

EFFECTS OF FLOW REGIME AND CYPRINID PREDATION ON A HEADWATER STREAM¹

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Abstract. We used descriptive and experimental approaches on Gould Creek, a first-order tributary of the Mississippi River near Lake Itasca, Minnesota to assess the influence of (1) flow regime on the colonization dynamics and abundance of invertebrates and cyprinids, and (2) cyprinid predation on invertebrates and fishes. Stream flow varied annually during the 3-yr (1984–1986) period. One dry year (1984), with few periods of elevated flow, was followed by two wet years (1985–1986), with prolonged elevated (nonscouring) discharge. The density of benthic and drifting invertebrates increased dramatically with elevated flow. Benthic riffle invertebrates in particular increased, from a maximum of 9000 individuals/m² in 1984 to 91 000 individuals/m² in 1985 and 51 000 individuals/m² in 1986. Larval Hydropsychidae and Simuliidae were the primary groups increasing in abundance during elevated flow. To assess directly the influence of flow regime on benthic insect densities, flow was manipulated in six subsections of a riffle and colonization of natural rock substrates monitored. Total insect abundance was higher under elevated (nonscouring) vs. low flow within 6–8 d; after 24 d insect abundance was three times as high under elevated flow. Insect families responded differently to elevated flow, with the largest increase resulting from a pulse of colonization by larval Hydropsychidae in 6–8 d.

Cyprinid density in Gould Creek also increased with elevated flow from 0.1–0.3 cyprinids/m² in 1984 to 1–2 cyprinids/m² in 1985 and 1986. The increased fish density was most pronounced during spawning periods in spring (May–June) and consisted primarily of older individuals. All cyprinids, except the creek chub (*Semotilus atromaculatus*), decreased in abundance 4–5 wk after spring colonization, regardless of flow conditions and invertebrate abundance. All cyprinids in Gould Creek selected pool habitats. Experiments in an artificial stream on Gould Creek indicated cyprinids influenced invertebrate abundance, but the effect of cyprinid predation was variable among habitats. Invertebrate abundance decreased most in structurally complex pools but exhibited little response to cyprinid predation in shallow riffle and raceway habitats. Because predation intensity varied among habitats, pool-dwelling invertebrates such as Chironomidae and Crustacea decreased more in the presence of cyprinid predation than riffle-dwelling Hydropsychidae and Simuliidae. However, if Simuliidae occurred in pool habitats, they were strongly selected by cyprinids, resulting in a significant depression in prey size in pools. Experiments in the artificial stream indicated creek chubs preyed on adult cyprinids, but larger species (adults 70–80 mm) were less susceptible to predation than smaller species (adults 50–60 mm). However, even taxa with small adult size were preyed on at a low rate, and all cyprinids strongly selected pools, with creek chubs having minimal effect on habitat use.

These results suggest that (1) the hydrologic regime has broad and pronounced effects on the colonization dynamics and abundance of invertebrates and fishes in headwater streams, and (2) cyprinid predation has weaker but variable effects on the abundance of stream organisms. Predation intensity varies (a) over short temporal scales, because of the dynamic nature of flow regime and the rapid colonizing ability but short post-spawning persistence of cyprinids, (b) over small spatial scales, because of increased abundance of cyprinids in pool vs. riffle habitats, (c) between invertebrate and vertebrate trophic levels because the creek chub is a relatively ineffective piscivore, and (d) between small and large fish because many minnows have a size refuge from creek chubs.

Key words: beaver pond; benthic invertebrate; cyprinid; fishes; flow regime; headwater stream; landscape ecology; Minnesota; minnows; predator–prey interactions.

INTRODUCTION

A basic and enduring question in ecology concerns the relative influence of abiotic variability and biotic interactions on population, community, and ecosystem

characteristics (Horwitz 1978, Allan 1982, 1983, Fisher et al. 1982, Fisher 1983, Hemphill and Cooper 1983, Peckarsky 1983, Reice 1983, Roughgarden 1983, Strong 1983, Strong et al. 1984, Power et al. 1985). Current paradigms in stream ecology imply that both abiotic and biotic factors are likely to be important in determining the distribution and abundance of stream or-

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ganisms, and that the relative influence of these variables is likely to change in aquatic environments across the landscape (Cummins 1975, Vannote et al. 1980, Minshall et al. 1983, 1985, Statzner and Higler 1985). However, few studies in lotic ecosystems, especially at higher trophic levels, have jointly assessed the influence of abiotic variability and biotic interactions on biological characteristics. Our objective in this study was to evaluate simultaneously (1) the influence of a key abiotic variable, flow regime, on the colonization dynamics and abundance of invertebrates and cyprinids in a headwater stream, and (2) the influence of a potentially important biotic interaction, cyprinid predation, on the distribution and abundance of invertebrates and small fishes.

We focused on fluctuations in stream discharge because they influence a wide range of physical variables affecting stream biota, including nutrient, organic, and sediment transport (Wallace et al. 1982, Tate and Meyer 1983), production processes at lower trophic levels (Fisher et al. 1982), habitat availability (Schlosser 1982, Peckarsky 1983, Schlosser and Toth 1984, Reice 1985), and the three-dimensional characteristics of the stream channel (Leopold et al. 1964). We evaluated the role of cyprinid predation because cyprinids are a predominant component of the fish fauna in small streams throughout much of the eastern United States, and because vertebrate predation has been widely reported as a major organizing force in other aquatic communities (Brooks and Dodson 1965, O'Brien 1979, Carpenter et al. 1985, Carpenter and Kitchell 1987). However, the importance of vertebrate predation in determining the abundance of stream organisms has been questioned (Allan 1982, Reice 1983).

Specifically, in this paper we combine descriptive and experimental approaches to: (1) examine the association between annual variation in stream flow and annual variation in benthic invertebrate and drift density, (2) manipulate flow regime in a natural riffle to assess directly the influence of elevated (nonscouring) vs. low flow conditions on colonization of natural substrates by aquatic insects, (3) examine the association between seasonal and annual variation in stream flow and the colonization dynamics and densities of stream cyprinids in riffle and pool habitats, and (4) use an experimental stream to evaluate (a) the influence of predation by cyprinids on the abundance of aquatic invertebrates, and (b) the effect of the primary aquatic piscivore in the stream (creek chub; *Semotilus atromaculatus*) on survival and habitat use of cyprinid prey.

STUDY SITE

We conducted the study on Gould Creek, a headwater tributary of the Mississippi River, located ≈ 4 –6 km west of the University of Minnesota Forestry and Biological Station at Lake Itasca. Gould Creek is a high

gradient (10m/km) stream with well-developed pool and riffle habitats originating as the drainage outlet of Beaver Lake. Beaver Lake is a natural lake which was increased in area and depth by a 2 m high beaver dam at its outlet. The dam has been in place almost permanently since at least the 1940s according to local landowners. The fish fauna of the stream is predominantly cyprinids, although the brook stickleback (*Culaea constans*) is common in the lower part of the creek. In addition, small numbers of younger age classes of lake fishes, particularly Ictaluridae and Centrarchidae, also occur in the stream during summer months.

METHODS

Annual variation in precipitation, stream flow, and water temperature in Gould Creek

We obtained daily precipitation records from the University of Minnesota weather station at Lake Itasca. Stream stage was measured with a Leopold and Stevens Type F continuous stage recorder in the lower part of the drainage basin. Stream stage was a reliable indicator of the frequency of elevated stream flow during the 3-yr study period. However, because of channel sedimentation in the vicinity of the gauge in late 1985, stream stage was not a reliable indicator of relative discharge. Stream temperature was recorded 100 m downstream from the beaver dam with a Ryan Model J continuous recording thermograph.

Annual variation in invertebrate abundance in Gould Creek

To assess the association between annual variation in stream flow and invertebrate abundance, we sampled benthic and drifting invertebrates at monthly intervals from May–September 1984 and April–September 1985–1986. We sampled benthic invertebrates in a riffle and shallow pool 70–100 m downstream from the beaver dam using a Surber sampler (0.093 m²) with 240- μ m mesh net. Five Surber samples were taken from each habitat and pooled for later enumeration. While five Surber samples would not adequately assess the number of individuals per species (Needham and Usinger 1956, Chutter 1972), it would assess the relative abundance of the common taxa (Hynes 1970, MacKay and Waters 1986). We normally sampled invertebrate drift below a riffle for 1 h, within 2 h after sunset, with a 30 \times 45 cm tapered net (360- μ m mesh). The net was emptied every 20 min during elevated flow conditions to avoid clogging and backwash effects. Volume of water sampled was determined based on average water depth and velocity at the net mouth and drift density was expressed as number of organisms per 100 m³ of water. Drift samples were subsampled as described by Waters (1969). We subsampled benthic samples after elutriation of invertebrates from substrates. One-eighth of each benthic or drift sample was counted.

