Experimental evidence that stream macroinvertebrate community structure is unaffected by different densities of coho salmon fry

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Abstract. Manipulative field enclosure/exclosure experiments were carried out in Carnation Creek, British Columbia to determine if patch-restricted coho fry (*Oncorhynchus kisutch*) affected the distribution and abundance of macroinvertebrates in the drift or benthos. Enclosures/exclosures with standardized substrate, detritus, and current velocity were buried in the streambed during the low discharge period, and four treatments used: no fish, ambient fish, double ambient fish, and quadruple ambient fish densities. Density, biomass, and size distribution of macroinvertebrates in the drift were not significantly affected by fish density treatment. Additionally, with the exception of large swimming larvae of *Ameletus* sp. and *Baetis tricaudatus*, macroinvertebrate density, size distribution, and biomass in the benthos were also not significantly affected by fish density treatments. Thus, despite fish densities being increased from two to four times above ambient patch levels, patch-restricted coho fry had little measureable effect on macroinvertebrate distribution and abundance in Carnation Creek during the low discharge period of August to September.

Key words: community structure, predator-prey, streams, benthos, coho, fish.

Predation by fish is often cited as an important biotic process structuring prey communities in freshwater ecosystems (Andersson et al. 1978, Brooks 1968, Brooks and Dodson 1965, Connell 1975, Zaret 1980). Nevertheless, in stream ecosystems there is little evidence that fish predators have a direct effect on the distribution and abundance of their macroinvertebrate prey community. Allan (1982) reported that despite a 75-90% reduction of salmonid biomass within an experimental exclosure, benthic macroinvertebrate densities and drift rates in the experimental area were similar to those in uncontrolled areas with ambient predator densities, although he qualified his inability to demonstrate a predator effect because the high variability of the benthic and hyporheic communities had caused significant sampling variance in the prey density estimates.

The variance in the estimates of the prey community is not the only factor that complicates the interpretation of predator exclusion experiments such as those of Allan (1982), Choat and Kingett (1982), Flecker and Allan (1984), and Thorp and Bergey (1981). In this type of experimental design, the prey community is assumed to be subjected to uniform ambient levels of predation throughout the unenclosed area. However, if local patchiness in predator distribution occurs, the impact on the prey community may be patch-restricted, thereby invalidating a vital assumption of the experimental design (Choat 1982). Furthermore, the experimental containers may modify the abiotic environmental regime so that responses of the prey community to these changes and effects of predator on prey are difficult to distinguish (Hulberg and Oliver 1980). A more appropriate design is one that uses in situ containers to enclose fixed densities of predators as well as to exclude predators from patches of substrate (Walde and Davies 1984). Additionally, variability between containers can be greatly reduced by standardizing and monitoring important variables such as substrate composition, detritus source and quantity, and current velocity. Thus, macroinvertebrate carrying capacity potential for all enclosures will be similar, thereby ensuring that fish density is the only experimental variable likely to be affecting the benthic prey community.

Using enclosure/exclosure methods, this study examined whether the distribution and abundance of benthic macroinvertebrates in homogeneous patches of substrate were influenced by salmonid predator density. Coho salmon fry, *Oncorhynchus kisutch* (Walbaum), which feed on macroinvertebrates located on the substrate (Dill et al. 1981) or at the water surface and in the drift (Mundie 1971), were used because they were the most abundant fish species in Carnation Creek. The objectives of the field manipulation experiment were to investigate the effects of different coho fry densities on: (1) macroinvertebrate composition, densities, and biomasses within enclosures; and (2) drift rates out of enclosures.

