that from Wisconsin, we performed a simulation exercise that gave cumulative numbers of species in sets of lakes ranging from one to N_i lakes ($N_F = 113$, $N_W = 51$). For each region, a lake was chosen randomly (without replacement) from among the study lakes, and all species present in that lake were recorded. A second lake was chosen at random, and any species not present in the first lake were added to a cumulative list. This process was repeated until all lakes were selected. The whole procedure was then repeated 99 times. We used the resulting rate of species accumulation among lakes as an index of Whittaker's (1972) beta diversity, that is, the extent of change in species composition along a gradient. From the results of these simulations we also calculated the asymptotic number of species expected in sets of an infinite number of small lakes from each region using the Walford method for determining L_∞ from the von Bertalanffy model of growth (Ricker 1975).

Whittaker's alpha richness (or local richness) was measured as the number of fish species per lake. Local richness was compared between regions via the Kruskal-Wallis test. We also compared the relations of local to regional richness between Finland and Wisconsin. Ricklefs (1987; see also Terborgh and Faaborg 1980) suggested that this local-regional richness relation for a pair or group of sites could be used as an index of the relative importance of local (vs. regional) processes in determining local diversity. If local conditions dominate, then an increase in regional richness should have little effect on local richness, producing an asymptotic relation. If local diversity is sensitive to regional effects, then local richness should continue to rise with increases in regional richness.

Species distributions.—To investigate how specific lake features may have affected the distribution of individual species, we analyzed distribution patterns by the occurrence-sequence method (Schoener and Schoener 1983). For each region, we ranked lakes along sequences of increasing value for each environmental factor (pH, area, isolation, conductivity, maximum depth) and analyzed pat-

terns of occurrence of species along these sequences for ordered or haphazard distributions via Mann-Whitney U-tests. If the presence or absence of a species is related to an environmental variable, then the species' distribution should be concentrated at one end of the environmental sequence; if there is no relation, then the occurrence distribution should not reveal a pattern relative to the sequence. This analysis determines the precision of any presence-absence threshold of a species along an environmental gradient and has the advantage of making no a priori assumptions about the exact location of a threshold (Schoener and Schoener 1983; Cornell 1986). Because of limitations of the Mann-Whitney test, analyses were restricted to species found in more than five lakes.

To examine how pairs of species were distributed among lakes relative to each other, and thus investigate the potential effects of interspecific interactions in the two regions, we analyzed patterns of species co-occurrence. We used 2×2 contingency tables and Fisher's exact test to assess the degree of positive or negative association between pairs of species in each region. Fisher's test could not be used directly to test the null hypothesis that the two species of a pair were distributed independently among lakes, because the assumption that all observations are statistically independent is violated (Bowers and Brown 1982). Instead, we used the test to classify co-occurrences into three groups: (1) pairs having overall positive associations and $P < .05$ from the Fisher's test (*positive co-occurrences*); (2) pairs having negative associations and Fisher's probabilities less than .05 (*negative co-occurrences*); and (3) pairs in either direction having $P \geq .05$ (*neutral co-occurrences*). The distributions of species' pairs among these three groups were then tested for independence between Finland and Wisconsin via a G-test to compare patterns of co-occurrence between regions. As above, analyses were restricted to species found in more than five lakes.

Assemblage composition.—To examine compositional patterns of fish assemblages and relations among assemblages in Finland, we applied the multivariate community-analysis methods of ordination and classification to the lakes-by-species data matrix. By providing low-dimensional summaries of community data, these well-established analyses help ecologists identify the data's basic structure; hypotheses can then be generated concerning underlying causes of identified patterns (Gauch 1982; Hermy 1988). Because they are complementary in approach, a combination of ordination and classification applied to the same data set can be an especially useful and powerful tool for revealing the general structure of community data (Gauch 1982; Legendre and Legendre 1983).

Several specific techniques of ordination and classification are available; strengths and weaknesses of each have been the subject of numerous analyses and much discussion over the years, with no end in sight (Pielou 1984; Kent and Ballard 1988). We used primarily principal-components analysis (PCA) on the correlation matrix (Frane et al. 1983) for the purpose of ordering assemblages in a low-dimensional space (pattern analysis). Although criticized by some workers for giving misleading patterns under certain circumstances, PCA is, conceptually, the most straightforward ordination method, and it has proved suitable and useful for numerous community analyses, especially when beta diversity is low and the data set spans a short gradient or has a linear structure (Austin and Noy-Meir

1971; Legendre and Legendre 1983; Pielou 1984; Orlóci 1988). Preliminary analyses suggested that these traits applied to the Finnish data set; however, additional ordinations were performed using detrended correspondence analysis (DCA; Hill and Gauch 1980), a method designed for data with a nonlinear structure. To complement ordination, we also performed hierarchical classification (Ward's method with squared Euclidean distance and the RELOCATE procedure, as suggested in Wishart 1978).

For both classification and ordination, we omitted rare species, defined in earlier analyses as those occurring in five or fewer lakes. This eliminates a substantial number of zeros in the data matrix, which can adversely affect analyses (Legendre and Legendre 1983); with many multivariate methods, especially ordination, infrequent and irregular appearances of rare species also tend to add more noise than information because analyses "perceive rare species as outliers, thus obscuring the analysis of the data set as a whole" (Gauch 1982, p. 214).

The Finnish assemblages were analyzed on two scales, presence-absence and relative abundance. Community composition patterns among fish assemblages from Wisconsin (presence or absence only) have been described using ordination (Tonn and Magnuson 1982; Rahel 1984); we used a composite pattern (from Tonn et al. 1983) to classify the 51 Wisconsin assemblages in the present data set into recurrent groups of co-occurrent species, or "assemblage types."

Whereas identifying structure in community data sets, including the definition of any assemblage types, is accomplished by ordination or classification, environmental interpretation and the generation of ecological hypotheses about this structure require additional data and analyses (Gauch 1982; Legendre and Legendre 1983). To evaluate environmental distinctness among any identified groups of lakes and to identify environmental factors contributing to this distinctness, we applied multiple discriminant analysis (Jennrich and Sampson 1983), using the five environmental factors as variables. All factors except pH were log-transformed to stabilize variances. As with PCA, the discriminant-analysis model itself is not sensitive to departures from multinormality (Legendre and Legendre 1983). Environmental distinctness of lake groups was judged by the percentage of lakes correctly classified by the discriminant functions.

RESULTS

Limnological Conditions

Considerable overlap existed between Wisconsin and Finnish lakes for all characteristics (table 1). The two sets of study lakes were similar with respect to surface area and pH, being small and acidic. Study lakes from Finland were, as a set, deeper, less isolated, and higher in conductivity than those in Wisconsin. Greater isolation in Wisconsin resulted from a higher proportion of seepage lakes; stream gradients were steeper in Finland. Rather than eliminate lakes one by one in an attempt to achieve statistical homogeneity between regions, we concluded that the two sets of lakes were limnologically similar enough to use as whole units in our intercontinental comparisons.

