

SPATIAL VARIATION IN FISH ASSEMBLAGES ACROSS A BEAVER-INFLUENCED SUCCESSIONAL LANDSCAPE

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Abstract. Beavers are increasingly viewed as “ecological engineers,” having broad effects on physical, chemical, and biological attributes of north-temperate landscapes. We examine the influence of both local successional processes associated with beaver activity and regional geomorphic boundaries on spatial variation in fish assemblages along the Kabetogama Peninsula in Voyageurs National Park, northern Minnesota, USA. Fish abundance and species richness exhibited considerable variation among drainages along the peninsula. Geological barriers to fish dispersal at outlets of some drainages has reduced fish abundance and species richness. Fish abundance and species richness also varied within drainages among local environments associated with beaver pond succession. Fish abundance was higher in upland ponds than in lowland ponds, collapsed ponds, or streams, whereas species richness was highest in collapsed ponds and streams. Cluster analyses based on fish abundance at sites classified according to successional environment indicated that four species (northern redbelly dace, *Phoxinus eos*; brook stickleback, *Culaea inconstans*; finescale dace, *P. neogaeus*; and fathead minnow, *Pimephales promelas*), were predominant in all successional environments. Several less abundant species were added in collapsed ponds and streams, with smaller size classes of large lake species (e.g., black crappie, *Pomoxis nigromaculatus*; smallmouth bass, *Micropterus dolomieu*; yellow perch, *Perca flavescens*; and burbot, *Lota lota*) being a component of these less abundant species. The addition of smaller size classes of large lake species indicates that dispersal of early life-history stages from Kabetogama Lake played a role in determining the species richness and composition of less abundant species in successional environments on the peninsula. Furthermore, collapsed-pond and stream environments closer to Kabetogama Lake had higher species richness than similar successional sites located farther from the lake. Cluster analyses based on fish abundance at sites classified according to drainage indicated that species composition among drainages was influenced both by the presence or absence of geological barriers to fish dispersal and the nonrandom distribution of collapsed ponds and streams. Based on these results, we present a hierarchical conceptual model suggesting how geomorphic boundaries and beaver pond succession interact to influence fish assemblage attributes. The presence of a productive and diverse fish assemblage in headwater streams of north-temperate areas requires the entire spatial and temporal mosaic of successional habitats associated with beaver activity, including those due to the creation and abandonment of beaver ponds. The ultimate impact of the local successional mosaic on fishes, however, will be strongly influenced by the regional geomorphic context in which the mosaic occurs.

Key words: beavers; boundary effects; Castor canadensis; dispersal; fish assemblages; landscape; Minnesota; pond succession; spatial hierarchy; spatial scale; successional mosaic; Voyageurs National Park, Minnesota (USA).

INTRODUCTION

A fundamental shift has occurred in ecology, incorporating a broader geographic perspective (Brown 1987, Wiens 1989, Gilpin and Hanski 1991, Hanski and Gilpin 1997). Ecologists are increasingly examining spatial and temporal variation to understand how different processes become important in determining population dynamics, species interactions, and assemblage structure as ecosystems are viewed over hierar-

chically structured and scale-dependent levels of variation and complexity (Allen and Starr 1982, Naveh and Lieberman 1984). As different levels in the environmental hierarchy are transcended, variation in dispersal and invasion can affect population sizes, demography, and coadaptation, as well as food webs and assemblage structures (Tonn et al. 1990, Endler 1991). Furthermore, these hierarchies frequently occur within landscape mosaics that are normally characterized by dynamic successional patch structure (Pickett and White 1985, Chesson and Huntly 1997, Wiens 1997). Patch quality, connectivity, context, and boundary characteristics are, in turn, thought to have profound

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influences on dispersal and subsequent food web interactions (Pickett and White 1985, Wiens 1997). Consequently, a fundamental objective for ecology must be to understand how hierarchically dependent attributes of environmental variation interact to influence population dynamics and assemblage attributes in the context of landscape succession (Hanski and Simberloff 1997).

Modification of aquatic ecosystems by beaver has resulted in a shifting successional mosaic of aquatic patches embedded within the larger regional landscape (Johnston and Naiman 1987, 1990, Naiman et al. 1988, Pastor et al. 1993, Johnston 1995, Snodgrass 1997, Schlosser 1998, Schlosser et al. 1998, Snodgrass and Meffe 1998). Since beaver ponds are created and maintained by living organisms, they are temporally dynamic, as stream reaches are colonized, flooded, and eventually abandoned by beaver. This results in both a spatial and temporal mosaic of aquatic patches on the landscape, including ponds, collapsed ponds, and streams (Naiman et al. 1988). Additional complexity occurs when these aquatic environments are placed in the context of the larger drainage network. Variation in valley shape, for instance, has a strong influence on pond morphology, creating either deep, narrow "upland" ponds in constrained valleys or broad, shallow "lowland" ponds in unconstrained reaches (Johnston and Naiman 1987). Spatial context within the longitudinal drainage network can also influence the magnitude of hydrologic fluxes through the ponds, and their spatial proximity to more stable aquatic ecosystems downstream, both of which are likely to impact dispersal and exchange processes. (Schlosser 1987, 1995a, b, Osborne and Wiley 1992). Finally, considerable temporal variation occurs in most north-temperate aquatic environments, associated with seasonal and annual variation in temperature and oxygen, with the potential for oxygen depletion being particularly severe in small, organically rich ponds and lakes in north-temperate areas (Tonn and Magnuson 1982, Rahel 1984, Johnston and Naiman 1987, Magnuson et al. 1989, Schlosser et al. 1998).

Previous studies of fish assemblages in small lakes suggest a combination of factors interact to control fish assemblage attributes. In particular, the number, identity, and relative abundance of fish species in small lakes can be viewed as the product of a series of "filters" ranging from continental to local spatial scales (Tonn 1990, Tonn et al. 1990). At regional scales, critical filtering processes include the influence of watershed boundaries and geomorphic barriers on fish dispersal and colonization (Tonn 1990, Angermeier and Winston 1998). At local scales, the presence or absence of essential physical habitats, and the frequency and severity of harsh chemical conditions, especially hypoxia in winter, appear to be critical filtering processes determining species composition and the subsequent nature of biotic interactions (Tonn and Magnuson 1982,

Rahel 1984, Magnuson et al. 1989, Tonn 1990, Tonn et al. 1990, Magnuson et al. 1998).

Our objective was to assess how the shifting successional mosaic of local aquatic habitat patches created by beaver influences the number, identity, and relative abundance of fish species and place this in the context of processes operating at the spatial scale of drainage basins. Specifically, we first examine variation in fish abundance and species richness among drainages along the Kabetogama Peninsula in Voyageurs National Park in northern Minnesota, USA. We then explore how this variation relates to successional stages associated with beaver activity. Lastly, we examine how species composition of fish assemblages varies among successional environments and drainages.

STUDY AREA

The study was conducted along the 294-km² Kabetogama Peninsula in Voyageurs National Park. Glacial activity 10 000–12 000 yr BP created three large lakes surrounding the peninsula; Rainy Lake to the north, Namakan Lake to the east, and Kabetogama Lake to the south. Numerous drainages located along the southern edge of the Kabetogama Peninsula enter into Kabetogama Lake, ranging from Locator and Sucker Creek in the far northwest to Shoepack and East Shoepack in the southeast (Schlosser et al. 1998: Fig. 1). Two drainages located in the middle of the peninsula have potential barriers to fish movement between them and Kabetogama Lake. Clyde Creek exhibits a 5–10 m drop in elevation near Kabetogama Lake, associated with a series of small (0.5–1 m) boulder and bedrock waterfalls. A 1.5–2 m bedrock waterfall is also located at the outlet of the West Lost Ponds drainage. Since the early part of this century, increased beaver activity on the peninsula has transformed the >300 km of existing stream channel within the drainages (Naiman et al. 1988). Modification of the aquatic ecosystem by beaver has resulted in a spatial and temporal mosaic of habitats associated with age, stage of succession, and local environment of beaver ponds (Johnston and Naiman 1987, Naiman et al. 1988).