*Flow manipulation and insect
colonization in Gould Creek*

To assess experimentally the influence of stream flow on benthic invertebrates, flow was manipulated in a single riffle of Gould Creek ≈ 35 m below the beaver dam. The objective of the experiment was to examine colonization rates of insects on natural rock substrates under elevated (nonscouring) and low flow conditions to establish directly (1) if insect abundance increases under elevated flow, (2) the length of time elevated flow has to persist before an increase in insect abundance occurs, and (3) which insect taxa increase most under elevated flow.

We cleared a riffle of the large rocks, and the underlying gravel substrate was leveled. The riffle was divided longitudinally into six subsections by boards 2 m long spaced 0.3 m apart. Individual rocks served as the invertebrate sampling unit during the experiment. Rocks were collected in the creek, scraped clean of all organic debris, dried, and divided into groups of six by size, material, and texture. In an attempt to reduce any "rock bias" among subsections, only one of these six similar rocks was placed in the same location in each subsection. We placed rocks in subsections in a 3 across-stream and 10 downstream pattern. Volume of individual rocks varied from 150–520 mL, but rock volumes ($\bar{X} \pm 1$ se) in elevated (281.9 ± 10.6 mL) and low (282.9 ± 10.3 mL) flow treatments were not different ($t = 0.09$, $P > .05$). We manipulated flow so three subsections experienced low flow and three elevated (nonscouring) flow. Treatments alternated across the stream and discharge was manipulated by diverting flow from low to elevated flow subsections. Discharge was maintained at relatively stable levels during the experiment by siphoning water over the beaver dam with three, 5 cm diameter flexible plastic pipes. The water siphoned from the pond was mixed with water already in the stream, before the flow entered the riffle area, to reduce any differences in chemical characteristics of water in elevated and low flow subsections. Water depth and discharge were measured in each subsection during the experiment. All rocks were placed in the subsections on 28 July 1986, which was a period of decreasing stream discharge. We removed three rocks from a priori randomly determined locations within each of the subsections 1, 2, 4, 6, 8, 16, and 24 d after the experiment began. The experiment ended after 24 d because of insufficient water for diversion from the beaver pond. Front and back rows of rocks were not collected to avoid any potential "edge effects." Rocks were removed each collection day, thoroughly cleaned of organisms, and returned to their same location to maintain constant hydrologic conditions. We identified and counted five insect families: Hydropsychidae, Simuliidae, Chironomidae, Heptageniidae, and Baetidae. These families included at least 99% of the insects found on the rocks.

The effect of insect family, flow, and flow \times family interactions on colonization rate (change in number of individuals per rock per day) and density (number of individuals per rock) were analyzed using log-transformed data and a two-way analysis of variance with repeated measures (Winer 1971). The mean for the three rocks collected for a given treatment, date, and subsection was considered one replicate. Since the replicates were sequentially collected in the same subsections of the stream, the date a sample was collected was considered a repeated factor and the analysis did not assume successive dates were independent of each other. A useful discussion of the appropriate error terms, calculation of degrees of freedom, and assumptions of the repeated measures ANOVA is provided by Vanni (1986). Colonization rate and abundance of each insect family, on each day of the experiment, under elevated vs. low flow were also compared using standard t tests. Since the t tests involved multiple comparisons, seven for each taxon and treatment, the Bonferroni correction was used to determine an appropriate significance level of .007 by letting alpha equal $(1 - 0.95^{1/7})$.

Cyprinid abundance in Gould Creek

Four minnows in Gould Creek were intensively sampled over a 3-yr period (1984–1986): brassy minnow (*Hybognathus hankinsoni*), northern redbelly dace (*Phoxinus eos*), fathead minnow (*Pimephales promelas*), and creek chub (*Semotilus atromaculatus*). These four species usually comprised 70–80% of the fish in the stream. Fish were sampled with two techniques; electro-seining and minnow trapping.

Electro-seining established the distribution of minnows in riffles vs. pools and the size (age) structure of the fish populations. 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), totaling 140 m in length, were normally sampled directly below the beaver dam. However, in August 1986 only four riffles were sampled because one riffle had been modified for the previously described flow manipulation experiment. 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 upper and lower ends of each habitat prior to sampling. Each area was electro-seined twice and fish were 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, 1985, 1987a) and ranges from 40–80% for minnows, averaging 50–60%. Total length of most individuals was measured in the field and fish were returned to the stream. Individuals were separated into four age groups based on size-frequency distributions; 0, I, II, and $> II$. The use of size-frequency distributions for aging fishes results in some misclassification be-

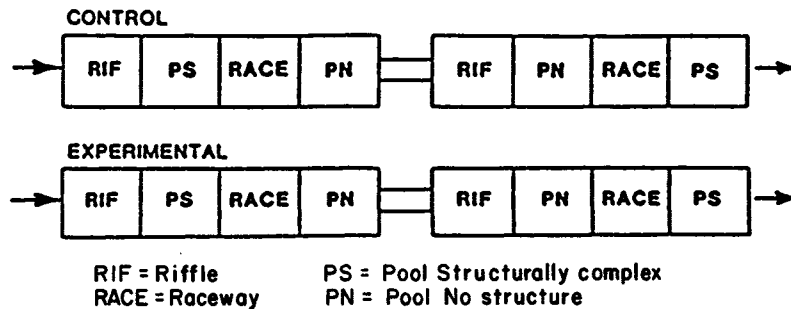


FIG. 1. Position of the experimental stream units below the beaver dam. Each stream unit contains four habitat compartments. Arrows indicate direction of stream flow.

cause of overlapping sizes of different age groups, and is most effective at segregating earlier age groups (Jerald 1983). Fish density was calculated using the area of each riffle and pool (product of its length and mean width). The influence of habitat, species, and habitat \times species interactions on fish density were analyzed on log-transformed data with a two-way analysis of variance with repeated measures; time of sampling was the repeated factor.

Minnow trapping established more precisely the temporal colonization dynamics of the cyprinids. Minnows were sampled for 2 d, every 2 wk, from June–September in 1984 and April–September in 1985–1986 with standard, unbaited Gee's minnow traps (40 \times 19 cm, opening 2.5 cm, mesh 0.5 cm). Three traps were placed in each of the five pools for a total of 15 traps. The traps were anchored with metal frames on the bottom and at the center of the pool, with one trap on each edge of the stream and one in the middle. We checked the traps every 24 h.

*Cyprinid predator and invertebrate
prey interactions in the
experimental stream*

The experimental stream has been previously discussed in detail (Schlosser 1987a). It is located in the uppermost reaches of Gould Creek just below the beaver dam and to the west of the main stream channel. Water was fed to the stream via flexible 5 cm diameter plastic pipes siphoning water over the dam. Standard valves on the pipes regulated flow.

There were two lines of streams, each consisting of two separate units, for a total of four units (Fig. 1). Each unit was screened (0.6-cm mesh) at upstream and downstream ends to prevent movement of fish between units. In addition to a 0.5 m long "headwater" box into which water for each unit was released, the units were partitioned into four compartments (each compartment 0.5 \times 1 m) by wooden dividers with holes cut to allow fish and water to move between compartments. Each compartment in all four units could be simultaneously isolated by metal drop gates so the distribution of fish and insects among compartments could be established. All compartments were covered

with 0.6-cm mesh hardware cloth lids to prevent access by terrestrial predators.

The compartments represented four habitats found in Gould Creek. Riffles were shallow (4–6 cm), fast-water (2% slope) habitats with gravel substrates overlain by rocks >80 mm in diameter. Raceways were moderately deep (10–12 cm) and moderately fast-water (1% slope) habitats with gravel substrates overlain by rocks >100 mm in diameter. Pools were deep (40–45 cm), slow-water (1% slope) habitats with sand substrates. The slower velocities in pool vs. raceway habitats were due to identical discharge in these subsections but a larger volume in pools. In addition, one of the pools in each unit was made structurally complex by adding two 15 cm long sections of 10-cm polyvinyl chloride plastic pipe, to simulate holes in undercut banks, and three dendritic pieces of woody debris.

To assess the influence of cyprinids on invertebrate abundance, invertebrate densities in the four stream habitats were determined in the presence and absence of cyprinid predation. The experiment was conducted in the spring from 9 May–1 June 1986, a period of maximum cyprinid abundance in Gould Creek. Prior to initiation of the experiment, natural sand, gravel, and rock substrates were collected from Gould Creek. A fixed quantity of substrate was randomly placed in the appropriate compartments of the experimental stream. Additional insect colonization of the stream units was then allowed for 2 wk. The control (no cyprinid predators) and experimental (cyprinid predators present) units were run concurrently. To avoid position effects (Hurlbert 1984), the front unit was the control in one line and experimental in the other, with a coin toss used to determine the treatment in the two lines.

