Influence of Beavers on Stream Fish Assemblages: Effects of Pond Age and Watershed Position

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INFLUENCE OF BEAVERS ON STREAM FISH ASSEMBLAGES: EFFECTS OF POND AGE AND WATERSHED POSITION

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Abstract. We used a spatial survey of fish assemblage structure in streams and beaver ponds to: (1) determine the effects of beavers on fish assemblage structure at the reach and drainage basin scales, and (2) assess the influences of pond age, watershed position, and pond environment on fish assemblage structure within beaver ponds. Stream impoundment by beavers affected species richness at the reach scale, but this effect was highly dependent on pond age and drainage area above the pond. In headwater streams, species richness per pond increased to a high in ponds 9–17 yr old and then decreased to a low in ponds >17 yr old. Farther downstream, species richness showed little change with pond age. Assemblage structure varied significantly among unimpounded, impounded, and previously impounded stream reaches, and variation in assemblage structure among ponds was related to pond age and physical habitat. In large ponds there was a shift from lotic to lentic species, and as ponds aged, small-bodied minnows were replaced by larger predators. Because there was high species turnover among impounded and previously impounded reaches, beavers affected patterns of species richness at the drainage basin scale; we collected more species in first- and second-order streams (32 and 38, respectively) than in third-order streams (26). Taken together these results indicate: (1) that beavers have a positive effect on fish species richness in low-order, blackwater streams, but maintenance of this effect requires preservation of both spatial and temporal dynamics of beaver pond creation and abandonment, and (2) the positive relationship between stream fish species richness and drainage area described for many streams may be a recent phenomenon resulting from the extirpation of beavers from much of their historical range.

Key words: anoxic conditions; beaver ponds; Castor canadensis; *fish assemblages; fish predation; landscape position; patch dynamics; pond age; species richness.*

INTRODUCTION

Beaver (*Castor canadensis*) impoundment of low-order streams in North America greatly modifies ecosystem processes and influences biota. Beavers alter nutrient and carbon cycles (Francis et al. 1985, Naiman et al. 1991, Yavitt et al. 1992), nutrient availability (Wilde et al. 1950, Johnston and Naiman 1990, Pinay and Naiman 1991), nutrient and material standing stocks and their transport (McDowell and Naiman 1986, Naiman et al. 1986, Smith et al. 1991), decomposition dynamics (Hodkinson 1975), and water characteristics (Gard 1961, Smith et al. 1991). These changes result in increased standing stocks and production of invertebrate assemblages, as well as shifts in invertebrate assemblage structure (Hanson and Campbell 1963, McDowell and Naiman 1986, Smith et al. 1991, Clifford et al. 1993) and major changes in aquatic plant communities (Johnston and Naiman 1990, Feldmann 1995).

Relatively little is known of the effects of beavers on stream fish assemblages in North America. The expansion of a beaver population in a California stream increased trout production (Gard 1961). In Ontario

beaver ponds, harsh winter conditions influenced life history characteristics, demographics, and feeding behavior of pumpkinseed sunfish (*Lepomis gibbosus*) populations (Fox and Keast 1990, 1991), and fishes were predominantly of small body size and partitioned resources among species (Keast and Fox 1990). Schlosser (1995) presented evidence suggesting ponds support "source" populations that provide a supply of immigrants to "sink" populations in adjacent streams, and that the supply of immigrants is controlled by the influence of discharge on boundary characteristics between ponds and streams. Hanson and Campbell (1963) present the only information that compares fish assemblage structure among beaver ponds. In comparing three beaver ponds to other pool habitats in a Missouri stream, they found increased standing stocks and richness of fish in the ponds compared to adjacent natural pool habitats. No studies have described the temporal dynamics of stream fish assemblages as they are affected by beavers, or investigated the influences of pond watershed position, age, and physical habitat on fish assemblage structure within ponds. In addition, most studies of beaver pond ecology have been conducted in northern latitudes (>35° N) although the historic range of beavers included most of North America (Hill 1982).

In this study, we describe the influence of beaver impoundment of Southeastern blackwater streams on fish assemblage structure. Our goals are to: (1) compare fish assemblage structure among unimpounded, impounded, and previously impounded stream reaches; and (2) to investigate correlations among species richness and fish assemblage structure, and pond watershed position, pond age, and physical environment. We ask three specific questions: (1) how does impoundment of low-order streams influence stream fish species richness and assemblage structure at the reach scale (two to three pool–run sequences, Frissel et al. 1986) and at the drainage basin scale (e.g., across a third-order drainage basin); (2) are influences related to beaver pond watershed position and age; and (3) is beaver pond physical habitat related to pond watershed position and age? Because of the large temporal and spatial scales involved (ponds may persist for >100 yr and are found on first- through fourth-order streams) we take a natural experiment approach (sensu Diamand 1986) and compare ponds ranging from 1 to >17 yr old on first- through third-order streams.

METHODS

The study system

Beaver ponds and streams were sampled at the Savannah River Site (SRS) on the Upper Coastal Plain of South Carolina (USA). Large portions of this 780-km² site have been undisturbed since the SRS was established in the early 1950s by the U.S. Department of Energy. The beaver population on the SRS has recovered from a low of two stream-dwelling colonies in 1950 to ~37 stream-dwelling colonies in 1992 (Snodgrass 1996). At the SRS, beaver ponds are limited to first- through third-order streams. Local geomorphology is characterized by streams with broad, flat floodplains flanked by uplands with moderate topographic relief. This results in broad, shallow ponds with depths >1 m restricted mainly to areas of the old stream channel.

Streams of the SRS are low gradient (usually <2 m/km), with shifting sand bottoms. In streams that have not been impounded by beavers, wood (both dead and living) provides the main structure; waters are usually acidic to neutral (pH 5–7), near 80% saturated with dissolved oxygen, and range in annual temperature between 8° and 24°C (Newman 1986). In impounded or previously impounded streams, aquatic plants become quite dense (Feldmann 1995) and contribute substantially to fish habitat structure. Water temperatures in impounded reaches may fluctuate between 1° and 30°C annually, and during summer months daily dissolved oxygen levels may range between zero and super saturation (>100%; J. W. Snodgrass, *unpublished data*).

Fish collections and physical habitat measures

Thirty-one beaver ponds were identified on 1992 color infrared aerial photographs and sampled for fishes in April and May 1994. During this period, 11 unimpounded stream reaches also were sampled; nine had never been impounded and two were previously impounded. Four additional previously impounded stream sites were sampled during April 1995 to yield sample sizes of 31 and 15 for ponds and streams, respectively.

We sampled ponds with seines and backpack electroshockers. All mesohabitats (e.g., emergent marsh, open water) that were accessible with the electro-shocker (<1 m depth) were sampled until 20–30 min of effort yielded no new species. This was followed by sampling with seines. In ponds with open areas, we used a short, straight seine (2 m deep × 3.3 m long, 0.32-cm mesh) and a longer bag seine (1.3 m deep × 10 m long, 0.16-cm mesh). In two of the ponds, obstructions prevented the use of the longer seine. The number of species collected from these ponds was relatively high, so it is unlikely that the lack of use of the large seine affected estimates of species richness and assemblage structure. Again, we sampled all mesohabitats until 20–30 min of effort yielded no new species.

We sampled streams by blocking the upper and lower ends of 30–50 m reaches with straight seines and removing fishes with three consecutive passes of a backpack electro-shocker. The exact sample length was determined by the location of areas where stream physiography allowed effective block-netting. We chose reach lengths of 30–50 m because they contained two to three pool–run sequences, the main mesohabitat elements in these streams (Meffe and Sheldon 1988). In addition, the average length of stream affected by beaver dams at the SRS is ~40 m (Snodgrass 1996), and preliminary investigations indicated that slopes of species accumulation curves level off dramatically after 30–50 m of stream are sampled. Preliminary investigations also indicated that this method was effective at removing most of the fish >20 mm standard length (SL) from the stream; 90% of the individuals collected in six electro-shocker passes were removed in the first three passes, and we collected many small fish (20–30 mm SL).

