Effects of fish predation in erosional and depositional habitats in a temperate stream

Jordan Rosenfeld

Abstract: Combined effects of predation by benthic and drift-foraging fish (prickly sculpin (*Cottus asper*) and coho salmon (*Onchorhynchus kisutch*) parr) on benthic invertebrate community and trophic structure were evaluated in Mayfly Creek, a previously fishless stream in the Coast Range Mountains of British Columbia. The role of microhabitat (substrate) in mediating predation effects was assessed by comparing invertebrate community structure on unglazed ceramic tiles and gravel baskets nested within enclosures. The role of macrohabitat was evaluated by placing enclosures in pool and riffle habitats. Effects of fish predation were most pronounced on tile substrate and in riffle habitat and least pronounced on gravel substrate in pool habitat. The presence of fish caused a decrease in abundance of larger-bodied herbivores (primarily the mayflies *Ameletus* and *Baetis*) and had positive indirect effects on algae and smaller invertebrates (primarily Orthocladiinae chironomids and nemourid stoneflies), probably through competitive release. In contrast with herbivores, detritivorous invertebrates were less influenced by fish predation and more highly correlated with the abundance of organic detritus. The distribution and abundance of detritivores in Mayfly Creek appear to be primarily influenced by bottom-up forces (implying resource limitation), while grazers in algal-based food chains are more strongly influenced by top-down effects (fish predation).

Résumé : Les effets combinés de la prédation exercée par les poissons qui se nourrissent sur le fond et dans la colonne d'eau (chabot piquant (*Cottus asper*) et tacon de coho (*Oncorhynchus kisutch*)) sur la communauté d'invertébrés benthiques et la structure trophique ont été évalués dans le crique Mayfly, cours d'eau autrefois dépourvu de poissons de la chaîne côtière de la Colombie-Britannique. Le rôle du microhabitat (substrat) comme agent de médiation des effets de la prédation a été évalué en comparant la structure de la communauté d'invertébrés sur des tuiles de céramique non vernissées et dans des paniers de gravier installés dans des enclos. Le rôle du macrohabitat a été évalué en plaçant les enclos dans des fosses et des radiers. Les effets de la prédation exercée par les poissons étaient plus marqués sur les tuiles et dans les radiers et moins marqués sur le gravier dans les fosses. La présence de poissons a entraîné une diminution de l'abondance des herbivores de grande taille (surtout les éphémères des genres *Ameletus* et *Baetis*), et avait des effets positifs indirects sur les algues et les invertébrés de petite taille (principalement des chironomides de la famille des Orthocladiinae et des plécoptères de la famille des Nemuridae), effets probablement attribuables à une libération compétitive. Par contraste avec les herbivores, la prédation exercée par les poissons influait moins sur les invertébrés détritivores, qui présentaient une corrélation plus marquée avec l'abondance des détritus organiques. Il semble que la distribution et l'abondance des détritivores dans le crique Mayfly soient influencées principalement par des forces ascendantes (ce qui implique une limitation des ressources), tandis que les effets descendants (prédation exercée par le poisson) influent plus fortement sur les brouteurs dans les chaînes trophiques basées sur les algues.

[Traduit par la Rédaction]

Introduction

Predation can be a powerful force shaping the structure of prey communities (Hunter and Price 1992). Although several recent studies have demonstrated strong effects of fish predation on invertebrate community structure in streams (e.g., Power 1990; Bechara et al. 1992; Flecker 1992), many others have found at best weak effects (Allan 1982; Flecker and Allan 1984; Culp 1986), and much of the variance in predator impacts in streams remains unexplained (Wooster 1994).

