DISPERSAL, BOUNDARY PROCESSES, AND TROPHIC-LEVEL INTERACTIONS IN STREAMS ADJACENT TO BEAVER PONDS[1]

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Abstract. I combined long-term (10 yr) descriptive and short-term experimental studies in a headwater stream in northern Minnesota to assess: (1) the effect of annual variation in stream discharge and spatial proximity of beaver (*Castor canadensis*) ponds on lotic fish abundance and (2) the subsequent influence of discharge and fish predation on lotic invertebrate colonization. Considerable annual variation in fish density occurred in the stream over the 10-yr period, particularly in pool habitats. Increased fish density was associated with increased stream discharge and creation of beaver ponds downstream from the study site. Weir traps used to monitor directional (upstream vs. downstream) fish movement during the last 4 yr of the study indicated annual changes in fish density were associated with the amount of fish dispersal occurring along the stream segment. Downstream fish movement, out of an upstream beaver pond occurred primarily during periods of elevated stream discharge. Upstream movement, out of a downstream beaver pond, occurred over a broader range of discharge conditions. A controlled, "split-stream," experiment examining the effect of very low vs. elevated discharge on upstream fish movement indicated, however, that upstream movement of fish out of beaver ponds was also reduced by very low discharge conditions. Movement data for individual fish species revealed considerable variation among the taxa in the tendency for downstream vs. upstream movement, due to variation in the morphology of upstream vs. downstream beaver ponds and its subsequent effect on the composition of fish dispersing from these source areas. Most fish movement occurred over relatively brief time periods, suggesting life history and developmental processes were critical in influencing the timing of dispersal. Size structure of fishes captured in the stream indicated predominantly older age classes (>age I) of fish were dispersing along the stream. However, based on the occurrence of age 0 individuals only 1 of 12 species, the creek chub (*Semotilus atromaculatus*), routinely reproduced in the stream.

Experiments conducted in an artificial stream located below one of the beaver ponds indicated discharge and fish predation have potentially strong and interactive effects on invertebrate colonization in stream ecosystems. Differences in colonization of riffles and pools under low vs. elevated discharge and fish vs. no-fish treatments suggested, however, that the interactive effect of these factors on invertebrate colonization was variable over even small spatial scales. Elevated discharge increased invertebrate colonization in riffles but decreased invertebrate colonization in pools. Contrary to intuitive expectations, fish predation reduced invertebrate colonization more under elevated than low discharge conditions, particularly in pool habitats.

Taken together, these results suggest: (1) beaver ponds act as reproductive "sources" for fish on the landscape, while adjacent stream environments act as potential reproductive "sinks," (2) large-scale spatial relationships between beaver ponds and streams, along with the influence of discharge on the permeability of the boundaries between these habitats, are critical in controlling fish dispersal between ponds and streams and the subsequent abundance and composition of fish in lotic ecosystems, and (3) fish predation and discharge have potentially cascading effects on invertebrate colonization in lotic ecosystems.

Key words: beaver ponds; boundary processes; Castor canadensis; *colonization; fish assemblages; fish dispersal; invertebrates; landscape ecology; lotic ecosystems; Minnesota; predator–prey interactions; stream discharge; trophic-level interactions.*

INTRODUCTION

Many aquatic vertebrates exhibit complex life cycles, with various life history stages using widely separated habitats (Sale 1978, 1979, Wilbur 1980, Werner and Gilliam 1984). Future empirical and theoretical developments concerning the ecology of organisms

with such spatially complex life cycles require an integration of the influence dispersal-related processes and local trophic level interactions have on population and assemblage dynamics (Pulliam 1988, Roughgarden et al. 1988, Wiens 1989). Critical dispersal-related processes include: (1) the "supply" of juveniles or adults to the community, which can come from either local or distant habitat patches and hence may or may not be strongly influenced by local trophic interactions

(Sale 1978, 1979, Roughgarden et al. 1988), (2) the influence of environmentally mediated extinction–colonization processes with the associated exchange of individuals between discrete habitat patches (Hanski and Gilpin 1991), and (3) the role of boundary processes, which can regulate the nature of exchanges between adjacent landscape elements (Wiens et al. 1986, Hardt and Forman 1989, Dunning et al. 1992, Schlosser 1995). Local trophic interactions that are likely to be critical include the effect of size-specific predation between trophic levels (Kerfoot and Sih 1987), competitive bottlenecks within trophic levels (Osenberg et al. 1992), and the role of ontogenetic niche shifts in mediating both competitive and predator–prey interactions (Wilbur 1980, Mittelbach 1981, Werner and Gilliam 1984).

In this paper I combine a 10-yr descriptive study with a short-term experimental study to examine the influence of dispersal-related processes and local trophic level interactions on fish assemblages in streams adjacent to beaver (*Castor canadensis*) ponds. Specifically, I use a 10-yr data set to assess the effect of temporal changes in stream discharge and temporal changes in the spatial proximity of beaver ponds on the colonization, abundance, age structure, and recruitment of fish in stream ecosystems. I then conducted an experiment in an artificial stream below a beaver pond to assess the influence of discharge and fish predation on invertebrate colonization.

I focused on the influence of spatial proximity of beaver ponds on fish assemblages in adjacent stream environments because the boundary between beaver ponds and streams was, historically, a fundamental component of large-scale spatial heterogeneity in north temperate aquatic habitats (Naiman et al. 1986, 1988). I focused on the effect of discharge on interactions between ponds and streams because variation in discharge is a fundamental component of temporal environmental variability in streams (Resh et al. 1988) and because previous research suggested discharge was a critical abiotic variable influencing colonization of invertebrates and fish (Schlosser and Ebel 1989, Schlosser 1992). Finally, I focused on the interactive effect of discharge and fish predation on invertebrate abundance because exchange (immigration/emigration) processes, which are likely to be strongly influenced by stream discharge (Schlosser and Ebel 1989, Schlosser 1992), have been hypothesized as being critical in influencing the effect of predator–prey interactions on invertebrate abundance (Cooper et al. 1990, Flecker 1992, Sih and Wooster 1994). Furthermore, the "supply" of invertebrate resources is a potentially important competitive bottleneck for insectivorous fish production in small stream ecosystems (Mason 1976, Angermeier 1982, Schlosser 1987a, Schlosser and Angermeier 1990).

STUDY SITE AND SPATIAL DISTRIBUTION OF BEAVER PONDS

I conducted the study from 1983 to 1992 in Gould Creek, a headwater tributary of the Mississippi River. Gould Creek is located ≈4–6 km west of the University of Minnesota Forestry and Biological Station at Lake Itasca, Minnesota, USA. It is a high gradient (10 m/km), 2–3 m wide, stream with well-developed pool and riffle habitats. It originates as the drainage outlet of Beaver Lake (Fig. 1), which is a natural, 8 m deep pond that has been increased in area and depth by a 2 m high beaver dam at its outlet. Fish species commonly collected in Beaver Lake (I. J. Schlosser, *personal observation* and *unpublished data*) included northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*), pumpkinseed sunfish (*Lepomis gibbosus*), black bullhead (*Ictalurus melas*), yellow perch (*Perca flavescens*), blacknose shiner (*Notropis heterolepis*), common shiner (*Notropis cornutus*), and fathead minnow (*Pimephales promelas*).

Temporal variation in the spatial distribution of beaver dams and beaver ponds occurred along Gould Creek during the 10-yr study (Fig. 1). From 1983 to 1987 the only beaver dam on Gould Creek was at the outlet of Beaver Lake. This dam collapsed in July of 1987 due to extremely high precipitation and storm runoff (Stock and Schlosser 1991) but was rebuilt by the spring of 1988. Beaver activity subsequently increased along Gould Creek during the spring and summer of 1989, associated with increased abundance of beaver due to declining fur prices and reduced beaver trapping throughout the region. By mid-August of 1989 several new ponds were created in the lower reaches of Gould Creek and these ponds persisted through the summer of 1992 (Fig. 1). The ponds in the lower reaches of Gould Creek were shallower than Beaver Lake, with a maximum depth of 1.0–2.0 m. Fish species commonly collected in these ponds (I. J. Schlosser, *personal observation* and *unpublished data*) included the brook stickleback (*Culaea inconstans*), brassy minnow (*Hybognathus hankinsoni*), northern redbelly dace (*Phoxinus eos*), finescale dace (*Phoxinus neogaeus*), fathead minnow, creek chub (*Semotilus atromaculatus*), blackchin shiner (*Notropis heterodon*), and pumpkinseed sunfish.

METHODS AND MATERIALS

Seasonal and annual variation in precipitation and stream stage in Gould Creek.—I obtained precipitation records from the University of Minnesota weather station at Lake Itasca. Stream stage was routinely measured from mid-April to mid-August (1984–1992) ≈4 km downstream from Beaver Lake on Sucker Creek, with a Leopold and Stevens Type F continuous stage recorder. Stream stage was a reliable indicator of the frequency of elevated vs. low discharge during the 10-yr study. Stream stage was not, however, a reliable
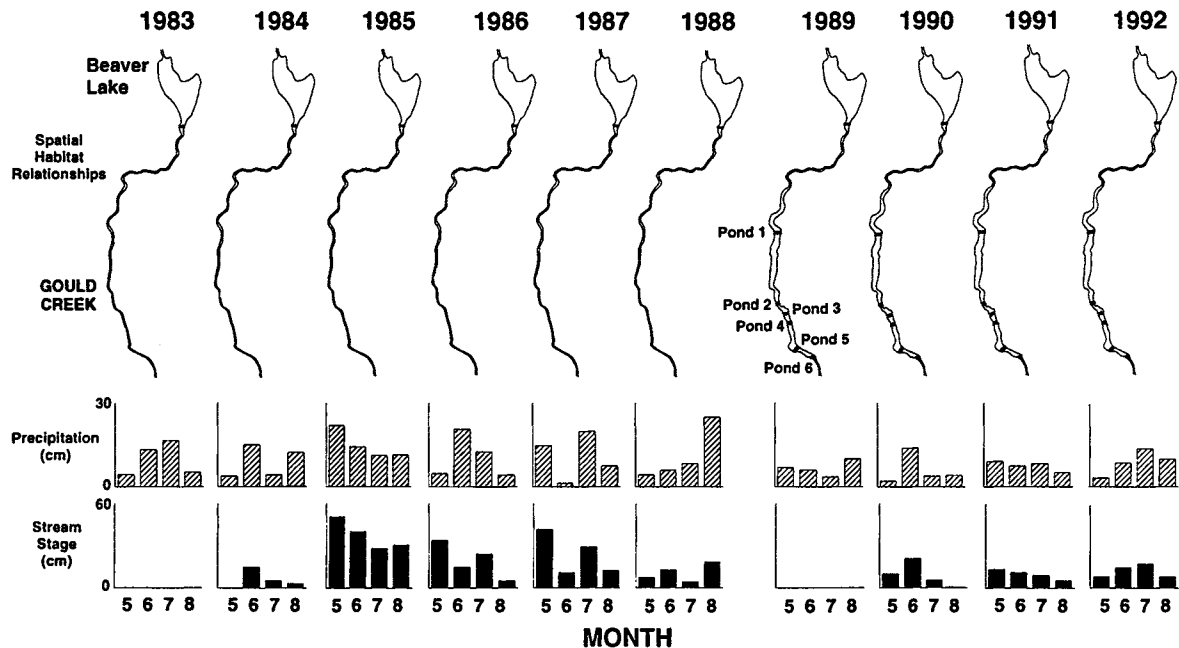
FIG. 1.   Spatial habitat relationships and environmental conditions in Gould Creek, Minnesota from 1983 to 1992. Note that stream stage data were not available for 1983 and 1989.