METHODS AND MATERIALS

Fish sampling

Fish were sampled at 23 sites in 12 drainages along the southern edge of the Kabetogama Peninsula (see Appendix A for a list of fish species). The drainages spanned 20–25 km along the peninsula, and the sites included all types of environments associated with beaver pond succession. The distribution of successional sites among drainages was dictated by their natural distribution on the landscape. Consequently, we could not achieve a fully balanced sampling design where all combinations of successional environments were sampled in replicate in the different drainages. However, our sampling approach did allow us to assess how the

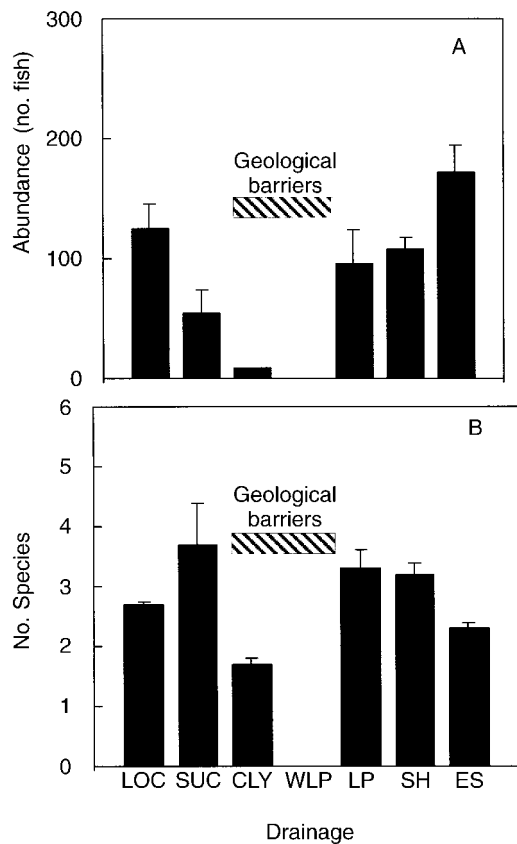


FIG. 1. (A) Total fish abundance and (B) species richness per minnow trap for the seven primary drainages along the Kabetogama Peninsula. Drainage basins are consecutively listed from northwest to southeast on the peninsula and include Locator (LOC), Sucker Creek (SUC), Clyde Creek (CLY), West Lost Ponds (WLP), Lost Ponds (LP), Shoepack (SH), and East Shoepack (ES). Histogram height is the mean, and vertical bar is 1 SE. Note that geological barriers occur at the outlets of Clyde Creek and West Lost Ponds.

natural distribution of successional environments impacted spatial variation in fish assemblages among drainages.

Each site was sampled once per year between mid-May and late July. Since the primary focus of the study was spatial variation in assemblage attributes, time of sampling was randomized within and between drainages to avoid bias due to site-by-time interactions. Most sites were sampled for three years (1993–1995), but two drainages (Clyde Creek and West Lost Ponds) were only sampled twice, because the presence of geological barriers on these drainages resulted in the absence of fish from West Lost Ponds and greatly reduced fish abundance in Clyde Creek. One successional site (East Deer Creek) was only sampled for one year because of logistical difficulty in returning to this location. Since geological barriers had such a strong influence on fish abundance and species richness in Clyde Creek and West Lost Ponds, we did not include the four sites in these drainages in the analysis of successional envi-

ronments. Instead, we sampled five additional sites to assure adequate representation of all environments associated with beaver pond succession.

Twelve unbaited Gee's minnow traps (40 × 19 cm, 2.5-cm opening, 0.5-cm mesh) were sampled for three days at each site. We restricted our sampling to the use of minnow traps for two reasons. First, it allowed standardization of sampling effort between sites that differed dramatically in size, spatial complexity, and ease of sampling with other gear. Second, many sites were extremely remote with difficult access, curtailing our use of more cumbersome sampling gear. Trapping effort among sites was standardized based on total shoreline length sampled, with approximately 100–150 m of shoreline sampled at each site. Sampling in pond and collapsed-pond environments was restricted to littoral regions, since previous research indicated the vast majority (>90–95%) of all fish were captured in littoral regions and no new species were added when minnow traps were suspended in pelagic zones (He and Lodge 1990, Schlosser et al. 1998; I. J. Schlosser, *unpublished data*). Most fish were identified in the field, and a subsample of up to 300 fish of each species measured for total length and returned to the water. Based on total number of fish captured, a catch-per-unit-effort (CPUE, number captured per trap per day) was calculated for each species, site and year. Since hybrids of northern redbelly dace and finescale dace were present in some drainages (Schlosser et al. 1998), a random sample of up to 250–300 dace was collected at each site and categorized as redbelly, finescale, and hybrids, using pharyngeal tooth counts and intestinal morphology (Elder and Schlosser 1995, Schlosser et al. 1998). Based on the total number of dace captured and the frequency of the three biotypes in the subsample, a CPUE was calculated for each species and the hybrids. Since the distribution and abundance of hybrids have been previously discussed in detail (Schlosser et al. 1998), they will not be discussed further. Hybrids have, however, been included in our estimates of total fish abundance.

Classification of sites according to successional stage

Twenty-one of the 23 sites could be classified into one of five successional environments based on physical–chemical characteristics, including upland ponds, lowland ponds, collapsed ponds with partially rebuilt dams, completely collapsed ponds, and streams (Appendix B). The latter three types of environments were easily classified based on their unique morphological characteristics. Streams were free-flowing reaches with no remnants of a beaver dam and no pooling of water out of the stream channel. Completely collapsed ponds were areas where the remnants of a dam were still present and water was partially ponded behind the dam, but at least part of the dam was fully breached and water was freely flowing through the breached area. Collapsed ponds with partially rebuilt dams were those

TABLE 1. Mean catch-per-unit-effort (number per trap per day) for the 16 species captured in the seven primary drainages sampled over a three-year (1993–1995) period along the Kabetogama Peninsula in Voyageurs National Park, Minnesota, USA.

Species	Drainage						
	Locator	Sucker	Clyde	West Lost	Lost Ponds	Shoepack	East Shoe
RED	62.3	19.3	38.1	32.1	141.2
FINE	6.5	9.9	6.0	9.0	9.6
FAT	0.3	2.2	10.1	5.3	17.7
BROOK	43.2	9.3	29.0	41.8	...
MUD	...	1.2	3.6
PEARL	...	0.8	4.2
GOLD	...	0.3
BRASS	...	3.1
BLACK	0.4
IOWA	0.4
JOHN
WHITE	...	<0.1
SMALL
CRAP
PERCH
BURBOT	...	<0.1
Total fish	115.3	46.1	8.3	...	78.3	88.2	168.6
Total species	4	10	4	0	4	4	3

Notes: species abbreviations are as follows: RED, northern redbelly dace (*Phoxinus eos*); FINE, finescale dace (*Phoxinus neogaeus*); FAT, fathead minnow (*Pimephales promelas*); BRASS, brassy minnow (*Hybognathus hankinsoni*); PEARL, pearl dace (*Semotilus margarita*); GOLD, golden shiner (*Notemigonus crysoleucas*); BLACK, blacknose shiner (*Notropis heterolepis*); BROOK, brook stickleback (*Culaea inconstans*); MUD, central mudminnow (*Umbra limi*); BURBOT, burbot (*Lota lota*); WHITE, white sucker (*Catostomus commersoni*); SMALL, smallmouth bass (*Micropterus dolomieu*); CRAP, black crappie (*Pomoxis nigromaculatus*); PERCH, yellow perch (*Perca flavescens*); IOWA, Iowa darter (*Etheostoma exile*); JOHN, Johnny darter (*Etheostoma nigrum*).

areas where the dam had been previously breached but had been partially rebuilt by beaver, so that pool behind the dam was deeper than in a fully collapsed pond, and there was no breached area with free-flowing water.