To sample physical habitat at each site we used a point transect method. At equally spaced points along each transect, substrate type, water column structure, depth, and current were recorded. For beaver ponds, 4–5 transects were spaced equally along the length of the pond, beginning 5 m above the dam. We recorded data at 5-m intervals in large ponds (>50 m wide) and 2-m intervals in smaller ponds. In streams, we spaced transects at 5-m intervals beginning at the downstream block net and recorded data at 0.25-m intervals. We recognized four substrate types (gravel, sand, silt, and detritus), and five water column structure types: aquatic vegetation, coarse wood (>5 cm diameter), fine wood (<5 cm diameter), coarse roots (>5 cm diameter), and fine roots (<5 cm diameter). Current was measured using a Marsh-McBirney current meter at 0.6 times depth at each point, and dissolved oxygen (DO) and

pH were measured at each site before sampling fish. In beaver ponds these measures were made at a point just before the water flowed over the dam; in streams they were made at the downstream end of the sample reach.

Determination of watershed position, pond age, and pond size

We described the landscape position of each sampling site using size of the drainage basin above the sampling site (henceforth referred to as drainage area); increasing drainage area indicates a movement from headwaters to downstream reaches. Other investigators (Osborne and Wiley 1992) have found other measures of landscape position to be better predictors of stream fish species richness; however, our preliminary investigations found that drainage area showed the strongest correlation with species richness and assemblage structure in our data set. Therefore, for simplicity we used only drainage area as a measure of landscape position. We determined drainage area by locating sites and drawing polygons on 1:24 000-scale U.S. Geological Survey quadrangle maps based on 10-foot (30.48-m) interval topographic contour lines. Polygons were digitized and areas calculated using a geographic information system (GIS).

Each pond was placed into one of three age categories based on its presence or absence on historical aerial photographs from 1978, 1986, and 1992. Ponds that were present in 1992, but not 1978 or 1986, were considered 1–8 yr old, or ''new'' ponds; ponds present in 1986 and 1992, but not 1978, were considered 9–17 yr old, or ''mid-aged'' ponds; and ponds present in 1978, 1986, and 1992 were considered >17 yr old, or ''old'' ponds.

For small ponds (<1 ha), pond surface areas were estimated from scale maps sketched at the time of sampling, and the length of stream impounded was determined by locating and measuring the old stream channel within the pond. For larger ponds (>1 ha), surface areas were estimated from polygons traced from aerial photographs. Polygons were digitized and areas calculated using GIS. Polygons for larger ponds were then intersected with a stream coverage for SRS to determine the length of stream impounded by each pond.

Data analysis

General approach.—For analysis we grouped sites into one of four types based on beaver impoundment history, defined as follows: streams—sites that had never been impounded; active ponds—sites where an active dam was being maintained; abandoned ponds—sites where a dam was no longer being maintained but was still impounding water on the floodplain; and recovering streams—sites that had been previously impounded, but where the riparian canopy had not returned, although the stream had returned to the channel. In comparing species richness and assemblage structure

among unimpounded, impounded, and previously impounded stream reaches we used these four site types.

Because sampling methods and total distance of stream sampled varied among site types, we used species richness per unit length of stream (in meters), hereafter expressed as species richness per meter, species richness per square meter of stream, and relative abundance of species for comparisons among site types. We used both species richness per meter and per square meter to investigate the role of area in producing differences in species richness among site types; a significant effect of site type for richness per meter, but not for richness per square meter, would suggest that increased surface area was responsible for the observed effect. For analysis of beaver ponds, we focused on individual ponds as the unit of analysis and used richness per pond and catch per unit effort (calculated as the total number of each species collected divided by the total shocking and seining time per pond) because all ponds were sampled using the same methods, but were not sampled to near depletion.

Physicochemical habitat.—Principal components analysis (PCA) was used to reduce the 13 physical habitat variables to a lower number of linear combinations of the original variables (Johnson and Wichern 1988). Average width, depth and current, and percentage occurrence of water column structure and substrate variables were used in the analysis. The variables used in PCA were plotted against each other and the plots inspected to determine the relationships among the variables. Where needed, we transformed variables to approximate more closely the linear relationship assumed in PCA. Because dissolved oxygen measures were significantly related to time of day, we standardized measures to 1200 (noon) following methods outlined in Snodgrass et al. (1996).

Effects of impoundment history, pond age and watershed position on fish-species richness relationships.—We used ANOVA to test for a significant difference in species richness per meter and species richness per square meter among site types and pond ages. Site types and pond ages were combined to produce eight categories (streams; new, mid-aged, and old active and abandoned ponds; and recovering streams). Species richness per meter was log transformed before analysis. Post hoc comparison of means for each impounded or previously impounded site type with unimpounded streams were made using t tests with a Bonferroni correction to maintain the experiment-wide error rate at $P = 0.05$ ($P = 0.05/7 = 0.007$ for individual comparisons). We estimated t statistics using pooled variance when variance differed significantly among groups; otherwise we used separate variance estimates.

The null hypothesis of no difference in the relationship between richness and drainage area among site types or pond age categories was tested using a homogeneity of slopes model (ANCOVA). A significant interaction term in this model indicates that the slope

of the line relating species richness to drainage area (the covariable) differs significantly between at least two of the categories (Johnson and Wichern 1988). A series of comparisons was made among site types and pond age categories. For site types we compared streams and each of the other site types (for a total of three comparisons), and for pond age categories we made all possible pairwise comparisons (for a total of three comparisons). Again, we controlled the experiment-wide error rate at $P = 0.05$ for each set of comparisons using a Bonferroni correction ($P = 0.05/3 = 0.017$ for individual comparisons).

Relative influence of physicochemical environment, watershed position, and pond age.—We used multiple regression to test the hypothesis that change in species richness per pond with pond age was a result of physical habitat changes. We used stepwise selection and backward elimination of watershed position and environmental variables (PCA scores and pond size) to build a multiple regression model to predict richness. Age categories were then coded as dummy variables, and their significance as predictors of richness was tested using stepwise selection of age categories after drainage area and environmental variables were forced into the model. If any of the age categories were retained in the final model, age would have significant ($P \leq 0.05$) predictive power beyond that of environmental variables.

Effects of impoundment history on fish assemblage structure.—We used ordination methods to analyze assemblage structure. Canonical correspondence analysis (CCA; CANOCO program; ter Braak 1988) was used to test for a significant effect of site type on fish assemblage structure. The relative abundance of species and site type, coded as a nominal response variable, was used in CCA. We used Monte Carlo permutations to test for a significant effect of site type on assemblage structure following ter Braak (1988). Ninety-nine permutations were used to develop expectations under the random model. Because preliminary analysis indicated that rare species dominated the ordination (i.e., differences among sites were due to the occurrence or lack of occurrence of a few rare species), they were downweighted in the final analysis. We used the same approach to test for a significant effect of drainage area and age on assemblage structure in active and abandoned beaver ponds, except that CPUE was used as the dependent variable.

Relative influence of watershed position, pond age, and physicochemical environment on fish assemblage structure of beaver ponds.—Using the same approach as described for richness, we tested the hypothesis that age had no significant effect on assemblage structure in active and abandoned ponds beyond that associated with habitat changes. Watershed position and environmental variables were used to build a model of assemblage structure for active and abandoned ponds. We then tested for a significant relationship between pond

age and assemblage structure after all significant watershed and environmental variables were forced into the model. Again, age was coded as a dummy variable.

RESULTS

Physicochemical habitat

Water chemistry and physical habitat variables for each sample site are given in the Appendix. PCA extracted two axes of variation from the physicochemical measures that accounted for 80% of the variation in these variables (Table 1). The first axis is related to physical habitat characteristics. It contrasts shallow, narrow sites that have faster current, abundant fine wood and roots, and sand and gravel substrates (low scores), with deep, wide sites that have slow current, abundant vegetation, and silty substrates (high scores). The second axis relates only to the occurrence of detritus substrates (Table 1).

Impoundment of streams by beavers influenced the physical habitat and water chemistry at the reach scale. Following impoundment, dissolved oxygen (DO) levels decreased, surface area of the stream increased, and physical habitat was characterized by wide, deep channels with abundant terrestrial and aquatic vegetation and silt substrates (PCA I scores increased; Fig. 1). Pond abandonment resulted in an increase in DO levels with age and a large reduction in pond surface area. While mean channel widths and depth decreased following abandonment (Appendix), vegetation and silty substrates remained abundant (PCA score remained elevated in relation to streams, Fig. 1). Although recovering streams exhibited DO levels, surface areas, and mean widths, depths and currents similar to unimpounded streams (Appendix), recovering stream PCA I scores remained elevated in relation to unimpounded streams, mainly as a result of the abundant aquatic vegetation found in these reaches.