indicator of absolute discharge over the 10-yr period because of channel sedimentation in the vicinity of the gauge in late 1985. To indicate general trends in seasonal and annual variation in precipitation and stream stage, I calculated total precipitation and mean stream stage for May–August during each of the 10 yr.

Temporal variation in abundance, age structure, and recruitment of fishes in Gould Creek.—To establish the influence of changes in spatial proximity of beaver ponds, stream discharge, and local habitat structure on the assemblage structure of fish in Gould Creek, I sampled the fish and habitat structure in the stream over the 10-yr period. Fish were sampled below Beaver Lake but above Pond 1 (Fig. 1) with two techniques, electro-seining (1983–1992) and minnow trapping (1984–1992).

Electro-seining was used to establish the distribution of fish in riffle vs. pool habitats and their age/size structure. Electro-seining was conducted twice per year in spring (mid–late May) and summer (mid–late August). Ten stream reaches (five pools and five riffles), with a combined length of 140 m, were normally sampled. However, only four riffles and four pools were sampled after August 1989 because one riffle and one pool had been modified for experimental purposes. Each riffle and pool was sampled separately. Sampling was conducted with a 7 m long electric-seine powered by a generator with a maximum capacity of 1500 V and 8.7 A at 60 Hz alternating current. Block seines (4.8 mm mesh) were placed at the upper and lower ends of each habitat prior to sampling. Each habitat was electro-seined twice and fish picked up with 4.8 mm mesh dip

nets. Absolute efficiency of the sampling procedure has been previously discussed in detail (Larimore 1961, Schlosser 1982, Schlosser and Ebel 1989) and ranges from 40 to 80% of the fish captured for most cyprinids, centrarchids, and catastomids, with an average of 50–60%. The procedure is not effective at capturing fish below ≈20 mm total length (I. J. Schlosser, *personal observation*). Most fish were measured to the nearest millimetre in the field and returned to the stream. Fish were separated into three age groups (0, I, and >I) based on size-frequency distributions. Use of size-frequency distributions for aging fish results in some misclassification because of overlapping sizes of different age groups. It is, however, most effective at segregating age 0 and I individuals (Jerald 1983). Habitat complexity, as indicated by depth, current, and substrate complexity was also measured in each riffle and pool immediately after fish sampling. The sampling protocol and method of calculating habitat complexity followed the procedures outlined by Gorman and Karr (1978) and Schlosser (1982).

I also sampled the fish in Gould Creek with minnow traps to assess if samples collected at a higher frequency exhibited patterns of annual variation in adult (>age 0) abundance similar to those documented with electro-seining. Fish were normally sampled from mid-April until mid-August for 2 d, every 2 wk with standard, unbaited Gee's minnow traps (40 × 19 cm, opening 2.5 cm, mesh 0.5 cm). Three traps were placed in each of the five pools, from 1984 to 1989, for a total of 15 traps. Only four pools were sampled from 1990 to 1992 because one pool had been modified for ex-

perimental purposes. The traps were anchored on the bottom with metal frames, with one trap on each edge of the stream and one in the middle. Fish were removed every 24 h, counted, and returned to the stream.

Directional fluxes of fish movement in Gould Creek.—I used weir traps during the last 4 yr of the study (1989–1992) to monitor seasonal and annual variation in upstream and downstream movement of adult fish (>age 0). Weir traps were part of a "split-stream" apparatus used in a flow manipulation experiment. The split-stream apparatus was located ≈60 m below the dam at Beaver Lake but ≈150 m above Pond 1 (Fig. 1). It consisted of a 10 m long riffle and 20 m long pool split into right and left halves by wooden boards, with 0.3 cm thick and 15 cm wide steel plates in a groove along the bottom edge of the boards. The steel plates were pounded into the substrates to assure water could not move from one side of the stream to the other. At the downstream end of the split-stream segment, "fish-tight" wooden and aluminum frames were constructed to hold four directional weir traps. Each of the four weir traps (two directed upstream and two downstream, alternating across the stream) were ≈30 × 30 × 30 cm in size and were constructed of 0.6 cm diameter steel rod, 2.5 cm diameter angle iron, and 0.6-cm mesh "hardware cloth." Smaller meshed hardware cloth could not be used because of excessive clogging of the screen by organic material transported downstream. Consequently, only fish >age 0 were effectively captured by the traps. Fish were "funneled" into small (5 × 10 cm) openings on the traps by v-shaped "wings" and lids on the traps were hinged to allow fish removal. Weir traps were run almost continuously from mid-April to mid-August in 1989–1992. Time and funding constraints prevented the traps from being operated from 1983 to 1988. Fish were normally removed from the traps and traps cleaned of debris twice each day; early morning (0700–0800) and evening (1900–2000). Traps were cleaned of debris more frequently during periods of elevated discharge. Fish were counted and returned to the stream in the direction they were moving. Stream stage was measured during the operation of the traps with a Leopold and Stevens Type F continuous stage recorder located in the pool directly upstream from the weir traps.

The descriptive association between stream stage and fish movement suggested downstream fluxes of fish movement occurred primarily during periods of high discharge but upstream fluxes occurred over a broader range of flow conditions. I conducted a controlled experiment to directly assess the influence of low vs. elevated discharge on reach selection by fish moving upstream. I elevated the discharge on one side of the split stream but kept the other as a low flow control to directly test the hypothesis that fish prefer to move upstream out of beaver ponds during elevated rather than low flow conditions. The experiment was conducted during a period of relatively stable but very low

discharges from 31 May to 28 June 1989. Discharge was elevated by siphoning water from Beaver Lake to the split-stream apparatus with three 5 cm diameter flexible plastic pipes. Valves on the pipes were adjusted daily to maintain relatively stable flow conditions. Stream stage at the outlet of the riffle in the split-stream apparatus was elevated by ≈2 cm throughout the 4-wk period in the elevated (experimental) relative to the low flow (control) side of the stream and discharge was more than doubled (experimental $\bar{X}$ = 5.75 L/s, control $\bar{X}$ = 2.47 L/s). Since weir traps were continuously monitored from mid-April until mid-August of 1989, pretreatment, treatment, and posttreatment data on fish movement were available from both the elevated and low flow sides of the stream.

Effect of discharge and fish predation on invertebrate colonization.—Since discharge appeared to strongly influence dispersal between beaver ponds and streams, I assessed how discharge and fish predation interacted to influence benthic invertebrate colonization in streams associated with beaver ponds. I conducted a factorial experiment in a series of artificial streams located in the uppermost reaches of Gould Creek, directly below the dam at Beaver Lake but to the west of the main stream channel (Schlosser 1987b, Schlosser and Ebel 1989). Water was fed to the experimental streams via flexible 5 cm diameter plastic pipes that siphoned water over the beaver dam. Standard valves on the pipes regulated discharge.

There were four lines of experimental streams, each consisting of two separate subunits, for a total of eight subunits. In addition to a 0.5 m "headwater" box into which water for each subunit was released, the subunits were partitioned into four habitat compartments (each compartment 0.5 × 1.0 m) by wooden dividers with holes cut that would potentially allow fish, insects, and water to move between compartments. The compartments represented two habitats typically found in Gould Creek. Riffles were shallow (4–6 cm maximum depth), fast water (2% slope) habitats with gravel substrates overlain by rocks 80–110 mm in diameter. Pools were deep (40–45 cm maximum depth), slow water (1% slope) habitats with sand substrates. Riffle and pool habitats alternated in the 8 subunits so there were a total of 16 riffle-pool sequences. The fish treatment in any given riffle-pool sequence was maintained by 0.6-cm mesh screening at the upstream and downstream end of the sequence. In addition, all compartments were covered with 0.6-cm mesh hardware cloth lids to prevent access by terrestrial predators.

To examine the simultaneous influence of discharge and fish predation on invertebrate colonization, invertebrate densities in riffle-pool sequences were determined at the end of a 5-wk colonization period under two different flow regimes and in the presence and absence of fish predators. The experiment was conducted from 16 May to 19 June 1991, which was a seasonal period when a large amount of postwinter re-

colonization of Gould Creek by fish and invertebrates normally occurred (Schlosser and Ebel 1989, Schlosser 1992). Prior to the start of the experiment, natural sand, gravel, and rock substrates were gathered from Gould Creek and allowed to air-dry. A fixed quantity of substrate was then placed in the appropriate compartments of the experimental stream. One of four different treatments was established in a given pool-riffle sequence; low discharge (0.30–0.33 L/s) with fish, low discharge no fish, elevated discharge (1.35–1.45 L/s) with fish, and elevated discharge no fish. Two of the stream lines were low discharge treatments and two were elevated discharge treatments. All treatments were run concurrently but constraints on water availability prevented each subunit within a line from having an independent water supply. To minimize the potential influence of bias due to either position or contagion effects (Hurlbert 1984), the front riffle-pool sequence in each stream line was not used and the three replicates of each treatment were randomly assigned to the remaining riffle-pool sequences.