Segregation of upland and lowland ponds required a more objective and quantitative approach. As described by Johnston and Naiman (1987), upland ponds are located in the upper reaches of drainages on the Kabetogama Peninsula and are created by short dams in incised valleys, resulting in narrow but potentially deep ponds. In contrast, lowland ponds are created by long dams placed across broader and flatter reaches of valley drainages, creating wider and potentially shallower ponds. Based on these morphological differences one would also expect upland and lowland ponds to exhibit different patterns of oxygen profiles, since the relative surface area of water exposed to organically rich pond bottoms would be higher in lowland than upland ponds. In light of these expected differences in upland and lowland ponds, we used six physical–chemical characteristics to quantitatively separate ponds into upland and lowland environments, including: (1) distance between the pond and Kabetogama Lake, (2) dam length, (3) mean pond depth, (4) maximum pond depth, (5) maximum dissolved oxygen, and (6) water depth at which the pond becomes hypoxic (<1.0 mg/L O₂). Of the six variables, numbers 1–4 were only measured once, while 5–6 were based on means over three years of sampling. A hierarchical cluster analysis using standardized data, a Euclidean distance metric, and single

linkage (nearest neighbor) clustering technique (SPSS 1996) clearly distinguished two different clusters, representing upland and lowland ponds (I. J. Schlosser and L. Kallemeyn, unpublished data).

Two of the 23 sites could not be effectively classified according to successional stage (Appendix B). These two sites were relatively small and recently constructed ponds with standing timber present in the water. These sites were included in the analysis of differences in fish assemblages among drainages, but were not included in the analysis of successional environments.

Statistical analyses

Because the primary objective of our analysis was to evaluate spatial variation in fish assemblages, sites represented the individual replicate in all analyses, and species richness and fish abundance for each site was based on mean values calculated from the three years of sampling. Species richness and total fish abundance across drainages and among successional sites were compared using a one-way ANOVA on log₁₀-transformed data, with the relatively conservative Tukey's multiple comparison follow-up test. To assess the influence that distance from Kabetogama Lake had on species richness in collapsed ponds and streams, we ranked correlated species richness with their distance from the lake. Hierarchical cluster analyses, using fish abundance data standardized with z scores, a Euclidean distance metric, and single linkage (nearest neighbor) technique, were used to separately cluster drainages,

successional environments, and species. We also simultaneously clustered species within drainages and species within successional environments. In the species-by-drainage and species-by-successional environment analyses, rows and columns in the data matrices were permuted according to the algorithm in Gruvaeus and Wainer (1972). All statistical analyses were performed using SYSTAT version 6.0 for Windows (SPSS 1996).

RESULTS

Fish abundance and species richness among drainages

Fish abundance varied among the seven primary drainages located along the Kabetogama Peninsula (one-way ANOVA, $F_{6,11} = 55.31$, $P < 0.001$), with primary drainages defined as those with at least two sample sites. Low abundance in the middle of the peninsula was associated with geological barriers at outlets to two drainages (Fig. 1A). No fish were present in West Lost Ponds, and fish abundance in Clyde Creek was only 5–15% of fish abundances in other drainages (Tukey's multiple comparison, $P < 0.05$). Abundance in Sucker Creek was intermediate between Clyde Creek and the rest of the drainages (Fig. 1A) but differed only from the East Shoepack drainage (Tukey's multiple comparison, $P < 0.05$). Fish abundances in Locator, Lost Ponds, Shoepack, and East Shoepack did not differ (Tukey's multiple comparison, $P > 0.05$).

Species richness per trap also differed among drainages (one way ANOVA, $F_{6,11} = 33.70$, $P < 0.001$). Once again, species richness per trap was lower in Clyde Creek and West Lost Ponds, relative to all other drainages (Tukey's multiple comparison, $P < 0.05$; Fig. 1B). Species richness per trap in Sucker Creek was the highest of all drainages but not significantly so (Tukey's multiple comparison test, $P > 0.05$). In addition, the number of species captured in Sucker Creek (10) over the three-year period was 2–3 times the number of species captured in other drainages (3–4; Table 1). The dramatic difference in species richness for mean values per trap (Fig. 1B) and total number of species captured over the three-year period (Table 1) indicates the additional species captured in Sucker Creek were relatively rare.

Fish abundance and species richness among successional environments

Total fish abundance differed among successional environments (one-way ANOVA, $F_{4,12} = 4.19$, $P < 0.05$). Abundance was nearly four times higher in upland ponds than lowland ponds (Tukey's multiple comparison, $P < 0.05$; Fig. 2A). Collapsed ponds, streams, and partially rebuilt ponds exhibited intermediate levels of abundance that did not significantly differ (Tukey's multiple comparison, $P > 0.05$).

Species richness per trap also differed among suc-

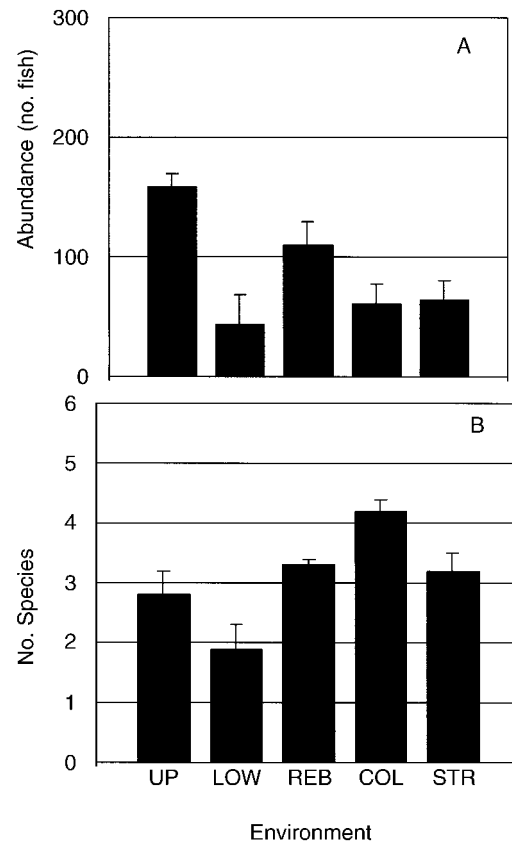


FIG. 2. (A) Total fish abundance and (B) species richness per trap for five different environments associated with beaver pond succession on the Kabetogama Peninsula, including upland ponds (UP), lowland ponds (LOW), collapsed ponds with partially rebuilt dams (REB), collapsed ponds (COL), and streams (STR). Histogram height is the mean and vertical bar is 1 SE.

cessional environments (one-way ANOVA, $F_{4,12} = 3.99$, $P < 0.05$). Mean richness was twice as high in collapsed ponds as in lowland ponds (Tukey's multiple comparison test, $P < 0.05$; Fig. 2B), with other environments exhibiting intermediate and similar species richness (Tukey's multiple comparison test, $P > 0.05$). The tendency for collapsed ponds to exhibit higher richness than upland, lowland, and partially rebuilt ponds was even greater when we compared the total number of species captured over the three-year period (Table 2). Furthermore, although the mean number of species per trap was not higher for streams compared to other environments (Fig. 2B), the total number of species in streams (13) approached that of collapsed ponds (15). The large difference in species richness per trap (Fig. 2B) and total number of species (Table 2) indicates that many of the additional species captured in collapsed ponds and streams were relatively rare.

Variation in species composition among successional environments

Four species (redbelly dace, brook stickleback, fat-head minnow, and finescale dace) were predominant in

TABLE 2. Mean catch per unit effort (number per trap per day) for the 16 species captured in five different successional environments sampled over a three-year (1993–1995) period along the Kabetogama Peninsula in Voyageurs National Park. Species abbreviations are defined in the notes to Table 1.