<div align="center">TABLE 1</div>

<div align="center">ENVIRONMENTAL FACTORS AND SPECIES RICHNESS OF THE SMALL FOREST LAKES FROM
FINLAND AND WISCONSIN EXAMINED IN THIS STUDY</div>

	FINLAND		WISCONSIN		KRUSKAL-WALLIS H
VARIABLE	$\bar{X}$	Range	$\bar{X}$	Range	(df = 1)
Environmental factors:					
pH	6.2	4.3–7.5	6.0	4.3–8.0	1.68
Lake area (ha)	9.5	.2–64.0	14.0	.2–86.9	.18
Lake isolation[a]	49	0–188	78	0–156	5.82*
Conductivity (μS at 20°C)	28	3–96	27	8–145	10.2**
Maximum depth (m)	9.6	1.5–27.0	4.8	1.2–10.0	32.9***
Species richness:					
Regional fish fauna (no. of species)	37[b]	65[c]			
Small-forest-lake fauna (no. of species)	20		23		
Single-lake species richness (no. of species)	3.7	1–10	4.4	1–11	2.57

NOTE.—Finland, $N = 113$; Wisconsin, $N = 51$.
[a] See App. B for definition and formula.
[b] Includes "freshwater" and "holoeuryhaline" species (Koli 1984).
[c] Species in Forest, Iron, Oneida, and Vilas counties, from distribution maps in Becker 1983.
* $P < .05$.
** $P < .01$.
*** $P < .001$.

Species Richness

At a regional level (gamma richness), northern Wisconsin contains 1.8 times as many species of freshwater fishes as does Finland (table 1); these regional faunas can be treated as "mainland" or source pools for small lake "islands." However, we found nearly as many species in small forest lakes of Finland (20) as in northern Wisconsin (23; App. A). The 20 Finnish species represent a significantly higher proportion of the regional fauna than do the 23 species in Wisconsin (z-test, $P < .01$). At the level of individual lakes (alpha richness), no significant difference in average species richness existed between Finland and Wisconsin (table 1). Species-area regressions for the two regions also did not differ ($F = 0.9$, df = 2,160, $P = .4$); the regression equation for Wisconsin was $\log S = 0.30 + 0.32\log A$, $R^2 = 0.41$; the equation for Finland was $\log S = 0.23 + 0.34\log A$, $R^2 = 0.40$.

On the basis of our simulation of species accumulation (fig. 1), a set of 51 small lakes in Finland would have an average of 16.1 species, which still represents a significantly higher proportion of the regional fauna than what we found in 51 Wisconsin lakes (z-test, $P < .01$). Species initially accumulated more rapidly in Wisconsin than in Finland, suggesting a higher beta richness in Wisconsin. Despite this initial difference in cumulative richness, lake sets from the two regions would eventually converge with regard to richness of their small-forest-lake fish faunas. Values of S_∞ calculated from the simulation were 22.9 species for Finnish lakes and 24.5 for Wisconsin. Because alpha richness did not differ between
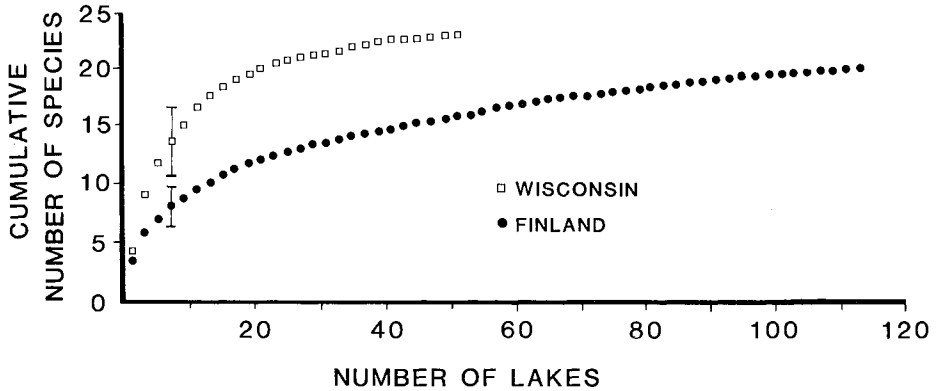
FIG. 1.—The total (cumulative) number of species in a set of small forest lakes versus the number of lakes in the set, based on a random-lakes selection-simulation exercise (see the text). Data used in the simulation were from the study lakes in Finland ($N = 113$) and Wisconsin ($N = 51$). As an example of the variability among individual simulations ($N = 100$), 95% confidence limits are given for sets of seven lakes.
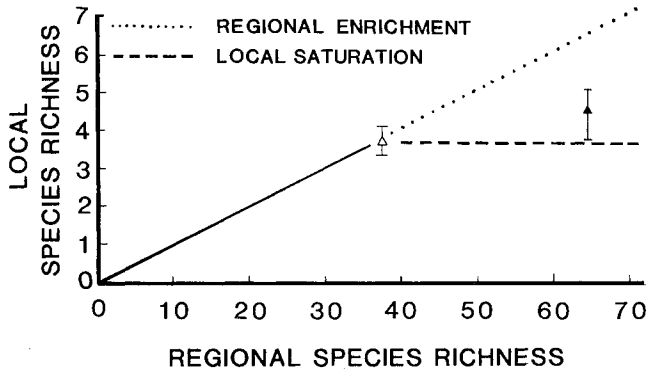

FIG. 2.—Relations between local and regional species richness for fish assemblages of small forest lakes in Finland (*open triangle*) and Wisconsin (*solid triangle*). The relation for Wisconsin was compared with a model of local saturation (*dashed line*) and regional enrichment (*dotted line*), on the basis of the relation observed in Finland. Values for local richness are means of individual assemblages; vertical lines are 95% confidence intervals.

regions, the relation of local to regional richness was nearly asymptotic (fig. 2), suggesting that ecological saturation in local assemblages predominated.

Fish Distributions

Occurrence sequences.—With the consistent exception of crucian carp, nearly all species examined in Finland had significantly ordered sequences of occurrence for pH, area, isolation, and conductivity (table 2). Moreover, significantly more Finnish species than expected were distributed in the same direction along gra-

TABLE 2

OCCURRENCE SEQUENCES WITH FIVE ENVIRONMENTAL VARIABLES FOR FISHES IN
SMALL LAKES OF FINLAND AND WISCONSIN

ENVIRONMENTAL VARIABLE	SIGNIFICANT z VALUES*		TOTAL z VALUES		
	Positive	Negative	Positive	Negative	P†
Finland:					
pH	0	7	0	9	.004
Lake area	0	7	1	8	.040
Lake isolation	7	0	9	0	.004
Conductivity	0	7	0	9	.004
Maximum depth	0	1	1	8	.040
Wisconsin:					
pH	1	7	1	11	.006
Lake area	1	5	2	10	.038
Lake isolation	4	0	8	4	.388
Conductivity	0	4	4	8	.388
Maximum depth	2	2	7	5	.744*

NOTE.—Species occurring in more than five lakes were analyzed (for Finland, $N = 9$; for Wisconsin, $N = 12$). Standard normal variates (z values) were determined from Mann-Whitney U-tests. Positive z values indicate a tendency for species to be present in lakes with smaller values of the environmental variables; negative z values show a trend toward occurrence in lakes with larger values.
* $P < .05$.
† Probability that at least the observed number of the total negative (or positive for isolation) z values occurred by chance, on the basis of the binomial distribution.

dients of all five environmental factors. Lakes in which these Finnish species were present were less acidic, larger, higher in conductivity, deeper, and less isolated than lakes without these species.