All fish used in the experiment were collected with minnow traps in Gould Creek. The experiment was initiated by starting the flow in the streams and placing two individuals of four different species in the appropriate riffle-pool sequence. The species and total lengths of fish ($\bar{X} \pm 1$ SE) were chosen to mimic the predominant taxa and size classes of fish in Gould Creek. They included the brook stickleback (Culae inconstans; 56.6 ± 1.1 mm), northern redbelly dace (Phoxinus eos; 59.8 ± 0.9 mm), brassy minnow (Hybognathus hankinsoni; 67.3 ± 1.1 mm), and creek chub (Semotilus atromaculatus; 56.8 ± 1.6 mm). The density of fish, 2 fish/m² per species and 8 fish/m² for all species combined, was above the average density of fish in Gould Creek when all the available habitat area was included in the density calculation. Because these species tend to aggregate in schools the density was, however, below the maximum density of fish commonly observed feeding within a given patch of habitat in the stream (I. J. Schlosser, personal observation).

At the end of the experiment, flow was stopped and all compartments were simultaneously isolated with metal drop gates. The water in each compartment was filtered, substrates removed, and invertebrates elutriated from the substrates. All invertebrates from each compartment were then subsampled according to the procedure outlined by Waters (1969). All of the invertebrates in one-eighth of the sample were then enumerated and head capsule widths of insects measured with an ocular micrometer.

RESULTS

Temporal variation in precipitation and stream stage in Gould Creek

Substantial annual variation occurred in the amount of precipitation over the 10-yr period (Fig. 1). Total
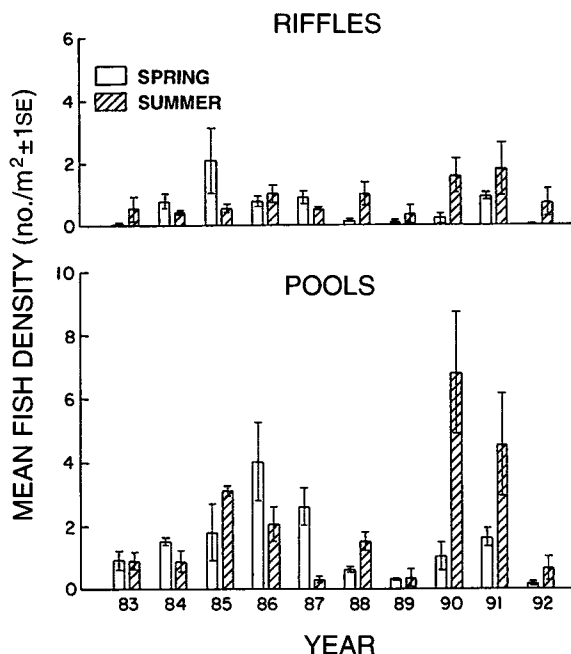

FIG. 2. Fish density in riffle and pool habitats of Gould Creek during spring (May) and summer (August) from 1983 to 1992.

precipitation from May to August varied between years by as much as 2.4-fold; from a low of 24.2 cm in 1990 to a high of 59 cm in 1985. In general, 1983–1984 exhibited relatively normal levels of precipitation, 1985–1987 were relatively wet, and 1988–1992 were relatively dry (Fig. 1).

Stream stage exhibited strong annual variation associated with changes in moisture conditions. Frequent and prolonged periods of elevated stream stage occurred throughout 1985 and to a lesser degree in 1986 and 1987 (Fig. 1). Although brief periods of elevated stream stage occurred in 1988–1992, mean stream stage was relatively low during this period (Fig. 1).

Temporal and spatial variation in fish assemblage structure in Gould Creek

Total fish abundance.—Fish density in Gould Creek exhibited striking annual variation during the 10-yr period, particularly in pool habitats (Fig. 2). Temporal variation in fish density appeared to be associated with annual variation in stream discharge and the creation of downstream beaver ponds. Repeated-measure ANOVAs for either spring or summer samples (Table 1) revealed significant ($P < 0.05$) annual variation in fish density in riffle and pool habitats, no significant habitat × time interaction ($P > 0.30$), but a marginally significant ($0.05 < P < 0.10$) effect of habitat. Fish density was high in pools and riffles during elevated discharge conditions in 1985–1986 and then increased again in 1990–1991, 1–2 yr after the creation of the downstream beaver ponds (Fig. 2). Fish density then decreased

TABLE 1. Summary of repeated-measures ANOVA for spring and summer samples examining the effect of habitat type (riffle vs. pool) and year on the number of fish per square metre during 10 yr of sampling in Gould Creek, Minnesota. Sample sites with missing values are not included in the analysis.

Source of variation	Spring				Summer			
	df	MS	F	P	df	MS	F	P
Habitat	1	7.39	7.03	0.057	1	4.22	4.22	0.095
Error	4	1.05			5	1.00		
Year	9	1.69	6.25	<0.01	9	1.17	2.60	<0.05
Year × Habitat	9	0.25	0.92	>0.50	9	0.52	1.15	>0.30
Error (Year)	36	0.27			45	0.45		

again in 1992, $\approx$3 yr after the creation of the downstream beaver ponds. Pools tended to have higher densities of fish than riffles, with the difference between riffles and pools being greatest during periods of elevated fish density in 1985–1987 and 1990–1991 (Fig. 2).

Considerable annual variation also occurred in seasonal timing of peak fish density (Fig. 2). From 1983 to 1987 fish densities were either higher in spring than summer (1984, 1986, 1987) or similar between the two seasons (1983, 1985). Peak fish densities after 1988 occurred in summer, particularly during the years of increased fish density in 1990 and 1991 (Fig. 2).

Stepwise multiple regression, with forward selection of independent variables based on the amount of variance each variable explained (Ray 1982), was used to examine the influence of several environmental parameters on fish abundance in riffles and pools of Gould Creek (Table 2). This analysis reaffirmed the overriding importance of seasonal and annual environmental variability, rather than local stream habitat complexity, in influencing fish abundance in Gould Creek (Table 2). Season accounted for most of the variation in fish abundance in riffles and pools, followed by year and then local habitat complexity. Local habitat complexity accounted for <1% of the variation in fish abundance in pools and only $\approx$5% in riffles after season and year were included in the model (Table 2).

TABLE 2. Summary of stepwise multiple regression with forward selection of independent variables, assessing the influence of habitat area, habitat complexity, number of species, season, and year on the total number of fish in riffle and pool habitats of Gould Creek, Minnesota.

Step	Variable entered	Partial R^2	Model R^2	F	P
Pools					
1	Season	0.4097	0.4097	62.46	0.001
2	Year	0.0175	0.4273	2.72	0.10
3	Habitat Com	0.0057	0.4330	0.88	0.34
4	Species	0.0051	0.4380	0.78	0.37
Riffles					
1	Season	0.3898	0.3898	52.38	<0.001
2	Year	0.0242	0.4140	3.34	0.071
3	Habitat Com	0.0504	0.4644	7.52	<0.010
4	Species	0.0105	0.4749	1.58	0.21

Species composition of fishes: electro-seining.— Strong annual variation occurred in the relative abundance of fish species in Gould Creek (Fig. 3). Repeated-measure ANOVAs, using log density of individual taxa captured during electro-seining and a Greenhouse-Geisser (1955) correction for heterogeneity of variance, revealed significant ($P < 0.001$) time × species interactions. This indicates the various fish taxa exhibited fundamentally different patterns of annual variation in abundance. Several species, including the largemouth bass, black bullhead, blacknose shiner, common shiner, fathead minnow, and redbelly dace exhibited increased abundances during some of the high discharge years in 1985–1987 but were less abundant from 1988 to 1992 (Fig. 3). Several other species, including the brook stickleback, pumpkinseed sunfish, creek chub, and yellow perch exhibited relatively low abundances in 1983–1987 but increased abundances in 1988–1992 (Fig. 3).

Species composition of fishes: minnow trapping.— Minnow trap samples, which were collected at a higher frequency than electro-seine samples, also revealed strong annual variation in the relative abundance of species over the 9 yr of sampling (Fig. 4). Furthermore, the patterns of annual variation in species' abundances were qualitatively similar to those observed with electro-seining. Largemouth bass, black bullhead, blacknose shiner, common shiner, and fathead minnow all tended to be more abundant in the stream from 1984 to 1987 than from 1988 to 1992. In contrast, the brook stickleback, pumpkinseed sunfish, creek chub, and yellow perch all exhibited increased abundances between 1988 and 1992. Finally, all of the species exhibited substantial temporal variation in abundance within years, with many taxa exhibiting increased abundances during only one or two of the sampling periods (Fig. 4).