Methods

Study area

The experiment was conducted in a riffle (2 m long \times 3 m wide) approximately 20 m downstream of the main discharge gauging weir (B weir) of Carnation Creek, British Columbia, a third order stream (sensu Strahler 1957) described in Culp and Davies (1985). Throughout this stream reach the riparian vegetation consisted primarily of red alder (Alnus rubra Bong.), salmonberry (Rubus spectabilis Pursh), and salal (Gaultheria shallon Pursh). Resident fish species in the stream include coho salmon, rainbow trout (Salmo gairdneri Richardson), coastal cutthroat trout (Salmo clarki clarki Richardson), aleutian sculpin (Cottus aleuticus Gilbert), and prickly sculpin (Cottus asper Richardson), with coho fry being eight times more abundant than any other species (Andersen 1984). During the period of low discharge (August to September) when the experiment was performed, current velocities in the riffles were 5-20 cm/s with minimal suspension and deposition of organic and inorganic sediment which did not vary significantly among gravel, pebble, and cobble substrates (Culp and Davies 1985, Culp et al. 1983).

Experimental design

Four experimental containers with different coho fry densities were established: $(0 \times)$ no fish; $(1 \times)$ ambient densities $(12/m^2; 25 \text{ g/m}^2);$ $(2 \times)$ double the ambient densities $(24/m^2; 53 \text{ g/m}^2);$ and $(4 \times)$ quadruple the ambient densities $(48/m^2; 101 \text{ g/m}^2)$. Ambient coho fry densities were based on observations made in the riffle immediately before the experiment and are slightly higher than the density estimates for this reach measured by the Department of Fisheries and Oceans of Canada (Andersen 1984). Before the experiment began, substrate for the containers was collected from dry areas of the streambed and sieved into sand (4.0-9.5 mm), gravel (9.5-16.0 mm), and pebble (16-31 mm) size classes. Detritus was removed from this substrate and the three size classes mixed in a 1:1:1 volumetric ratio similar to the natural substrate. The source and type of detritus in the experimental containers were standardized using leaves of red alder that had begun falling into the stream about two weeks beforehand. These leaves were mechanically shredded in a blender and wet-sieved into fine (230-850 μ m) and coarse (850–2000 μ m) fractions which were mixed in a 1:1 ratio. This standardized detritus was added to the sand, gravel, and pebble mixture to produce a standardized substrate with a quantity of detritus (100 g/m^2 dry mass) equivalent to amounts found in the natural streambed.

The experimental containers consisted of open-ended galvanized troughs (1.2 \times 0.3 \times 0.3 m) that were imbedded side-by-side 10 cm into the streambed in the experimental riffle which had uniform low current velocity (12 ± 2) cm/s). Temporary polyethylene seals were placed at each end of the troughs while a 10cm deep layer of the standardized substrate and detritus mixture was gently and evenly spread over the bottom so that this substrate was flush with the streambed outside the troughs. Four 10-cm diameter stones were placed on the substrate surface in a side-to-side alternating pattern to provide refugia for the fry. Any suspended detritus was allowed to settle before the seals were removed. Each container therefore represented a streambed patch 10 cm in depth with standardized detritus and substrate composition, and similar current velocity. The substrate in the troughs was allowed to be colonized by macroinvertebrates for 21 d (August to September 1982). Because the bottom and sides of the troughs were solid, macroinvertebrate colonization occurred largely by upstream and downstream movements of the macroinvertebrates in the substrate, and by downstream drift.

After the 21-d colonization period, squaremesh screens with a diagonal opening of 9 mm were placed over both ends of the troughs to prevent coho fry from entering or leaving the enclosures, while not restricting the movement of macroinvertebrates or measurably modifying the current. Although the troughs extended well above the water surface, wire mesh was placed across the top of the troughs to prevent fish from leaping out of the enclosures. One day after the placement of the wire screens, predator densities of $0 \times$, $1 \times$, $2 \times$, and $4 \times$ were established using fish of known weight. Throughout the experiment, small amounts of organic detritus and filamentous algae that collected on the screens were removed by gently brushing with a nylon brush three times per day. Otherwise, the experimental containers were maintained without disturbance or loss of fry for a 16-d period (14–30 September 1982).

Macroinvertebrate drift from all the troughs was sampled 1 d before the addition of fish, and 1, 7, and 14 d thereafter. Each day macroinvertebrate drift collections were made: (a) 1 hr before until 1 hr after sunrise (06:00–08:00); (b) 1 hr at midday (12:45–13:45); and (c) 1 hr before until 2 hr after sunset (18:45–21:45) using 15 × 15 cm nets (230 μ m mesh) positioned at the downstream outflow of each trough. Current velocity was measured at the front of each net with a Marsh McBirney Model 201 current meter. The nets were emptied into 106- μ m sieves at 30-min intervals throughout the sampling periods and preserved in 10% formalin.