J. Rosenfeld. Department of Zoology, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

[1]Present address: B.C. Ministry of Fisheries, Fisheries Research, 2204 Main Mall, Vancouver, BC V6T 1Z4, Canada. e-mail: jordan.rosenfeld@gems4.gov.bc.ca

The degree to which predation influences community structure will depend on a variety of biotic and abiotic factors (Hunter and Price 1992), including the attributes (e.g., size, intrinsic rate of growth) of the primary producer trophic level (Power 1992*a*), the functional role and spatial distribution of dominant predator taxa (Dahl and Greenberg 1996), and differences in prey movement rates (Cooper et al. 1990; Englund 1997) between habitat patches. In physically complex systems like streams, substrate heterogeneity can also play a key role in mediating predation effects through the availability of refuges. For example, fish predation caused a strong trophic cascade on smooth boulder substrate but not over gravel in the Eel River, California, which was attributed to the availability of interstitial refuges in gravel substrate (Power 1992*b*). Independent of substrate heterogeneity, the differentiation of aquatic invertebrates into discrete functional feeding groups may also affect their vulnerability to shared predators depending on whether the resources that they consume are in habitats that are more or less exposed to

fish predation (Kohler and McPeek 1989; Bechara et al. 1992). In particular, herbivorous invertebrates may be constrained to foraging on algae on the upper surfaces of rocks, while detritivores feed on detrital accumulations in substrate interstices, leading to the prediction that direct and indirect fish predation effects should be greatest in habitats with an algal carbon base, i.e., where the majority of food resources are on upper substrate surfaces.

Habitat and substrate heterogeneity, in addition to influencing the availability of refuges, will also affect the relative abundances of algal and detrital organic matter in different habitat types. (These two sources of organic carbon for invertebrates in streams (detrital organic matter versus living plant tissue) will, for simplicity, subsequently be referred to as algal and detrital carbon.) Because of the nature of bedload transport in streams, depositional habitats (pools) and microhabitats (substrate interstices) tend to accumulate detrital carbon (Rabeni and Minshall 1977; Huryn and Wallace 1987), while erosional habitats (riffles) and microhabitats (upper rock surfaces) tend to support algal production (Rosenfeld and Hudson 1997). If functional groups of invertebrates differ in their vulnerability to predation, then small-scale differences in the carbon base of patches within a stream may lead to differences in the impact of local predation in a spatially heterogeneous environment.

Most studies of fish effects in streams have been within fish-bearing streams where fish effects are likely to be smaller or expressed as differences in behavioural responses to predation risk (e.g., McIntosh and Townsend 1996) rather than as radical changes in species composition. An alternative approach for studying the effects of fish predation is to examine the impact of introducing a foreign predator to a previously fishless system. For example, the first study to clearly demonstrate the impact of fish predation on zooplankton was based on the introduction of freshwater herring to a lake without fish adapted to planktivory (Brooks and Dodson 1965). While the impact of fish predation on a naive invertebrate community may be exaggerated (Neill 1994), effects may be clearer than in a fish-bearing system, and the mechanisms and pathways of predator impacts on prey should be similar (Rosenfeld 2000).

The experiment described in this study examined the impact of fish predation on invertebrate community structure in a previously fishless stream. Specific objectives were to assess (*i*) whether membership in different invertebrate functional feeding groups influenced vulnerability to predation and (*ii*) how habitat (pool versus riffle) and microhabitat (gravel versus tile) modified local predator impacts. Simplistic expectations for a three-link food chain (algae/detritus–invertebrates–fish) were that predator impacts should be greatest on simple substrates lacking refugia and on grazing invertebrates in predominantly algal-based food chains.

Materials and methods

Study site

The study was carried out in Mayfly Creek, a second-order stream in the Coastal Western Hemlock biogeoclimatic zone of British Columbia. Mayfly Creek is located 60 km northeast of the city of Vancouver in the University of British Columbia Malcolm Knapp Research Forest (49°18′40″, 122°32′40″) at an elevation of 350 m in the Coast Range Mountains. Streams in coastal British Columbia receive large amounts of rainfall and tend to be moderately oligotrophic. Mayfly Creek flows through second-growth forest with a partially open canopy dominated by western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and Douglas-fir (*Pseudotsuga menziesii*), with red alder (*Alnus rubra*) and salmonberry (*Rubus spectabilis*) common in the riparian zone. Experiments were performed in the upper fishless reach of Mayfly Creek above a series of cascades, which provide a barrier to resident cutthroat trout (*Oncorhynchus clarki*). Research was done during summer baseflow when minimum discharge can be as low as 30 L·s⁻¹ and wetted width is between 2 and 5 m. The stream gradient in this reach averages 1%, and the substratum is dominated by gravel, cobble, and sand in a channel with well-developed pools and riffles. Canopy cover is moderate with occasional gaps, and the stream is cool, rarely exceeding 17.5°C (Richardson 1991).