Species	Successional environment				
	Upland	Lowland	Rebuilt	Collapsed	Stream
RED	105.4	10.6	35.3	22.9	19.4
FINE	10.5	1.7	6.2	9.2	8.7
FAT	13.6	1.7	5.8	2.5	3.2
BROOK	21.3	25.0	39.5	12.5	16.5
MUD	...	3.2	...	1.1	<0.1
PEARL	0.4	0.3
GOLD	0.3	...
BRASS	3.9	0.2
BLACK	<0.1	...
IOWA	0.2	<0.1
JOHN	<0.1
WHITE	<0.1	0.2
SMALL	<0.1	...
CRAP	<0.1	<0.1
PERCH	0.1	0.8
BURBOT	<0.1	2.8
Total fish	150.8	42.3	87.0	53.4	52.3
Total species	4	5	4	15	13

all successional environments, so that variation in species composition among environments was due to the addition of less abundant species (Table 2). Analyses based on capture rates for all species standardized with z scores and clustered according to successional environment (Fig. 3, upper panel), species (Fig. 3, middle panel), and species by successional environment (Fig. 3, lower panel), indicated that 11 of the 12 upland, lowland, and rebuilt pond sites formed a single cluster, due to the predominance of the four widely distributed species in those environments (Fig. 3, lower panel; see also Table 2). In contrast, the stream and collapsed pond sites varied as to their clustering relative to pond sites. Two stream sites (2 and 3) clustered with pond sites due to the predominance of the same four species and absence of any rare species. However, the other two streams sites (1 and 4) and all three of the collapsed pond sites each contained relatively distinct assemblages due to the addition of less abundant species (Fig. 3, Table 2).

Species richness of streams and collapsed ponds was strongly and negatively correlated with distance from Kabetogama Lake ($r_s = -0.95$, $P < 0.01$). The most unique stream (1) and collapsed pond (1) sites in the cluster analysis (Fig. 3, upper and lower panels), and those with the largest number of rare species, were those closest to Kabetogama Lake. In contrast, stream sites 2 and 3, which lacked any rare species and clustered with pond sites (Fig. 3, lower panel), were farthest from Kabetogama Lake. Several species reproducing in lakes (e.g., black crappie, smallmouth bass, yellow perch, and burbot) were predominantly represented by smaller size classes (Fig. 4) in collapsed pond and stream environments closest to Lake Kabetogama.

Variation in species composition among drainages

In light of the role geological barriers play in influencing colonization of drainages (Fig. 1, A,B) and the difference in species richness and composition among successional environments (Table 2, Fig. 3), what pattern of variation in species composition do we see among drainage basins and what role does the spatial distribution of successional environments play in causing this variation? Analyses based on capture rates for all species standardized with z scores and clustered according to drainage (Fig. 5, upper panel), species (Fig. 5, middle panel), and drainages by species (Fig. 5, lower panel), revealed four patterns. First, species composition varied dramatically between drainages having and lacking geological barriers. West Lost Pond sites had no fish and formed a unique cluster (Fig. 5, upper panel). The two sites in Clyde Creek also formed a unique cluster that lacked the four widespread species (Table 1). The only species present in Clyde Creek were blacknose shiner, Iowa darter, central mudminnow, and pearl dace. Second, in all drainages without geological barriers, the four widespread species were predominant (Table 1). Third, variation in species composition between drainages was primarily due to the addition of several less abundant species (Table 1). Fourth, sites in Sucker Creek formed their own distinct cluster, being the only drainage with several less abundant species (Fig. 5, Table 1). Furthermore, all sites in Sucker Creek were either streams (3) or collapsed ponds (1 and 2; Appendix B), indicating the nonrandom distribution of successional sites among drainages was critical in determining among-drainage variation in species richness and composition.

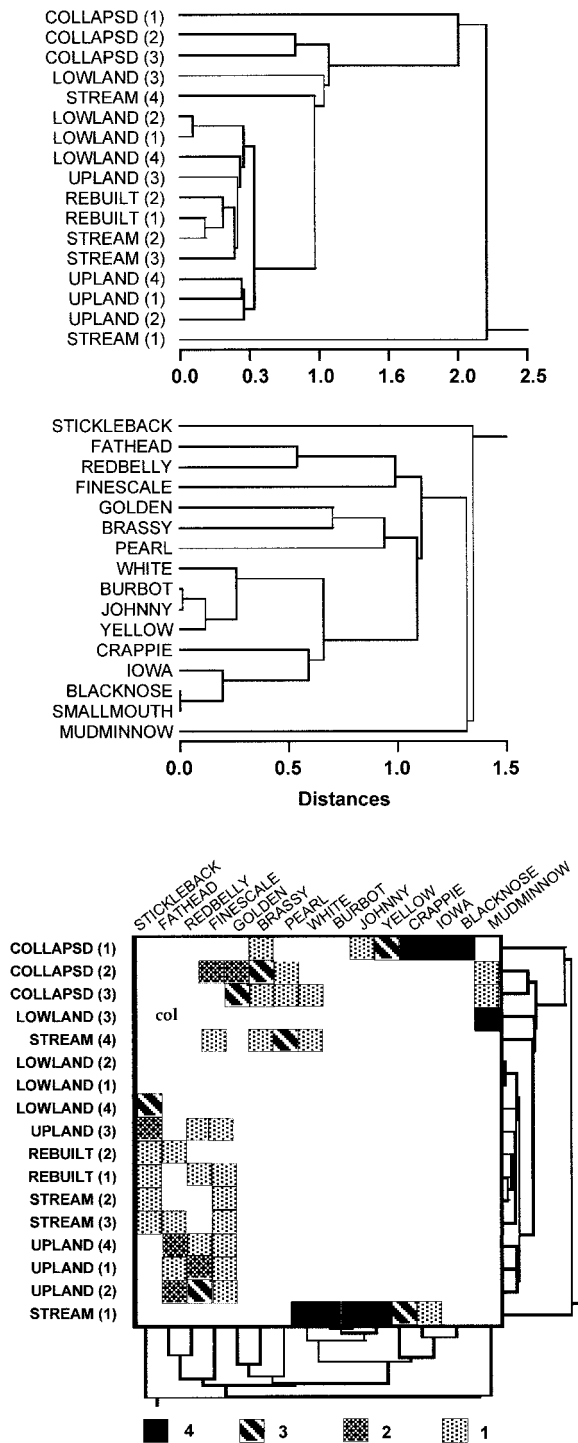


FIG. 3. Hierarchical cluster analyses of successional environments (upper panel), species (middle panel), and species by successional environments (lower panel), using standardized fish abundance data. A Euclidean distance metric was used in all analyses. Different shadings in the lower panel represent the magnitude of values in the species-by-environment matrix, and only values ≥ 1 are shown.

DISCUSSION

A fundamental challenge ecologists face is understanding how hierarchically organized attributes of environmental variation interact across spatial scales to influence dispersal and ecological success in successional landscapes (Allen and Star 1982, Pickett and White 1985, Hanski and Simberloff 1997, Weins 1997). Tonn (1990) and Tonn et al. (1990) suggest environmental filters acting across the spatial hierarchy, from the continental to the local scale, determine fish assemblage attributes in small north-temperate lakes. Our results extend their model to the uppermost reaches of north temperature drainages, where a successional mosaic associated with beaver activity is the primary factor determining the nature of local aquatic habitats within drainages. Specifically, our data indicate regional geomorphic boundaries act in conjunction with local successional environments created by beaver to strongly influence fish assemblage attributes in this landscape (Fig. 6).

Regional geomorphology is an especially important factor influencing local fish assemblages, since it controls the nature of dispersal corridors between adjacent aquatic environments (Tonn 1990, Tonn et al. 1990, Angermeier and Winston 1998). The regional landscape characterized by the Kabetogama Peninsula is the result of continental glaciation approximately 10 000–12 000 yr BP. This glaciation resulted in a regional landscape characterized by multiple drainages of variable size, juxtaposition of large lakes and small streams, and geological barriers to dispersal between surrounding lakes and peninsular streams. In turn, these geomorphic attributes strongly influence critical ecological factors determining the attributes of local fish assemblages, including the nature of hydrologic fluxes, and whether boundaries between aquatic environments are relatively open or closed to fish movement (Fig. 6).