All minnows used in the experiment were collected with minnow traps from Gould Creek. The experiment began by placing four individuals per species in each experimental unit, one per compartment. Size of fish (total length; $\bar{X} \pm 1$ SE) used in the experiment reflected the predominant size classes in Gould Creek; brassy minnow (67.0 \pm 3.4 mm), northern redbelly dace (54.6 \pm 1.2 mm), fathead minnow (62.1 \pm 3.4 mm), and creek chub (61.6 \pm 6.1 mm). The density of fish, 2 fish/m² per species and 8 fish/m² for all species com-

TABLE 1. Summary of conditions for predatory fish and minnow prey experiments in the experimental stream. Predator species is *Semotilus atromaculatus* in all cases. Lengths are given as $\bar{X} \pm \text{SE}$.

	Prey species		
	<i>Hybognathus hankinsoni</i>	<i>Phoxinus eos</i>	<i>Pimephales promelas</i>
Prey total length (mm)	73.9 \pm 1.4	55.7 \pm 0.5	56.5 \pm 0.8
Number of prey per stream unit	16	16	16
Predator total length (mm)	168.5 \pm 3.2	166.1 \pm 3.3	168.0 \pm 3.0
Water temperature ($^{\circ}\text{C}$)	18–22	16–20	18–23
Stream discharge (L/s)	2–2.5	2–2.5	2–2.5
Number of replicates	8	8	8

bined, was above the average density of minnows in Gould Creek, when all available habitat area was included in the density calculation, but below the maximum density of minnows commonly observed feeding within a given patch of habitat in the stream. Water temperature (15°–22°C) and discharge (2–2.5 L/s) were measured throughout the experiment.

Fish were allowed to feed for 10 d. Flow was then stopped and all compartments simultaneously isolated. The water in each compartment was filtered, substrates removed, and invertebrates elutriated and subsampled. Invertebrates in one-eighth of the sample were then enumerated. Insect head capsule widths were measured with an ocular micrometer. The effects of habitat, predation, and habitat \times predation interactions on total invertebrate abundance were analyzed with a two-way ANOVA on log-transformed data.

*Aquatic piscivore and cyprinid
prey interactions in the
experimental stream*

Preliminary observations of cyprinids in the absence of the predominant aquatic piscivore in Gould Creek (creek chubs; *S. atromaculatus*) indicated a preference for pools in both Gould Creek and the experimental stream. Furthermore, in natural streams, piscivores are normally in deep habitats with shallow areas serving as prey refugia (Schlosser 1982, 1987a, b, Power 1984, 1987). In light of these patterns, the experiments were designed to assess simultaneously: (1) the effectiveness of adult creek chubs at capturing minnows in the stream when shallow refugia exist, (2) the effect of the presence of creek chubs in pools on the habitat selection patterns of minnow prey, and (3) the influence of structural complexity of pool habitats on the interaction between creek chubs and their prey.

To achieve these objectives, habitat selection and mortality rates of three predominant minnows in the stream, brassy minnow, redbelly dace, and fathead minnow, were determined in the absence (controls) and presence (experimentals) of adult creek chubs. Two control and two experimental units were always run concurrently, but the constraint of four stream units required that any more than two replicates, and the different prey taxa, be run sequentially. There were no major weather changes during the experiments; flow

was constant and water temperature nearly constant (Table 1).

All fish used in the experiments were collected with minnow traps from Gould Creek and reflected the size composition of fishes in the natural stream. Experiments began by placing 16 prey in each stream (Table 1), 4 prey per compartment. All prey fish were used only once. Minnows were introduced 10–15 min before predators. Three creek chubs were placed in each pool (Table 1), mimicking the clumped distribution of adult creek chubs found in pools of natural headwater streams (Fraser and Sise 1980, I. J. Schlosser, *personal observation*). Experiments were run for 3 d. At the end of the 3rd d, between 0800–1000, fish were trapped in all compartments by releasing the metal drop gates and halting the flow. Fish in each compartment were dipnetted and counted. Since 98–99% of all fish were recaptured in control streams, including dead fish, absence of fish was attributed to predation by creek chubs.

Predation rates on the three prey species were compared using a one-way ANOVA with Tukey's range test. The behavioral response (habitat use) of the prey taxa to creek chubs was analyzed on log-transformed data for each prey taxon with a two-way analysis of variance with repeated measures. This design tested for the effects of habitat, predation, and habitat \times predation interactions on minnow abundance. Since the replicates were sequentially repeated in the same experimental units, using the same predators, the date a trial was conducted was considered a repeated factor and we did not assume successive trials were independent of each other.

RESULTS

*Annual variation in precipitation,
stream flow, and water temperature in
Gould Creek*

There was considerable annual variation in precipitation and stream flow during the 3-yr study (Fig. 2). The 1st yr (1984) was relatively dry, with low flow conditions throughout most of the year. Beginning in May 1985, and persisting through most of the summer of 1986, rainfall increased. Numerous rainstorms occurred during the summer of 1985, resulting in frequent and prolonged periods of elevated discharge (Fig. 2).

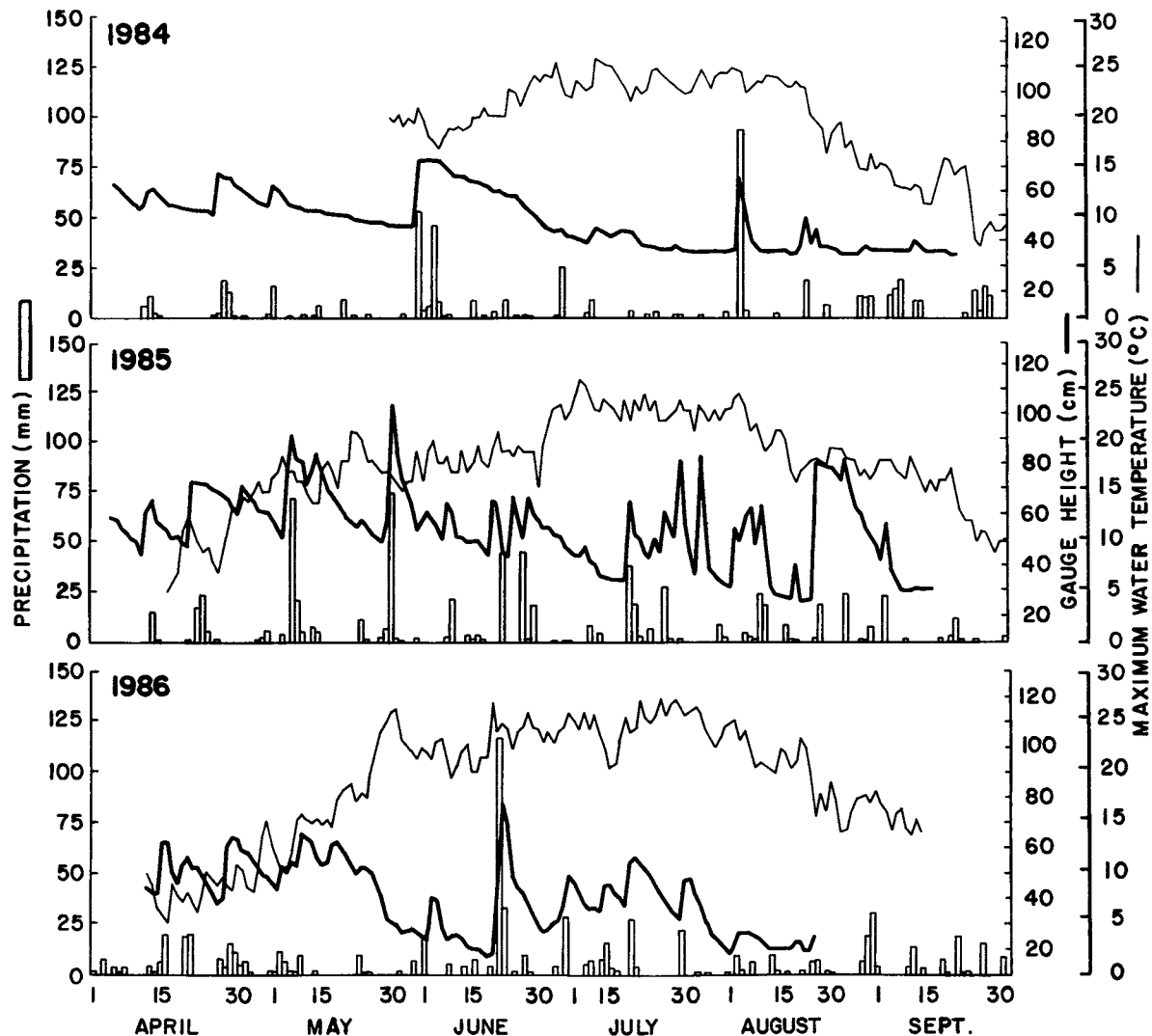


FIG. 2. Daily precipitation, stream stage, and maximum daily water temperature during the 3-yr study period (1984–1986).