Age structure and recruitment of fishes.—A limited number of age classes were present for most of the fish species in Gould Creek, suggesting only a portion of their life cycle was spent in the stream (Appendix). Colonization of the stream in May, for instance, was predominantly by fish >age I, especially among those species (e.g., black bullhead, fathead minnow, common shiner, and brassy minnow) that were abundant during
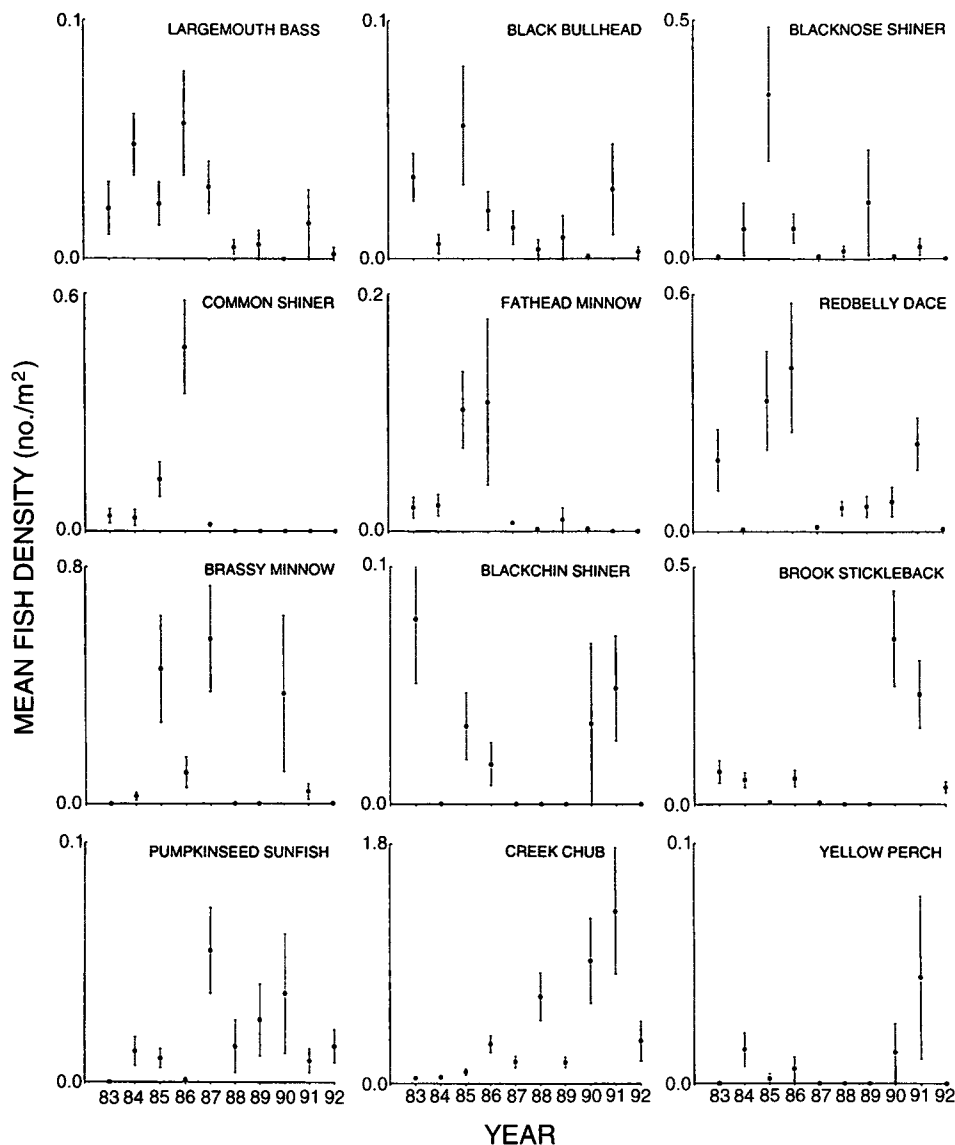
FIG. 3. Density of 12 fish species in Gould Creek from 1983 to 1992. Values based on electro-seine samples collected in riffle and pool habitats during spring (May) and summer (August). The circles are mean density, narrow vertical bars are ± 1 SE. Note that the magnitude of the values on the ordinate varies among the taxa.

the high discharge conditions of 1985–1987. Creation of downstream beaver ponds in 1989 was associated with increased age structure complexity for some species, e.g., brook stickleback, but most species still exhibited few age classes. The blackchin shiner, for example, was one of the most abundant fish during the period of increased fish abundance in the spring of 1990 but virtually all of these fish were age I individuals (Appendix).

Furthermore, most of the fish species did not reproduce in Gould Creek (Table 3). Age 0 largemouth bass were captured in Gould Creek in 8 of the 10 yr (Table 3) but bass >age I were never captured or observed in the stream (Appendix). This suggests adult largemouth

bass reproduced in other habitats, probably Beaver Lake (I. J. Schlosser, *personal observation*), with some young subsequently moving into the adjacent stream environment. Furthermore, age 0 individuals were either rarely or never present for several of the other species (Table 3). Age 0 fathead minnow, common shiner, and blacknose shiner were never captured in Gould Creek during the entire 10-yr period. Age 0 brassy minnow and blackchin shiner were present in only 1 of 10 yr and redbelly dace, brook stickleback, and yellow perch in 3 of 10 yr. The only fish species, other than the largemouth bass, with age 0 fish present during >5 of the 10 yr was the creek chub (Table 3), a species widely documented as completing its life cy-
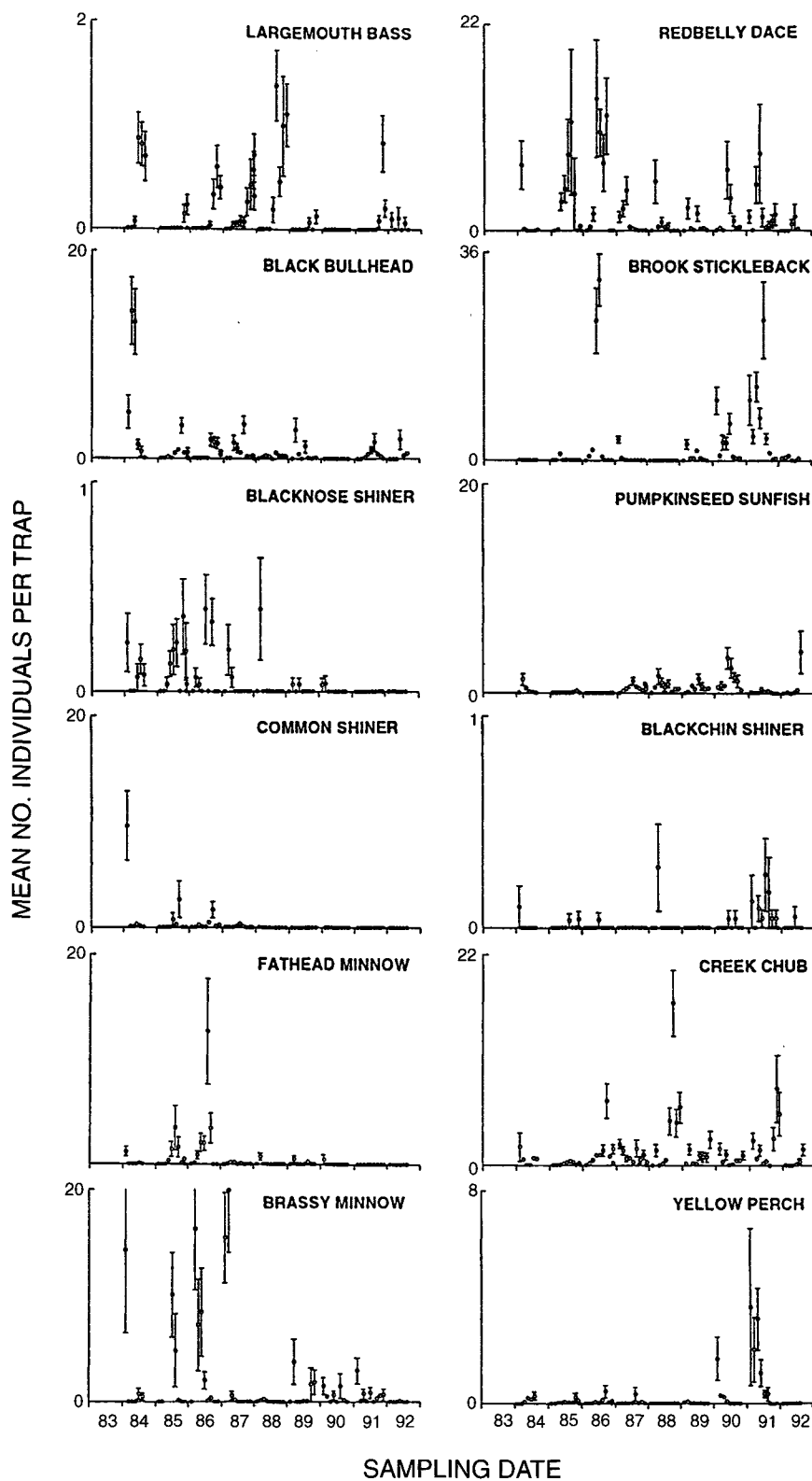
FIG. 4.   Mean number of fish per minnow trap (± 1 SE) for 12 fish species in Gould Creek from 1984 to 1992. Note that the magnitude of the values on the ordinate varies among the taxa.

TABLE 3. Presence of age 0 fish during August in Gould Creek, Minnesota from 1983 to 1992.

Species	Year										No. years
	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	
Largemouth bass	*	*	*	*	*	*	*		*		8
Black bullhead	*	*				*	*		*		5
Fathead minnow											0
Common shiner											0
Blacknose shiner											0
Brassy minnow								*			1
Redbelly dace								*	*	*	3
Brook stickleback	*							*		*	3
Pumpkinseed sunfish											0
Blackchin shiner								*			1
Creek chub				*	*	*	*	*	*	*	7
Yellow perch		*	*	*							3

cle in small headwater streams. Interestingly, the highest number of cyprinid species present as age 0 fish (4) occurred in 1990 (Table 3), the 2nd yr after the creation of beaver ponds below the sampling area.

Directional movements of fishes in Gould Creek

Total numbers of fish.—Large fluxes of fish movement in either upstream or downstream directions normally occurred over a very short time period (Fig. 5). For instance, 33% of the fish moving upstream during the entire May–August period in 1990 moved during 2 d in late June (Fig. 6). Similarly, 48% of all fish moving downstream during May–August in 1991 moved during 1 d in mid-July.

The number of fish moving downstream in Gould Creek was significantly, but weakly, correlated ($r = 0.31, P < 0.05$) with stream stage (Fig. 6). Large increases in the downstream movement of fish only occurred if stream stage was >12–14 cm (Fig. 6). This was also the approximate stage when water began moving over and around the dam at the outlet of Beaver

Lake (I. J. Schlosser, *personal observation*). The occurrence of elevated stream stage (>12–14 cm) did not, however, always result in increased downstream fish movement (Fig. 6). Sometimes very large numbers of fish moved downstream during periods of elevated discharge (Fig. 6), as in July 1991 (Fig. 5), but at other times there was virtually no downstream movement associated with elevated discharge, as in August 1992 (Figs. 5 and 6). Upstream fluxes of fish movement were not significantly correlated ($r = 0.09, P > 0.05$) with elevated stream stage, as major fluxes of upstream movement occurred over a broader range of flow conditions (Fig. 5).