At the end of the experiment, the coho fry were removed from the troughs and the wet weight determined (± 0.01 g). Then four samples of benthic macroinvertebrates were collected successively in an upstream direction from each trough using a modified Neil (1937) sampler (0.03 m²) with 230 μ m mesh and were preserved in 10% formalin. Macroinvertebrates from the drift and benthic samples were sorted under 12× magnification, identified to the lowest taxonomic level possible, and enumerated. The macroinvertebrates in each taxon were split into two size classes (>3 mm and <3 mm total length), and the wet and dry (40°C for 24 hr) biomass measured using a Cahn 25 automatic electrobalance. Note that macroinvertebrate wet weights were determined in order to facilitate comparisions with fry wet weight.

Statistical methods

Simple linear regression (Zar 1984) was used to determine whether the slope of the regression lines for mean benthic macroinvertebrate densities or biomasses on fish density or biomass in treatments $0 \times$, $1 \times$, $2 \times$, and $4 \times$ was ≥ 0 . Thus, rejection of this directional null hypothesis would indicate that increasing fish density from $0 \times$ to $4 \times$ significantly decreased benthic macroinvertebrate density or biomass. Regression analysis was also used to establish whether the mean 30-min densities or biomasses of macroinvertebrates drifting from the containers at sunrise, midday, or sunset were significantly decreased by fish density treatments $0 \times$ to $4 \times$ on each of the 4 d that drift was sampled: 1 d before, and 1, 7, and 14 d after fish addition. For both the benthic and drift analyses, the null hypotheses were tested for the following taxonomic and size class categories of macroinvertebrates: (1) order with all size classes pooled; (2) species with all size classes pooled; (3) order with individuals <3mm; (4) order with individuals >3 mm; (5) species with individuals <3 mm; and (6) species with individuals >3 mm. Rare taxa (<1% of total density or drift) were omitted from the analyses. Hypothesis rejection was performed at the α =0.05 level of probability.

Results

Although the original experimental design provided for replication of the treatments, a moderate increase in discharge during the 21-d colonization period overturned several of the experimental troughs. Thus, at the start of the fish density experiment only one replicate enclosure per treatment could be established. The lack of replication makes the experimental design pseudoreplicated (Hurlbert 1984) and statistical testing was restricted to regression analysis. Sample variance was used to calculate the smallest difference from a slope of 0 that could be statistically detected for each regression relationship. These calculations indicate that negative functional relationships between the biomasses of macroinvertebrate taxa and fish density which produced slopes <-0.1 caused rejection of the null hypothesis. When analyzing macroinvertebrate densities on fish density, slopes <-0.3 would lead to null hypothesis rejection for most taxa, the exceptions being Diptera (<-0.5), Trichoptera (<-0.6), and Plecoptera (< -0.7).

On all 4 d that drift was sampled, the densities and biomasses of macroinvertebrate orders, species, or size classes in the drift were not significantly affected by fish density treatment. Although the results for biomass, species, and size class were analyzed, only the trends

TABLE 1. Mean 30-min drift density/100 m³ of Diptera, Ephemeroptera, Plecoptera, and Trichoptera from the treatments without fish $(0\times)$, and with ambient $(1\times)$, double ambient $(2\times)$, and quadruple ambient $(4\times)$ fish densities for samples collected 1 d before the addition of fish, and 1, 7, and 14 d after the fish additions.