Site scores on PCA axis II and pH showed no relationship to site type or beaver pond age (Fig. 1). pH showed a positive relationship with drainage area that

TABLE 1. Loadings of physical habitat variables on the first two principal components and the proportion of variance explained by each component. For clarity, only loadings >0.30 and <-0.30 are listed.

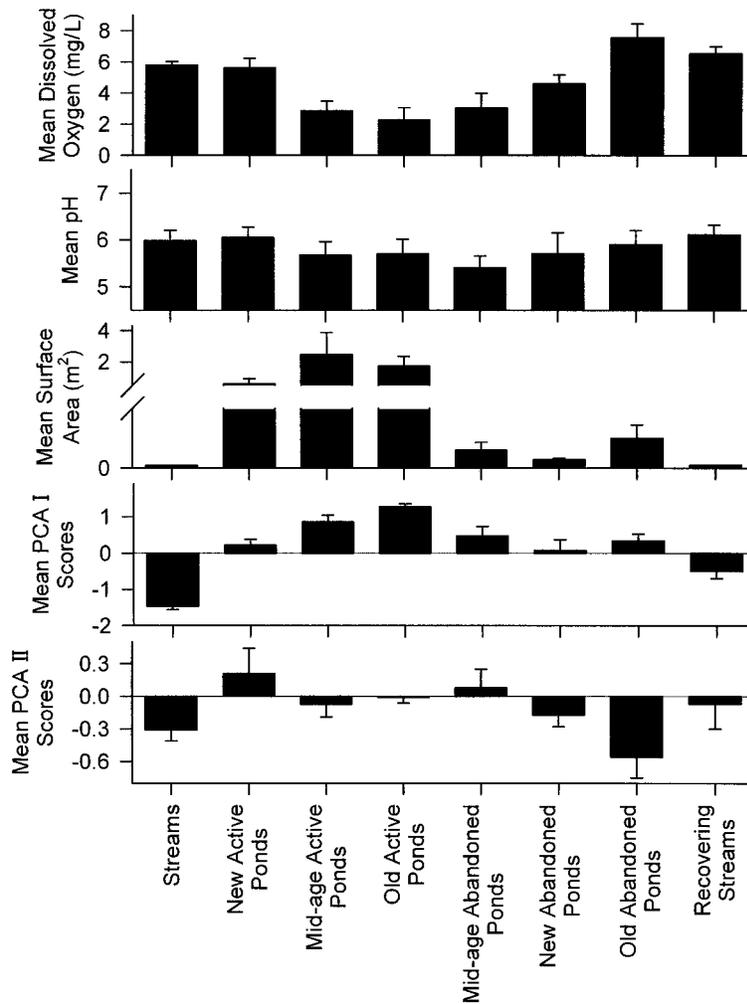| Variable	PCA I	PCA II
Mean depth	0.85	
Mean width	0.91	
Mean current	−0.86	
Aquatic vegetation (%)	0.84	
Coarse wood (%)		
Fine wood (%)	−0.58	
Fine roots (%)	−0.58	
Coarse roots (%)		
Silt (%)	0.87	−0.37
Sand (%)	−0.85	
Gravel (%)	−0.40	
Detritus (%)		0.95
Variance explained (%)	63.9	16.3

FIG. 1. Relationship between site type and mean physicochemical environment in unimpounded, impounded, and previously impounded stream reaches. Error bars represent 1 SE.

appeared to be eliminated by beaver impoundment (Fig. 2); however, the values recorded are within the range reported to be tolerable by the fishes encountered in this study, and pH did not appear to affect species richness (e.g., 16 species were collected from the active pond with the lowest recorded pH value, 4.2). For simplicity and the above stated reasons, we do not consider PCA II scores or pH in further analysis.

Fish species richness

A total of 40 fish species was collected among the four site types (Table 2). Among the more abundant species (>40 individuals collected), three (blackbanded sunfish, bluespotted sunfish, and lined topminnow) occurred almost exclusively in active or abandoned ponds, and one (sawcheek darter) occurred exclusively in streams that were or had been previously impounded by beavers. Of the more abundant species, none was found exclusively in streams or recovering streams.

Effects of site type, pond age and watershed position

on species richness.—At the reach scale, beaver impoundment had a significant effect ($P = 0.0007$) on species richness per meter; however, this effect was not always positive (Fig. 3). Mean species richness per meter for old active ponds was significantly lower ($P < 0.0001$) when compared to unimpounded streams; mean species richness per meter for mid-aged, abandoned ponds was significantly ($P = 0.001$) higher. These differences were large, with mean species richness per meter 10 times lower in old active ponds and 3 times greater in mid-aged abandoned ponds (Fig. 3).

While there were significant effects of site type on species richness per square meter these effects were always negative (Fig. 3), suggesting that increased species richness per meter in mid-aged, abandoned ponds was a result of increased stream surface area. Significantly lower species richness per square meter in all ages of active ponds and lower mean species richness per square meter in abandoned ponds and recovering streams also suggested that increases in surface area
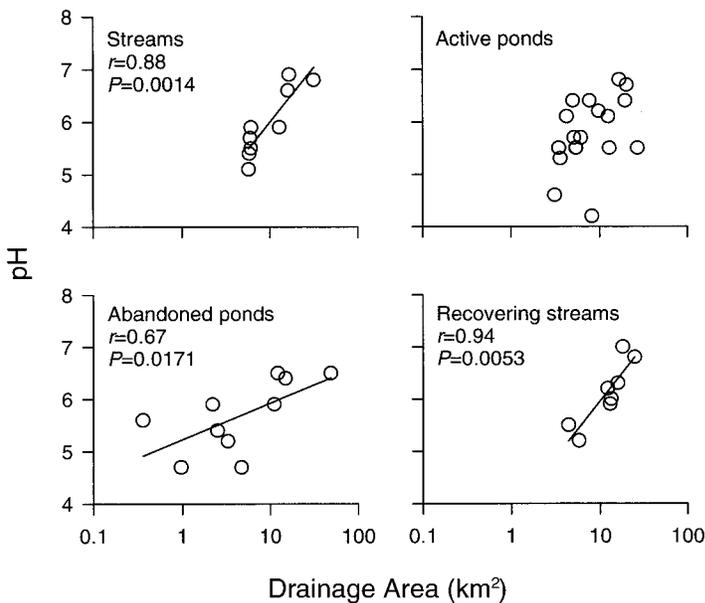
FIG. 2. Relationship between pH and drainage area among the different site types created by beaver impoundment.

produced by beaver impoundment did not always produce proportional increases in species richness per meter.

None of the interaction terms of the ANCOVA models comparing the slope of the drainage area–species richness line among streams and the other site types were significant ($P < 0.10$). This resulted from a lack of relationship between drainage area and species richness per meter or square meter among most site types (Table 3).

The relationship of species richness per pond changed significantly among pond age categories (Table 4). The slope of the line relating species richness to drainage area decreased from new to mid-aged ponds and then increased from mid-aged to old ponds (Fig. 4). Species richness was not related to physiochemical habitat (Fig. 5). Stepwise selection of drainage area, PCA I scores (related to physical environment of the pond), DO, and pond surface area retained drainage area only as a predictive variable of species richness ($r^2 = 0.31$). After drainage area was forced into the model, stepwise selection did retain the dummy variable "old pond age" ($r^2 = 0.58$), indicating that age had predictive power beyond that of physicochemical variables.

To examine patterns of richness at the drainage basin scale, we combined our data from streams, impounded streams, and previously impounded streams, for first-through third-order streams (the highest order stream impounded by beaver at the study site; Snodgrass, *in press*), to estimate the total number of species collected from each stream order. The total number of species collected was highest in second-order streams and lowest in third-order streams (Fig. 6).