Annual variation in fish density in Gould Creek during the 1989–1992 period was directly associated with annual variation in the amount of fish movement, particularly in the upstream direction. Total fish density in electro-seine samples in August of a particular year was strongly correlated (Spearman rank correlation = 1.0, $P < 0.05$) with the average number of fish moving per day through upstream weir traps during the June–August period (Figs. 2 and 5).
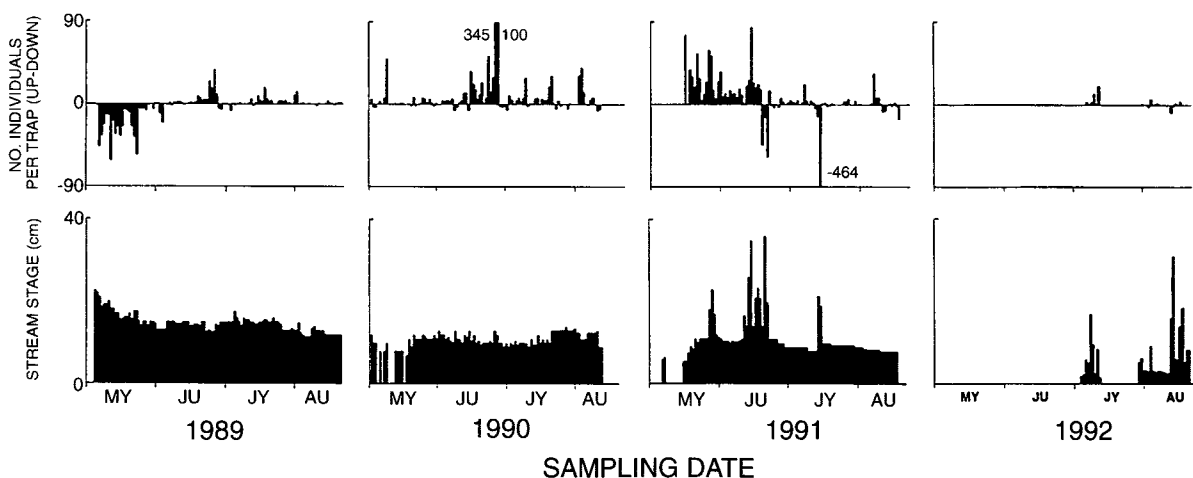

FIG. 5. Stream stage (cm) and net fluxes of fish movement in Gould Creek from 1989 to 1992. Net fluxes of fish movement represented as the number of fish captured in weir traps that were moving upstream minus the number moving downstream.

FIG. 6. Stream stage vs. the number of fish moving per day through downstream weir traps in Gould Creek from 1989 to 1992. Circled numbers indicate number of data points with similar position on the graph.
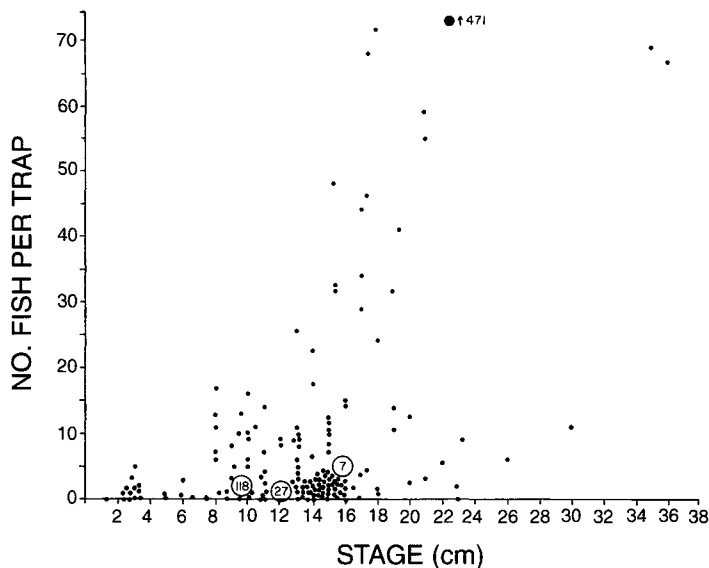
Species composition.—Individual fish taxa revealed considerable variation in their tendency for downstream vs. upstream movement. Largemouth bass, black bullhead, and fathead minnow exhibited predominantly downstream movement, especially during periods of elevated discharge (Fig. 7). Pumpkinseed sunfish, blackchin shiner, creek chub, and yellow perch exhibited predominantly upstream movement (Fig. 8). Brassy minnow, redbelly dace, and brook stickleback exhibited primarily downstream movement during high discharge conditions but upstream movement under other flow conditions (Figs. 7 and 8).

Major periods of fish movement for individual species were temporally quite restricted (Figs. 7 and 8). Several species exhibited significant movement in only 1 of 4 yr, including the largemouth bass (1991), fathead minnow (1989), blackchin shiner (1990), and yellow perch (1991). Furthermore, most of the fish movement within a year usually occurred over a very short time interval. For instance, over the 4-yr sampling period, 25% of the upstream movement of brook stickleback, 44% of the upstream movement of blackchin shiner, and 95% of the downstream movement of largemouth bass each occurred within different 2-d periods. Finally, the movement data for individual species indicate the increase in fish abundance in Gould Creek in 1990 and 1991 relative to 1989 (Fig. 2) was associated with the increased upstream movement of brassy minnow, northern redbelly dace, brook stickleback, pumpkinseed sunfish, blackchin shiner, and yellow perch (Figs. 7 and 8).

Experimental test of elevated vs. low discharge on upstream movement by fishes.—Upstream movement of fish during the pretreatment period was not significantly different (Wilcoxon paired sample test, $n = 28$, $T = 115$, $P > 0.05$) on the control (low discharge) and experimental (elevated discharge) sides of the split stream (Fig. 9, 1 May–27 May). Upstream movement of fish was significantly higher (Wilcoxon paired sample test, $n = 31$, $T = 102$, $P < 0.01$) on the elevated flow (experimental) side of the split stream during the treatment period (28 May–28 June; Fig. 9). The increase in upstream movement of fish under elevated discharge was, however, quite variable over time and between species. Approximately 60% of the fish moving upstream during the treatment did so during the 10 d from 13 June to 22 June (Fig. 9). Furthermore, of the seven predominant species moving upstream on the elevated flow side of the stream, three species (brook stickleback, pumpkinseed sunfish, and black bullhead) accounted for 84% of the individuals.

Effect of discharge and fish predation on invertebrate colonization in the experimental stream

In light of the critical role discharge potentially played in controlling the exchange of fish between the beaver ponds and Gould Creek, I conducted an experiment to assess how discharge and fish predation interacted to influence lotic invertebrate colonization. Discharge and fish predation had strong and interactive effects on the abundance of invertebrates colonizing the experimental stream (Fig. 10). A significant habitat × flow interaction (Table 4) indicated colonization of riffles and pools responded differently to low vs. elevated discharge. In the absence of fish, riffles exhibited significantly higher invertebrate abundance under elevated than low discharge conditions (Tukey's multiple comparison test, $P < 0.05$), while pools exhibited significantly ($P < 0.05$) lower invertebrate abundance under elevated than low discharge conditions (Fig. 10). Increased invertebrate abundance in riffles under elevated discharge was primarily due to increased abun-
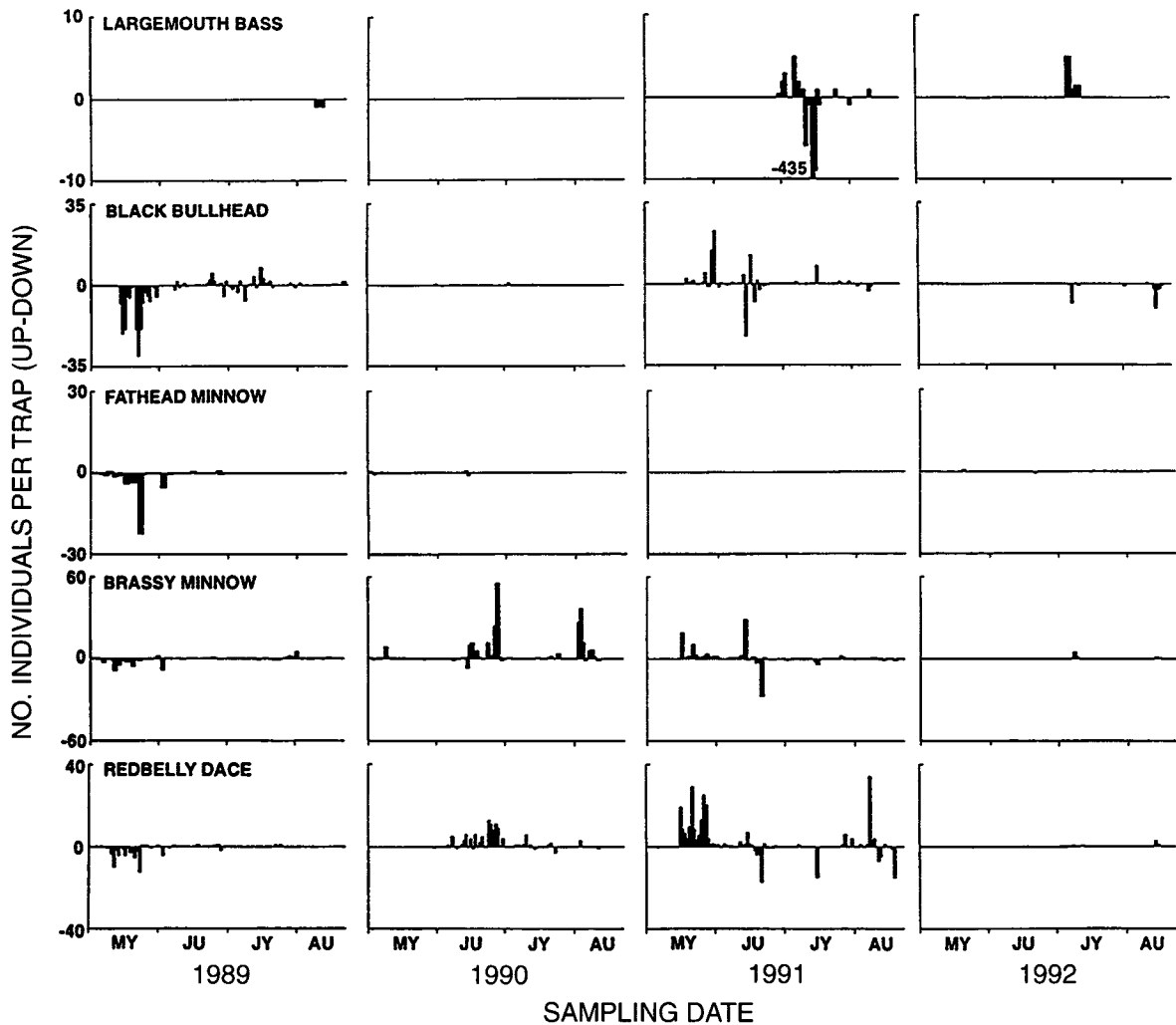
FIG. 7.   Net fluxes of largemouth bass, black bullhead, fathead minnow, brassy minnow, and northern redbelly dace movement in Gould Creek from 1989 to 1992. Net fluxes of fish movement represented as the number of fish captured in weir traps that were moving upstream minus the number moving downstream. Note the magnitude of the values on the ordinate varies among the taxa.

dance of Chironomidae (Tanypodinae and Chironominae), Simuliidae, and Oligochaeta, while decreased abundance of invertebrates in pools during elevated discharge was primarily due to decreased Cladoceran abundance (I. J. Schlosser, *unpublished data*). The significant effect of predation on invertebrate abundance (Table 4), but the absence of any significant interactions involving habitat, suggested predation had similar effects on invertebrate abundances in either riffles or pools. Fish treatments had significantly (Tukey's multiple comparison test, $P < 0.05$) lower invertebrate abundances than non fish treatments in all discharge and habitat combinations except low discharge riffles (Fig. 10). The marginally significant ($P = 0.056$) flow × predation interaction (Table 4) suggested, however, that fish predation did not have equal effects on invertebrate abundance under low and elevated discharge. Fish predation appeared to have a stronger ef-

fect on invertebrate abundance under elevated than low discharge in either riffle or pool habitats (Fig. 10).