TABLE 2. Benthic insect densities (no./m²) over a 3-yr period in riffle and pool habitats of Gould Creek. Each number based on five Surber samples. Other insect orders combined comprised $\leq 1\%$ of the samples.

	1984					1985		
	May	Jun	Jul	Aug	Sep	Apr	May	Jun
Riffle								
Diptera	4953	1238	1066	2752	2666	3801	20 020	14 671
Simuliidae*	2984	490	77	51	138	1737	13 966	344
Trichoptera	430	172	4042	3818	4145	2855	946	25 593
Ephemeroptera	17	95	77	1918	542	103	17	1943
Coleoptera	100	198	...	138	1342	275	120	585
Total	5460	1703	5185	8626	8833	7034	21 103	42 792
Pool								
Diptera	628	95	1293	206	1152	3939	206	2855
Simuliidae	9	69	52
Trichoptera	9	52	86	17	86	1685
Ephemeroptera	34	43	34	17	17	241
Coleoptera	...	17	17	...
Total	671	155	1327	275	1255	3956	309	4281

* Individuals of the family Simuliidae were numerically predominant representatives of the Diptera under elevated flow conditions.

† ... No individuals were found in the sample.

There was so much standing water in the drainage basin by August 1985 that beaver dams had to be removed in the drainage basin above Beaver Lake to prevent flooding of nearby roads. This resulted in a major period of elevated flow in the stream (Fig. 2). Wet conditions in the drainage basin in autumn of 1985 maintained elevated flows in the stream throughout the winter and spring of 1986. Stream flow decreased in early June of 1986, but by late June and early July another series of thunderstorms resulted in elevated flows that persisted until early August.

Stream temperature exhibited less annual variation than precipitation and stream flow (Fig. 2). The primary feature of annual variation in temperature was the timing of the abrupt increase in temperature associated with summer conditions. For the first 2 yr (1984–1985) the increase occurred from mid to late June. However, in 1986, warm air temperatures in early to mid-May resulted in temperatures of $\approx 25^{\circ}\text{C}$ by late May rather than late June (Fig. 2).

Annual variation in invertebrate abundance in Gould Creek

Benthic insect densities increased dramatically in association with elevated stream flow in 1985 and 1986, especially during summer in riffles (Table 2). Maximum insect densities in riffles increased from ≈ 9000 insects/ m^2 in 1984 to 91 000 insects/ m^2 in July 1985 and 51 000 insects/ m^2 in July 1986. Trichoptera and Diptera larvae, especially Simuliidae, were the primary taxa causing increased insect densities in riffles during elevated flow. Simuliidae tended to be most abundant in spring (April–May), while Trichoptera were most abundant in summer (June–August). Increased abundance of Trichoptera during elevated flow conditions was due to increased abundance of all size classes (I. J. Schlosser, *personal observation*). Benthic insects, especially Diptera, were also more abundant in pools in

1985–1986, but the increase was not as dramatic as that observed for riffles (Table 2).

Higher drift densities also occurred during elevated flow (Table 3), particularly in spring (April–May) 1986, when an extremely large increase in crustacea occurred. However, insect densities also increased in the drift during the summer and early autumn of 1985–1986, especially Diptera and Trichoptera (Table 3).

Flow manipulation and insect colonization in Gould Creek

To assess experimentally the effect of stream flow on insect colonization rates and abundance, flow was manipulated in a single riffle of Gould Creek. The flow treatments created during the experiment were relatively constant over the 24-d period (Fig. 3), with only a slight decrease in the elevated flow due to low precipitation and a decrease in the amount of water available in Beaver Lake for diversion. Flows were well within the range normally observed in Gould Creek. Water depth under elevated flow was usually 2 cm or more above the upper surface of the rocks, but under low flow varied from 80–100% coverage of the rock surface area.

Flow regime had pronounced effects on insect abundance (Fig. 4). Total insect abundance under low flow conditions stabilized after 6–8 d, while insect abundance under elevated flow was still increasing after 16–24 d (Fig. 4, Tukey's Studentized Range Test; $P < .05$). By day 8 of the experiment there were significant differences in insect abundance in the elevated and low flow treatments (Fig. 5) and after 24 d there were 480 and 150 insects per rock, respectively, under the elevated and low flows.

The general pattern of increased insect abundance under elevated flow was a composite response of five families: Hydropsychidae, Simuliidae, Chironomidae, Heptageniidae, and Baetidae, which represented 99%

TABLE 2. Continued.

1985			1986					
Jul	Aug	Sep	Apr	May	Jun	Jul	Aug	Sep
16 735	1479	1772	29 584	39 818	8428	3990	1909	3285
...	103	258	24 854	34 864	103	34	51	...
70 520	16 409	11 713	2735	2890	17 131	43 894	29 308	6983
3630	1359	258	...	1204	4317	1978	3302	1600
602	310	550	120	170	430	1236	1600	2959
91 487	19 557	14 293	32 439	44 082	30 306	51 098	36 119	14 827
4352	2631	1875	12 745	2494	14 964	4145	4525	6794
120	17	...	103	155	17
912	568	344	86	172	189	275	34	17
17	...	52	...	17	...	34	...	52
...	34	34	17	17
5281	3199	2271	12 831	2683	15 817	4488	4626	6880

TABLE 3. Drift density (no./100 m³) of insects and crustacea over a 3-yr period in Gould Creek.

	1984					1985		
	May	Jun	Jul	Aug	Sep	Apr	May	Jun
Diptera	131	230	34	...*	...	39	344	55
Trichoptera	40	32
Ephemeroptera	...	18	5	10
Coleoptera
Crustacea	2630	1029	4904	1538	49
Total	2761	1277	39	4953	1922	136

* No individuals were found in the sample.

of the insects collected during the experiment. Colonization rate and abundance of the individual families were influenced differently, as is shown by a significant flow \times family interaction (Table 4). The effect of elevated flow on colonization rates was especially evident for Hydropsychidae larvae on days 6–8 (Fig. 5), when there was a significant difference in colonization rate in elevated (36.8 individuals/d) vs. low (1.8 individuals/d) flow. No other insect family exhibited a significant difference in colonization rate under the two flow treatments at any time during the experiment (Fig. 5).

Only Hydropsychidae exhibited a consistent effect of elevated flow on abundance (Fig. 5). Hydropsychidae increased precipitously on days 6–8 of the experiment, resulting in significantly more Hydropsychidae under elevated vs. low flow conditions as early as day 8 and continuing through day 24 (Fig. 5). Most other insect families tended to be more abundant under elevated flow (Fig. 5) but there was no statistical effect of flow on abundance of these taxa.

In summary, elevated (nonscouring) flow was associated with a dramatic increase in density of benthic and drifting invertebrates in Gould Creek. The most dramatic increase occurred for Hydropsychidae, and

to a lesser extent Simuliidae, in riffles in late spring and early summer. Experiments indicated increased insect abundance under elevated flows can occur in as little as 8 d, primarily due to colonization by larval Hydropsychidae.

Cyprinid abundance in Gould Creek

As with invertebrates, the density of cyprinids increased dramatically in conjunction with increased stream flow; from 0.1–0.3 fish/m² in 1984 to 1–2 fish/m² in 1985–1986 (Fig. 6). Increased fish density under elevated flow conditions was especially pronounced during spring spawning periods (May–June) and was primarily due to increased abundance of age II or older individuals (Fig. 7). Species with relatively short lifespans (2–3 yr; brassy minnow, northern redbelly dace, and fathead minnow) exhibited large decreases in abundance during the summer, even if elevated flow conditions persisted (Fig. 6). Only the creek chub, with a maximum lifespan of 6–7 yr, did not exhibit a large decrease in abundance between spring and summer. Furthermore, the creek chub was the only species exhibiting significant recruitment (age 0), but this occurred in only 1 of 3 yr (1986, Fig. 7).

The cyprinid species did not vary in their relative use of riffle vs. pool habitats (Table 5, Species \times Habitat; $P > .05$). However, as a group, cyprinids did differ ($P < .01$) in their relative use of riffles vs. pools (Table 5); normally densities were higher in pools than in riffles (Fig. 6). The differential use of riffles and pools

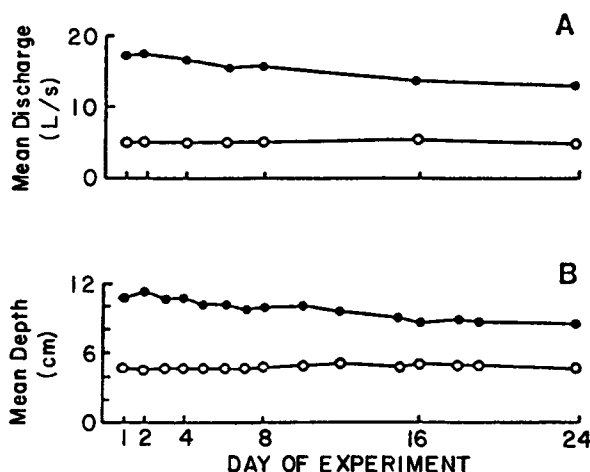


FIG. 3. Mean discharge (A) and depth (B) for the elevated (nonscouring; ●) and low flow (○) subsections of Gould Creek during the flow manipulation experiment. The standard errors ranged from 0.45–0.96 L/s for discharge and 0.29–0.66 cm for depth.