Fish assemblage structure

Site type had a significant ($P = 0.01$) effect on assemblage structure; however, site type accounted for only a small portion of the variation in assemblage structure among sites (Table 5). In Fig. 7, species scores from CCA, which represent approximate optima of the species, are plotted in multivariate space. Arrows represent the directional influences of the different site types on assemblage structure and are derived from the correlations between site types and the species axes, eigenvalues of the axes, and their standard deviation (Jongman et al. 1987). CCA axis I separates active and abandoned ponds from streams and recovering streams, axis II separates recovering streams from other site types, and axis III separates active and abandoned ponds (Table 5). Because the amount of variation explained by the CCA axes decreases with axis number, this indicates that the largest differences in assemblage structure existed between impounded (active and abandoned ponds) and free-flowing (streams and recovering streams) stream reaches. In general, most species showed a strong preference for one site type as indicated by the clustering of species near the heads of arrows in Fig. 7.

Only among active ponds was assemblage structure significantly ($P = 0.01$) correlated with pond age and drainage area. CCA axis I of the active pond analysis was related to drainage area and its interaction with age, and axis II was related to age (Table 6; Fig. 8, interpreted as in Fig. 7, but arrows represent gradients in environmental variables). We included the interaction term in the model because of the strong interaction of drainage area and pond age in relation to species richness per pond. The CPUE of most species was re-

TABLE 2. Total number, relative abundance, and rank of species collected at all sites, and by stream stages. Common and scientific names with abbreviation (in parentheses) used in Figs. 6 and 7 are provided.

Scientific name, common name, (abbreviation)	Total no. (relative abundance, rank)				
	All sites	Streams	Active ponds	Abandoned ponds	Recovering streams
Notropis lutipinnis, yellowfin shiner (lut)	935 (0.16, 1)	538 (0.60, 1)	91 (0.04, 8)	145 (0.08, 4)	161 (0.23, 1)
Gambusia holbrooki, mosquitofish (hol)	892 (0.16, 2)	5 (0.01, 15)	406 (0.17, 1)	481 (0.27, 1)	0
Lepomis marginatus, dollar sunfish (mar)	671 (0.12, 3)	23 (0.03, 6)	398 (0.17, 2)	216 (0.12, 3)	34 (0.05, 8)
Notropis cummingsae, dusky shiner (cum)	620 (0.11, 4)	0	238 (0.10, 3)	257 (0.15, 2)	125 (0.18, 2)
Erimyzon sucetta, lake chubsucker (suc)	296 (0.05, 5)	13 (0.01, 11)	128 (0.05, 6)	133 (0.08, 5)	22 (0.03, 9)
Notropis chalybaeus, ironcolor shiner (ncha)	257 (0.05, 6)	0	186 (0.08, 4)	70 (0.04, 6)	1 (<0.01, 29)
Erimyzon oblongus, creek chubsucker (obl)	255 (0.04, 7)	55 (0.06, 3)	91 (0.04, 9)	66 (0.04, 7)	43 (0.06, 5)
Aphredoderus sayanus, pirate perch (say)	239 (0.04, 8)	61 (0.07, 2)	108 (0.05, 7)	53 (0.03, 8)	17 (0.02, 10)
Enneacanthus chaetodon, blackbanded sunfish (echa)	164 (0.03, 9)	1 (<0.01, 24)	163 (0.07, 5)	0	0
Lepomis auritus, redbreast sunfish (aur)	155 (0.03, 10)	12 (0.01, 12)	62 (0.03, 12)	25 (0.01, 16)	56 (0.08, 3)
Esox americanus, redfin pickerel (ame)	144 (0.03, 11)	23 (0.03, 7)	84 (0.04, 10)	26 (0.01, 15)	11 (0.02, 14)
Enneacanthus gloriosus, bluespotted sunfish (glo)	114 (0.02, 12)	0	84 (0.04, 11)	30 (0.02, 12)	0
Fundulus lineolatus, lined topminnow (lin)	105 (0.02, 13)	1 (<0.01, 25)	55 (0.02, 14)	44 (0.02, 9)	5 (0.01, 21)
Lepomis punctatus, spotted sunfish (pun)	98 (0.02, 14)	5 (0.01, 16)	26 (0.01, 18)	27 (0.02, 14)	40 (0.06, 6)
Nocomis leptocephalus, bluehead chub (lepa)	96 (0.02, 15)	51 (0.06, 4)	2 (<0.01, 27)	4 (<0.01, 25)	39 (0.05, 7)
Etheostoma serriferum, sawcheek darter (ser)	87 (0.02, 16)	0	31 (0.01, 17)	6 (<0.01, 23)	50 (0.07, 4)
Notemigonus crysoleucas, golden shiner (cry)	87 (0.02, 17)	15 (0.02, 10)	36 (0.02, 16)	33 (0.02, 11)	3 (<0.01, 24)
Lepomis gulosus, warmouth (gul)	77 (0.01, 18)	2 (<0.01, 19)	45 (0.02, 15)	27 (0.02, 13)	3 (<0.01, 25)
Centrarchus macropterus, flier (mac)	74 (0.01, 19)	0	57 (0.02, 13)	11 (0.01, 18)	6 (0.01, 19)
Esox niger, chain pickerel (enig)	57 (0.01, 20)	2 (<0.01, 20)	18 (0.01, 20)	36 (0.02, 10)	2 (<0.01, 26)
Ameiurus platycephalus, flat bullhead (pla)	47 (0.01, 21)	25 (0.03, 5)	7 (<0.01, 21)	14 (0.01, 17)	4 (0.01, 23)
Etheostoma fricksium, Savannah darter (ser)	43 (0.01, 22)	21 (0.02, 8)	3 (<0.01, 23)	3 (<0.01, 29)	16 (0.02, 11)
Etheostoma olmstedi, tessellated darter (olm)	41 (0.01, 23)	19 (0.02, 9)	0	11 (0.01, 19)	11 (0.02, 15)
Anguilla rostrata, American eel (ros)	20 (<0.01, 24)	2 (<0.01, 21)	3 (<0.01, 24)	10 (0.01, 21)	5 (0.01, 22)
Micropterus salmoides, largemouth bass (sal)	20 (<0.01, 25)	0	20 (0.01, 19)	0	0
Noturus gyrinus, tadpole madtom (gyr)	19 (<0.01, 26)	10 (0.01, 13)	1 (<0.01, 30)	0	8 (0.01, 17)
Ameiurus natalis, yellow bullhead (nat)	17 (<0.01, 27)	0	3 (<0.01, 25)	2 (<0.01, 30)	12 (0.02, 13)
Acantharchus pomotis, mud sunfish (pom)	15 (<0.01, 28)	3 (<0.01, 17)	4 (<0.01, 22)	8 (<0.01, 22)	
Noturus leptacanthus, speckled madtom (lepb)	14 (<0.01, 29)	1 (<0.01, 26)	0	5 (<0.01, 24)	8 (0.01, 16)
Notropis petersoni, coastal shiner (pet)	13 (<0.01, 30)	2 (<0.01, 22)	0	11 (0.01, 20)	0
Elassoma zonatum, banded pygmy sunfish (zon)	9 (<0.01, 31)	1 (<0.01, 27)	2 (<0.01, 28)	4 (<0.01, 26)	2 (<0.01, 27)
Percina nigrofasciata, blackbanded darter (pnig)	7 (<0.01, 32)	0	0	0	7 (0.01, 18)
Pteronotropis hypselopterus, sailfin shiner (hyp)	6 (<0.01, 33)	0	0	0	6 (0.01, 20)

TABLE 2.　Continued.