A comparable, common pattern of similar distributions did not exist for Wisconsin species (table 2); the distributions of more than half of the species were significantly ordered only along the pH gradient. For lake area and isolation, northern pike, black bullhead, white sucker, and yellow perch had ordered sequences, occurring significantly more frequently in larger, less isolated lakes. Pike and bullhead were found more often in shallow lakes, whereas bluegill and largemouth bass occurred more frequently in deeper lakes. Only for gradients of pH and lake area were significantly more Wisconsin species than expected distributed in the same direction (table 2); lakes containing these species had higher pH's and larger areas than lakes lacking them.

Species co-occurrence.—Of 36 species pairs examined in Finland, 23 (64%) showed positive co-occurrences, 12 (33%) exhibited a pattern of neutral co-occurrence, and only 1 (crucian carp and perch) displayed negative co-occurrence. Each of the 9 species examined in Finland exhibited positive co-occurrence patterns with at least 2 other species; most co-occurred positively with more than half of the others. In contrast, of 66 pairwise comparisons made among Wisconsin species, only 11 (17%) revealed positive co-occurrences, whereas 50 (76%) exhibited neutral co-occurrence patterns and 5 (8%) displayed negative patterns; all 5 negative co-occurrences involved central mudminnows, with pi-

scivorous largemouth bass and northern pike and the associated bluegill, pumpkin-seed, and white sucker. Overall, patterns of co-occurrence differed significantly between regions ($G = 22.1$, df $= 2$, $P < .001$).

Connor and Simberloff (1983, p. 461) pointed out that general procedures for examining co-occurrence fail to account for expected co-occurrences caused by the "omnipresent" species-area relationship. For our Finnish data set, such omnipresent patterns also included relations of richness with pH, isolation, conductivity, and depth (table 2). To correct for similar species-environment relations, we repeated our co-occurrence analyses, except that for each pair of species, we included only lakes having at least as many species as the most depauperate assemblage in which the two species were found. In this reanalysis, the number of positive co-occurrences in Finland dropped to only 9 (25%), increasing the number of neutral pairs to 26 (72%). These changes reflected the common pattern of occurrence sequences described above. Few changes occurred in pairwise comparisons for Wisconsin; 3 additional negative co-occurrences involved northern redbelly dace with the piscivorous largemouth bass, northern pike, and yellow perch. Despite these changes, overall distributions remained different between regions ($G = 6.4$, df $= 2$, $P < .05$).

Patterns of Species Composition

Wisconsin.—An earlier study (Tonn et al. [1983], which used the data set of Tonn and Magnuson [1982] and a portion of Rahel's [1984] data) divided fish assemblages of small, northern Wisconsin lakes into three assemblage types (mudminnow, pike, bass; table 3). Although Rahel (1984) subsequently subdivided the mudminnow assemblage type into two (*Umbra-Perca* and cyprinid) because of the absence of many cyprinid (minnow) species in bog lakes of low pH, that finer-scale subdivision was not evident in analyses of our larger data set. Rahel's "centrarchid" assemblages are equivalent to our bass assemblage type.

Multiple discriminant analysis correctly classified 84% of the lakes in terms of which assemblage type they contained (table 4; see also table 9). Combinations of environmental severity (low pH, low winter oxygen), biotic severity (especially predation), and the presence or absence of refuges from these conditions appeared to be largely responsible for the composition and occurrence pattern of assemblage types. Mudminnow assemblages were found in small, shallow, isolated lakes that frequently had low levels of dissolved oxygen during the winter (Tonn and Magnuson 1982; Tonn and Paszkowski 1986). These assemblages lacked specialized piscivores (largemouth bass, northern pike) and were dominated by small, soft-rayed species (central mudminnow, northern redbelly dace, golden shiner, and other cyprinids), many of which rarely occurred in the other assemblage types. Bass assemblages also occurred in small, isolated lakes, but only in lakes that were deeper and therefore had higher levels of winter dissolved oxygen (Tonn and Magnuson 1982; Rahel 1984). In addition to largemouth bass, these assemblages were composed primarily of large, spiny-rayed species. Pike lakes were larger and more productive than mudminnow or bass lakes, and although they were shallow and had low levels of dissolved oxygen during the winter, they were well connected to streams that could provide refuges from seasonally harsh

TABLE 3

RELATIVE FREQUENCIES OF OCCURRENCE OF FISH SPECIES, AND OTHER COMMUNITY CHARACTERISTICS, IN
THREE ASSEMBLAGE TYPES IN NORTHERN WISCONSIN LAKES

| | ASSEMBLAGE TYPE | | | |
SPECIES	Pike (N = 8)	Bass (N = 23)	Mudminnow (N = 20)	ALL LAKES (N = 51)
Yellow perch	.88	.91	.60	.78
Central mudminnow	.12	.43	.90	.57
Largemouth bass	.25	.78	. . .	.39
Bluegill	.38	.52	. . .	.29
White sucker	.88	.26	.05	.27
Black bullhead	1.00	.09	.20	.27
Pumpkinseed	.75	.30	. . .	.25
Golden shiner	.38	.17	.30	.25
Northern pike	1.00	.13	. . .	.22
Yellow bullhead	.25	.30	. . .	.18
Black crappie	.25	.22	. . .	.14
Northern redbelly dace	. . .	. . .	.30	.12
Brook stickleback	. . .	. . .	.25	.10
Rock bass	.50	.04	. . .	.10
Iowa darter	.25	. . .	.15	.10
Blacknose shiner	.12	. . .	.15	.08
Finescale dace	. . .	. . .	.15	.06
Fathead minnow	. . .	. . .	.15	.06
Bluntnose minnow	.25	. . .	. . .	.04
Pearl dace	. . .	. . .	.10	.04
Common shiner	.12	. . .	. . .	.02
Redhorse	.12	. . .	. . .	.02
Smallmouth bass	. . .	.04	. . .	.02
Total no. of species	17	13	12	23
Species richness:				
Mean no. of species[a]	7.5‡	4.2†	3.3†	4.4
Range	5–10	2–7	1–11	
No. of unique species[b]	1	0	5	

[a] Means with the same symbol are not significantly different from each other (Tukey-Kramer test). Overall ANOVA, $F = 11.3$, df = 2,48, $P < .001$.

[b] Species that occur in two or more lakes but in only one assemblage type.

abiotic conditions. Like bass assemblages, pike assemblages consisted primarily of large, spiny-rayed species. These patterns and ecological relationships are discussed in detail elsewhere (Tonn and Magnuson 1982; Rahel 1984; Magnuson et al., in press).