Experimental design

Experimental units consisted of five enclosures placed in separate channel units (three in riffles, two in pools) spaced 20–100 m apart over a 400-m reach of stream. Enclosures were constructed of a wooden frame supported by 19-mm-diameter, concrete-reinforcing rods (iron rebar), with plywood sides embedded in the stream channel and 6.5-mm galvanized steel mesh across the upstream and downstream ends (Fig. 1). The 6.5-mm-mesh opening was large enough to permit free movement of most stream organisms, with the exception of larger larvae of the tailed frog (*Ascaphus truei*), but small enough to retain fish. Enclosures were 6 m long, 2 m wide, and 1 m high and were divided internally into a larger upstream section and two lower sections (Fig. 1). Each lower section was 2 m long and 1 m wide. The upper sections of all enclosures were in pools and the lower sections were either in slow riffles, where current velocity averaged 16.4 ± 1.8 cm·s⁻¹ (range 11–22 cm·s⁻¹), sufficient to prevent deposition of fine particulate organic matter on upper substratum surfaces, or in pools with much lower current velocity (4.9 ± 1.2 cm·s⁻¹, range 2–7 cm·s⁻¹). Velocities were measured once during baseflow at four points along transects across lower enclosure sections using a Marsh-McBirney model 2000 flowmeter.

Lower enclosure sections were used for fish treatments and controls. Design and interpretation of enclosure experiments in streams are complicated by naturally high background movement rates of prey that may swamp the effects of predation in inappropriately small enclosures (Cooper et al. 1990; Englund 1997), leading to underestimates of predation effects as an artifact of enclosure size. This was of concern in fishless Mayfly Creek, where there was an unknown potential for invertebrate densities and drift rates to be higher than in a fish-bearing stream. To minimize the probability of fish effects in lower enclosure sections being obscured by high immigration rates of prey from fishless areas upstream, upper enclosure sections were also stocked with fish.

To evaluate fish predation effects in different microhabitat types, four 15 × 15 cm unglazed ceramic tiles and five open gravel baskets were placed in each lower enclosure section for colonization by algae and invertebrates. Tiles were used in this experiment as rock surrogates, since regularity in size, shape, and surface texture reduces variance, and benthic community structure on unglazed ceramic tiles has been shown to be similar to that on rock substrate (Lamberti and Resh 1985). Gravel baskets were 30 cm long, 20 cm wide, 5 cm deep, and were made of 6.5-mm-mesh hardware cloth buried flush with the streambed in each lower enclosure section. Baskets were filled with approximately 2.5 L of 4- to 7-cm-diameter river-washed gravel; an additional 1 L of sand and fine gravel was added to partially fill gravel interstices.

One lower section of each enclosure was stocked with coho salmon (*Onchorhynchus kisutch*) parr (mean (± SD) length 50.2 ± 6.5 mm, mean weight 1.6 ± 0.6 g) and prickly sculpin (*Cottus*