Discharge and fish predation also had significant effects on the size structure of insects colonizing riffles and pools in the experimental stream. All comparisons of insect size distributions in fish vs. no fish treatments within a habitat type and discharge regime revealed significant (*G* test, $P < 0.01$) effects of fish predation. Similarly, all comparisons of size distributions in elevated vs. low discharge treatments within a habitat type and fish predation regime revealed significant (*G* test, $P < 0.01$) effects of discharge. These results suggest fish predation and discharge had strong individual effects on the size structure of lotic insects. Elevated discharge increased the abundance of larger (>0.50 mm head width) insects in either riffles or pools, while fish predation decreased the abundance of these size classes (Fig. 11). Examination of the insect size dis-
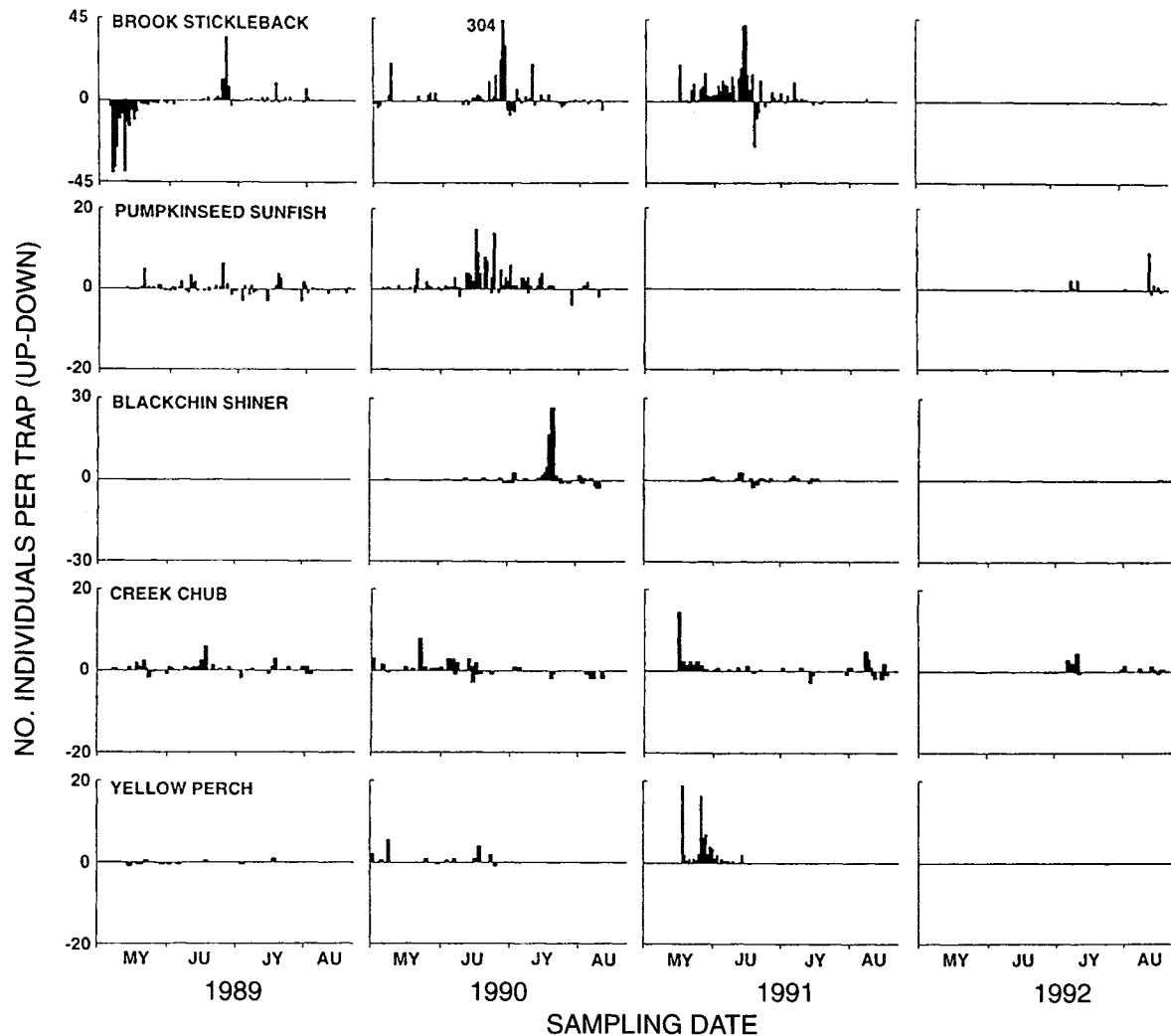
FIG. 8.   Net fluxes of brook stickleback, pumpkinseed sunfish, blackchin shiner, creek chub, and yellow perch movement in Gould Creek from 1989 to 1992. Net fluxes of fish movement represented as the number of fish captured in weir traps that were moving upstream minus the number moving downstream. Note the magnitude of the values on the ordinate varies among the taxa.
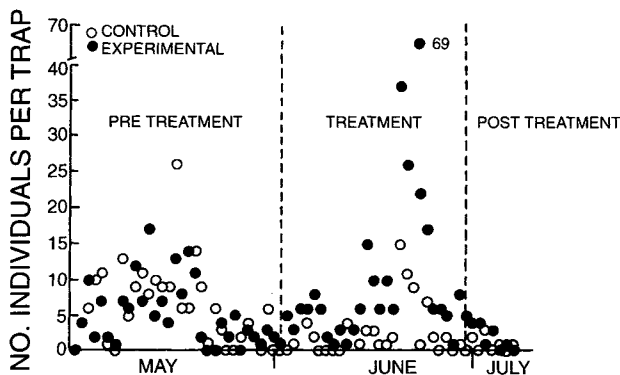

FIG. 9.   Number of fish per weir trap moving upstream on the control (base flow) and experimental (elevated flow) sides of the split stream.

tributions under the various treatments (Fig. 11) indicated, however, that, as with total invertebrate abundance, the effect of fish predation on insect size distribution did not appear to be equal under the two discharge treatments. In particular, fish predation appeared to have a stronger effect on the abundance of large insects under elevated vs. low discharge conditions in either riffles or pools (Fig. 11).

DISCUSSION

Fish assemblages in streams adjacent to beaver ponds: the role of dispersal across habitat boundaries

Beaver had, historically, strong effects on small streams throughout north-temperate areas (Naiman et
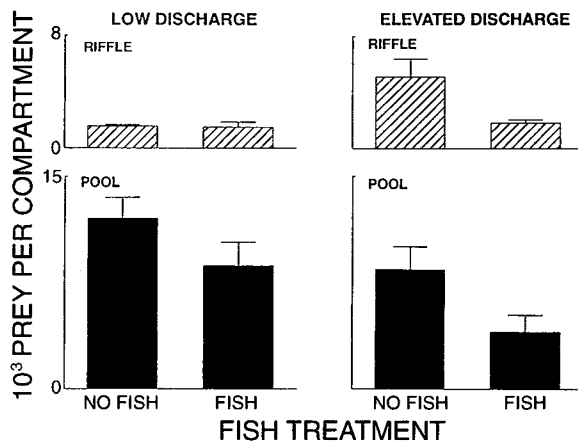
FIG. 10. Total number of invertebrate prey in riffle and pool habitats of the experimental stream under low vs. elevated discharge and fish vs. no fish treatments. Height of histogram bar is mean abundance, narrow vertical bar is 1 SE.

al. 1988). The creation of beaver ponds along stream ecosystems results in increased nitrogen fixation (Naiman and Melillo 1984, Francis et al. 1985), supply and retention of coarse particulate organic matter (Naiman et al. 1986), downstream export of fine particulate organic matter (Naiman et al. 1986), invertebrate production (McDowell and Naiman 1986), and boundary complexity (Johnston and Naiman 1987). Increased boundary complexity associated with beaver ponds includes lateral complexity between littoral and pelagic areas, vertical complexity between upper aerobic and lower anaerobic regions, and longitudinal complexity between the pond or dam and upstream and downstream areas (Johnston and Naiman 1987).

The results in this paper strongly suggest dispersal-related processes across longitudinal boundaries between beaver ponds and streams are critical in determining the dynamics of fish assemblages in adjacent lotic ecosystems. Beaver ponds appear to be key "source" areas (sensu Pulliam 1988) on the landscape (Fig. 12), where much fish production occurs (Gard 1961). At least some of the fish produced in these source areas disperse along associated stream corridors. The ultimate reasons for this dispersal were not established by this study. However, it probably at least partially involves an attempt by these fishes to colonize new "unexploited" ponds continuously being created by beaver activity (Naiman et al. 1988).

Substantial spatial and temporal variation occurs, however, in the abundance and composition of fish dispersing between pond and stream environments, resulting in considerable temporal and spatial variation in the structure of fish assemblages in adjacent lotic ecosystems. Variability in these dispersal-related processes results from a number of physical and biological factors interacting to influence fish dispersal between ponds and streams. These factors are likely to include beaver pond age, beaver pond morphology, permeability of the boundary between beaver ponds and streams, and life history processes within the fish fauna.