Finland.—Ordination of Finnish fish assemblages based on species' presence or absence did not identify distinct assemblage types (Tonn et al., unpublished data); rather, a hierarchical continuum of species richness based on species addition was suggested. To facilitate analysis of this continuum, we divided the assemblages into three groups based on species richness (table 5): group I included assemblages with 1–3 species; group II assemblages contained 4–6 species; and group III lakes had 7–10 species. Examination of these groups revealed a nested pattern of assemblage composition. This continuum of species composition paralleled an environmental continuum (table 6). Area was the most

TABLE 4

MEAN VALUES OF ENVIRONMENTAL FACTORS FOR THREE FISH ASSEMBLAGE TYPES IN
NORTHERN WISCONSIN LAKES

| | ASSEMBLAGE TYPE | | | |
| | Pike | Bass | Mudminnow | UNIVARIATE F |
FACTOR	($N = 8$)	($N = 23$)	($N = 20$)	(df $= 2,48$)
pH	7.2	5.8	5.7	10.7***
Lake area (ha)	41.6	6.1	3.5	23.2***
Lake isolation[a]	0.7	73.4	72.2	49.1***
Conductivity (μS at 20°C)	59.3	12.3	19.0	22.1***
Maximum depth (m)	2.1	6.3	3.5	25.4***

NOTE.—All factors except pH were log-transformed before analyses. Equations for the two canonical variables (X, Y) from a discriminant analysis are as follows: $X = -1.01 + 1.73\log(\text{isolation} + 1) + 0.24\log(\text{depth}) - 1.04\log(\text{area} + 1) - 0.62\log(\text{conductivity}) - 0.03\,\text{pH}$; $Y = -3.27 - 0.62\log(\text{isolation} + 1) + 4.88\log(\text{depth}) + 1.85\log(\text{area} + 1) - 2.86\log(\text{conductivity}) + 0.53\,\text{pH}$.
 [a] See App. B for formula and description.
 *** $P < .001$.

TABLE 5

RELATIVE FREQUENCIES OF OCCURRENCE OF FISH SPECIES, AND OTHER COMMUNITY CHARACTERISTICS, IN
THREE SPECIES-RICHNESS GROUPS IN FINNISH LAKES

| | GROUP I | GROUP II | GROUP III | |
| | 1–3 Species ($N = 58$) | 4–6 Species ($N = 41$) | 7–10 Species ($N = 14$) | ALL LAKES ($N = 113$) |
SPECIES				
Core species:				
Eurasian perch	.86	1.00	1.00	.92
Northern pike	.50	.98	.93	.72
Roach	.14	.80	1.00	.48
Burbot	.07	.85	1.00	.46
Ruffe	.14	.56	1.00	.39
Secondary species:				
Crucian carp	.14	.07	.57	.17
Bream	...	.07	.79	.12
Bleak	...	.12	.50	.11
Tench	...	.05	.50	.08
Satellite species:				
Minnow	.03	.02	...	.03
Rudd	...	.07	...	.03
Ninespine stickleback	...	.02	...	.01
Dace	...	.02	...	.01
Miller's thumb	...	.02	...	.01
Vendace	...	.02	.14	.04
Smelt	...	...	.21	.03
Ide	...	...	.14	.02
White bream	...	...	.14	.02
Zander	...	...	.14	.02
Whitefish	...	...	.07	.01
Total no. of species	7	15	16	20
Mean species richness	1.9	4.8	8.1	3.7
No. of unique species[a]	0	1	4	

 [a] Species that occur in two or more lakes but in only one species-richness group.

TABLE 6

MEAN VALUES OF ENVIRONMENTAL FACTORS FOR THREE SPECIES-RICHNESS GROUPS IN FINNISH LAKES

FACTOR	GROUP I 1–3 Species (N = 58)	GROUP II 4–6 Species (N = 41)	GROUP III 7–10 Species (N = 14)	UNIVARIATE F (df = 2,110)
pH	5.9	6.4	6.6	18.3***
Lake area (ha)	3.1	10.2	13.8	29.7***
Lake isolation[a]	45.5	11.3	7.9	19.2***
Conductivity (μS at 20°C)	19	24	40	8.8***
Maximum depth (m)	7.6	8.1	10.2	1.3

NOTE.—All factors except pH were log-transformed before analyses.

[a] See App. B for formula and description.

*** $P < .001$.

important environmental factor distinguishing the species-richness groups, increasing from the depauperate group I lakes to the more species-rich group III lakes. Other important variables included lake isolation (greatest in group I) and pH (highest in group III).

Five core species (Hanski 1982) appeared in all three richness groups and were nearly ubiquitous in group III lakes (table 5). Perch and pike were usually present in group II lakes and in 63% of two-species lakes; perch were found in 68% of single-species lakes. Secondary and satellite species were generally absent from depauperate lakes, occurring with greater frequency in progressively richer assemblages. Crucian carp, a secondary species, was an important exception to this pattern, occurring in 21% of single-species lakes.

For Finnish assemblages, we were also able to perform our multivariate community analyses on a second scale, using biomass relative abundance. Rather than a single continuum, three groups were distinguishable, each with a different predominant species (fig. 3; table 7); DCA ordination gave similar results (Tonn et al., unpublished data). The three assemblage types consisted of 58 assemblages dominated by perch, 47 assemblages dominated by roach (or, rarely, pike), and 8 assemblages dominated by crucian carp. The dominant species usually contributed at least twice as much biomass as did the second-ranked species. As expected from the presence-absence analyses, assemblage types did not differ greatly in species composition; few species were restricted to one asemblage type (table 7).

Environmental characteristics of the lakes of each Finnish assemblage type were relatively distinct, as indicated by discriminant analysis (table 8). This five-variable analysis, comparable to one performed on Wisconsin lakes, correctly classified 68% of the lakes (table 9). The index of local isolation was the most important factor distinguishing the three groups; roach lakes were significantly less isolated than either perch or crucian carp lakes. Other important variables included maximum depth (lower in crucian carp lakes) and pH (higher in roach lakes).
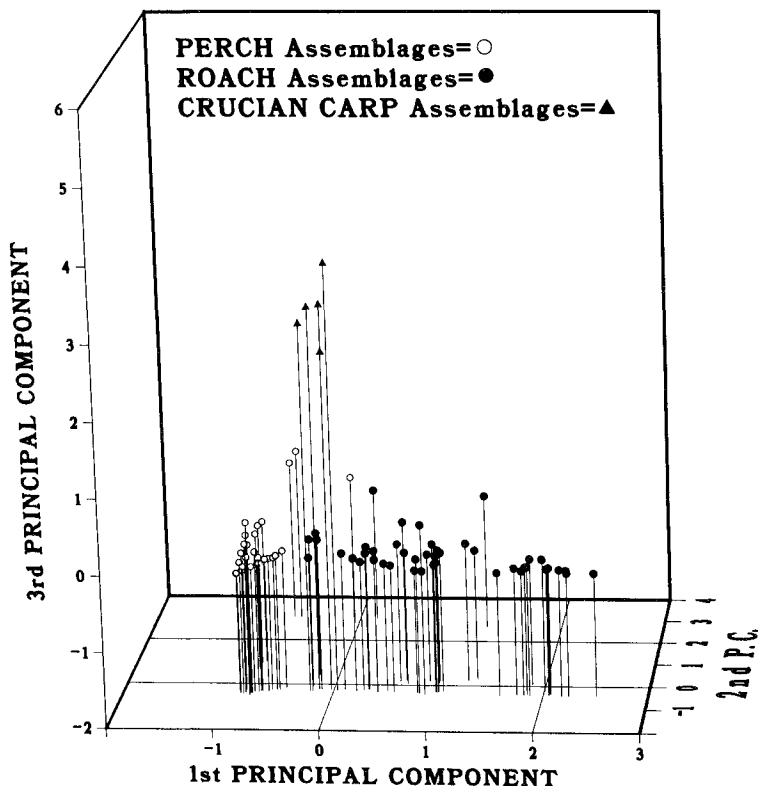
Fig. 3.—Ordination of fish assemblages in 113 Finnish lakes, based on the relative abundance of species. Three types of assemblages are distinguished, identifiable by the predominant species in the assemblages. The first three principal components explained 20%, 16%, and 13% of the total variance, respectively.