	Time . Period	Before Fish Treatment			1 d After Fish Treatment			7 d After Fish Treatment			14 d After Fish Treatment						
Taxa		0×	$1 \times$	2×	4 ×	0×	1×	2×	4×	0×	1×	2×	4×	0×	1×	2×	4×
Diptera	Sunrise	92	51	70	119	84	115	128	134	30	34	16	25	105	87	61	57
-	Midday	71	73	48	31	66	101	55	73	17	58	17	10	76	72	33	44
	Sunset	101	168	156	106	156	210	159	192	92	97	89	96	87	105	55	81
Ephemeroptera	Sunrise	18	6	9	8	10	18	17	15	5	5	6	0	11	11	12	17
	Midday	9	0	18	0	0	0	0	9	0	0	0	0	0	0	0	0
	Sunset	9	5	5	15	29	59	15	36	10	28	0	10	39	22	21	17
Plecoptera	Sunrise	5	19	8	9	0	11	0	0	8	0	5	0	7	· 0	0	0
	Midday	0	0	7	0	0	0	8	0	0	0	8	0	0	0	0	0
	Sunset	20	18	9	24	22	40	13	22	13	9	12	8	10	11	13	9
Trichoptera	Sunrise	24	10	0	26	33	0	0	33	0	5	0	0	10	7	0	0
	Midday	0	27	18	17	0	9	0	0 ·	0	0	0	0	0	0	0	0
	Sunset	15	11	15	24	26	24	15	24	12	13	8	13	22	50	17	28

TABLE 2. Total macroinvertebrate wet biomass (mg/enclosure) in the drift from the treatments without fish $(0 \times)$ and with ambient $(1 \times)$, double ambient $(2 \times)$, and quadruple ambient $(4 \times)$ fish densities for samples collected between 06:00 and 21:45 hr, 1 d before the addition of fish, and 1, 7, and 14 d after the fish additions.

	Treatment					
	0×	1×	2×	4×		
Before fish	54	31	50	37		
1 d after fish	34	39	36	55		
7 d after fish	16	18	10	12		
14 d after fish	15	10	17	10		

for the density of macroinvertebrate orders in the drift are presented (Table 1) as they are similar to the trends shown for all analyses. Throughout the experimental period in all treatments and diel periods, Diptera larvae (largely Chironomidae) formed the major component of the macroinvertebrate drift with their highest levels occurring at sunset (Table 1). Diel drift rates for the Ephemeroptera, Plecoptera, and Trichoptera were also highest at sunset. Terrestrial insects constituted <1% of the drift density or biomass recorded.

The drift measurements at sunrise, midday, and sunset were used to calculate the total biomasses of macroinvertebrates drifting through each enclosure from 06:00 to 21:45 hr. Midday



FIG. 1. Mean final benthic densities (± 1 SE) of Diptera, Ephemeroptera, Plecoptera, and Trichoptera in the treatments without fish ($0 \times$) and with ambient ($1 \times$), double ambient ($2 \times$), and quadruple ambient ($4 \times$) fish densities.



FIG. 2. Mean final benthic biomasses (± 1 SE) of Diptera, Ephemeroptera, Plecoptera, and Trichoptera in the treatments without fish (0×) and with ambient (1×), double ambient (2×), and quadruple ambient (4×) fish densities.

values were the best estimate for the periods 08:00 to 12:45 hr and 13:45 to 18:45 hr when no samples were collected. These calculations indicate that the total biomass of macroinvertebrates drifting through an enclosure between dawn and dusk never exceeded 55 mg wet wt/ container on any day (Table 2) and drifting macroinvertebrates were generally <3 mm in body length.

Benthic densities or biomasses of macroinvertebrate orders, species, or size classes were not significantly affected by the treatments except for *Ameletus* sp. and *Baetis tricaudatus* Dodds nymphs >3 mm which decreased with increased fish density or biomass (Appendices 1 and 2; Figs. 1 and 2). Mean macroinvertebrate densities in all treatments were similar, with Plecoptera (*Capnia* sp., *Sweltza* sp.) having the

TABLE 3. Initial and final mean wet weights (g) of fry ± 1 SE, the total fry weight gain per treatment, and the mean weight gain per fry (g) in the treatments with ambient (1×), double ambient (2×), and quadruple ambient (4×) fry densities.