Fig. 1. Design of experimental enclosures. Stippled rectangles represent gravel baskets, diamonds represent tiles, and broken lines denote permeable mesh.
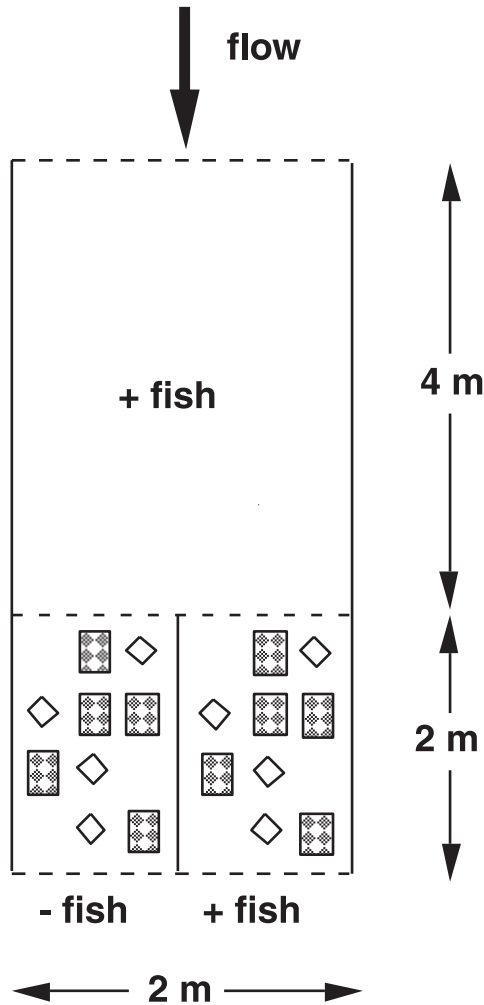
asper) (mean length 72.8 ± 9.8 mm, mean weight 4.3 ± 1.9 g) at a density of 2 and 1 fish·m^{-2}, respectively, and the other lower section was left as a fishless control. Each upper enclosure section was stocked with fish at the same density; coho in upper sections were partially restocked when the smallest fish escaped through the 6.5-mm mesh, so that final densities of coho in upper sections averaged 3 fish·m^{-2}. Average coho and sculpin weight in all enclosure sections combined increased by 95 and 13%, respectively, during the course of the experiment, with a range in final weight of 1.2–9.8 g for coho and 2.6–8.9 g for sculpin. Positive growth suggests that fish densities were not excessive for the productivity of the system. The appropriate ambient density of fish was determined by electrofishing reaches in nearby streams of similar size and water chemistry (J. Rosenfeld, unpublished data). Coho and sculpin used during the experiment were collected from the Allouette River downstream of Mayfly Creek by electrofishing or baited minnow traps.

Fish were stocked during May 18–20, 1993, 1 week after substrates were placed in enclosures. Lengths and weights of all fish were measured at the beginning and end of the experiment. To ensure that upper Mayfly Creek remained fishless, sculpin were sexed using the morphology of the anal papilla, and only males were used. Several impassable falls downstream ensured that any escaped coho would be unable to return to the stream to spawn af-

ter running to the ocean. Juvenile coho were used rather than resident cutthroat trout to ensure that escaped fish would not colonize the stream. Fish were collected from enclosures by electroshocking at the end of the experiment, following removal of artificial substrates. Voltage was turned up to 700 V and the entire enclosure thoroughly shocked to ensure mortality of any fish that escaped capture.

Tiles and gravel baskets were sampled from August 26 to 31, 101 days after fish introduction, by carefully lifting each substrate off of the stream bottom into a 150-µm-mesh Surber sampler held immediately downstream. Invertebrates were rinsed off of individual tiles into a bucket using a wash bottle and brush, and the contents of the Surber sampler were also backwashed into the same bucket. After collection with a Surber sampler, contents of individual gravel baskets were emptied into a 10-L basin and agitated, and water in the basin was repeatedly decanted into a 150-µm net until the gravel was clean of organic matter and invertebrates. Water containing invertebrates and detritus from gravel and tile baskets was separately filtered through 150-µm-mesh sieves and the filter contents were preserved in 5% formalin. Invertebrates larger than 1 mm were later sorted from samples in the laboratory and identified to genus using Merritt and Cummins (1984), with the exception of chironomids, which were identified to subfamily. Samples from gravel baskets were split into quarters when the volume of detritus in the sample exceeded 200 mL. Chironomids were sorted and counted from randomly chosen subsamples until a minimum of 200 chironomids were counted. Counts were only split for chironomids, which were the most abundant invertebrate; all other taxa were completely sorted from each sample. Lengths of a total 26 000 invertebrates were measured to the nearest 0.05 mm using a digitizing system and a Wild M5 dissecting scope equipped with a drawing tube.