Intercontinental Comparisons of Assemblage-Environment Relations

From the above community analyses, it appeared that fish-assemblage types of the two regions were distributed in similar ways along environmental gradients (cf. tables 4 and 8). Characteristics of lakes containing perch, roach, and crucian carp assemblages in Finland paralleled those of bass, pike, and mudminnow lakes, respectively, in Wisconsin. Roach and pike lakes were generally larger, less acidic, and less isolated, relative to the other lake types. Crucian carp and mudminnow lakes tended to be small, shallow, and isolated, whereas perch and bass lakes were typically isolated but relatively deep.

To investigate this apparent pattern, we used discriminant functions from one region as a priori predictors for the second region (rather than as descriptors of the original data set, as used above; see also Cody 1978; Tonn et al. 1983). We calculated canonical variate scores for each Finnish lake using functions generated by the discriminant analysis of Wisconsin lakes (table 4) and calculated canonical variate scores for the Wisconsin lakes using discriminant functions from

TABLE 7

MEAN RELATIVE ABUNDANCE OF FISH SPECIES, AND OTHER COMMUNITY CHARACTERISTICS, IN THREE
ASSEMBLAGE TYPES IN FINNISH LAKES

	ASSEMBLAGE TYPE			
SPECIES	Roach (N = 47)	Perch (N = 58)	Crucian Carp (N = 8)	ALL LAKES (N = 113)
Eurasian perch	.23	.86	.06	.53
Northern pike	.18	.06	.08	.11
Roach	.50	.00[a]	.00[a]	.20
Burbot	.02	.02	...	.02
Ruffe	.02	.04	.00[a]	.03
Crucian carp	.00[a]	.00[a]	.85	.05
Bream	.03	.00[a]	...	.01
Bleak	.00[a]	.00[a]	...	.00[a]
Tench	.00[a]	.00[a]	...	.00[a]
Total no. of species	17	16	5	20
Species richness:				
Mean no. of species[b]	2.7†	5.3‡	2.0†	3.7
Range	1–9	1–10	1–5	
No. of unique species[c]	2	1	0	

NOTE.—Only species occurring in five or more lakes are listed.

[a] Present in at least one assemblage.

[b] Means with the same symbol are not significantly different from each other (Tukey-Kramer test).
Overall ANOVA, F = 28.1, df = 2,110, P < .001.

[c] Species that occur in two or more lakes but in only one assemblage type.

TABLE 8

MEAN VALUES OF ENVIRONMENTAL FACTORS FOR THREE ASSEMBLAGE TYPES IN FINNISH LAKES

	ASSEMBLAGE TYPE			
FACTOR	Roach (N = 47)	Perch (N = 58)	Crucian Carp (N = 8)	UNIVARIATE F (df = 2,110)
pH	6.5	5.9	6.0	14.0***
Lake area (ha)	9.6	6.1	2.2	10.9***
Lake isolation[a]	8.7	40.5	50.3	18.9***
Conductivity (µS at 20°C)	30.2	19.4	16.7	7.6***
Maximum depth (m)	8.1	8.7	3.3	8.7***

NOTE.—All factors except pH were log-transformed before analyses. Equations for the two canonical variables (X, Y) from a discriminant analysis are as follows: $X = 5.23 + 1.21\log(\text{isolation} + 1) - 0.16\log(\text{depth}) - 0.31\log(\text{area} + 1) - 0.24\log(\text{conductivity}) - 1.00\text{pH}$; $Y = 1.59 + 0.52\log(\text{isolation} + 1) + 2.73\log(\text{depth}) + 1.34\log(\text{area} + 1) + 1.04\log(\text{conductivity}) - 0.67\text{pH}$.

[a] See App. B for formula and description.

*** P < .001.

TABLE 9

Classification Matrices Resulting from Discriminant-Function Analyses

Lake Environment Type	Fish Assemblage Type			Lake Environment Type	Fish Assemblage Type		
	Pike	Bass	Mudminnow		Roach	Perch	Crucian Carp
N	8	23	20	N	47	58	8
Pike:				Roach:			
W	8	1	2	W	34	12	1
F	8	1	2	F	35	13	1
Bass:				Perch:			
W	0	20	3	W	9	33	1
F	0	17	4	F	9	36	1
Mudminnow:				Crucian carp:			
W	0	2	15	W	4	13	6
F	0	5	14	F	3	9	6
% correct:				% correct:			
W	100	87	75	W	72	57	75
F	100	74	70	F	74	62	75

Note.—Lakes of each fish assemblage type were classified into groups according to discriminant functions from environmental analyses. Presented are the number of lakes of each assemblage type that were classified into each lake environment type and the percentage of lakes that were correctly classified. W (Wisconsin) and F (Finland) are the sets of lakes from which the discriminant functions were derived.

the comparable five-variable analysis of the lakes in Finland (table 8). Using these between-region canonical variate scores, new discriminant analyses were then performed for each region to determine whether relations that separated lakes of different assemblage types on one continent could successfully distinguish lakes containing analogous assemblage types on the other continent.

Discrimination among assemblage types using these between-region analyses was nearly as good as in the original within-region analyses (table 9). Distributions of Finnish lakes having perch, roach, and crucian carp assemblages differed significantly from each other in discriminant space using the two canonical variables derived from Wisconsin lakes (multivariate analysis of variance, MANOVA, $P < .001$). Canonical variables derived from the Wisconsin discriminant functions correctly classified 73 of the 133 Finnish lakes (65%), compared with 77 correct (68%) based on functions derived from the Finnish lakes themselves. This was a significantly greater number of correct classifications than 40 (36%), the average of 20 cross-continental analyses in which each Finnish lake was randomly assigned to an assemblage type, with the restriction that the total number of lakes in each type was the same as in the original analysis ($t = 6.9$, df $= 19$, $P < .001$).

Distributions of Wisconsin lakes with bass, pike, and mudminnow assemblages also differed from each other along canonical variables derived from Finnish lakes (MANOVA, $P < .001$). These canonical variables correctly classified 39 of 51 Wisconsin lakes (76%) versus 43 correct with the original Wisconsin variables (84%); this was greater than the 22 correct (43%) produced, on the average, with

20 analyses in which lakes were randomly assigned to the three assemblage types ($t = 5.9$, df $= 19$, $P < .001$). Analogous assemblage types are indeed distributed in environmental space in parallel ways on the two continents.

<div style="text-align: center;">DISCUSSION</div>

Our comparative analyses of fish assemblages in a Nearctic and Palearctic region reveal community-level patterns that reflect joint but variable influences of phenomena that are local and contemporary and those that are regional and historical. Although our assessment of the relative roles of these two groups of processes frequently, and by necessity, relied on indirect evidence, it is apparent that certain features of fish assemblages are influenced primarily by phenomena on one scale, whereas processes operating on the alternative scale dominate other features. Clearly, ecologists must be aware of these differences and study processes on the scale appropriate to the community trait being investigated (Allen and Starr 1982).