Regional analysis of fish assemblage attributes among drainages revealed decreased fish abundance and species richness in two drainages having geomorphic barriers to fish dispersal at their outlets. This indicates that open or closed nature of geomorphic boundaries to dispersal can profoundly influence regional variation in fish assemblages (Tonn 1990, Tonn et al. 1990). Such differences in boundary permeability to fish dispersal can occur over very small spatial scales, as in West Lost Ponds (fishless) vs. Lost Ponds (with fish), whose outlets to Kabetogama Lake are only 200–300 m apart. Lastly, the regional juxtaposition of a large lake and small streams strongly influenced the composition of fish colonizing the drainages, with smaller life stages of predatory lake fishes being a component of fish assemblages in some peninsular drainages.

Within drainages, the critical local factor influencing fish assemblages was the nature of habitat succession associated with beaver activity (Fig. 6). These succes-

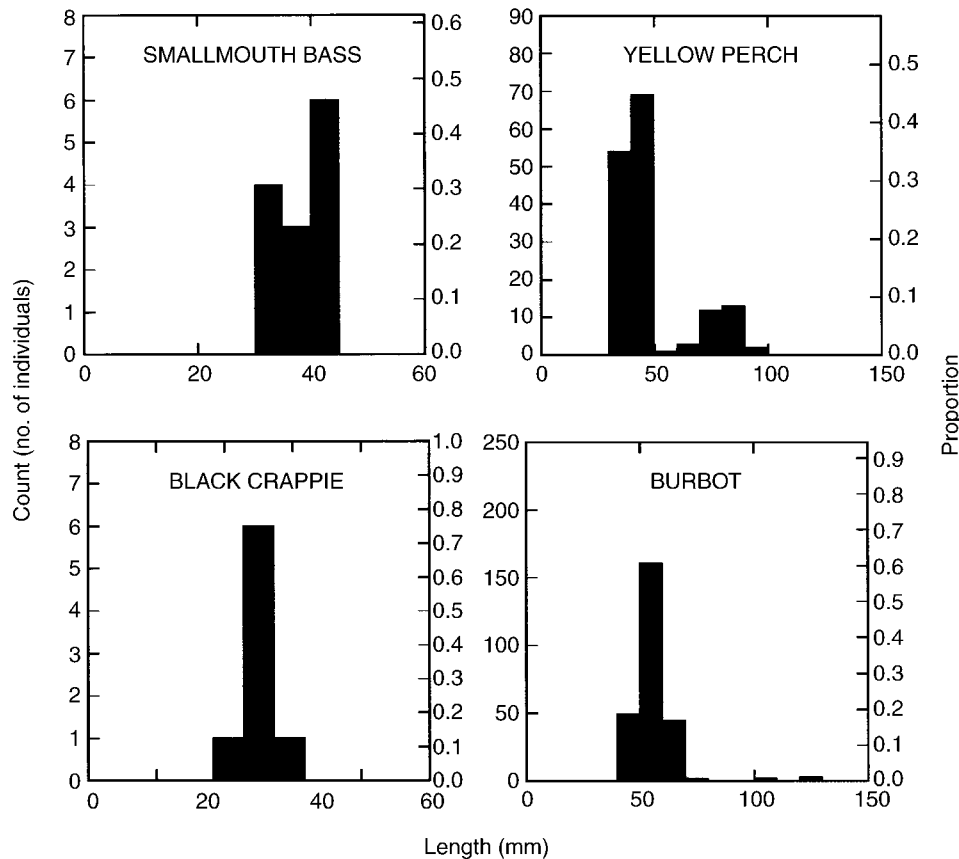


FIG. 4. Size-structure of black crappie, smallmouth bass, yellow perch, and burbot in collapsed-pond and stream environments along the Kabetogama Peninsula over the three-year sampling period.

sional processes appeared to result in a switch from relatively "closed" habitat patches, with either complete dams or partially rebuilt dams at their outlets, to relatively "open" habitat patches without intact dams. Associated with this succession, were fundamental differences in fish assemblages. Fish abundance was highest in closed environments, particularly upland ponds, whereas species richness was highest in collapsed ponds and streams. A similar pattern of species addition in collapsed ponds and streams has been documented in less intensively studied sites on the north side of the peninsula (L. Kallemeyn, *unpublished data*), suggesting that this pattern may occur throughout the region.

The presence or absence of intact beaver dams at the outlet of successional environments influences two key factors affecting fish assemblages (Fig. 6). First, intact dams will decrease the potential for fish colonization from downstream sources (Schlosser 1995a). Although beaver dams are semipermeable to water fluxes, they can be effective barriers to fish movement, especially during periods of low discharge (Schlosser 1995a). Since most recolonization of fish in small streams after extreme physical-chemical conditions (e.g., droughts, winter periods, etc.) is from downstream sources that exhibit greater environmental stability and species rich-

ness (Schlosser 1987, Osborne and Wiley 1992), the presence of downstream dams will significantly reduce the potential for colonization of peninsular drainages from Kabetogama Lake. Furthermore, our results and those of others (Magnuson et al. 1998) indicate the spatial proximity of these downstream colonization sources to successional environments will play a critical role in determining the likelihood of successful fish colonization and subsequent species richness. Size structure of less abundant species captured in collapsed pond and stream environments further supported the contention that dispersal of early life history stages of large predatory lake fishes was critical in determining species richness and species composition in successional environments. Second, beaver dams will have a dramatic impact on the rate of hydrologic exchange through the successional environments and the subsequent nature of the physical-chemical habitats available to colonizing fish (Fig. 6). The absence of intact dams in collapsed ponds and streams increases this rate, creating physical habitats associated with increased current and firm substrates. Collapsed ponds, in particular, exhibited a combination of stream and pond habitats (I. J. Schlosser, *personal observation*) and several of the less abundant species occurring in these

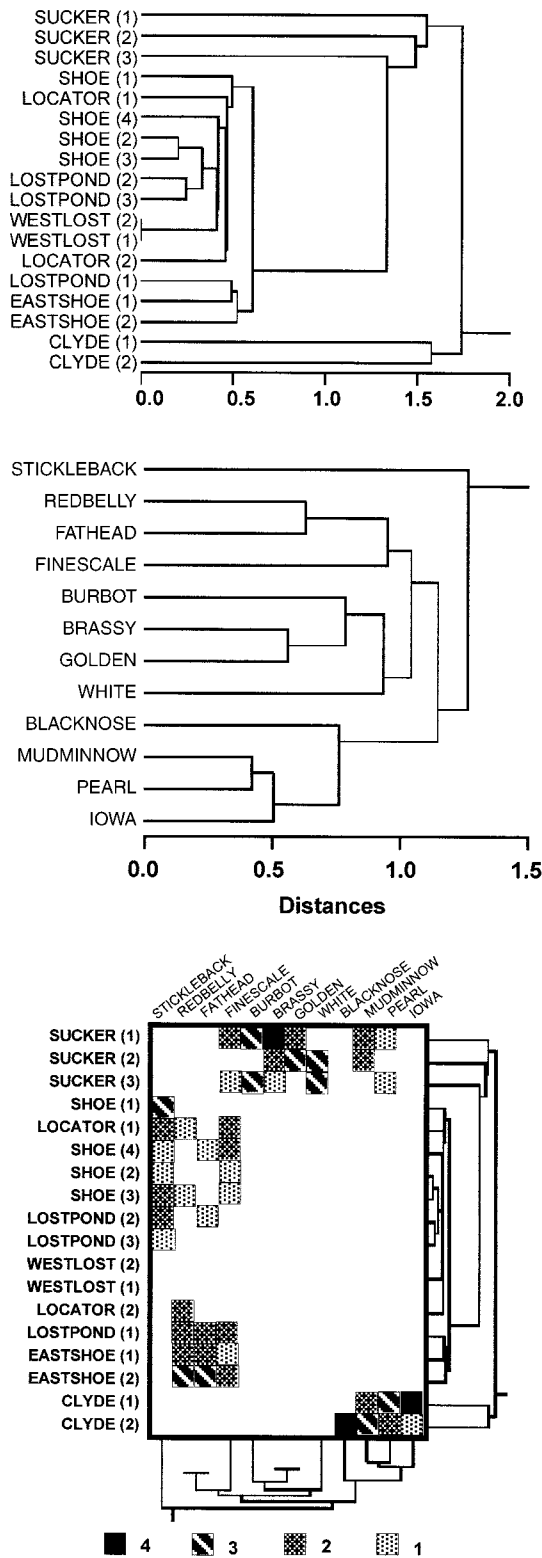


FIG. 5. Hierarchical cluster analyses of drainages (upper panel), species (middle panel), and species by drainages (lower panel), using standardized fish abundance data. A Euclidean distance metric was used in all analyses. Different shadings in the lower panel represent the magnitude of values in the species-by-drainage matrix, and only values ≥ 1 are shown.