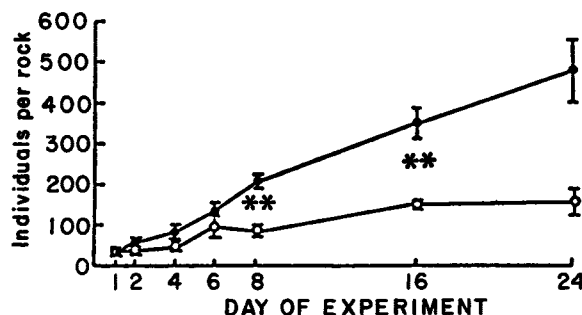


FIG. 4. Total number of insects colonizing rocks in Gould Creek under elevated (●) and low flow (○) conditions. Symbol is mean, vertical bar is ± 1 standard error. Double asterisks indicate significant differences ($P < .007$) between elevated and low flow conditions.

TABLE 3. Continued.

1985			1986					
Jul	Aug	Sep	Apr	May	Jun	Jul	Aug	Sep
65	90	255	424	205	141	77	25	42
28	...	29	12	34	2031	4	...	21
19	...	7	8	34	197	...	25	...
9	16
...	...	7	71 601	63 481	381
121	90	298	72 061	63 754	2750	81	50	63

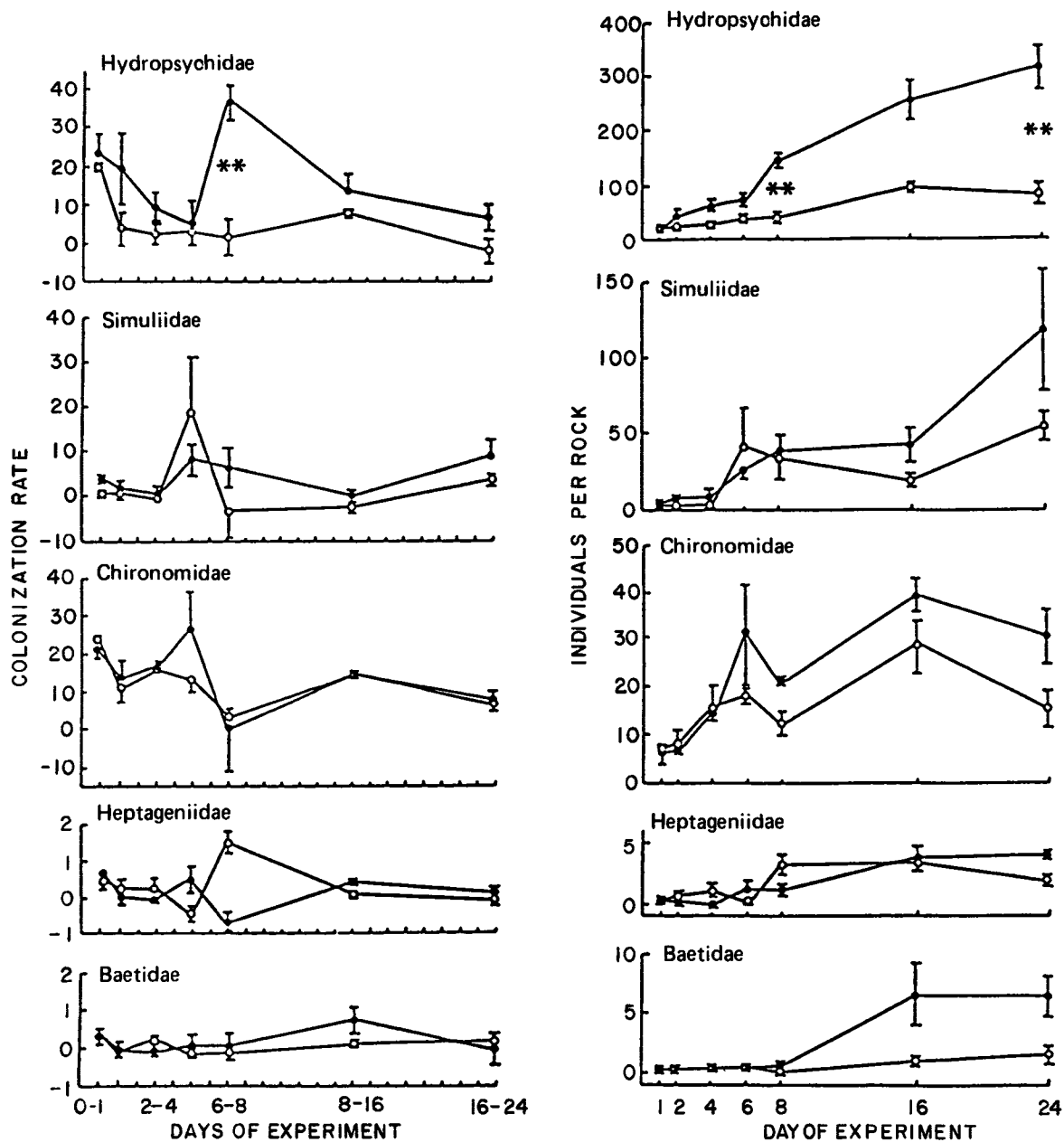


FIG. 5. Colonization rate (change in number of individuals per rock per day) and abundance (number of individuals per rock) for five insect families in Gould Creek under elevated (●) and low (○) flow conditions. Symbol is mean, vertical bar is ± 1 standard error. Double asterisks indicate significant differences ($P < .007$) between elevated and low flow conditions.

TABLE 4. Summary of the effects of flow, family, and flow \times family interactions on colonization rate (change in the number of individuals per rock per day) and abundance (number of individuals per rock) of benthic insects in riffle habitats of Gould Creek.

Source of variation	Criterion variable						
	Colonization rate				Abundance		
	df	MS	F	P	MS	F	P
Flow	1	413.2	39.3	<.01	1.29	14.3	<.01
Family*	4	888.5	84.6	<.01	17.20	191.1	<.01
Flow \times family	4	260.5	24.8	<.01	0.28	3.1	<.05
Error	20	10.5			0.09		

* Five insect families were examined: Hydropsychidae, Simuliidae, Chironomidae, Heptageniidae, and Baetidae.

by minnows was even more pronounced when absolute minnow abundance in these habitats was compared; 84% of all minnows were captured in pools and 16% in riffles.

Minnow trap sampling indicated few cyprinids were present in the stream in early April (Fig. 8). Rapid pulses of cyprinid colonization occurred from mid-

May through mid-June. Less intensive minnow trapping in Beaver Lake and ≈ 6 km downstream, suggested the minnows colonized Gould Creek from downstream areas rather than Beaver Lake (I. J. Schlosser, *personal observation*). Brassy minnows were the first to colonize the stream in early May, followed by redbelly dace in late May to early June, and fathead minnows and creek chubs in mid to late June. Brassy minnows, redbelly dace, and fathead minnows all exhibited large decreases in abundance within 4–5 wk after their initial colonization (Fig. 8).

In summary, cyprinid densities below the beaver pond exhibited a dramatic increase in 1985–1986 with

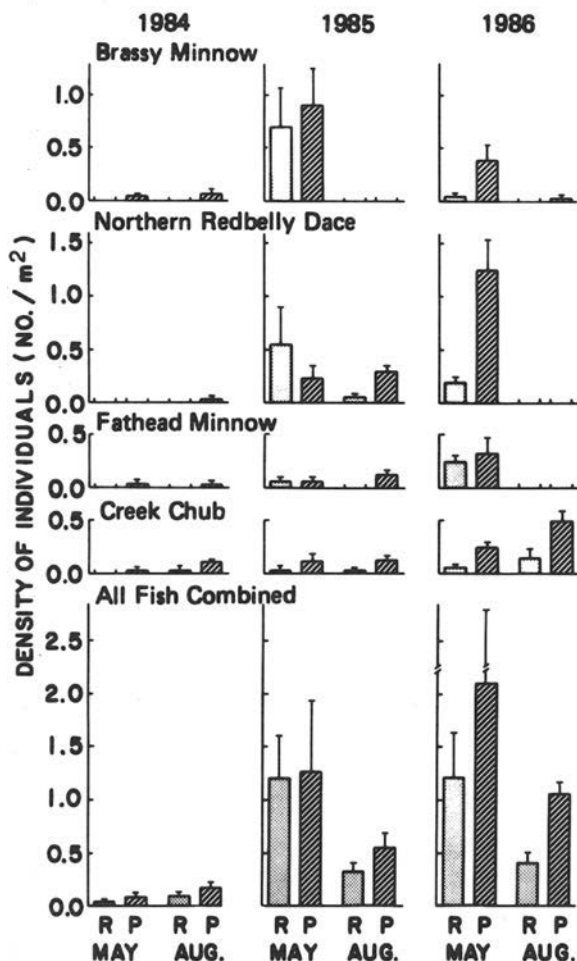


FIG. 6. Density of fishes in riffle (R) and pool (P) habitats of Gould Creek during spring (May) and summer (August) from 1984–1986. Height of histogram bar is mean density, narrow vertical bar is ± 1 standard error.