Species Richness

Historical factors are generally recognized as contributing to differences in regional species richness (Westoby 1988). Although many families of freshwater fishes are Holarctic in distribution as a result of Cenozoic connections between North America, Europe, and Asia (Briggs 1986), differing effects of Pleistocene glaciation resulted in a more depauperate fauna in northern Europe than in climatically similar regions in central North America. Because of the lack of nearby refuges (Bănărescu 1975), widespread selective extinction occurred within the northern European fauna, with conditions favoring large, long-lived, and migratory species (Mahon 1984; Moyle and Herbold 1987). In contrast, Wisconsin's fish fauna enjoyed a large, nearby refuge (and a center of speciation) in the Mississippi River basin (Burr and Page 1986), with conditions favoring small, short-lived species or species using relatively narrow ranges of habitats (Mahon 1984).

Mahon (1984) suggested that low species richness in the northern European fauna and the absence of a number of North American families (e.g., Centrarchidae, Ictaluridae) promoted intraspecific competition and development of broad habitat-use patterns in Europe. A large proportion of the European fauna can be found in rivers, streams, large lakes, and small forest lakes, whereas North American species tend to be more specialized, each occurring in fewer types of habitat (Muus and Dahlstrøm 1978; Becker 1983). Only a third of freshwater fishes in northern Wisconsin occur in small forest lakes, and beta richness is significantly higher there than in Finland. Greater specialization and higher spatial turnover may be a common pattern for small-bodied species (Brown and Maurer 1989), which make up a significant part of the Wisconsin, but not Finnish, fauna.

Postglacial Fennoscandia has been covered by several bodies of brackish and fresh water (Svärdson 1970, 1976), in which most species of the modern regional fauna probably lived (Nordqvist 1903). Because small lake basins had already formed by the time of Ancylus Lake (8,500–8,000 yr ago), Nordqvist believed that

most fishes simply remained in the smaller basins as water levels dropped and persisted as long as conditions remained suitable. If so, a large set of forest lakes contains a high proportion of the regional freshwater fauna not only because of their ecological generality but because the forest lake fauna is a remnant from Ancylus Lake. Therefore, historical extinctions may have been more important than colonizations in determining the species richness and composition of individual lakes. The absence of large pro-glacial lakes in northern Wisconsin (Attig 1984) suggests that although less isolated regionally from glacial refuges, Wisconsin lakes were more isolated from local sources of immigrants than were Finnish lakes. Despite differences in gamma (regional) and beta (among-lake) richness, fish assemblages within individual lakes of the two regions revealed convergent and similar levels of richness. Lakes of the two regions had similar areas and water chemistry, both of which could have contributed, directly or indirectly, to similar levels of local richness (Eadie and Keast 1984). Greater depth and less isolation both should have favored greater richness in Finnish lakes, all else being equal; the increased beta richness in Wisconsin, suggested by figure 1, and an increased degree of habitat specialization in the North American fauna (Mahon 1984) could have compensated for the higher regional richness in Wisconsin. The range of local species richness in our study lakes also approximated that found in similarly sized lakes of Vologda and Jaroslavl provinces, USSR (Zhakov 1974), Sweden (Alm 1960, 1961), and Ontario (Eadie et al. 1986).

The nearly asymptotic relation of local to regional richness (fig. 2) can be viewed as an indication of the relative importance of local (vs. regional) processes in determining local diversity (Ricklefs 1987). The asymptotic relation also has been found in terrestrial and marine systems (Cody 1966; Heck 1979; Bohnsack and Talbot 1980; Terborgh and Faaborg 1980), suggesting some generality of the pattern.

Standard explanations have stressed that saturation would occur because competition imposes a fixed limit on the number of coexisting species (Cornell 1985). Competition probably has contributed to increased habitat specialization of eastern North American fishes relative to those in northern Europe (Mahon 1984). However, the isolation, ecological impoverishment, and habitat severity of small forest lakes and the occurrence of size-limited predation also have structured fish assemblages in small Wisconsin lakes (Rahel 1984; Tonn and Paszkowski 1986, 1987; Magnuson et al., in press). These factors are probably more important than competition in limiting the number of species in individual Wisconsin lakes to levels similar to those occurring in Finland.

An asymptotic relation between local and regional richness is not universal. Lawton (1984) and Cornell (1985, 1986) both found strong correlations between alpha and gamma richness for host-herbivore systems, which led them to conclude that these assemblages were not saturated and that local interactions among species were not important. Causes behind the different patterns are not clear. Potential influences on the type of relation observed between local and regional richness involve the sizes of local assemblages and regional species pools in the systems being compared (J. Lawton, personal communication). Pool "exhaus-

tion" (Lawton and Strong 1981, p. 326) can produce an asymptotic relation; alternatively, richness in systems reported to have linear relations might level off if localities with larger regional pools are discovered. Finally, there simply appear to be different "kinds" of communities for which different processes, operating on different scales, are important (Schoener 1986a; Westoby 1988). Currently, a general explanation accounting for various local-regional relations cannot be provided.

Fish Distribution and Assemblage Composition

A proximate factor involved in the higher beta richness of Wisconsin was the irregular patterns of occurrence of Wisconsin species along environmental gradients, whereas most species in Finland displayed similar, regular occurrence patterns along the same gradients. Results of co-occurrence analysis and the occurrence sequences of individual species suggest that individualistic responses to the environment, rather than biotic interactions among species, played major roles in creating overall patterns of occurrence and assemblage composition in Finland at the level of species' presence or absence. Strong, biotic interactions that can eliminate species from otherwise favorable lakes could well have resulted in haphazard occurrence sequences along environmental gradients. Nearly all species examined in Finland had significantly ordered sequences of occurrence for four of five environmental factors; combined with exceptionally low numbers of negative co-occurrences, this suggests that negative interactions were not important. Rather, it seems that species were responding independently in similar ways to an overall environmental gradient. These patterns are consistent with the observation that, on the scale of species' presence or absence, Finnish assemblages present a continuum rather than discrete groups; that is, assemblages are nested in a hierarchical fashion (table 5; see also Cornell 1986; Schoener 1986b).

Zhakov (1974) also noted a continuum of species richness and composition, with the same five core species being ubiquitous in richer assemblages; he also described a regular pattern of species loss. Zhakov interpreted this as a form of succession, "regular transformations of certain ichthyocoenoses into others," and he believed that "this process is accompanied by reduction in the number of species and a continuously increasing degree of co-adaptation of species to each other" (1974, p. 213).

Alternatively, the continuum can be viewed in terms of the regional and historical process first outlined by Nordqvist (1903), in which nearly all species present in the fauna gained access to small lake basins at the time of Ancylus Lake. As climatic and limnological conditions changed within individual basins, more sensitive species emigrated or perished. In this view, the current ordered richness gradient reflects a gradient of species tolerance to the filtering effect of progressively deteriorating environments of small, isolated forest lakes, compared with conditions in earlier large lakes. Likely factors contributing to this deterioration include the increased acidity and decreased habitat complexity that develop as a floating bog mat encircles the shoreline (Rahel 1984) and the increased probability of winterkill as organic matter accumulates and depth decreases (Tonn and Mag-

nuson 1982). Thus, environmentally induced extinction, augmented by recolonization in less isolated lakes, is proposed as the primary ecological process behind the observed presence-absence continuum in Finland.