Chlorophyll *a* was measured only on gravel substrata. Five pieces of gravel were randomly removed from the surface of separate gravel baskets on each enclosure side, and algae on individual gravel pieces were extracted for chlorophyll *a* in 90% acetone in 250-mL glass jars on ice in the dark overnight. Chlorophyll *a* fluorescence was measured the next day using a Turner Designs model 10-005 R fluorometer. Chlorophyll *a* abundance was corrected for the upper surface area of each stone (measured by tracing outlines on paper) and is expressed as milligrams per square metre. Chlorophyll *a* was not measured on tiles because of logistic difficulties subsampling tiles for chlorophyll *a* and because periphyton abundance was visually similar on both tile and gravel. Chlorophyll *a* measurements from a subsequent predation experiment in the same enclosures the following year demonstrated that chlorophyll *a* levels were roughly equivalent on both substrate types (2.9 ± 1.0 mg·m^{-2} on tile, 4.5 ± 1.7 mg·m^{-2} on gravel; Rosenfeld 1997*a*).

Ash-free dry mass of all organic matter greater than 150 µm associated with each substrate was measured by drying organic matter from each sample to a constant weight in a preashed aluminium boat at 75°C and then combusting samples in a muffle furnace for 4 h at 550°C. Organic matter on tiles in riffles consisted primarily of periphyton and fine particulate organic matter, while organic matter in gravel baskets and on tiles in pools also included coarser detritus.

Data analysis

Data analysis was performed using PC SAS version 6.03. Invertebrate abundance data were (log + 1) transformed, proportional data were arsine square root transformed, and predator impact (PI) indices (described below) were square root transformed to maximize normality of distributions and equalize variances. Statistical significance was accepted at α = 0.05. Fish effects on chlorophyll *a* were analyzed as a paired t test (the difference between predator and control treatments within each enclosure) for pools (*n* = 2) and riffles (*n* = 3) separately. Fish effects on total invertebrate abun-

1372

Can. J. Fish. Aquat. Sci. Vol. 57, 2000

dance and individual taxa were analyzed as a split-plot design with enclosures as blocks ($n = 5$), fish presence/absence as the main effect (two levels within each block), and substrate (two levels) as a subplot within each main plot (total $n = 20$) (Snedecor and Cochran 1989); habitat type (pool versus riffle) was not included in this analysis because of insufficient degrees of freedom. Critical significance levels for evaluating the significance of fish effects on individual taxa were adjusted with a sequential Bonferroni correction (Sokal and Rohlf 1997) for multiple tests (first critical $\alpha = 0.05/9 = 0.0056$). If there was a significant fish by substrate interaction, the effect of fish predation was analyzed separately for tile and gravel substrate as a randomized block design without replication (Sokal and Rohlf 1997) ($n = 5$ blocks, two fish levels, total $n = 10$). Invertebrate – organic matter relationships were evaluated using analysis of covariance (ANCOVA) with organic matter as the covariate. In order to simplify interpretation of the results, untransformed data were used for ANCOVA of total invertebrate – organic matter relationships (total $n = 20$), since distribution of residuals from regression with untransformed data was not significantly different from normal (Shapiro–Wilke normality test, $W = 0.93$, $P = 0.40$).

Because differences in densities between taxa may lead to biases in objectively scaling predation effects, a modification of the PI index described by Cooper et al. (1990) was used to assess predation effects on total invertebrate abundance. In addition to standardizing for differences in density between taxa, the PI index has the advantage of equivalently scaling increases and decreases relative to a control. PI is calculated as the natural logarithm of the ratio of prey densities in predator treatments to prey densities in controls (PI = $\ln(N_P/N_C)$. The negative sign used by Cooper et al. (1990) was dropped from the PI expression so that a positive or negative PI corresponds to an increase or decrease in prey abundance in the presence of predators.

Differences in community structure between combined substrate and habitat types were evaluated using principal components analysis. The correlation matrix was used as this reduces the influence of invertebrate abundance and has been demonstrated to give the most consistent results in ordination. In order to provide sufficient data points for a meaningful analysis of community structure, data from individual tiles and gravel baskets were used for the ordination rather than the enclosure means.