Scientific name, common name, (abbreviation)	Total no. (relative abundance, rank)				
	All sites	Streams	Active ponds	Abandoned ponds	Recovering streams
Semotilus atromaculatus, creek chub (atr)	6 (<0.01, 34)	3 (<0.01, 18)	0	2 (<0.01, 31)	1 (<0.01, 30)
Noturus insignis, margined madtom (ins)	6 (<0.01, 35)	6 (0.01, 14)	0	0	0
Umbra pygmaea, eastern mudminnow (pyg)	4 (<0.01, 36)	0	0	4 (<0.01, 28)	2 (<0.01, 28)
Minytrema melanops, spotted sucker (mel)	4 (<0.01, 37)	0	0	4 (<0.01, 27)	0
Etheostoma fusiforme, swamp darter (fus)	3 (<0.01, 38)	0	3 (<0.01, 26)	0	0
Amia calva, bowfin (cal)	2 (<0.01, 39)	0	2 (<0.01, 29)	0	0
Perca flavescens, yellow perch (fla)	2 (<0.01, 40)	2 (<0.01, 23)	0	0	0
Total	5722	902	2357	1768	712
Richness	40	27	30	31	30

lated to age (i.e., the centroids of most species are near the axis of the arrow related to age in Fig. 8). As active ponds aged, small-bodied, insectivorous species (mosquitofish, lined topminnow, lake and creek chubsuckers, sawcheek and Savannah darters, and ironcolor, dusky and golden shiners) declined in abundance, and predator abundance increased (redfin and chain pick-
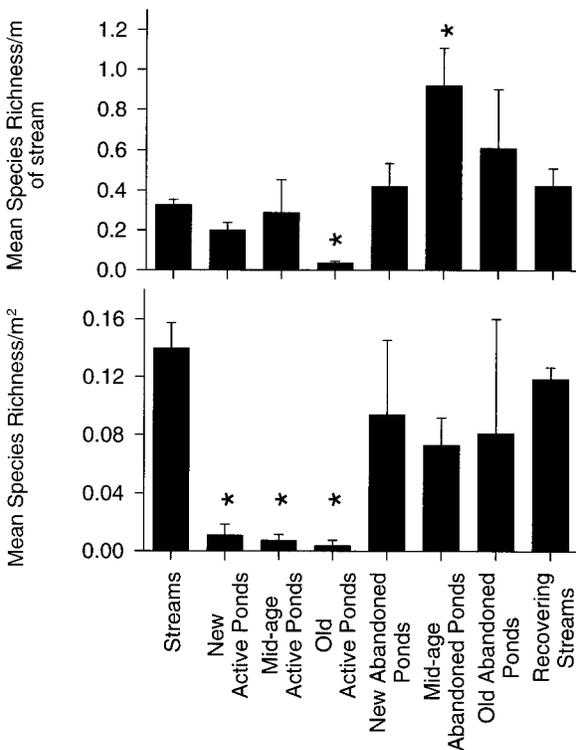

FIG. 3.　Relationship of mean fish species richness per unit length and area of stream by site type. Asterisks indicate that points differed significantly from unimpounded streams, and bars represent 1 SE.

erels, mud, redbreast and dollar sunfish, warmouth, and flier).

Positive and negative regression coefficients for age and the interaction term of drainage area with age (Table 6) in the active pond model indicates that increasing drainage area offsets the effects of age. This interaction involved differences in the response of small-body insectivores and larger bodied predators to pond age in upstream (drainage area <10 km^2) and downstream ponds (drainage area >10 km^2). In upstream ponds, small-bodied insectivores increased in abundance from new to mid-aged ponds and then decreased substantially in old ponds, while downstream they increased with pond age (Fig. 9). The abundance of large-bodied predators generally increased with pond age in both upstream and downstream active ponds (Fig. 9).

Forward selection of environmental variables retained PCA I scores ($P = 0.01$) and drainage area ($P = 0.04$) as significant predictors of assemblage structure among active ponds and PCA I scores ($P = 0.01$) only among abandoned ponds. Among active ponds, pond age was only marginally ($P = 0.06$) related to variation in assemblage structure beyond that accounted for by environmental variables, suggesting that changes in assemblage structure with age are a result of changes in the physical environment of active ponds with age. Assemblage structure in abandoned ponds was related to the gradient in physical habitats among ponds. In small ponds with relatively high current and abundant sand and gravel substrates (similar to unimpounded streams), assemblages were dominated by lotic species, and in larger ponds with little or no current and abundant silt substrates and aquatic vegetation (similar to active ponds) assemblages were dominated by lotic species.

DISCUSSION

Effects of beavers on stream fish assemblages

Beavers substantially affected the stream habitat studied, including decreasing current and increasing

Table 3. Pearson correlation coefficients among watershed area and measures of species richness for the four different site types.

Measure of species richness	Streams	Active ponds	Abandoned ponds	Recovering streams
Richness per stream meter	0.7425*	0.2831	0.1637	0.7408
Richness per square meter of stream	−0.1726	−0.0431	0.0222	0.5149

* Coefficient is significant at an experiment-wide error rate of $P < 0.05$ using a Bonferroni correction for individual comparisons.

stream depth and width and the occurrence of silty substrates and aquatic vegetation. These habitat changes influenced fish species richness at the reach scale (50–100 m of stream); however, the direction and magnitude of that influence depended on watershed position and pond age. In downstream reaches, richness was similar across all site types and pond ages; however, in upstream locations, richness peaked in abandoned mid-aged ponds, and was lowest in old, active ponds. Changes in species richness appeared to result from increased stream surface area, but increases in species richness were not directly proportional to increases in surface area, so that unimpounded streams maintained the highest species densities per square meter.

While assemblage structure varied significantly among site types and among beaver pond age categories, multivariate models of assemblage structure based on these variables explain only a small portion of the variation in assemblage structure. This resulted from the fact that within site types and pond age categories there was a large turnover in species among stream reaches. For example, there was a total of 30 species collected in recovering streams; however, the largest number of species collected in a single recovering stream was 16. Thus, a large amount of diversity exists among individual recovering stream reaches.

This among-site diversity resulted in large effects on patterns of species richness at the drainage basin scale. Fourth-order streams are the largest found in our study area. Paller (1994) made 47 collections in the same first- through fourth-order blackwater streams that we studied and found species richness to increase with stream order to a maximum of 22 species in fourth-order streams. We collected 31 and 37 species in first- and second-order streams respectively, almost twice the number collected by Paller in these stream orders (Fig. 6). The pattern of species richness among stream orders matches the preference of beavers for certain stream sizes; in our study area beavers preferentially impound second-order streams and rarely impound third-order streams (Snodgrass, *in press*). Thus, when beaver pond habitats are considered, stream fish species richness peaks in headwater streams as a function of the amount of beaver impoundment present. This pattern contrasts with theoretical models of stream ecosystem structure and function that predict that species richness will peak in mid-order streams (Vannote et al. 1980)

Beaver ponds have the potential to affect drainage basin scale patterns of species richness in unimpounded stream reaches through source/sink population dynamics (Pulliam 1988). Schlosser (1995) observed large

Table 4. Results of ANCOVA comparing the relationship between watershed size and species richness (per pond) among pond age categories.

Comparison Source	df	MS	F	P
Old vs. mid-aged ponds				
Age	1	0.0897	13.05	0.0019
Watershed size	1	0.1431	20.83	0.0002
Interaction	1	0.0555	8.08	0.0104
New vs. old ponds				
Age	1	0.4372	12.71	0.0031
Watershed size	1	0.6639	19.29	0.0006
Interaction	1	0.2958	8.62	0.0108
Mid-aged vs. old ponds				
Age	1	0.9116	32.12	0.0001
Watershed size	1	0.7019	24.73	0.0001
Interaction	1	0.5221	18.39	0.0005

Note: The experiment-wide error rate is controlled at $P < 0.05$ using a Bonferroni correction; individual interaction terms are considered significant at $P < 0.05/3 < 0.017$.
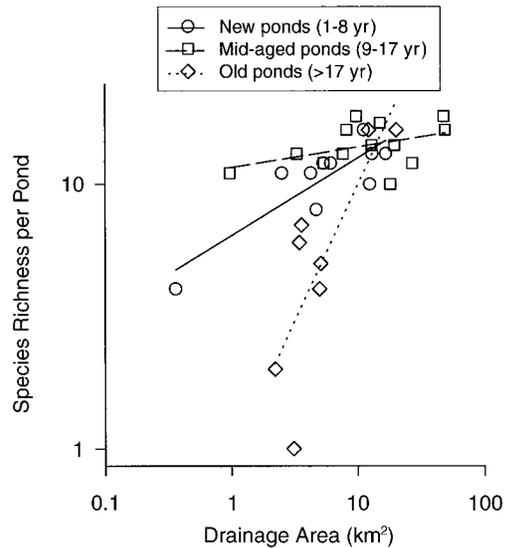