In contrast, less regular and consistent patterns of occurrence sequences for Wisconsin fishes suggest that distinct groups of species are more specialized for specific lake environments and/or that biological interactions within or among these groups are important in determining species' presence or absence. The negative co-occurrences, involving small-bodied, soft-rayed fishes and either piscivores or other large-bodied, spiny-rayed species associated with piscivores, are also consistent with the existence of discrete assemblage types in Wisconsin and suggest the importance of predation in determining species composition (Tonn and Magnuson 1982; Rahel 1984; Magnuson et al., in press). We believe that a major reason for differences between Wisconsin and Finland in community-level patterns on the scale of species' presence or absence is the ability of North American piscivores to exclude many small prey species, for example, central mudminnow, northern redbelly dace, and others (see also Tonn and Paszkowski 1986; Robinson and Tonn 1989). In contrast, predators and prey coexist in Finland, at least in part because most soft-rayed species in northern Europe, including cyprinids, resemble white suckers in Wisconsin in that they can grow large enough to acquire a size refuge from predation (Tonn et al. 1989).

Biotic interactions can also be important in structuring Finnish assemblages, but on the scale of relative abundance rather than presence or absence. In most lakes where roach was dominant, perch populations were much reduced, often making up less than 10% of total biomass. Competition is the primary mechanism behind the frequent dominance by roach in more productive lakes (Sumari 1971; Persson 1986). Roach is a more efficient planktivore than is perch; in addition, blue-green algae and detritus serve as exclusive resources for roach (Persson 1983, 1987). Both factors give roach a competitive advantage where these resources are relatively abundant. In contrast, perch lakes were more isolated, more acidic, smaller, and lower in conductivity than were lakes dominated by roach. Many perch lakes, in fact, contained only perch or perch and pike, with low pH apparently acting as an effective filter against cyprinids such as roach (Overrein et al. 1981). Environmental characteristics of particular lakes may modify or override biotic interactions and thus have broader, assemblage-wide consequences (Persson et al. 1988).

Isolated, small, and shallow lakes dominated by crucian carp were environmentally most distinct. This type of lake frequently experiences severe winter hypoxia and therefore offers an unfavorable environment to most fishes. However, crucian carp are physiologically well adapted for surviving winter hypoxia (Holopainen and Hyvärinen 1985; Hyvärinen et al. 1985; Piironen and Holopainen 1986) and frequently attain high densities in these severe and depauperate lakes (Holopainen and Pitkänen 1985). In benign lakes with richer assemblages, only sparse populations of large crucian carp occur (table 7; Hamrin 1979; Piironen and Holopainen 1988) as a result of predation and/or interspecific competition (Svärdson 1976; Tonn et al. 1989). The availability of a body-size refuge to many Finnish species,

together with their use of structural refuges (Holopainen et al. 1988), may prevent complete exclusion of prey species from lakes containing piscivores.

Intercontinental Comparisons of Assemblage-Environment Relations

Because of strong and similar relations between local environmental factors and the composition of local assemblages in both regions, we were able to make and successfully test intercontinental predictions of fish assemblage type. This ability, using assemblage types of largely unrelated species, is ecologically significant (Orians and Paine 1983), suggesting that some of these intercontinental relations reflect similar operations of local biotic or abiotic processes.

The combination of winter hypoxia and lake isolation prevents most species from establishing and maintaining populations in mudminnow and crucian carp lakes. Despite phylogenetic and morphological differences, both central mudminnows (Umbridae) and crucian carp (Cyprinidae) have developed ways of surviving this type of environmental severity (Gee 1981; Magnuson et al. 1983; Holopainen and Hyvärinen 1985). However, both species also are vulnerable to biotic interactions such as size-limited predation (more so for mudminnows) and enjoy their greatest success in single-species lakes (Tonn 1985; Tonn and Paszkowski 1986; Paszkowski et al. 1989).

Somewhat less similar ecologically are the component species and organizing processes of bass (Wisconsin) and perch (Finland) assemblages. Abiotic factors (primarily low levels of pH, nutrients, and structural diversity, combined with high isolation) exclude several species, creating fundamental assemblages for these environments that can then be shaped further into realized assemblages by biotic interactions. The environmental filter is especially effective in perch lakes (mean richness, 2.7 species), restricting the establishment of cyprinids and often leaving only the physiologically tolerant and ecologically generalized perch and, to a lesser extent, pike to dominate the assemblages (Rask and Arvola 1985). Low pH also restricts cyprinids from many bass lakes (Rahel 1984), but even where the environment is more benign, predation by largemouth bass can prevent the establishment of these and other small species (Carpenter et al. 1987). Other core species of bass assemblages, yellow perch and bluegill, are physiologically tolerant, are ecologically generalized, and have morphologies that reduce vulnerability to predation by piscivores (Wahl and Stein 1988; Robinson 1989). With the exception of perch, the regional absence of species having all three of these characteristics in Finland may contribute to the lower average richness of perch assemblages in comparison with bass assemblages.

Most dissimilar ecologically are pike (Wisconsin) and roach (Finland) assemblages. Lakes of these two types are the largest, least isolated, least acidic, and probably most productive of the study lakes; their environmental filters should be more porous than those of other lake types, and it is unlikely that many species are excluded at this level. In roach lakes, predators are also unable to exclude or even regulate many prey populations (Persson et al. 1988); a large proportion of the fish biomass in these assemblages is composed of the competitively dominant roach. It is not clear, however, to what extent the competitive dominance by

roach results in the exclusion of other species. In contrast, predation is most likely responsible for the absence of most minnows and other small-bodied species in pike assemblages in Wisconsin (Tonn and Magnuson 1982). Thus, although local environments are similar in both regions and associated with distinct assemblage types, dominant species in each region are ecologically different and influence assemblages via different processes. Historical factors responsible for the presence of large-bodied cyprinids in Finland and small-bodied species in Wisconsin appear important in the ecological differences observed between analogous assemblage types.

<center>CONCLUSIONS</center>

Our comparative, multiple-scale approach allowed us to examine important questions not typically amenable to investigation by manipulative methods. By employing intercontinental comparisons of fish assemblages from historically distinct faunas occurring in environmentally similar local environments, we were also able to expand the geographical and historical scope of our investigation and assess the relative roles of local and regional processes (Ricklefs 1987). From complementary multivariate analyses, we were able to extract overall structural patterns from the community data sets; by relating these patterns to our multivariate analyses of the lakes' environmental features, we were then able to generate hypotheses and initiate the ecological interpretation of the community-level patterns. A series of analyses of lower-level phenomena—for example, the distribution of individual species, the co-occurrence of species pairs, and the accumulation of species among individual lakes—aided our interpretation, strengthened our hypotheses, and identified processes that contribute to community-level patterns. Some of these process-oriented hypotheses, associated with lower-level phenomena, are amenable to direct, experimental testing (Tonn and Paszkowski 1986; Tonn et al. 1989). However, we stress that, although many community-level patterns may be interpreted in terms of the population- and individual-level processes of autecology, it is unlikely that autecological studies will actually discover such patterns. And without studies of large-scale phenomena, it is difficult to draw useful generalizations from even a large number of microecological manipulations (Brown and Maurer 1989). A balanced, complementary approach is called for.

An outcome of this approach is our view that local fish assemblages in small forest lakes are products of a series of filters that operate, along with unique or unpredictable events, on several spatial and temporal scales (fig. 4; see also Simpson 1953; Smith and Powell 1971; Holmes 1986; Tonn 1990). Higher levels of biological organization act as filters, with only a portion of the properties passing through and influencing lower levels. Although these larger-scale filters directly affect characteristics at the adjacent lower level, they also can influence levels farther down by determining which species are available to enter subsequent filters.