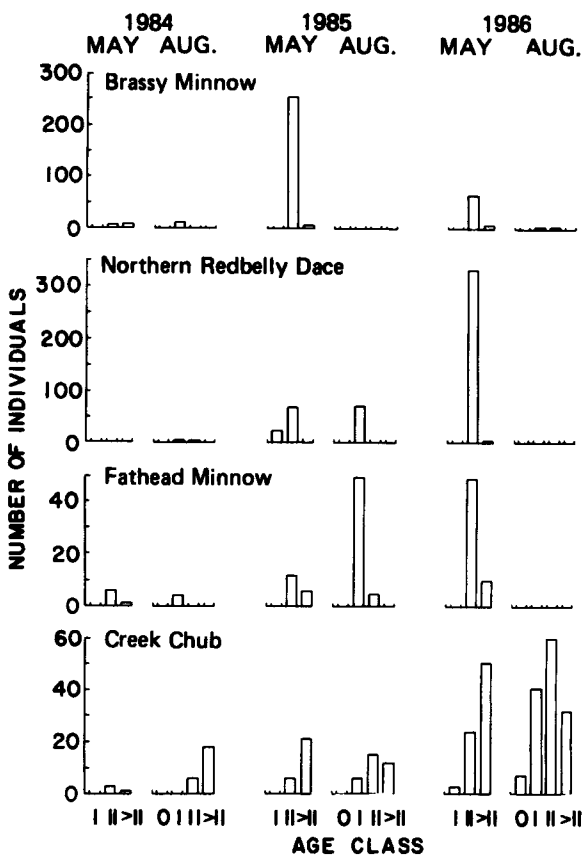


FIG. 7. Age structure of cyprinid populations in Gould Creek in spring (May) and summer (August) from 1984–1986.

TABLE 5. Summary of the effects of species, habitat, and species \times habitat interactions on fish density (number/m²) in Gould Creek.

Source of variation	df	MS	F	P
Species*	3	0.019	3.16	<.05
Habitat†	1	0.089	14.83	<.01
Species \times habitat	3	0.002	0.33	>.05 (NS)
Error	32	0.006		

* Species included were brassy minnow (*Hybognathus hankinsoni*), northern redbelly dace (*Phoxinus eos*), fathead minnow (*Pimephales promelas*), and creek chub (*Semotilus atromaculatus*).

† The habitats were riffles and pools.

elevated stream flow. Increased abundance of cyprinids was most pronounced in late spring and early summer due to rapid pulses of colonization by age II or older individuals. Large decreases in the abundance of short-lived cyprinids occurred shortly after colonization, even if elevated flow conditions persisted. The cyprinids inhabited predominantly pool habitats.

*Cyprinid predator and invertebrate
prey interactions in the
experimental stream*

Habitat type significantly affected total invertebrate abundance (Table 6) with total invertebrate abundance increasing dramatically in structurally complex pools (Fig. 9). The increase in invertebrate abundance in structurally complex pools was primarily due to an

TABLE 6. Summary of the effects of habitat, cyprinid predation, and habitat \times cyprinid predation interactions on the total number of invertebrate prey in the experimental stream.

Source of variation	df	MS	F	P
Habitat	3	0.218	27.25	<.01
Predation	1	0.093	11.62	<.01
Habitat \times predation	3	0.029	3.62	.06
Error	8	0.008		

increased abundance of crustacea and to a lesser degree chironomid larvae. Most of the crustacea were copepods (50–55%) and cladocera (35–45%), with the remainder being amphipods.

Cyprinid predation significantly affected invertebrate abundance, but there was also a marginally significant ($P = .06$) interaction between habitat and predation (Table 6). The interaction term suggests that the influence of cyprinid predators on invertebrates varied among the habitats. Cyprinids had the greatest impact on invertebrates in structurally complex pools, with less effect in shallow riffle or raceway habitats (Fig. 9). In addition, since invertebrate taxa differed in their distribution among habitats (Fig. 9), cyprinid predation had a larger impact on the abundance of chironomid larvae and crustacea than hydroptychid and simuliid larvae.

Associated with the increased abundance of Hydroptychidae and Simuliidae in riffles and raceways was an increase in insect size (Fig. 10). Fish predation had

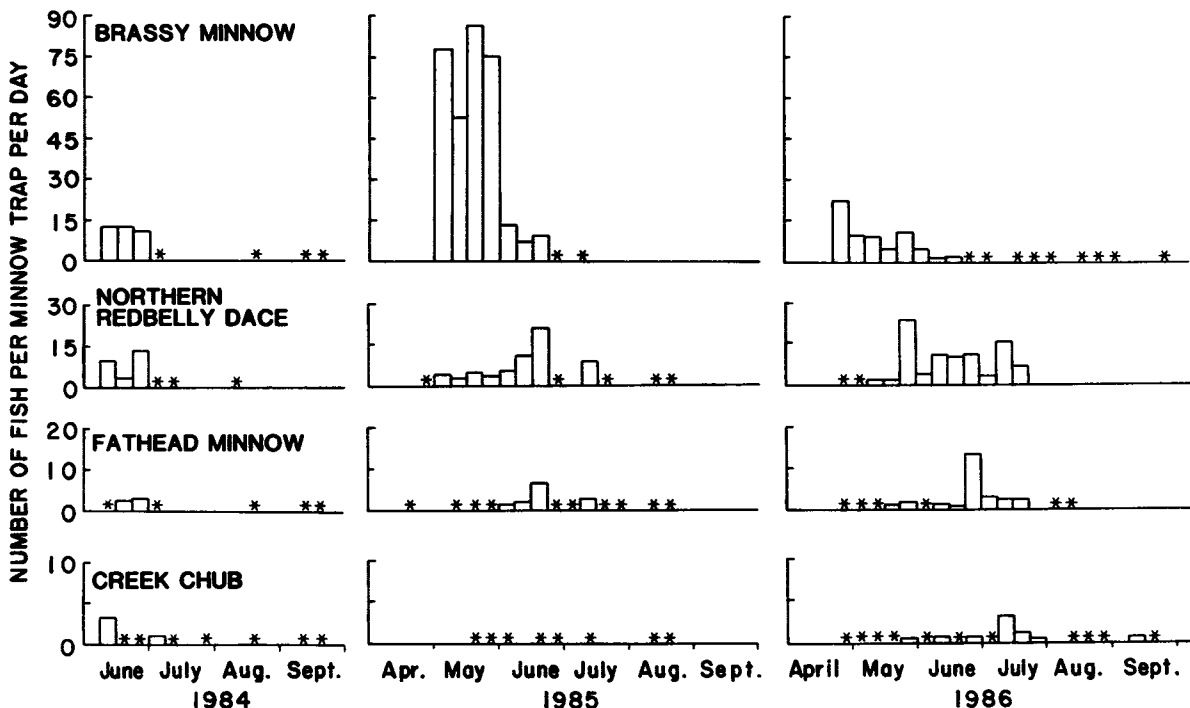


FIG. 8. Number of fish captured per minnow trap per day in Gould Creek during the three-year study period (1984–1986). Asterisks indicate that <1 fish per trap was captured.