The contribution of fish predation as a source of variation in total invertebrate abundance and abundance of individual taxa was calculated using variance components, as described by Sokal and Rohlf (1997), for tile and gravel separately (randomized block design without replication, $n = 5$ blocks, two fish levels, total $n = 10$). Abundance of invertebrates and organic carbon covaried at two distinct spatial scales in the experimental design: within enclosures (between replicate substrates) and between enclosures. The correlation of invertebrate abundance with organic matter, for all invertebrates and taxa individually, was partitioned into within- and between-enclosure components for gravel and tile separately using sequential sums of squares. The variance in abundance due to organic matter within enclosures was calculated as the residual variance after enclosure effects (the block) were used to remove the effects of average organic matter abundance per enclosure in multiple regression ($n = 40$ for tile, four tiles per enclosure side; $n = 50$ for gravel, five gravel baskets per enclosure side). The variance in invertebrate abundance due to differences in average organic matter per enclosure was calculated by subtracting the variance due to organic matter within enclosures from the total variance due to organic matter both within and between enclosures. The regression mean square was used as the error term to evaluate the significance of organic matter both within and between enclosures.

Research in aquatic systems has demonstrated that large-bodied invertebrate taxa are typically more vulnerable to fish predation (Allan 1978). To test for differences in predation effects as a function of prey size, invertebrates were divided into small (<3 mm), medium (≥3 mm, <6 mm), and large (≥6 mm) size-classes based on total length. These size-class divisions roughly correspond to <0.1, 0.1–1.0, and >1.0 mg weight-classes based on length–weight regressions from Smock (1980). These weight-classes were identified by Allan (1981) as being approximately representative of the vulnerability of invertebrates to drift-foraging fish; invertebrates <0.1 mg show a lower vulnerability to fish predation and propensity for diurnal drift periodicity, whereas those >1 mg are preferentially selected by fish and tend to drift primarily at night (Allan 1984). Because abundances of different size-classes of invertebrates from an individual substrate are not independent, the effect of fish predation on invertebrate abundance in different size-classes was analyzed as a split-plot design with enclosures as blocks ($n = 5$), fish presence (two levels) as the main effect, and size (three levels) as a subplot (or repeated measure) within a plot (total $n = 30$) for tile and gravel separately (Snedecor and Cochran 1989). A split-plot design is an appropriate method for dealing with the nonindependence of repeated measures when the order of replicate measurements is unimportant (Snedecor and Cochrane 1989).

Results

Fish effects on chlorophyll *a*

Impacts of fish on algae were consistent with the expectation of greater fish effects in habitats dominated by herbivorous invertebrates. Chlorophyll *a* was significantly higher on gravel substrate in riffles in the presence of fish (paired *t* test, $t_2 = 4.41$, $P = 0.05$) (Fig. 2), but there was no apparent effect of fish on chlorophyll *a* in pools (paired *t* test, $t_1 = 0.66$, $P = 0.63$). Variance of chlorophyll *a* within enclosures was also significantly lower in the absence of fish in riffles (paired *t* test, $t_2 = 6.1$, $P = 0.03$) (Fig. 2), indicating more uniform grazing activity by herbivores in the absence of predation, but variance was unaffected in pools (paired *t* test, $t_1 = –0.96$, $P = 0.52$).

Invertebrate community structure and organic matter relationships

The combined ordination of substrate samples ($n = 50$ for gravel, $n = 40$ for tile) demonstrated that invertebrate communities on different substrate and habitat types are well separated (Fig. 3). The first principal component (PC1) explained 46.7% of the variation in the data set, and the second principal component (PC2) explained an additional 19.6%. There is a positive correlation between PC1 and the abundance of primarily detritivore taxa (e.g., *Despaxia* sp., *Zapada* sp., *Paraaleptophlebia* sp., and Tipulidae) (see axis labels in Fig. 3); PC1 appears to be an axis representing detritivore abundance and separates tile from gravel substrate, indicating that detritivores are proportionally more abundant on gravel substrate. PC2 is positively correlated with the abundance of grazing mayflies and negatively correlated with the abundance of chironomids and appears to be an axis separating pool and riffle habitats, indicating that grazing mayflies are proportionately more abundant in riffles.