Fig. 4. Relationship between fish species richness per pond and drainage area among beaver pond age categories.
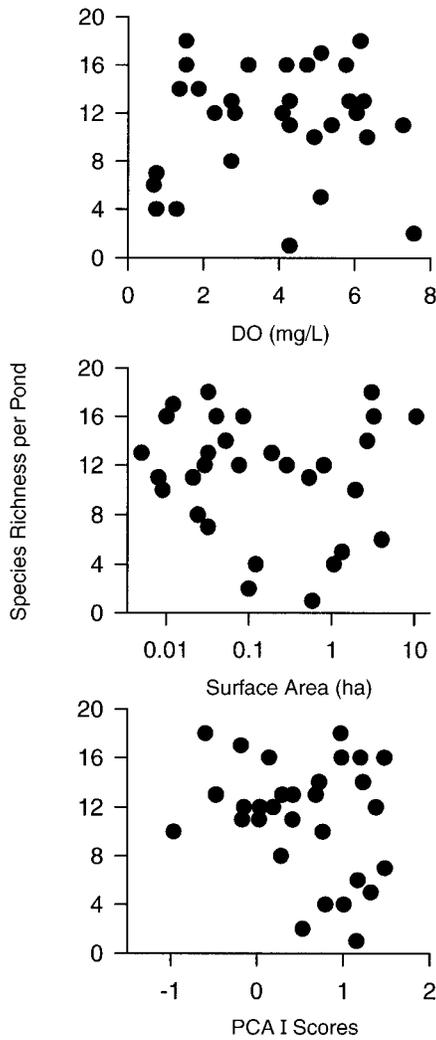
FIG. 5. Relationship between species richness per pond and dissolved oxygen, pond surface area, and pond physical environment (PCA I scores). With increasing PCA I scores, pond environments change from shallow, narrow ponds with abundant fine roots, wood, and sand and gravel substrates, to deep, wide ponds with abundant aquatic vegetation and silty substrates.
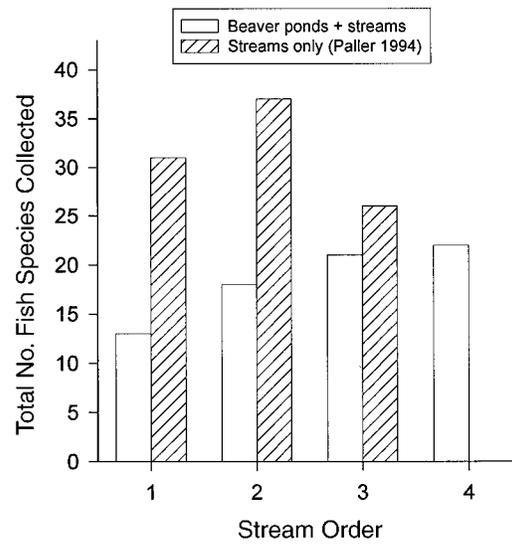

FIG. 6. Comparison of the total number of species collected per stream order in this study (including beaver-created habitats) with results reported by Paller (1994) who sampled 47 unimpounded stream reaches.

ness gradients in drainage basins with varying levels of beaver impoundment.

Consideration of the distribution of species among unimpounded, impounded, and previously impounded reaches suggests that beavers have influenced the evolution of stream fishes. When Meffe and Sheldon (1988) conducted a similar analysis at the smaller scale of individual pools and runs in these blackwater streams they found that congeneric or confamilial species clustered together in multivariate space. They suggested that this implied a strong role of ecological preferences, expressed at the genus or family level, rather than diversification of closely related taxa. In contrast to their results, congeneric or confamilial species often showed a great deal of separation at the larger scale

TABLE 5. Results of CCA of the effects of site type on fish assemblage structure. The overall model was significant at $P = 0.01$.

Statistic	Axis I	Axis II	Axis III
Cumulative percentage variance			
Species data	9.5	12.5	14.5
Species–environment relation	65.6	86.3	100.0
Regression/canonical coefficients for standardized variables			
Streams	0.29	−1.35	−0.31
Active ponds	−0.86	−1.13	−0.63
Abandoned ponds	−0.65	−1.27	0.49
Recovering streams	0.00	0.00	0.00
Correlations of environmental variables with axes			
Streams	0.70	−0.37	−0.12
Active ponds	−0.55	0.03	−0.41
Abandoned ponds	−0.26	−0.20	0.49
Recovering streams	0.31	0.67	0.07

numbers of fishes moving out of beaver ponds into unimpounded stream reaches in a Minnesota stream. Fish species richness has been found to increase with drainage area across a range of latitudes and stream types (e.g., Larimore and Smith 1963, Sheldon 1968, Horwitz 1978, Angermeier and Schlosser 1989). Because these relationships are used in developing expectations for biological assessment and monitoring measures, such as the ''index of biotic integrity'' (Karr 1981, Karr et al. 1986), it is important to understand the influence of beaver ponds on these patterns. We expect that beavers will decrease the slope of the line relating species richness to drainage area; however, testing this hypothesis will require comparisons of rich-
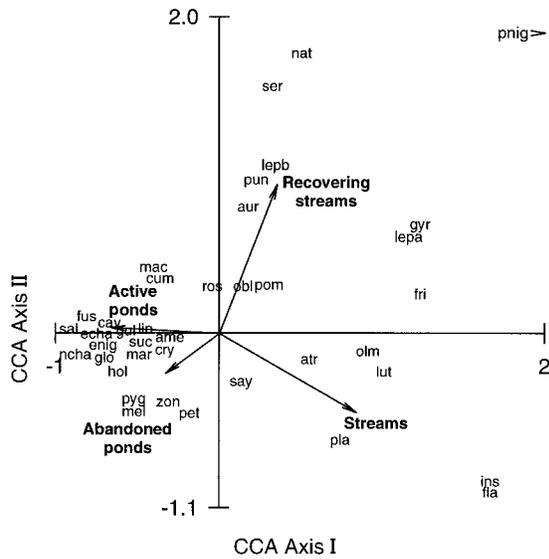
FIG. 7. Ordination diagram depicting the effects of pond creation and abandonment and stream recovery on fish assemblage structure in Southeastern blackwater streams. Arrows indicate the direction in multivariate space that different stream classes move assemblage structure. Points indicate the approximate location of species optima. The designation pnig> indicates that *Percina nigrofasciata* extends outside the axis boundaries. Species abbreviations are given in Table 2.

TABLE 6. Results of CCA of the effects of drainage area and age on assemblage structure in active beaver ponds. The overall model was significant at $P = 0.04$.

Statistic	Axis I	Axis II	Axis III
Cumulative percentage variance			
Species data	12.3	21.0	23.9
Species–environment relation	51.3	87.8	100.0
Regression/canonical coefficients for standardized variables			
Drainage area	0.28	0.60	3.32
Age	0.28	1.36	1.18
Drainage area × age	0.61	−1.33	−3.54
Correlations of environmental variables with axes			
Drainage area	0.74	−0.39	0.28
Age	0.52	0.70	−0.18
Drainage area × age	0.87	−0.14	−0.51

studied here. For example, darters (Percidae) and madtoms (*Noturus*), both of which showed similar habitat preference at the individual pool or run scale (Meffe and Sheldon 1988), showed a large degree of separation in this study (Fig. 7). This suggests that the spatial mosaic of habitat types created by beavers acts as another axis along which resources are partitioned.

Richness and assemblage structure in beaver ponds

In upstream ponds species richness per pond increased initially and then declined, while in downstream ponds species richness showed little change with age. Clearly, the increase in richness of young upstream ponds is a result of colonization of the newly created habitat. This process appears to be rapid and much of it was probably missed by our relatively coarse temporal scale. For example, at one of our study sites on Meyers Branch, 158 fish and 11 species were collected from a 45-m reach of unimpounded stream. Approximately 3 mo later, following beaver impoundment of the reach, only 11 fish and 3 species were collected from the same stream reach (J. W. Snodgrass, *unpublished data*). Additionally, low numbers of fish species typically found in mid-aged beaver ponds were collected in less than a year following impoundment of this stream reach.