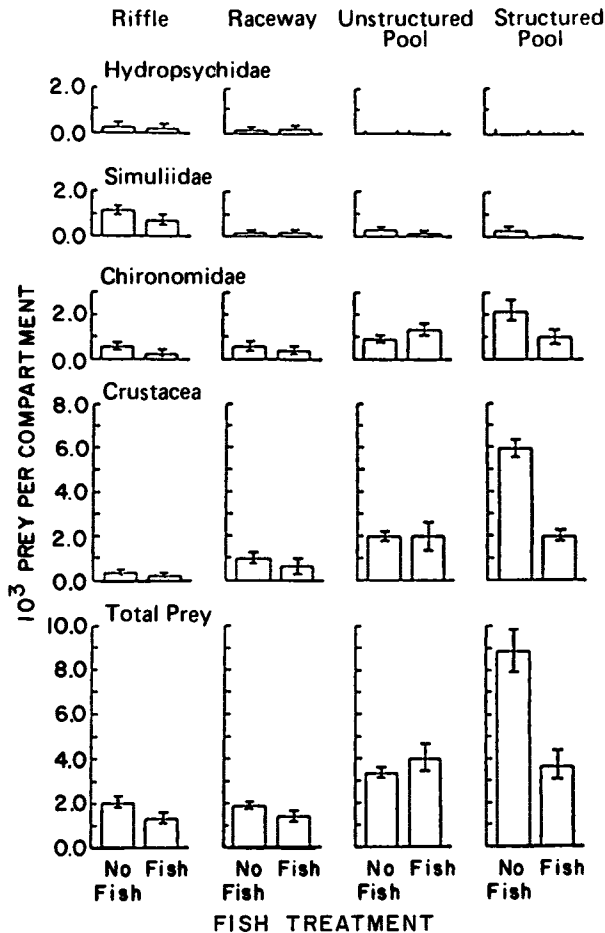


FIG. 9. Abundance of four invertebrate taxa and total invertebrate abundance, in riffle, raceway, unstructured pool, and structured pool habitats of the experimental stream in the presence and absence of cyprinid predation. Height of histogram bar is mean abundance, narrow vertical bar is ± 1 standard error.

little effect on size of insects in riffles but depressed insect size in pools, primarily due to the selective removal of simuliid larvae from pool habitats (Fig. 10).

Aquatic piscivore and cyprinid prey interactions in the experimental stream

Even though shallow water refugia were present in the experimental stream, successful predation by creek chubs on adult cyprinids occurred (Fig. 11). However, there were significant ($F = 7.49$, $P < .01$) differences in the rate of predation on the three prey species. The species with the largest adult size (brassy minnow; \bar{X} total length = 73.9 mm) was less ($P < .05$) susceptible to predation than the two species with smaller adult size (fathead minnow; $\bar{X} = 56.5$ mm and redbelly dace; $\bar{X} = 55.7$ mm). However, even the smaller species were preyed on at a relatively low rate (0.25–0.30 fish per day per predator; Fig. 11).

Analysis of the spatial distribution of the prey species in the presence and absence of creek chubs indicated that habitat significantly ($P < .01$) affected the distribution of two of the three prey species and was marginally significant ($.05 < P < .10$) for the third (Table 7). There were no significant habitat \times predation interactions (Table 7). All three minnow species predominantly selected pool habitats (Fig. 12), and while all taxa exhibited a tendency to modify their use of structured or unstructured pool habitats in the presence of creek chubs, the tendency for habitat shifts to occur was relatively weak, with little consistency in the response of the prey fishes to the chubs.

In summary, cyprinids had the greatest impact on abundance and size composition of invertebrates in structurally complex pool habitats. Insects in shallow riffle and raceway habitats exhibited little response to cyprinid predation. Creek chubs were ineffective predators on adult minnows, especially minnows with large body size, and creek chubs had weak and inconsistent effects on the use of pools by adult minnows.

DISCUSSION

Effects of flow regime on the abundance of stream organisms

Our results indicate that frequent and prolonged periods of elevated (nonscouring) discharge cause dramatic increases in colonization and abundance of invertebrates and cyprinids in headwater streams. Increased invertebrate abundance during elevated flow does not appear to be merely a function of increased habitat availability. In the flow manipulation experiment, habitat area was 10–20% greater under elevated flow, but insects were three times as abundant after 24 d. The effects of elevated stream flow on water velocity or the amount of organic material transported are likely to be more important factors causing increased insect abundance (Naiman and Melillo 1984, MacKay and Waters 1986). This is supported by the observation that the taxa exhibiting the largest increase under elevated flow, Hydropsychidae and Simuliidae, have specific velocity requirements and feed primarily on organic matter transported in the water column (Merritt and Cummins 1984).

The flow manipulation experiment also indicated that some insect taxa respond rapidly (6–8 d) to increased discharge. The estimates of response rate are probably biased toward minimal response time because of the reduced spatial scale of the experiment, resulting in minimal colonization distances from low flow to elevated flow habitat. A better estimate of the time of invertebrate response to flow variation will require ecosystem-level manipulations (see also Fisher 1987 and Peckarsky 1987).

One question based on the invertebrate data yet to be addressed is why do Hydropsychidae become so abundant during elevated flow? At least three not nec-

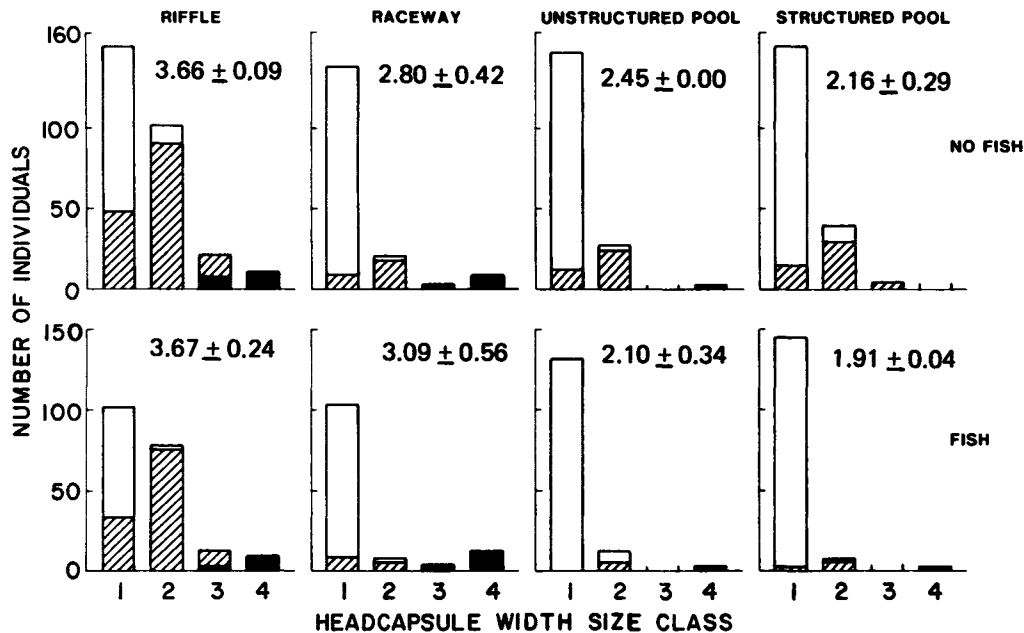


FIG. 10. Size distribution based on head capsule width for three insect taxa in riffle, raceway, unstructured pool, and structured pool habitats of the experimental stream in the presence and absence of cyprinid predation. ■ Hydropsychidae, ▨ Simuliidae, □ Chironomidae. Size classes: 1(0–0.3 mm), 2(0.3–0.6 mm), 3(0.6–0.9 mm), 4(>0.9 mm). Head capsule width ($\bar{X} \pm 1 \text{ SE}$) for all taxa combined is provided for each habitat and fish treatment.

essarily mutually exclusive hypotheses can be proposed to explain this. First, the habitat created and organic matter transported during elevated flow may be more suitable for larval Hydropsychidae than other taxa. Second, the rapid colonization rate and aggressive behavior of Hydropsychidae may make them more effective at pre-empting space under elevated flow, including active defense of feeding territories and occasional predatory behavior (Glass and Bovbjerg 1969, Jansson and Vuroisto 1979, Hildrew and Townsend 1980, Wiley and Kohler 1981, Hemphill and Cooper 1983, R. J. MacKay, *personal communication*). Lastly, because of their life history characteristics there may be a larger pool of Hydropsychidae available for colonization of substrates during summer (MacKay 1979, Williams 1981). Distinguishing among these hypotheses will require detailed analyses of the life histories of all insect taxa and controlled manipulations of physical variables and species interactions.

As with invertebrates, the increased abundance of cyprinids associated with elevated flow was probably due to a variety of factors correlated with increased discharge, including increased food availability, habitat space and volume, and ease of colonization of upstream areas. A striking aspect of the response of stream fishes to elevated flow was the role of spawning time and longevity. Brassy minnows are early spawners with maximum longevity of 2–3 yr (Becker 1983). Age II brassy minnows were abundant during elevated flow early in the spring but exhibited low post-spawning abundances the remainder of the summer, regardless of flow conditions and invertebrate abundance. In con-

trast, creek chubs spawn at higher temperatures and live 6–7 yr (Becker 1983). Creek chubs colonized the stream later than the brassy minnows and, apparently because of lower post-spawning mortality and/or emigration, were present in the stream throughout the summer. These results suggest the timing of critical life history events and the physiological characteristics of the biota, in relation to the timing and magnitude of abiotic variability, has major effects on the population

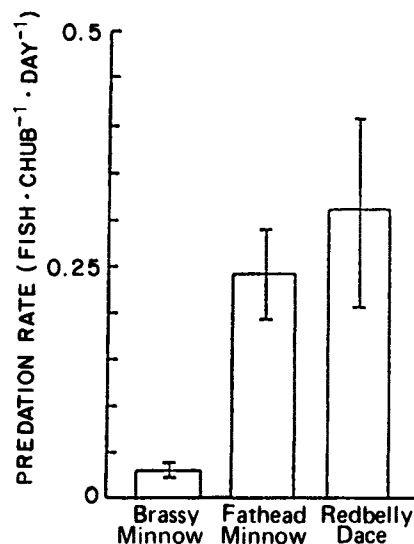


FIG. 11. Predation rate by adult creek chubs (*Semotilus atromaculatus*) on adults of three species of cyprinid prey in the experimental stream. Height of histogram bar is mean rate, narrow vertical bar is ± 1 standard error.