environments, including blacknose shiners, Iowa darters, and Johnny darters, are associated with sand and gravel substrates lacking in most soft-bottomed beaver impoundments (Becker 1983).

The increased rate of hydrologic exchange in collapsed ponds or streams will also decrease the potential severity of oxygen stress during both summer (Schlosser et al. 1998, I. J. Schlosser, unpublished data) and winter (Tonn and Magnuson 1982, Magnuson et al. 1989, I. J. Schlosser, unpublished data), reducing the intensity of selection for fish tolerant to hypoxia (Fig. 6). Previous studies suggest the four predominant species occurring in ponds (redbelly dace, finescale dace, fathead minnows, and brook stickleback) are all tolerant of oxygen stress (Cooper and Washburn 1946, Gee et al. 1978, Klinger et al. 1982, Tonn and Magnuson 1982, Rahel 1984, Schlosser et al. 1998), indicating hypoxia is likely to be a particularly strong environmental filter determining fish species composition in these assemblages (Tonn and Magnuson 1982, Rahel 1984, Magnuson et al. 1989, Tonn 1990). Species less tolerant of oxygen stress (e.g., black crappie, smallmouth bass, and burbot) were only added to fish assemblages in relatively more open and highly oxygenated collapsed ponds and streams, and in drainages characterized by these environments.

The role of winter hypoxia in influencing species richness and species composition in beaver-influenced drainages undoubtedly exhibits geographic variation associated with climate. Consistent with our results, Snodgrass and Meffe (1998) observed increased species richness in streams and collapsed ponds, relative to active beaver ponds in more moderate temperate areas in the southeastern United States. However, they also observed the addition of centrarchid species and the reduction of cyprinid species over time in active beaver ponds, particularly in ponds close to downstream colonization sources. Unlike Snodgrass and Meffe (1998), we could not directly evaluate the impact of pond age on fish assemblage attributes. The absence of standing wood in virtually all of our ponds, and the historical pattern of beaver recolonization in the area, strongly suggests ponds were >20 – 25 yr old, with some as old as 35–40 yr (Naiman et al. 1988). Yet even in these very old ponds centrarchids were virtually absent. Thus, limited time for colonization was probably not what differentiated our northern Minnesota ponds from those in the southeastern United States. Rather, the absence of centrarchids in our ponds was undoubtedly due to severe oxygen stress during winter in the more extreme northern climate (Tonn and Magnuson 1982, Magnuson et al. 1989). Our limited sampling of upland ponds, lowland ponds, and partially rebuilt ponds in winter indicated virtually all of them were hypoxic, with O_2 concentrations throughout the water column being <0.4 mg/L (I. J. Schlosser, unpublished data), which is likely to be well below the O_2 tolerance of most centrarchids.

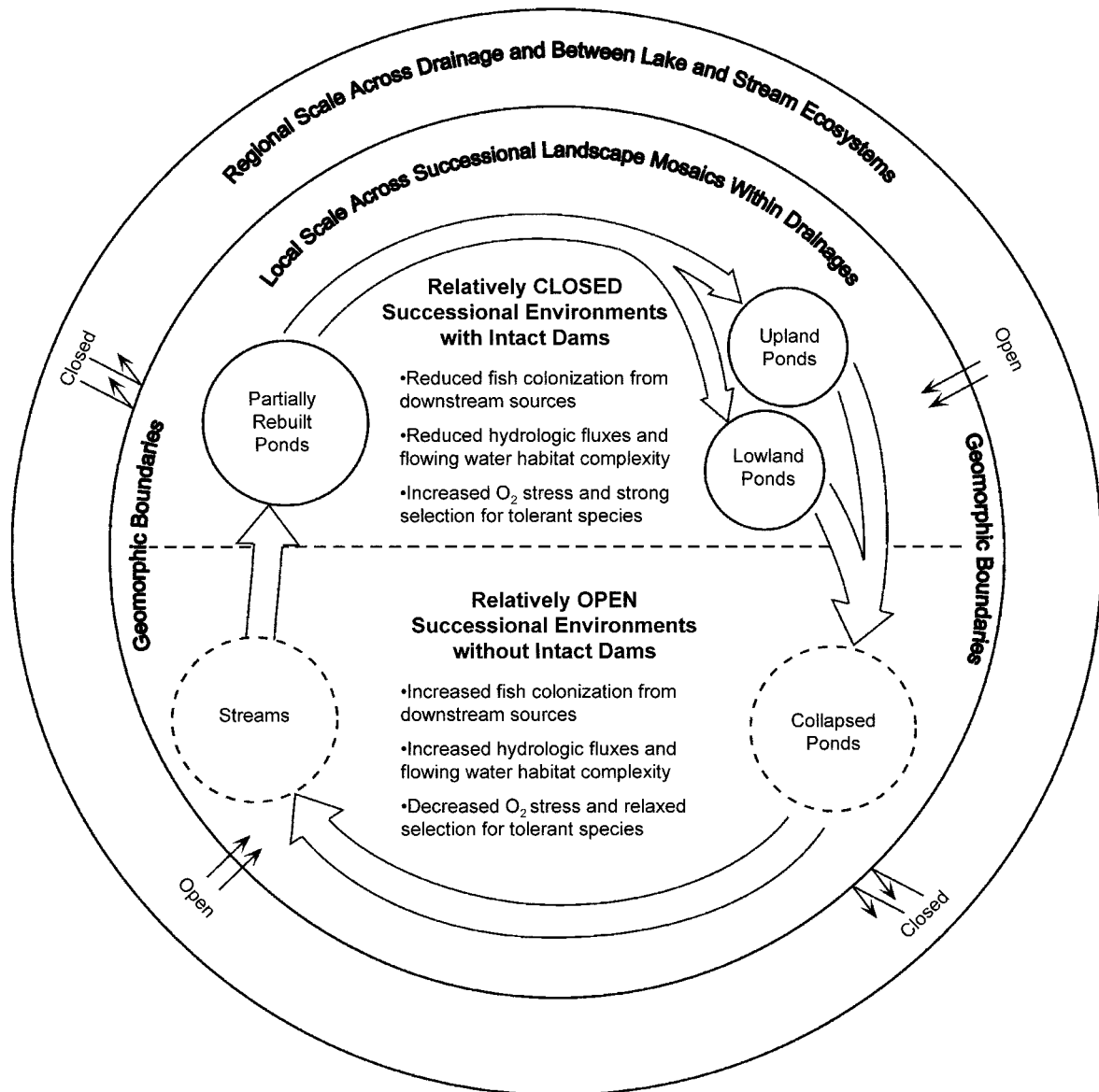


FIG. 6. Conceptual framework suggesting how regional geomorphic boundaries and local succession influence fish assemblage attributes in north-temperate landscapes modified by beaver activity.