	Treatment					
	1×	2×	4 ×			
Mean initial weight Mean final weight Total weight gained	2.1±0.2 2.6±0.2 2.5	2.2±0.2 2.8±0.2 6.1	2.1±0.1 2.7±0.1 12.3			
Mean weight gain/fry	0.5	0.6	0.6			

highest benthic densities in all treatments, followed by Trichoptera (Limnephilidae), Diptera (Chironomidae), and Ephemeroptera (*B. tricaudatus*, *B. hageni* Eaton, *Paraleptophlebia* sp.). These densities are similar to those recorded in the natural substrate of this stream reach (unpublished data). In all treatments, Ephemeroptera had the highest biomasses, followed by Plecoptera, Trichoptera, and Diptera (Fig. 2).

The initial and final weights of fry, and the average weight gain per fry, were similar in all treatments (Table 3). In all treatments the average wet weight gain per fry was approximately 40 mg/d; thus, coho fry growth rate was not affected by density treatments $1 \times$, $2 \times$, or $4 \times$. This rate of growth per individual translates to an average daily increase in total fish biomass of approximately 200 mg/d in treatment $1 \times$, 400 mg/d in treatment $2 \times$, and 800 mg/d in treatment $4 \times$.

Discussion

If patch-restricted coho fry affected the distribution of macroinvertebrates, then macroinvertebrate abundance (density or biomass) would be expected to decrease as fish density within an area of the streambed increased, provided immigration did not counter this loss. Alternatively, a decrease in benthos abundance might come about through the avoidance by macroinvertebrates of areas of habitat with fish. An increase in the abundance of some macroinvertebrate taxa could result if the fish predator regulates the abundance of a prey species which is itself regulating other prey species (Paine 1980). However, the results of the field experiment provide evidence that, for most of the macroinvertebrate taxa, these salmonid predators did not influence the distribution or abundance of macroinvertebrates in either the benthos or the drift. Therefore, alternative hypotheses that may account for the lack of an effect of salmonids on macroinvertebrates will be discussed.

The enclosure/exclosure experimental design fixed the densities of predators and standardized other important environmental variables. Because this design ensured that fish density was the only experimental variable, the absence of a treatment effect cannot be attributed to inadequacies in the sampling design. The densities of fish used in the two highest density treatments $(2 \times, 4 \times)$ might have increased mutual interference among the coho fry, thereby reducing their searching efficiency for prey items. However, since the growth rates of fish in all treatments were similar (Table 3) and at least as high as in adjacent areas of the stream (Andersen 1984), changes in search efficiency cannot explain the lack of an effect of coho fry on benthic abundance.

Allan (1982) suggested that the effect of salmonid predators on prey populations is trivial when compared to natural variation in prey density. However, in the Carnation Creek experiment, variation was greatly reduced by rigorous standardization of the environmental factors in the experimental containers. Because detritus source and quantity, which are very important factors affecting macroinvertebrate colonization in Carnation Creek at this time of the year (Culp and Davies 1985, Culp et al. 1983), were standardized among enclosures, benthic density variance was low. The field experimental results showed no density-dependent trend for any order, species, or macroinvertebrate size class category in the drift or the benthos with the exception of the surface swimmers Ameletus sp. and B. tricaudatus.

Even though the diet of coho fry was not directly investigated during the experiment, macroinvertebrate drift did not appear to be a significant component of coho fry diet because there was no significant difference in the number, composition, or size of invertebrates drifting through the containers without fish and the number drifting through containers with fish during daylight. Although macroinvertebrate drift occurs throughout the period of darkness in Carnation Creek (Culp et al. 1986), these animals would not be available to the fry because Mundie (1971) showed that coho fry cease feeding at night. More importantly, the total biomass of macroinvertebrates drifting through a container never exceeded 55 mg (wet)/enclosure during daylight, which is considerably less than the 200 to 800 mg (wet)/d increase in total fish biomass in the treatments. Thus, the coho fry must have been consuming significant quantities of benthos from the substrate.