As beaver ponds age they exhibit successional processes involving creation of the dam and pond, exploitation of available forage by the beaver, pond abandonment, and eventual collapse of the dam (Johnston and Naiman 1987, Naiman et al. 1988). Associated with these successional stages, one would expect fish to exhibit successional cycles involving colonization of new ponds, rapid reproduction to exploit new habitat, and eventually dispersal as fish population sizes increase (Hansson 1991) or dams collapse (Stock and Schlosser 1991). Thus, the amount of dispersal between beaver ponds and streams is likely to be strongly influenced by pond age. The potential effect of pond age on dispersal may partly explain the strong temporal variation of fish abundance in Gould Creek from 1989 to 1992 (Fig. 2), even though the spatial distribution of beaver ponds was relatively stable during this period.

Substantial variation also occurs in beaver pond morphology (Fig. 12) because of the influence of geological history on the shape of the valley floor in which the dam is placed (Johnston and Naiman 1987). Ponds can vary from very shallow (<1 m maximum depth) to almost lake-like conditions (e.g., Beaver Lake), which, in turn, has strong effects on physical–chemical attributes of the pond and composition of the fish assemblage (Tonn and Magnuson 1982). Deep ponds, which are less prone to winterkill than shallow ponds, usually exhibit increased piscivore abundance but decreased abundance of small soft-rayed fishes (Tonn and Magnuson 1982, Tonn et al. 1992).

TABLE 4. Summary of analysis of variance examining the effect of habitat, stream flow, and fish predation on total invertebrate abundance per compartment in the experimental stream.

Source of variation	df	MS	F	P
Habitat	1	1.807	59.84	0.0000
Flow	1	0.002	0.06	>0.75
Predation	1	0.370	12.26	0.0030
Habitat × Flow	1	0.501	16.57	0.0009
Habitat × Predation	1	0.000	0.00	>0.75
Flow × Predation	1	0.128	4.22	0.0566
Habitat × Flow × Predation	1	0.010	0.34	>0.25
Error	16	0.030		

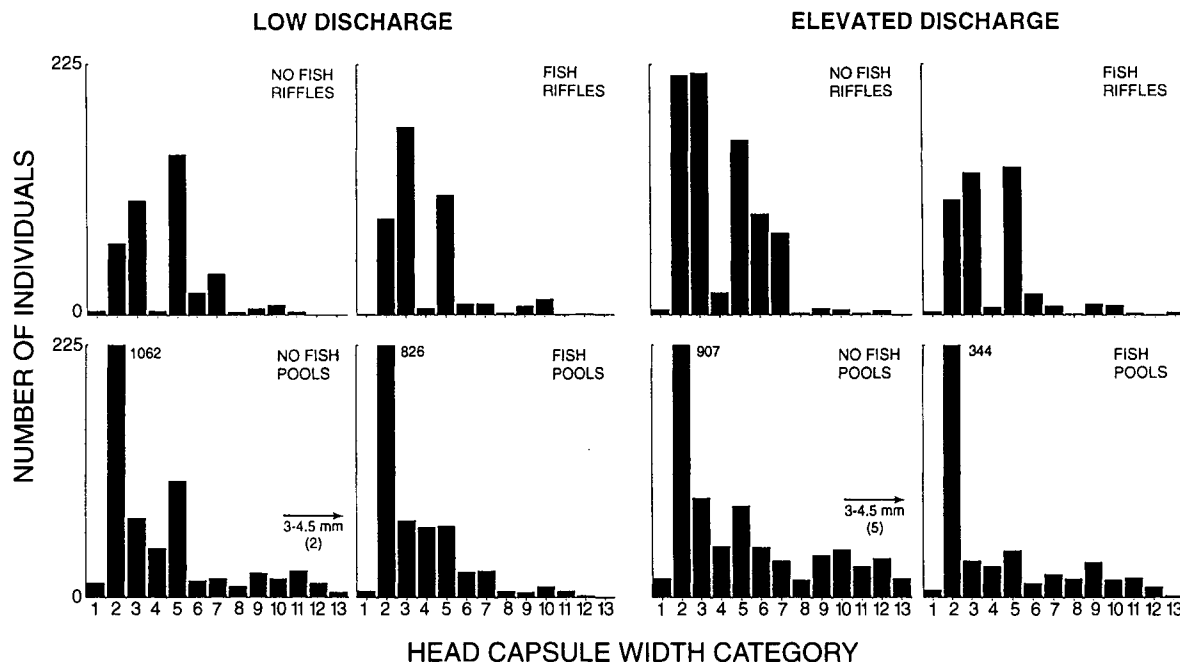LOW DISCHARGE   ELEVATED DISCHARGE

FIG. 11. Size distribution, based on head capsule width (mm), of insects in riffle and pool habitats of the experimental stream under low vs. elevated discharge and fish vs. no fish treatments. Insect size classes: 1 (0.00–0.10 mm), 2 (0.11–0.20 mm), 3 (0.21–0.30 mm), 4 (0.31–0.40 mm), 5 (0.41–0.50 mm), 6 (0.51–0.60 mm), 7 (0.61–0.70 mm), 8 (0.71–0.80 mm), 9 (0.81–0.90 mm), 10 (0.91–1.00 mm), 11 (1.01–1.10 mm), 12 (1.11–1.20 mm), 13 (1.21–1.30 mm).

Spatial variation in pond morphology will, therefore, be a fundamental factor determining spatial variation in the taxa of fish exchanged between ponds and streams. This is probably why basic differences occurred in the composition of fish moving downstream out of the larger and deeper Beaver Lake (e.g., largemouth bass, black bullhead, common shiner), relative to those moving upstream (e.g., brook stickleback,

FIG. 12. Conceptual framework for viewing exchanges between beaver pond and stream environments at the fish trophic level. Arrows indicate dispersal or attempts at dispersal. Hatched and unhatched areas represent beaver ponds of differing morphology. Beaver dams represented as boundaries that are semipermeable to fish movement.

blackchin shiner, and redbelly dace) out of the smaller and shallower ponds on Gould Creek.

Spatial variation in pond morphology and piscivore abundance also potentially influence the amount and timing of fish dispersal between ponds and streams. He and Kitchell (1990), for instance, experimentally demonstrated the importance of the indirect effect of predators (e.g., *Esox lucius*) on prey fish in small ponds by increasing emigration rates of cyprinids, particularly early in the spring. Differences in piscivore abundance between Beaver Lake and the smaller downstream ponds on Gould Creek (I. J. Schlosser, *personal observation*) may at least partially explain why most of the downstream emigration of small fish out of Beaver Lake occurred in spring (May–June), while most of the upstream emigration out of the smaller ponds occurred in summer.

The effect of discharge on the permeability of the habitat boundary between beaver ponds and streams also appears to create substantial temporal and spatial variation in fish dispersal between these environments (Fig. 12). Naiman et al. (1989) hypothesized that hydrologic fluxes and boundary permeability interact to have strong effects on ecological exchanges in lotic habitats. The results in this paper suggest downstream boundaries between beaver dams and streams are semipermeable to fish movement (Fig. 12), only allowing significant amounts of downstream fish dispersal during periods of elevated discharge. In fact, beaver normally seal the inside of their dam with mud and veg-
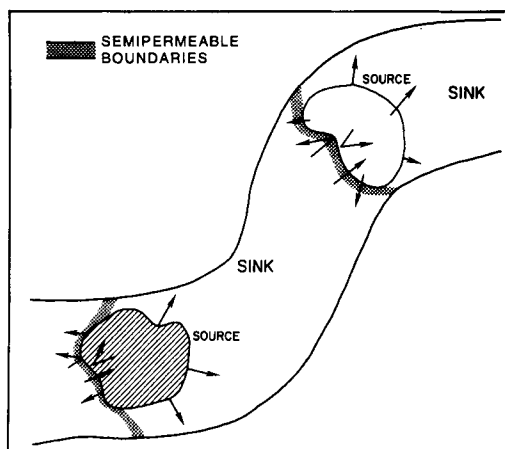
etation during low discharge conditions (I. J. Schlosser, *personal observation*), reducing surface water loss to downstream areas and decreasing the potential for exchange of fish between pond and stream environments. In contrast, upstream boundaries between ponds and streams appear more permeable to fish movement (Fig. 12), allowing exchanges of fish to occur across a broader range of discharge conditions. The split-stream experiment in which discharge was manipulated on one side of a stream above a beaver pond indicated, however, that even upstream movement of fish is likely to be reduced by very low discharge conditions but probably less so than downstream movement.

Temporal variation in the life history attributes of the fish fauna also appeared to cause considerable variability in the timing and amount of dispersal between pond and stream environments. All of the fish species in this study exhibited the vast majority of their dispersal during very brief time intervals. In fact, in some years the fish exhibited little or no dispersal across the habitat boundaries I monitored. The extreme temporal variation in dispersal probably reflects the need for appropriate physiological, developmental, and/or reproductive states of the fish to coincide with appropriate boundary conditions for dispersal to occur. Spatially explicit models of fish population and assemblage dynamics in stream ecosystems will, therefore, need to link the basic life history processes involved in fish reproduction (e.g., spawning migrations, dispersal of larval and juvenile fish, etc.) with large-scale models of spatial and temporal variation in habitat structure and boundary conditions (Jones 1958, Northcote 1978, Frissell et al. 1986, Schlosser 1991, 1995).

Finally, the absence of age 0 individuals in Gould Creek for many of these fish species suggests the stream was a potential sink (sensu Pulliam 1988), where little juvenile production occurred (Fig. 12). One might argue that size selectivity of the electric-seine, with its inefficiency at capturing fish <20 mm, was causing the pattern of limited fish recruitment in Gould Creek. Gould Creek is, however, an extremely small, shallow, clear stream with low structural complexity, where large numbers of fish <20 mm in length would have easily been observed if they had been present.

The extent to which Gould Creek, or any other stream, ultimately acts as a reproductive sink will depend on two related factors. First, it will depend on the flexibility in the life history characteristics of the individual fish taxa and their ability to effectively complete their life cycle in either pond or stream environments. Second, it will depend on the large-scale (basin level) spatial distribution of suitable pond habitats and whether fish dispersing along the stream have access to and/or can locate the pond habitats. If large-scale spatial relationships between pond and stream environments are important in determining the reproductive success of the fishes, then the numerical mixture and spatial distribution of pond (source) and stream (sink)

habitats have the potential to profoundly influence the population and assemblage dynamics of these fishes at the drainage basin level (Pulliam 1988, Danielson 1991, Dunning et al. 1992, Schlosser 1995).