Whether or not successional environments associated with intact beaver dams are truly closed or open will, however, be strongly influenced by their regional geomorphic and hydrologic context (Schlosser 1995a, Snodgrass 1997, Snodgrass and Meffe 1998). Drainage basin size above the ponds, subsurface geology around the ponds, and regional precipitation regime will strongly influence the magnitude of hydrological fluxes and the relative degree to which ponds are open or closed. The intensive damming of drainages along the Kabetogama Peninsula by beavers during the last 60–70 yr (Johnston and Naiman 1987, Naiman et al. 1988, Johnston and Naiman 1980), the relatively normal-to-dry precipitation regime throughout the three-year study (Na-

tional Oceanic and Atmospheric Administration, NOAA, National Weather Service Office, International Falls, Minnesota), and the poor soil drainage in the stream valleys on the Kabetogama Peninsula likely reduced the magnitude of hydrologic fluxes, accentuating the relatively closed nature of the pond environments. Other geographic areas with increased precipitation, more permeable subsurface geology, and increased hydrologic fluxes will likely exhibit relatively more open pond environments (Snodgrass and Meffe 1998).

An important question yet to be addressed is how successional processes within drainages affect fish composition among drainages? One could argue that in the absence of a balanced design, in which all suc-

cessional environments would be sampled in replicate in all drainages, we could not effectively address this question. We believe, however, that the nonrandom distribution of successional environments on the landscape is in fact of most ecological interest. A cross-classification of fish assemblage attributes for different successional sites and drainages, combined with the distribution of successional sites among drainages, suggests that there is in fact a strong and nonrandom relationship between local successional processes and regional attributes of fish assemblages along the peninsula. Locator and East Shoepack are both relatively small drainages, with primarily upland ponds, located at the extreme ends of the peninsula. These drainages were characterized by relatively high fish abundance, but low species richness compared to the other drainages. In contrast, Sucker Creek, the largest drainage located near the center of the peninsula, contained only collapsed ponds and streams. The fish assemblage in Sucker Creek was characterized by low to moderate fish abundance but high species richness. These results suggest processes operating at the regional level among drainage basins (e.g., basin size, magnitude of hydrologic fluxes, successional patterns in terrestrial vegetation, and historic patterns of beaver colonization and abandonment) have strong effects on the distribution of local successional environments among drainages and subsequent variation in fish assemblage attributes among drainages. Additional study of the interrelationships between drainage basin processes, beaver pond succession, and fish assemblage attributes, is needed to further clarify the nature of these interactions.

Finally, our results have considerable implications for the management of north-temperate landscapes if the goal is to simultaneously assure both a diverse and productive fish assemblage. Our data clearly suggest that during beaver pond succession a shift occurs from shorelines in pond environments, with potentially high fish abundance and low species richness, to shorelines in collapsed ponds and streams, with low fish abundance but high species richness. Furthermore, this conclusion is conservative since it is based on CPUE values from traps sampled over similar shoreline lengths at different successional sites. When beaver invade a regional landscape or when humans remove beaver from the landscape, they change the relative amount of shoreline length in pond vs. collapsed-pond or stream environments even more than they change the relative number of different successional environments (Naiman et al. 1988, Broschart et al. 1989). Naiman et al. (1988) estimated that shoreline length increased 13.6-fold during the reinvasion of the Kabetogama Peninsula by beaver from 1940 to 1986. Consequently, changes in fish abundance and species richness associated with increased or decreased beaver activity will be even more accentuated, when comparisons incorporate actual shoreline lengths for each environment on the land-

scape. Based on our data and those of Snodgrass and Meffe (1998) beaver ponds should substantially increase overall production of fish across the landscape. However, effects of beaver activity on species richness will be strongly influenced by the impact of succession on spatial and temporal heterogeneity in the physical-chemical environment. If a primary goal of landscape management is to assure the presence of a highly productive and diverse fish assemblage, then the entire mosaic of successional habitats associated with beaver activity needs to be preserved.

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LITERATURE CITED

- Allen, T. F. H., and T. B. Starr. 1982. *Hierarchy*. University of Chicago Press, Chicago, Illinois, USA.
- Angermeier, P. L., and M. R. Winston. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology* **79**:911–927.
- Becker, G. C. 1983. *Fishes of Wisconsin*. University of Wisconsin Press, Madison, Wisconsin.
- Broschart, M. R., C. A. Johnston, and R. J. Naiman. 1989. Prediction of beaver colony density using impounded habitat variables. *Journal of Wildlife Management* **53**:929–934.
- Brown, J. H. 1987. Variation in desert rodent guilds: patterns, processes, and scales. Pages 185–203 in J. H. R. Gee and P. S. Giller, editors. *Organization of communities, past and present*. Blackwell, Oxford, UK.
- Chesson, P., and N. Huntley. 1997. The role of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist* **150**:519–553.
- Cooper, G. P., and G. N. Washburn. 1946. Relation of dissolved oxygen to winter mortality of fish in Michigan lakes. *Transactions of the American Fisheries Society* **76**:23–33.
- Elder, J. F., and I. J. Schlosser. 1995. Extreme clonal uniformity of *Phoxinus eos/neogaeus gynogens* (Pisces: Cyprinidae) among variable habitats in northern Minnesota beaver ponds. *Proceedings of the National Academy of Sciences (USA)* **92**:5001–5005.
- Endler, J. A. 1991. Genetic heterogeneity and ecology. Pages 315–334 in R. J. Berry et al., editors. *33rd Symposium of the British Ecological Society*. Blackwell Scientific Publications, Oxford, UK.
- Gee, J. H., R. F. Tallman, and H. J. Smart. 1978. Reactions of some Great Plains fish to progressive hypoxia. *Canadian Journal of Zoology* **56**:1962–1966.
- Gilpin, M., and I. Hanski, editors. 1991. *Metapopulation dynamics: empirical and theoretical investigations*. Academic Press, London, UK.
- Gruvaeus, G., and H. Wainer. 1972. Two additions to hierarchical cluster analysis. *British Journal of Mathematical and Statistical Psychology* **25**:200–206.