The mechanisms behind the decline in species richness in old ponds are less clear. The decrease in abundance of small-bodied species in old ponds and weak

increase in abundance of large-bodied predators with pond age suggests that predators eliminated prey species from old ponds. Harsh environmental conditions (low DO) also may have eliminated species from old ponds; however, several factors argue against this mechanism: (1) there was no relationship between DO and species richness, (2) the larger bodied predators should have experienced decreased relative abundance as a result of low DO levels before the smaller bodied species (Klinger et al. 1982), (3) species known to be tolerant of low DO levels, such as mosquitofish (Meffe and Snelson 1989), were absent from most old, upstream ponds, and (4) some of the small-bodied prey species (mosquitofish, lake chubsuckers, and bluespotted sunfish) are found in isolated wetlands where DO levels often are <4 mg/L (Snodgrass et al. 1996).
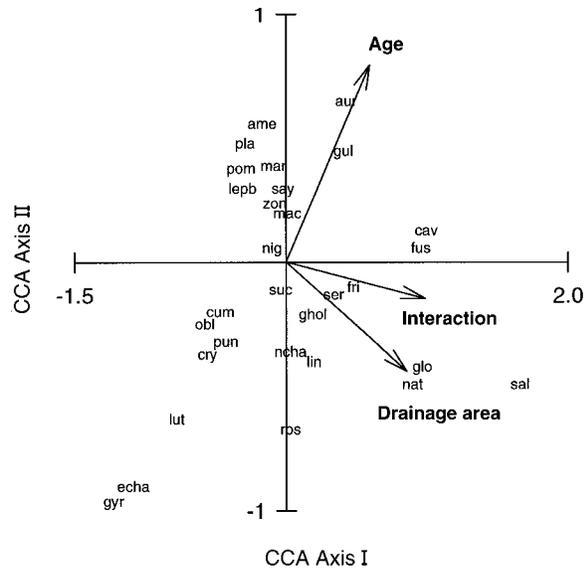
The weak increase in large-bodied predators with

FIG. 8. Ordination diagram depicting the effects of drainage area and pond age on fish assemblage structure in active beaver ponds. See the legend of Fig. 7 and the *Results* for interpretation. Species abbreviations are given in Table 2.
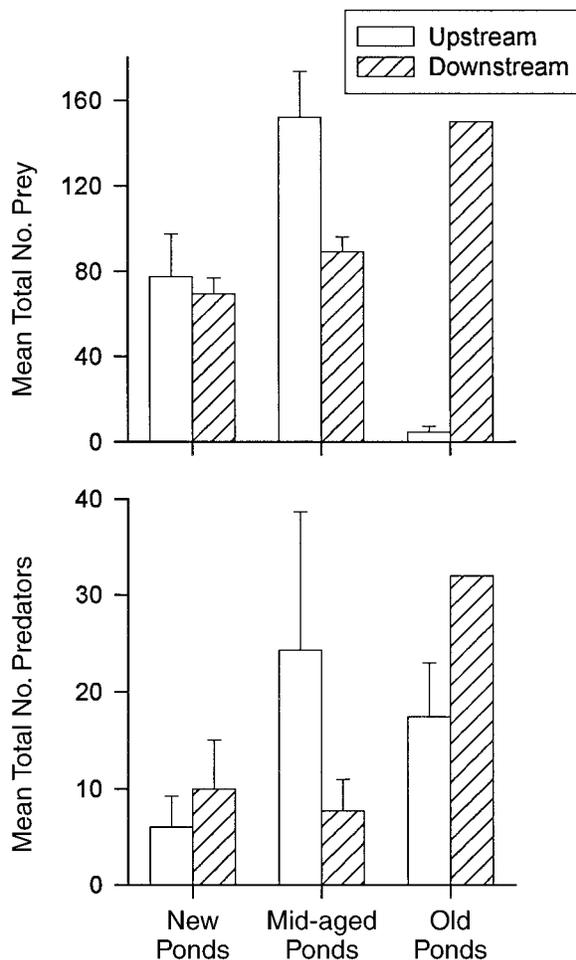
FIG. 9. Relationship of active pond age and the total number of prey (mosquitofish; lined topminnow; lake and creek chubsuckers; sawcheek and Savannah darters; and ironcolor, dusky, and golden shiners) and predators (redfin and chain pickerels; mud, redbreast, and dollar sunfish; warmouth; and flier) collected. Bars represent 1 SE. There is no error bar for downstream old ponds because of lack of replication (*n* = 1).

pond age suggests that other factors are involved in promoting the elimination of prey species from old ponds. A possible factor is boundary permeability of ponds. As active pond size increases in these systems, dam height and the transition zone between the stream and the pond increases, presumably reducing boundary permeability. Pond surface area was much greater in mid-aged and old, active ponds. This may have prevented prey species from avoiding predation by moving out of ponds. Additionally, species that require a number of different habitat types to complete their life cycle would be eliminated even in the absence of predation. For example, dusky shiners (*Notropis cummingsae*) spend the majority of the year in stream pools with moderate current, but move to backwater areas to spawn over sunfish (*Lepomis* spp.) nests during the spawning season (Fletcher 1993).

Finally, the reason for a lack of correlation between age and species richness in downstream ponds is also unclear, but may be related to the landscape position of ponds. Downstream ponds are located closer to a source of colonists than upstream ponds. Many of the lotic species found in beaver ponds are also found in the backwaters of fourth-order streams and the floodplain of the Savannah River (J. W. Snodgrass and G. K. Meffe, *personal observation*). It is possible that downstream ponds receive more colonists that prevent prey populations from going extinct through a "rescue effect" (Brown and Kodric-Brown 1977). If this is true, landscape position of ponds and boundary permeability would work in concert to allow predators to eliminate prey species from old upstream ponds.

Relationship to general models of aquatic community structure

Several diversity theories predict a unimodal pattern of richness with patch age. The intermediate disturbance hypothesis views richness as increasing as species colonize a habitat patch, but then decreasing as competition begins to eliminate species. Menge and Sutherland (1987) expanded this model by viewing richness as a function of recruitment rates and environmental stress. At low levels of recruitment and environmental stress, predation is responsible for reduced richness. As environmental stress levels increase, competition and then environmental stress reduce richness, producing a bimodal pattern. When mechanisms of competitive coexistence exist, or recruitment rates are low, competition will not affect richness, resulting in a unimodal pattern of richness at all levels of recruitment. Our results appear to fit this model in some respects. Predation appeared to reduce diversity when immigration rates were low, but high immigration rates appear to offset effects of predation.

Hypothesized mechanisms behind large-scale fish species richness patterns in aquatic systems have been based on colonization–extinction processes. In this model, assemblage structure depends on the ability of species to persist in the face of disturbance, or to recolonize following disturbance. In northern lake systems, extinction processes, in the form of anoxic conditions and predaceous elimination (Tonn and Magnuson 1982, Rahel 1984), play a major role in determining assemblage structure, except when immigration rates are high (Tonn et al. 1995). In stream systems, differences both in the ability of species to persist in the face of disturbance, and colonization following disturbance, are thought to structure assemblages (Osborne and Wiley 1992, Poff and Allan 1995). In contrast to lake systems, disturbance in stream systems is physical in nature (low- or high-flow events). In isolated wetlands of the Southeast, where disturbances are relatively harsh (complete drying of the wetland), differences in colonization ability were suggested as the dominant factor controlling fish assemblage structure

(Snodgrass et al. 1996). Beaver ponds appear to fit the model for small northern lake systems. Extinction processes in older ponds create variation in richness and assemblage structure among ponds except when immigration rates are high.

Although assemblage structuring mechanisms appear to be similar between small lakes and beaver ponds, there are two contrasts between the two systems. First, changes in local environmental conditions among small lakes were a function of lake morphometry (Tonn et al. 1990), whereas changes in beaver ponds were associated with age and pond abandonment. Second, predatory fishes were present in deep lakes or lakes connected to streams where a refuge from anoxic conditions was present, while in beaver ponds, predators were present in all ponds, but were only able to eliminate prey species in isolated (headwater) ponds where prey immigration rates presumably were lowest. This may be a result of differences in the severity of anoxic conditions between the two systems. In northern lakes studied by Tonn et al. (1990), anoxic conditions develop below winter ice cover throughout the entire lake (Magnuson et al. 1989). In contrast, anoxic conditions develop during warm, summer months in Southeastern beaver ponds, and are more patchy. For example, anoxic conditions do not develop in open-water areas of ponds where vegetation is absent or sparse, or in upstream portions of the pond where stream water enters (J. W. Snodgrass, *personal observation*).