Despite fish densities being increased from $2 \times$ to $4 \times$ above ambient density levels, coho fry had no measurable effect on macroinvertebrate distribution or abundance in these re-

stricted substrate patches in Carnation Creek. Similarly, Allan (1982) found the presence or absence of brook trout (Salvelinus fontinalis) did not play a major role in determining macroinvertebrate abundance or species composition in a Colorado stream. In both of these stream experiments, the salmonid predators appear to be "weak interactors" (sensu Paine 1980) in the food web rather than keystone predators, because their presence or absence has little or no effect on the structure of their macroinvertebrate prey community. Although salmonids forage extensively on macroinvertebrates, any local depletion of macroinvertebrates appears to be rapidly compensated through the movement of macroinvertebrates either via the drift and/or within the substrate. Thus, as suggested by Benke (1978) for lentic freshwater systems, in Carnation Creek the primary impact of fish predation on macroinvertebrates is likely to be an increase in secondary production rather than a lowering of standing crop.

In contrast to these results for coho fry, sculpin have been shown to reduce Chironomidae densities (Flecker 1984), and predatory plecopteran nymphs can depress the abundance of their macroinvertebrate prey (Peckarsky and Dodson 1980a, 1980b, Walde and Davies 1984). Thus, it appears that predators foraging within the substrate interstices (e.g., sculpin and Plecoptera) have a greater potential for influencing the distribution and abundance of benthic macroinvertebrates than predators (e.g., salmonids) feeding on substrate surfaces or on the drift. Indeed, the only macroinvertebrates that were affected by patch-restricted coho fry were those that swim along the substrate surface (Ameletus sp., B. tricaudatus). Coho fry may strongly affect the population dynamics of these surface dwellers.

This research has demonstrated that during the low discharge period when current velocity and sediment transport are low, benthic macroinvertebrate distribution and abundance in the streambed were not measurably affected by coho fry. Thus, although salmonid predation may affect the secondary production of macroinvertebrates, no measurable effect on macroinvertebrate standing crop was detected. However, it is stressed that these results only apply to the late-summer period of low flow and drift. Additional replications of this experiment must be conducted in other seasonal periods with different flow regimes and macroinvertebrate composition to more fully understand the importance of coho fry predation to this macroinvertebrate community.

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Appendix 1

Mean (± 1 SE) final benthic densities (/0.1 m²) of macroinvertebrate taxa in the treatment without fish (0×) and with ambient (1×), double ambient (2×), and quadruple ambient (4×) fish densities. Macroinvertebrate size class is indicated by L (>3 mm) or S (<3 mm), while * indicates a significant difference among the treatments.

	Size	Density					
Taxa	Class	0×	1×	2×	4×		
Diptera total		58.3 (12.3)	48.1 (12.9)	65.1 (17.7)	67.3 (21.3)		
Chironomidae	L	28.2 (8.1)	21.3 (8.9)	25.8 (7.5)	24.4 (6.9)		
Chironomidae	S	30.1 (10.2)	26.8 (9.7)	39.3 (8.1)	42.9 (11.6)		
Ephemeroptera total		36.6 (8.9)	30.1 (5.8)	34.4 (6.4)	38.3 (7.2)		
*Ameletus	L	6.6 (1.9)	5.3 (0.8)	2.3 (1.3)	0		
Ameletus	S	1.1 (0.3)	0	1.0 (0.6)	1.3 (0.7)		
Baetis hageni	S	4.7 (1.8)	6.0 (1.0)	8.4 (3.8)	10.0 (1.4)		
*B. tricaudatus	L	7.3 (2.5)	4.4 (2.1)	2.1 (0.8)	2.4 (0.6)		
Cinygmula ramaleyi	L	1.3 (0.4)	0	1.7 (0.7)	1.9 (1.3)		
C. ramaleyi	S	1.7 (0.2)	0	1.9 (0.9)	1.6 (1.1)		
Ephemerella	S	2.4 (0.5)	2.1 (1.6)	3.0 (2.1)	3.8 (1.6)		
Paraleptophlebia	L	2.9 (1.2)	4.7 (0.9)	7.3 (3.6)	6.9 (2.8)		
Paraleptophlebia	S	8.6 (3.4)	7.6 (2.5)	6.7 (1.6)	10.4 (4.9)		
Plecoptera total		174 (41.7)	204.5 (19.1)	177.6 (19.4)	182.4 (4.4)		
Sweltza	L	40.4 (8.2)	33.8 (3.6)	52.9 (4.9)	30.1 (5.1)		
Capnia	S	132.0 (37.9)	168.2 (13.2)	120.4 (22.5)	147.0 (7.5)		
Zapada	S	1.7 (0.5)	2.5 (0.6)	4.3 (2.3)	5.3 (2.2)		
Trichoptera total		64.2 (15.9)	87.0 (24.8)	65.4 (16.2)	84.2 (12.3)		
Hydroptilidae	S	1.9 (0.7)	4.1 (1.6)	4.1 (2.5)	1.8 (1.6)		
Limnephilidae	S	62.3 (16.8)	82.9 (24.2)	61.3 (16.5)	82.4 (10.9)		
Oligochaeta	L	16.0 (9.1)	10.7 (4.8)	21.5 (4.2)	13.7 (5.6)		