Invertebrate colonization in streams adjacent to beaver ponds: the role of discharge and fish predation

In addition to having strong effects on the dispersal of fish between beaver ponds and streams, the results in this paper indicate discharge subsequently interacts with fish predation to have strong effects on invertebrate colonization in stream ecosystems. Differences in the response of stream invertebrates to discharge and fish predation in riffles and pools suggest, however, that the influence of these factors on invertebrate colonization is likely to be quite variable over even small spatial scales (see also Power 1992). Elevated discharge resulted in increased invertebrate abundance in riffles but decreased invertebrate abundance in pools. Contrary to intuitive expectations, predation appeared to have a proportionately greater influence on invertebrate colonization under elevated than low discharge conditions, particularly in pools. This latter observation is consistent with Sih and Wooster's (1994) theoretical modelling effort, which suggested that under some circumstances increased prey exchanges in streams can increase, rather than decrease, the proportional loss rate due to predator impacts. Final elucidation of the mechanism(s) underlying these complex patterns in the response of invertebrates to discharge and vertebrate predation will require experiments in which measurements of invertebrate emigration/immigration are combined with an assessment of vertebrate immigration/emigration and the direct and indirect effect of vertebrate predation on individual habitat patches (Cooper et al. 1990, Forrester 1994, Sih and Wooster 1994).

Finally, the ability of these four fish species (brook stickleback, northern redbelly dace, brassy minnow, and creek chub) to collectively depress invertebrate abundance in the stream has potentially profound implications for fish population and assemblage dynamics. Resource availability, particularly during early life history stages, is widely recognized by fish biologists as being potentially critical in influencing fish recruitment in either lentic or lotic environments (Mittelbach 1984, Werner and Gilliam 1984, Schlosser 1987, Schlosser and Angermeier 1990, Osenberg et al. 1992). The results in this paper suggest the "top-down" exploitation of invertebrate prey by vertebrate predators can significantly depress the supply of invertebrate resources to fishes in stream ecosystems. Other experiments I have conducted in the experimental stream suggest, however, that the nature and intensity of these "top-down" trophic interactions may vary between "typical" pond (e.g., stickleback) and "typical" stream (e.g., creek chub) fishes. For instance, experi-

ments in the artificial stream examining the effect of various creek chub densities on fish growth and invertebrate abundance under low vs. elevated discharge conditions revealed relatively weak effects of creek chubs on benthic invertebrate abundance (I. J. Schlosser, *unpublished manuscript*). Instead, creek chubs appeared to predominantly feed on invertebrates in the water column or drift. If fundamental differences occur in the nature of the trophic level interactions exhibited by fish species typically found in pond vs. stream environments, then alterations in the spatial distribution of source (pond) areas on the landscape and their subsequent effect on fish dispersal into sinks (streams) has the potential for altering not only the composition of fish in associated stream environments but also the fundamental nature of the competitive and predator–prey interactions in these habitats. Mathematical modelling efforts by others (Danielson 1991) suggest these sorts of dispersal-related alterations in trophic interactions, which can be mediated by the relative location of sources and sinks on the landscape, have potentially profound effects on vertebrate population and assemblage dynamics (see also Dunning et al. 1992).

Conclusions

Because of the historical extirpation of beaver over much of its southern range, most lotic fish ecologists working in warmwater streams have not incorporated the influence of beaver into conceptual models of either population or assemblage dynamics. The results in this paper suggest the large-scale spatial distribution of beaver ponds and the permeability of the longitudinal boundaries between beaver ponds and streams are critical in controlling the timing and nature of fish dispersal into adjacent lotic environments. Current research emphasizing the importance of vertebrate-driven trophic level interactions in controlling the structure of lotic ecosystems (Power 1990, Fraser and Gilliam 1992) needs to increasingly incorporate the influence of vertebrate dispersal across habitat boundaries on the nature and intensity of those interactions.

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APPENDIX

Density (no./m^2) of age 0, I, and >I largemouth bass (BA), black bullhead (BB), fathead minnow (FM), common shiner (CS), blacknose shiner (BN), brassy minnow (BM), northern redbelly dace (NR), brook stickleback (BS), pumpkinseed sunfish (PS), blackchin shiner (BC), creek chub (CC), and yellow perch (YP) in Gould Creek during spring (May) and summer (August) from 1983 to 1992.

Year	Taxa	Spring		Summer			Taxa	Spring		Summer		
		I	>I	0	I	>I		I	>I	0	I	>I
1983	BA	0.00	0.00	0.05	0.00	0.00	BB	0.02	0.00	0.01	0.02	<0.01
1984		0.00	0.00	0.11	0.00	0.00		0.00	0.00	<0.01	<0.01	0.00
1985		0.00	0.00	0.04	0.00	<0.01		0.00	0.03	0.00	0.01	0.09
1986		0.00	0.00	0.09	0.01	0.00		0.00	<0.01	0.00	0.02	0.01
1987		0.00	0.00	0.07	0.00	0.00		<0.01	0.01	0.00	0.02	0.00
1988		0.00	0.00	0.01	0.00	0.00		0.00	<0.01	<0.01	0.00	0.00
1989		0.00	0.00	0.01	0.00	0.00		0.00	0.05	<0.01	0.00	0.02
1990		0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	<0.01
1991		0.00	0.00	0.06	0.00	0.00		0.01	0.02	0.04	0.03	<0.01
1992		<0.01	0.00	0.00	<0.01	0.00		0.00	<0.01	0.00	0.00	<0.01
1983	FM	0.00	0.02	0.00	0.02	<0.01	CS	0.00	0.00	0.00	0.05	<0.01
1984		0.00	0.03	0.00	0.02	0.00		0.00	<0.01	0.00	<0.01	0.06
1985		0.00	0.06	0.00	0.17	0.02		0.00	0.04	0.00	0.13	0.15
1986		0.00	0.25	0.00	<0.01	0.00		0.07	0.42	0.00	0.29	0.28
1987		0.00	0.01	0.00	0.00	0.00		0.00	0.02	0.00	0.00	0.02
1988		0.00	<0.01	0.00	0.00	<0.01		0.00	0.00	0.00	0.00	0.00
1989		0.00	0.00	0.00	0.00	0.03		0.00	0.00	0.00	0.00	0.00
1990		0.00	<0.01	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00
1991		0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00
1992		0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00
1983	BN	0.00	0.00	0.00	0.01	0.00	BM	0.00	0.00	0.00	0.00	0.00
1984		0.00	0.00	0.00	0.00	0.14		0.00	0.03	0.00	0.04	0.00
1985		0.00	0.02	0.00	0.85	<0.01		0.00	0.79	0.00	0.00	<0.01
1986		0.00	0.14	0.00	0.00	0.00		0.00	0.20	0.00	0.01	<0.01
1987		0.00	0.01	0.00	<0.01	0.00		0.00	1.33	0.00	0.00	0.00
1988		0.00	0.05	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00
1989		0.00	0.00	0.00	0.00	0.33		0.00	0.00	0.00	0.00	0.00
1990		0.00	0.00	0.00	0.00	0.02		0.00	0.00	0.34	0.75	0.03
1991		<0.01	0.01	0.00	0.00	0.00		0.00	<0.01	0.00	0.08	0.06
1992		0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	<0.01
1983	NR	0.00	0.11	0.00	0.18	0.03	BS	0.02	0.13	0.01	0.00	0.00
1984		0.00	0.00	0.00	<0.01	<0.01		0.10	0.03	0.00	0.00	0.00
1985		0.07	0.22	0.00	0.24	<0.01		<0.01	<0.01	0.00	0.00	0.00
1986		0.00	0.91	0.00	0.00	0.00		0.00	0.10	0.00	0.00	0.00
1987		0.00	0.02	0.00	0.00	0.00		0.00	<0.01	0.00	0.00	0.00
1988		0.00	0.13	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00
1989		0.00	<0.01	0.00	0.10	0.04		0.00	0.00	0.00	0.00	0.00
1990		0.00	0.01	0.07	0.16	0.00		0.08	0.02	0.65	0.03	0.00
1991		<0.01	0.26	0.01	0.23	0.02		0.18	0.21	0.00	0.06	0.00
1992		0.00	0.00	<0.01	0.02	0.00		0.00	0.06	<0.01	0.01	0.00
1983	PS	0.00	0.00	0.00	0.00	0.00	BC	0.02	0.03	0.00	0.11	0.00
1984		0.00	0.00	0.00	0.02	0.01		0.00	0.00	0.00	0.00	0.00
1985		0.00	<0.01	0.00	0.01	<0.01		<0.01	0.00	0.00	0.08	0.00
1986		0.00	0.00	0.00	0.00	<0.01		0.00	0.03	0.00	0.00	0.00
1987		0.00	0.00	0.00	0.07	0.03		0.00	0.00	0.00	0.00	0.00
1988		0.03	0.02	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00
1989		0.01	0.04	0.00	0.02	0.02		0.00	0.00	0.00	0.00	0.00
1990		0.01	0.03	0.00	0.04	0.06		0.46	<0.01	<0.01	2.12	0.00
1991		0.00	0.03	0.00	0.00	0.00		0.02	0.05	0.00	0.00	0.07
1992		0.00	0.02	0.00	0.02	0.00		0.00	0.00	0.00	0.00	0.00
1983	CC	0.00	0.00	0.00	0.04	0.04	YP	0.00	0.00	0.00	0.00	0.00
1984		0.00	0.02	0.00	0.00	0.10		0.00	0.00	0.03	0.00	0.00
1985		0.00	0.08	0.00	0.02	0.09		0.00	0.00	<0.01	<0.01	0.00
1986		<0.01	0.20	0.03	0.13	0.34		0.00	0.00	0.01	0.00	0.00
1987		0.02	0.14	0.08	0.00	0.04		0.00	0.00	0.00	0.00	0.00
1988		0.05	0.04	1.37	<0.01	<0.01		0.00	0.00	0.00	0.00	0.00
1989		0.03	0.03	<0.01	0.13	0.17		0.00	0.00	0.00	0.00	0.00
1990		0.00	0.07	2.04	<0.01	0.01		0.05	0.00	0.00	0.00	0.00
1991		0.16	0.23	1.81	0.14	0.06		0.13	0.03	0.00	0.00	0.00
1992		0.00	<0.01	0.68	0.00	0.01		0.00	0.00	0.00	0.00	0.00