Angermeier and Schlosser (1989) suggested that in systems where emigration/extinction and colonization processes are important in structuring assemblages, there should be little relationship between habitat features such as patch size or volume. They hypothesized that the weaker relationships they observed between habitat volume and complexity, and species richness in Minnesota streams, when compared with streams in Illinois and Panama, was the result of increased environmental variability and harsher winters. Snodgrass et al. (1996) suggested that high disturbance frequencies in isolated wetlands resulted in a dependence of fish assemblage structure on differences in immigration rates between species, and thus a lack of relationship between wetland size and assemblage richness. Also, predation may have the same destabilizing effect on physical habitat and assemblage structure relationships (Schoener 1986). The lack of relationship between size and richness in beaver ponds observed in this study supports the generality of this idea. In addition, a relationship between richness and watershed position in both streams and ponds suggests that proximity to source populations, and thus immigration and extinction processes, are important in these blackwater systems. This leads to a second generality: when emigration/extinction and colonization processes are important determinants of assemblage structure, landscape position will have a strong influence on assemblage structure. Thus, in systems where physical (e.g., an-

oxia) or biological (predation) disturbances are frequent, assemblages may not be in equilibrium with the physical environment but may reflect an equilibrium determined by landscape position and patch boundary permeability.

In summary, the results presented here indicate that beaver ponds increase fish species richness in headwater streams, that this effect is highly dependent on the dynamics of pond creation and abandonment, and that large-scale (drainage basin) patterns of fish species richness were probably altered by the extirpation of beavers from most North American streams. Thus, management plans with the goal of maintaining biodiversity will need to include steps that preserve or reintroduce temporal, as well as spatial, beaver pond dynamics. In addition, variation in pond assemblage structure and environment with age and watershed position suggests that harsh environmental conditions, predation, pond boundary characteristics, and immigration from downstream source populations are significant assemblage structuring mechanisms within ponds; however, more rigorous experimental approaches are needed to more clearly determine interactions between, and the relative importance of, these factors.

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APPENDIX

Physical characteristics, site types, pond age categories, and total number of species collected at unimpounded, impounded, and previously impounded stream reaches on the upper coastal plain of South Carolina, United States. Site types are: stream, never impounded; active pond, dam impounding water across its entire length; abandoned pond, dam impounding water across only a portion of its length; recovering stream, stream that has returned to the channel but riparian vegetation has not recovered. Age categories were determined from historical aerial photographs. Dissolved oxygen was standardized to 1200 (noon) following methods in Snodgrass et al. (1996).

Sample site identification number	Standardized dissolved oxygen (mg/L)	pH	Total no. species	Mean depth (cm)	Length (m)	Mean width (m)	Mean current (m/s)	Surface area (m²)	Drainage area (km²)	Pond age category (yr)	Site type
MB-DS1	5.49	6.8	16	22.95	34	4.11	0.1290	0.014	31.82		stream
MB-DS4	5.11	6.6	14	12.90	37	3.07	0.1359	0.011	16.23		stream
MB-DS5	4.19	6.9	15	10.17	43	2.05	0.0270	0.009	16.72		stream
MB-US1	5.96	5.1	9	14.67	35	2.41	0.1400	0.008	5.75		stream
MB-US3	6.43	5.9	9	8.78	32	2.34	0.1472	0.008	12.91		stream
TB-DS1	6.05	5.9	12	11.14	30	1.49	0.1530	0.004	6.15		stream
TB-US1	6.15	5.5	8	12.02	33	2.28	0.2095	0.007	6.12		stream
TB-US2	6.62	5.7	9	17.55	35	2.36	0.1669	0.008	6.00		stream
TB-US3	5.96	5.4	9	13.36	28	2.29	0.1645	0.006	5.87		stream
MB-DS2	4.28	6.8	13	23.70	52	25.40	0.0032	0.191	16.72	1–8	active pond
ME31_2	6.33	6.1	10	64.58	96	37.58	0.0000	1.935	12.54	1–8	active pond
TB-BP	6.05	5.7	12	13.52	46	11.83	0.0448	0.029	6.15	1–8	active pond
TC005	7.28	6.1	11	24.48	40	24.49	0.0111	0.538	4.26	1–8	active pond
TC7_1	4.09	5.5	12	22.94	111	30.82	0.0254	0.288	5.37	1–8	active pond
ME31	1.36	5.5	14	87.79	237	75.10	0.0000	2.688	12.96	9–17	active pond
PE1	2.29	5.5	12	76.46	264	117.00	0.0000	0.806	27.06	9–17	active pond
PE2	1.86	6.4	14	60.88	11	40.00	0.0140	0.052	19.62	9–17	active pond
RE1	5.86	6.4	13	44.57	50	16.48	0.0195	0.188	7.68	9–17	active pond
ST11	1.53	6.2	18	32.28	357	79.50	0.0012	3.037	9.79	9–17	active pond
TC7_2	2.82	5.5	12	29.10	33	21.20	0.0345	0.076	5.41	9–17	active pond
UTR3	4.19	4.2	16	69.26	758	113.09	0.0000	10.480	8.18	9–17	active pond
LTR64	0.75	5.3	7	56.40	255	210.15	0.0000	0.032	3.60	>17	active pond
PE3	1.53	6.7	16	95.76	338	97.29	0.0000	3.226	20.25	>17	active pond
PE51	4.28	4.6	1	47.97	71	46.25	0.0001	0.591	3.11	>17	active pond
UTR1_1	5.11	5.7	5	53.87	73	100.16	0.0000	1.344	5.12	>17	active pond
UTR1_2	1.28	6.4	4	51.57	91	106.04	0.0000	1.075	5.00	>17	active pond
UTR5	0.68	5.5	6	58.47	366	92.46	0.0000	4.032	3.46	>17	active pond
MB-US4	6.24	5.9	13	31.15	16	2.93	0.0394	0.005	13.04	1–8	abandoned pond
fourm	0.75	5.6	4	44.31	42	29.00	0.0092	0.122	0.36	1–8	abandoned pond
MC5	5.39	5.4	11	26.79	26	6.65	0.0989	0.008	2.51	1–8	abandoned pond
PE8	3.18	5.9	16	45.60	35	39.30	0.0865	0.085	11.19	1–8	abandoned pond
TC008	2.73	4.7	8	29.59	25	16.38	0.0261	0.024	4.72	1–8	abandoned pond
MB-DS3	4.93	7.0	11	11.90	14	6.63	0.0488	0.009	18.19	9–17	abandoned pond
LTR61	4.28	4.7	11	29.65	12	26.10	0.0010	0.021	0.97	9–17	abandoned pond
LTR63	2.73	5.2	13	33.98	12	34.87	0.0382	0.032	3.30	9–17	abandoned pond
ME1_2	5.11	6.4	17	21.72	14	10.50	0.0221	0.012	15.06	9–17	abandoned pond
MED1	6.15		18	17.18	16	29.15	0.0222	0.032	47.78	9–17	abandoned pond
MED2	4.74	6.5	16	21.65	85	11.08	0.0685	0.040	48.97	9–17	abandoned pond
fpond	7.57	5.9	2	29.02	32	15.00	0.0325	0.100	2.22	>17	abandoned pond
ME1	5.77	6.5	16	12.47	15	8.88	0.1005	0.010	12.24	>17	abandoned pond
MB-REC	7.47	6.3	11	27.53	43	2.30	0.1667	0.010	15.98		recovering stream
MB-US2	5.86	5.2	9	12.73	28	2.42	0.1604	0.007	5.79		recovering stream
MIB-US5	4.93	6.0	16	38.22	27	4.47	0.0244	0.012	13.42		recovering stream
MC-REC1	7.85	6.2	15	34.99	47	2.94	0.1397	0.014	12.23		recovering stream
MC-REC2	7.19	6.8	14	31.09	18	5.68	0.1495	0.010	24.98		recovering stream
TC-REC	8.04	5.5	11	23.86	40	3.12	0.0992	0.012	4.40		recovering stream