A significant positive relationship was observed between total invertebrate abundance on tiles and organic matter (ANCOVA, $F_{1,7} = 30.1$, $P = 0.001$, total $n = 10$ fish for treatment means) (Fig. 4A), suggesting limitation of invertebrate abundance by organic carbon (periphyton and fine particulate detritus) on tile surfaces. There was also a significant difference in intercept for pools and riffles (ANCOVA,

Fig. 2. Chlorophyll *a* concentration (±1 SD) on gravel substrate in individual pool and riffle enclosures in the presence and absence of fish. Solid circles represent fish treatments and open circles represent fishless controls.
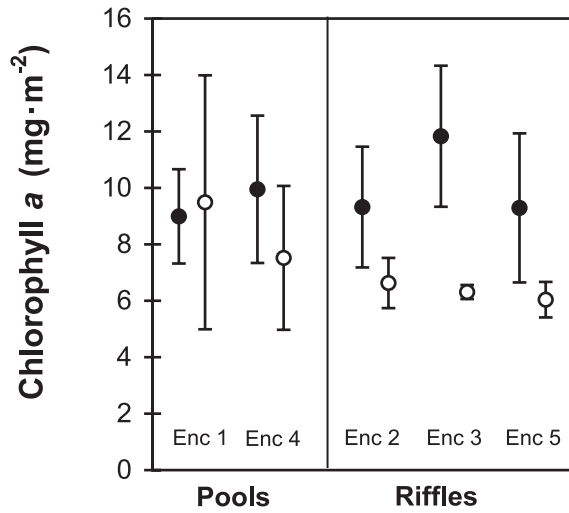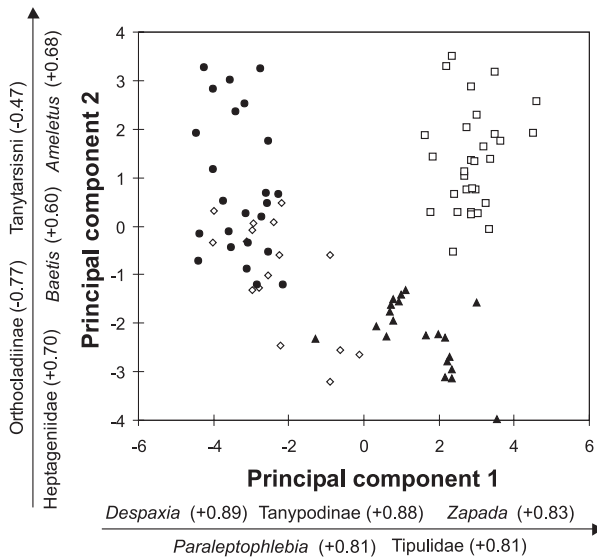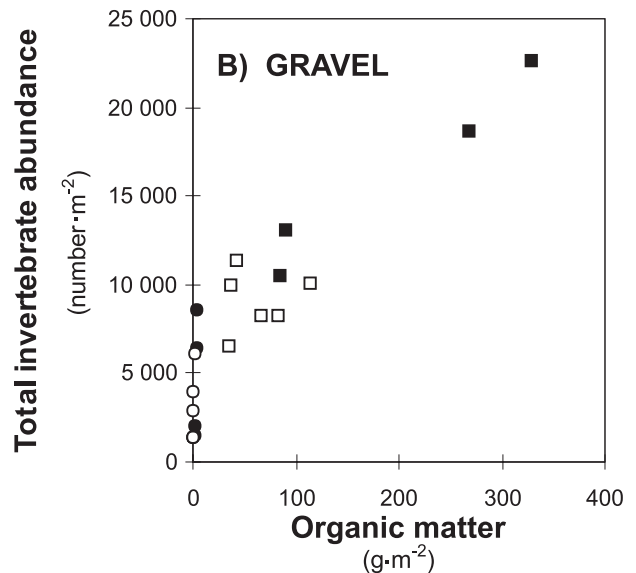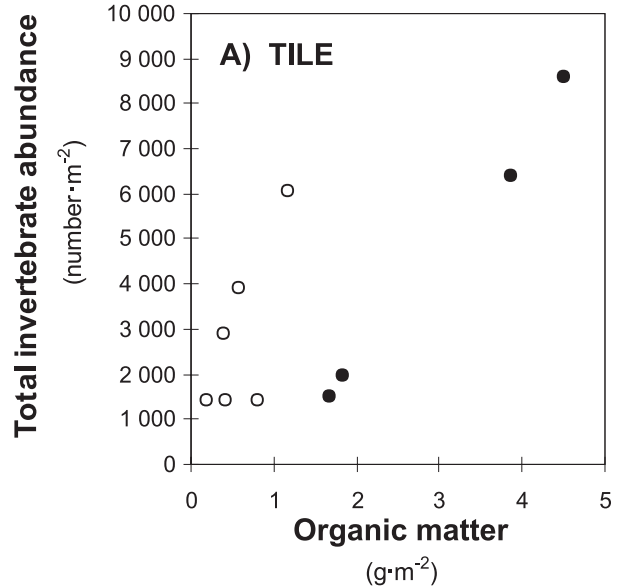