- Hanski, I., and M. Gilpin, editors. 1997. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego, California, USA.
- Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application. Pages 5–26 in I. Hanski, and M. Gilpin, editors. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego, California, USA.
- He, X., and D. M. Lodge. 1990. Using minnow traps to estimate fish population size: the importance of spatial distribution and relative species abundance. *Hydrobiologia* **190**:9–14.
- Johnston, C. A. 1995. Effects of animals on landscape pattern. Pages 57–80 in L. Hansson, L. Fahrig, and G. Merriam, editors. *Mosaic landscapes and ecological processes*. Landscape ecology study series, Volume 2. Chapman and Hall, New York, New York, USA.
- Johnston, C. A., and R. J. Naiman. 1987. Boundary dynamics at the aquatic–terrestrial interface: the influence of beaver and geomorphology. *Landscape Ecology* **1**:47–57.
- Johnston, C. A., and R. J. Naiman. 1990. Aquatic patch creation in relation to beaver population trends. *Ecology* **71**:1617–1621.
- Klinger, S. A., J. J. Magnuson, and G. W. Gallep. 1982. Survival mechanisms of the central mudminnow (*Umbra limi*), fathead minnow (*Pimephales promelas*) and brook stickleback (*Culea inconstans*) for low oxygen in winter. *Environmental Biology of Fishes* **3**:7–31.
- Magnuson, J. J., C. A. Paszkowski, F. J. Rahel, and W. M. Tonn. 1989. Fish ecology in severe environments. Pages 487–515 in R. R. Sharitz and J. W. Gibbons, editors. *Freshwater wetlands and wildlife conference*. DOE Symposium Series Number 61. USDOE Office of Scientific and Technical Information, Oak Ridge, Tennessee, USA.
- Magnuson, J. J., W. M. Tonn, A. Banerjee, J. T. Toivonen, O. Sanchez, and M. Rask. 1998. Isolation versus extinction in the assembly of fishes in small northern lakes. *Ecology* **79**:941–2956.
- Naiman, R. J., C. A. Johnston, and J. C. Kelly. 1988. Alteration of North American streams by beaver. *BioScience* **38**:753–762.
- Naveh, Z., and A. S. Lieberman. 1984. *Landscape ecology: theory and application*. Springer-Verlag, New York, New York, USA.
- Osborne, L. L., and M. J. Wiley. 1992. Influence of tributary position on the structure of warmwater fish communities. *Canadian Journal of Fisheries and Aquatic Sciences* **49**:671–681.
- Pastor, J., J. Bonde, C. A. Johnston, and R. J. Naiman. 1993. A Markovian analysis of the spatially dependent dynamics of beaver ponds. Pages 5–27 in R. H. Gardner, editor. *Predicting spatial effects in ecological systems*. American Mathematical Society, Providence, Rhode Island, USA.
- Pickett, S. T. A., and P. S. White, editors. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida, USA.
- Rahel, F. J. 1984. Factors structuring fish assemblages along a bog lake successional gradient. *Ecology* **65**:1276–1289.
- Schlosser, I. J. 1987. A conceptual framework for fish communities in small warmwater streams. Pages 17–24 in W. J. Matthews and D. C. Heins, editors. *The ecology and evolution of North American stream fish communities*. University of Oklahoma Press, Norman, Oklahoma.
- Schlosser, I. J. 1995a. Dispersal, boundary processes, and trophic level interactions in streams adjacent to beaver ponds. *Ecology* **76**:908–925.
- Schlosser, I. J. 1995b. Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia* **303**:71–81.
- Schlosser, I. J. 1998. Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. *Oecologia* **113**:260–268.
- Schlosser, I. J., M. R. Doeringsfeld, J. F. Elder, Jr., and L. F. Arzayus. 1998. Niche relationships of clonal and sexual fish in a heterogeneous landscape. *Ecology* **79**:953–968.
- Snodgrass, J. W. 1997. Temporal and spatial dynamics of beaver-created patches as influenced by management practices in a south-eastern North American landscape. *Journal of Applied Ecology* **34**:1043–1056.
- Snodgrass, J. W., and G. K. Meffe. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. *Ecology* **79**:928–942.
- SPSS. 1996. SYSTAT 6.0 for Windows: Statistics. SYSTAT, Chicago, Illinois, USA.
- Tonn, W. M. 1990. Climate change and fish communities: a conceptual framework. *Transactions of the American Fisheries Society* **119**:337–352.
- Tonn, W. M., and J. J. Magnuson. 1982. Patterns in the species composition and richness of fish assemblages in northern Wisconsin lakes. *Ecology* **63**:1149–1166.
- Tonn, W. M., J. J. Magnuson, M. Rask, and J. Toivonen. 1990. Intercontinental comparison of small-lake fish assemblages: the balance between local and regional processes. *American Naturalist* **136**:345–375.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385–397.
- Wiens, J. A. 1997. Metapopulation dynamics and landscape ecology. Pages 43–62 in I. Hanski and M. Gilpin., editors. *Metapopulation biology: ecology, genetics and evolution*. Academic Press, San Diego, California, USA.

APPENDIX A

A list of common and scientific names for the fish species captured along the Kabetogama Peninsula is available in ESA's Electronic Data Archive: *Ecological Archives* E081-015-A1.

APPENDIX B

A table presenting mean catch per unit effort for 16 species of fish sampled over 1993–1995 at 23 sites along the Kabetogama Peninsula in Voyageurs National park is available in ESA's Electronic Data Archive: *Ecological Archives* E081-015-A2.

APPENDIX A

Common and scientific names for the fish species captured along the Kabetogama Peninsula, Minnesota, USA, along with species abbreviations used in the text but not necessarily the figures.

Common name	Scientific name	Abbreviation
Northern redbelly dace	<i>Phoxinus eos</i>	RED
Finescale dace	<i>Phoxinus neogaeus</i>	FINE
Fathead minnow	<i>Pimephales promelas</i>	FAT
Brassy minnow	<i>Hybognathus hankinsoni</i>	BRASS
Pearl dace	<i>Semotilus margarita</i>	PEARL
Golden shiner	<i>Notemigonus crysoleucas</i>	GOLD
Blacknose shiner	<i>Notropis heterolepis</i>	BLACK
Brook stickleback	<i>Culaea inconstans</i>	BROOK
Central mudminnow	<i>Umbra limi</i>	MUD
Burbot	<i>Lota lota</i>	BURBOT
White sucker	<i>Catostomus commersoni</i>	WHITE
Smallmouth bass	<i>Micropterus dolomieu</i>	SMALL
Black crappie	<i>Pomoxis nigromaculatus</i>	BLACK
Yellow perch	<i>Perca flavescens</i>	PERCH
Iowa darter	<i>Etheostoma exile</i>	IOWA
Johnny darter	<i>Etheostoma nigrum</i>	JOHN

APPENDIX B

Mean catch per unit effort (number per trap per day) for 16 species of fish sampled over a 3-yr (1993–1995) period at 23 sites along the Kabetogama Peninsula in Voyageurs National Park (Minnesota, USA). Sites are classified according to drainage and successional state. See Appendix A for species abbreviations.

Site	Drain- age†	Stage‡	Species					
			RED	FINE	FAT	BROOK	MUD	PEARL
1	LC	Upland	57.6	11.1	...	70.2
2	LC	Unclass.	72.9	2.0	0.6	16.2
3	SU	Collapsed	35.1	16.1	4.2	12.6	1.7	0.7
4	SU	Collapsed	12.7	6.2	2.4	12.3	1.6	0.4
5	SU	Stream	10.0	7.5	0.1	3.0	0.3	1.2
6	CL	Upland	3.2	4.7
7	CL	Rebuilt	4.0	3.7
8	WLP	Rebuilt
9	WLP	Lowland
10	LP	Upland	81.7	11.6	19.1	14.9
11	LP	Rebuilt	22.9	4.0	7.4	42.6
12	LP	Unclass.	9.7	2.5	3.9	29.4
13	SH	Lowland	21.3	3.6	4.7	83.4
14	SH	Stream	31.9	8.7	3.4	21.9
15	SH	Rebuilt	47.8	8.5	4.3	36.4
16	SH	Stream	27.6	15.0	8.8	25.4
17	ES	Upland	127.4	7.6	12.6
18	ES	Upland	155.1	11.7	22.8
19	CO	Lowland	8.3	0.2	2.0	8.7
20	HP	Lowland	3.3	0.8	...	5.2
21	LB	Lowland	9.6	2.2	...	2.8	13.0	...
22	DC	Stream	8.1	3.6	0.5	15.9
23	JL	Collapsed	21.0	5.3	1.0	12.5	...	0.1

† Drainages include Locator (LC), Sucker Creek (SU), Clyde Creek (CL), West Lost Ponds (WLP), Lost Ponds (LP), Shoepack (SH), East Shoepack (ES), Cutover (CO), Horon Pond (HP), Deer Creek (DC), Lost Bay (LB), and Jorgens Lake (JL).

‡ Successional stages include upland ponds, lowland ponds, partially rebuilt ponds, fully collapsed ponds, streams, and unclassified sites that could not be easily categorized.

APPENDIX B. Extended.

Species										Total species
GOLD	BRASS	BLACK	IOWA	JOHN	WHITE	SMALL	CRAP	PERCH	BURBOT	
...	3
...	4
0.4	5.9	0.1	9
0.6	2.8	0.1	9
...	0.7	0.1	0.1	9
...	0.7	3
...	...	0.8	0.2	4
...	0
...	0
...	4
...	4
...	4
...	4
...	4
...	4
...	4
...	4
...	3
...	3
...	4
...	3
...	4
...	4
...	0.1	0.1	0.5	...	0.1	3.3	11.2	10
...	3.1	0.1	0.5	0.1	0.1	0.4	...	11