Appendix 2

Mean (± 1 SE) final benthic dry biomasses (mg/0.1 m²) of the macroinvertebrate taxa in the treatment without fish (0×) and with ambient (1×), double ambient (2×), and quadruple ambient (4×) fish densities. Macroinvertebrate size class is indicated by L (>3 mm) or S (<3 mm), while * indicates a significant difference among the treatments.

	Size	Biomass						
Taxa	Class	0×	1×	2×	4 ×			
Diptera total		2.4 (0.9)	1.7 (0.8)	3.2 (1.9)	2.7 (1.9)			
Chironomidae	L	1.7 (0.7)	1.0 (0.3)	2.3 (1.3)	1.9 (0.9)			
Chironomidae	S	0.7 (0.3)	0.7 (0.4)	0.9 (0.7)	0.8 (0.6)			
Ephemeroptera total		12.8 (5.6)	16.4 (4.4)	10.8 (4.2)	9.5 (3.9)			
*Ameletus	L	7.2 (2.7)	9.2 (2.8)	5.5 (2.5)	0			
Ameletus	S	0.2 (0.1)	0	0.1 (0.1)	0.1 (0.1)			
Baetis hageni	S	0.1 (0.1)	0.1 (0.1)	0.2 (0.1)	0.2 (0.1)			
*B. tricaudatus	L	2.5 (1.1)	1.6 (0.9)	0.8 (0.3)	0.7 (0.3)			
Cinygmula ramaleyi	L	0.5 (0.2)	0	0.9 (0.4)	2.7 (1.6)			
C. ramaleyi	S	0.1 (0.1)	0	0.1 (0.1)	0.1 (0.1)			
Ephemerella	S	0.1 (0.1)	0.1 (0.1)	0.2 (0.1)	0.2 (0.1)			
Paraleptophlebia	L	1.7 (0.9)	4.6 (1.4)	2.4 (1.5)	4.7 (2.7)			
 Paraleptophlebia 	S	0.4 (0.2)	0.8 (0.3)	0.6 (0.2)	0.8 (0.5)			
Plecoptera total		6.7 (1.2)	8.5 (1.0)	10.2 (2.6)	8.7 (1.2)			
Sweltza	L	2.5 (1.4)	3.1 (0.6)	6.7 (2.5)	4.2 (1.4)			
Capnia	S	3.8 (1.3)	5.2 (0.7)	3.2 (0.5)	3.9 (0.3)			
Zapada	S	0.4 (0.1)	0.2 (0.1)	0.3 (0.2)	0.6 (0.3)			
Trichoptera total		4.7 (1.2)	10.3 (3.6)	4.5 (1.2)	10.0 (5.2)			
Hydroptilidae	S	0.1 (0.1)	0.3 (0.1)	0.6 (0.3)	0.5 (0.4)			
Limnephilidae	S	4.6 (1.1)	10.0 (3.6)	3.9 (1.3)	9.5 (5.5)			
Oligochaeta	L	0.3 (0.1)	0.2 (0.1)	0.2 (0.1)	0.2 (0.1)			