TABLE 7. Summary of the effects of habitat, creek chub (*Semotilus atromaculatus*) predation, and habitat \times predation interactions on the abundance of minnow prey in the experimental stream. The prey species were brassy minnow (*Hybognathus hankinsoni*), fathead minnow (*Pimephales promelas*) and northern redbelly dace (*Phoxinus eos*).

Source of variation	df	Brassy		Fathead		Redbelly	
		MS	F	MS	F	MS	F
Habitat	3	2.44	20.33**	1.32	2.86	1.77	13.61**
Predator	1	0.01	0.08	0.01	0.02	0.01	0.08
Habitat \times predator	3	0.31	2.58	0.11	0.24	0.01	0.08
Error	8	0.12		0.46		0.13	

** $P < .01$.

dynamics of stream fishes (see also Fisher et al. 1982, Fisher 1983, Sousa 1984, Pickett and White 1985, Schlosser 1985).

The role of predator-prey interactions

In contrast to the broad and dramatic effects of flow regime on invertebrates and fishes, the effects of cyprinid predation appeared relatively weak. However, the ability to generalize regarding the influence of cyprinid predation is constrained by two factors.

First, the conclusions regarding the effect of cyprinid predation need to be placed in the context of the experimental biases. The experimental stream mimicked

the natural headwater stream reasonably well with respect to temperature, spatial variation in insect abundance, and habitat heterogeneity (Schlosser 1987a). It was, however, reduced in scale relative to the natural stream and restricted fish dispersal. This reduction in scale and dispersal would, if anything, accentuate the intensity of trophic interactions by forcing predators and prey into close proximity (Schlosser 1988a). Thus, the conclusion that cyprinids have weak effects on invertebrates in shallow areas and adult minnows in pools is strengthened by the experimental biases.

Second, the ability to generalize regarding cyprinid predation is constrained by its variation across temporal and spatial scales, between invertebrate and vertebrate organisms, and for different prey sizes. Temporal variation in the intensity of predation occurs over short time intervals (2–3 wk) because of the dynamic nature of stream flow and rapid colonization but short lifespan of most stream cyprinids. Variation in intensity of cyprinid predation over small spatial scales occurs because of increased abundance of cyprinids in pools vs. riffles. Cyprinids in Gould Creek probably restrict their distribution to deep, structurally complex habitats to minimize exposure to terrestrial wading predators (e.g., herons, minks, and raccoons), which frequently feed in shallow areas of headwater streams (Power 1984, 1987, Schlosser 1988b, I. J. Schlosser, *personal observation*). As a result, the greatest influence of cyprinids on benthic invertebrates was in structurally complex pools, with little effect on invertebrates in shallow habitats. Spatial variation in cyprinid predation on invertebrates has several important implications. It suggests cyprinids can locally depress resources, resulting in food limitation and increased competitive interactions, especially during low flow conditions. It also provides a partial explanation for the frequently observed complementarity in distribution of small fishes in pools and large invertebrates in riffles of many small streams (Bowly and Roff 1986). Lastly, it may explain some of the conflicting conclusions in the literature regarding the influence of vertebrates on invertebrate prey in streams. Vertebrate predators may have little influence on the abundance of invertebrates in shallow, rocky habitats (Reice 1983, Flecker and Allan 1984) or on the density of drifting invertebrates originating from these areas (Allan 1982).

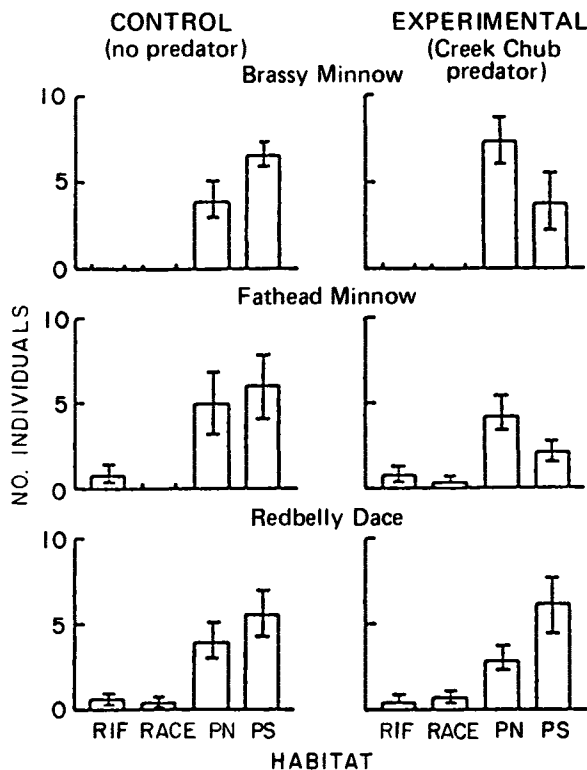


FIG. 12. Habitat selection by three species of cyprinids in the experimental stream in the absence (control) and presence (experimental) of adult creek chubs (*Semotilus atromaculatus*). Habitat types: riffle (RIF), raceway (RACE), pools without structure (PN), and pools with structure (PS). Height of histogram bar is mean abundance, narrow vertical bar is ± 1 standard error.

However, they may have a dramatic effect on invertebrate abundance in pools (Cooper 1984, Angermeier 1985). Incorporation of greater habitat heterogeneity into experiments exploring vertebrate predator and invertebrate prey interactions will allow more realistic generalizations regarding the role of vertebrate predators in structuring stream communities.

Finally, the influence of predatory cyprinids appears to vary between invertebrates and vertebrates because adult creek chubs are ineffective piscivores. The relatively low predation rate of creek chubs on adult cyprinid prey suggests that while creek chubs may cause subtle alterations in the way minnows relate to structural complexity in pools (Fraser and Cerri 1982, Fraser and Emmons 1984), it is unlikely *Semotilus* is more important than colonization and post-spawning emigration and/or mortality in determining the abundance of adult cyprinids (see also Moyle and Li 1979, Grossman and Freeman 1987). The ineffectiveness of the creek chub as a piscivore is probably related to its small body and mouth size, and generalized feeding behavior (Pflieger 1975, Schlosser 1988a).

The weak effect of *Semotilus* on adult minnows in Gould Creek does not mean aquatic piscivores are never important in determining the distribution and abundance of stream fishes. Our results suggest creek chubs will in fact have more effect on small, larval fishes. Considerable spatial variation also occurs within streams in the species composition and abundance of aquatic piscivores (Schlosser 1982, 1987b). Large centrarchid predators, such as smallmouth (*M. dolomieu*) and largemouth bass (*M. salmoides*), have higher predation rates (Schlosser 1987a) and cause pronounced shifts of small fishes to shallow habitats (Power and Matthews 1983, Power et al. 1985, Schlosser 1987a). To develop general models of the influence of aquatic piscivores on fishes in streams requires more complex predator-prey experiments with an array of predator taxa and different size classes of predators and prey.

Implications for landscape ecology

Previous conceptual models of aquatic environments envision streams as longitudinally interconnected channels with a continuum of gradually changing physical, chemical, and biological characteristics (Cummins 1975, Vannote et al. 1980). Recently Naiman et al. (1986) suggested that in natural, north temperate areas, conceptual models need to address the role of interruptions or discontinuities in the stream continuum, including lakes and beaver ponds (see also Ward and Stanford 1983). Other research indicates ponds or lakes have major effects on nutrient and organic cycling in outlet streams (Naiman and Melillo 1984, Francis et al. 1985, Naiman et al. 1986). Very high benthic invertebrate densities occur in these areas (Carlsson et al. 1977, Bronmark and Malmqvist 1984), with invertebrate density decreasing downstream from the lake or pond outlet (Statzner 1978, Oswood 1979,

Valett and Stanford 1987). These patterns suggest ecotones between beaver ponds or lakes and downstream areas are "hot spots" of productivity, which should play an important role in future models of north temperate landscapes. Specifically, these models should emphasize (1) the effect of hydrologic regime on nutrient and organic transport, and benthic and fish productivity in pond or lake outlets, and (2) the considerable temporal and spatial patchiness in the influence of trophic level interactions on these stream reaches.

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