Local assemblages are immediate products of local and contemporary processes, but if effects of regional and historical filters are strong, then the impact of
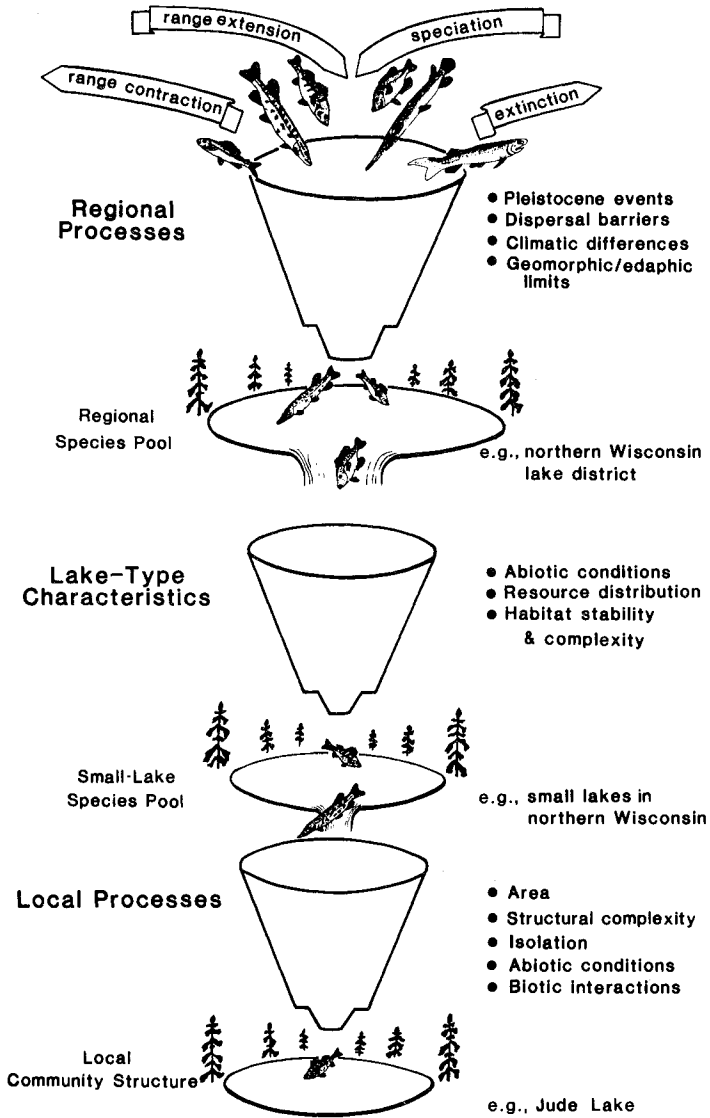
Fig. 4.—Conceptual model of the origin and maintenance of fish assemblages in small forest lakes, illustrating the effects of filters operating on faunal characteristics and community structure on different spatial and temporal scales. Modified from Tonn 1990.

these larger-scale factors on aspects of individual assemblages can be significant (Holmes 1986; Ricklefs 1987). Whether a trait like local community structure is similar or different in two regions depends not only on the match of local phenomena but also on the relative effects (e.g., "pore size" or "selectivity") of larger-scale filters. Similarities and differences between fish assemblages in small forest lakes of Finland and Wisconsin reflect similarities and differences of local and

regional filters, that is, the lakes in which the assemblages occur and the faunas from which they are derived.

SUMMARY

We compared characteristics of fish assemblages from Finland and northern Wisconsin on several scales to investigate community-level similarity in environmentally similar but faunistically different small lakes. Although Finland has only half as many fishes in its regional species pool, local species richness did not differ between the two regions. Variability in species composition among assemblages was lower in Finland, suggesting that a large proportion of the fauna could maintain populations across a broad range of environmental conditions, whereas the Wisconsin fauna was composed of more specialized species. Three types of fish assemblages were identified in Wisconsin based on species' presence or absence, whereas on the same scale, Finnish assemblages presented a hierarchical continuum based on species addition. These and other patterns suggest that habitat specialization and the exclusion of small prey species from lakes with piscivores contribute to the occurrence of presence-absence assemblage types in Wisconsin. Biotic interactions can affect population densities of Finnish species without exclusion, and assemblage types could be identified in Finland only on the basis of species' relative abundance. Finnish assemblages dominated by perch, roach, and crucian carp occurred in lakes that were environmentally similar to lakes in Wisconsin with bass, pike, and mudminnow assemblages, respectively. Because of these similar relations, discriminant functions from one region could successfully identify the assemblage types that occurred in lakes from the other region; this community-level predictability suggests that fish assemblage structures in northern forest lakes are influenced by common sets of environmental factors. Similarities and differences on different scales reflect the balance between local and regional processes; although local characteristics are well matched between regions, many regional and historical phenomena are dissimilar. Because of influences operating on several scales, viewed as a series of filters, community ecologists should not be content with simple acceptance or rejection of the convergence hypothesis. Greater understanding of communities will come from comprehensive studies that encompass a hierarchy of causes and effects.

APPENDIX A

FISH SPECIES FOUND IN 113 SMALL FOREST LAKES IN FINLAND AND IN 51 LAKES IN NORTHERN WISCONSIN

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

* Single individuals of four additional species thought not to be reproducing residents were caught but not included in the species list: grass pickerel, *Esox americanus vermiculatus* Lesueur; muskellunge, *Esox masquinongy* Mitchill; walleye, *Stizostedion vitreum vitreum* (Mitchill); and mottled sculpin, *Cottus bairdi* Girard.

APPENDIX B

DETERMINATION OF THE INDEX OF ISOLATION

To calculate this index, used in assessing the degree of insularity of each study lake, one of two formulas was used:

$$\text{for drainage lakes: } I = G ,$$

$$\text{for seepage lakes: } I = G + 3A + 90 ,$$

where I is the index of isolation, G is the vertical gradient (m km^{-1}) along a watercourse from the study lake to the next lake downstream, and A is the total altitudinal distance from the study lake to the nearest body of water (lentic or lotic) in the downstream direction. A is nearly always the difference in altitude between the study lake and the downslope water body; however, in a few complex landscapes, topographical irregularities were added to the vertical distances.

The vertical gradient or slope of the stream connecting two lakes is a simple but appropriate ecological yardstick of isolation for an upstream lake, measuring the difference in habitat that a stream would present to a lake-dwelling fish, thus creating a larger or smaller barrier to colonization. For study lakes lacking outlet streams directly connecting them to downstream sources, total vertical distance to the nearest downslope water body should be biogeographically more important than slope when considering past changes in water levels and/or postglacial isostatic rebound of land (Nordqvist 1903; Svärdson 1970). The term $3A + 90$ was used to weight this overland portion relative to any portion that was along a watercourse. To put A, which ranges from 0 to 30, on the same scale as G (0–90), A was multiplied by 3. We added 90 to the $3A$ term because we believed that the least isolated seepage lake ($A = 0$) is at least as ecologically isolated for fishes as the most isolated drainage lake ($G = 90$). The scaling factor $3A + 90$ was also appropriate for Wisconsin seepage lakes since, for all drainage lakes, $G < 90$.

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