Fig. 3. Ordination of the four substrate–habitat combinations in species space (using only those taxa contributing to at least 1% of the invertebrate community); *n* = 50 for gravel and *n* = 40 for tile. Those taxa with the highest correlations of density with principal component score (correlation coefficient in parentheses) are labeled on the axes. Circles represent tiles in riffles, diamonds represent tiles in pools, triangles represent gravel in pools, and squares represent gravel in riffles.

Fig. 4. Relationship between total invertebrate abundance and organic matter on (A) tiles and (B) gravel in pool and riffle habitat. Points represent enclosure treatment means (*n* = 10). The regression equation for tile is $N = 2520$(organic) − 4240 (habitat) + 1400, where habitat = 0 for riffle and 1 for pool. The regression equation for total invertebrate abundance on gravel is $N = 46.4$(organic) + 6600. Open circles represent tiles in riffles, solid circles represent tiles in pools, open squares represent gravel in riffles, and solid squares represent gravel in pools.

$F_{1,7} = 10.0$, $P = 0.016$), indicating that riffles supported more invertebrates for a given quantity of organic matter. There was a significant positive relationship between invertebrate abundance and organic matter on gravel substrate as well, but the slope of the relationship was significantly less than for tile (*t* test with unequal variances, Welch's approximate $t_9 = 17.04$, $P < 0.01$), and there was also no significant habitat (pool–riffle) effect for gravel (Fig. 4B), indicating

substantial differences in invertebrate abundance – organic matter relationships between tile and gravel substrate.

The fish treatment had no detectable effect on the abundance of organic matter on gravel substrate but caused a small but significant increase in organic matter biomass (periphyton and fine detritus) on tiles (analysis of variance (ANOVA), $F_{1,5} = 11$, $P = 0.03$, total $n = 10$ for treatment means); mean organic matter on tiles (as ash-free dry

1374

Can. J. Fish. Aquat. Sci. Vol. 57, 2000

Table 1. Results of split-plot ANOVA for the effect of fish predation and substrate type on total invertebrate abundance (log transformed).

Effect	Source	df	SS	MS	F	P
Main	Enclosure	4	0.519	0.130	13.19	0.014*
	Fish	1	0.177	0.177	17.98	0.013*
	Main plot error[a]	4	0.039	0.010	0.58	0.685
Subplot	Substrate	1	1.822	1.822	107.59	0.0001**
	Fish × substrate	1	0.124	0.124	7.34	0.027*
	Subplot error[b]	8	0.136	0.017		

Note: *Significant at $\alpha = 0.05$; **significant at $\alpha = 0.01$.
[a]Main plot error = (enclosure × fish).
[b]Subplot error = enclosure × substrate + enclosure × fish × substrate).

weight) averaged 1.7 g·m^{-2} in the fish treatment and 1.4 g·m^{-2} in the control.

Mean organic matter biomass (primarily detrital carbon) was two orders of magnitude higher on gravel than on tiles (ANOVA, $F_{1,7} = 142.5$, $P = 0.0001$, total $n = 10$ for enclosure side means) and three to five times higher in pools than in riffles (ANOVA, $F_{1,7} = 11.9$, $P = 0.011$, $n = 10$), averaging 0.58 ± 0.36 g·m^{-2} on tiles in riffles, 2.98 ± 1.76 g·m^{-2} on tiles in pools, 62.8 ± 20.7 g·m^{-2} on gravel in riffles, and 193 ± 149 g·m^{-2} on gravel in pools.

Predation effects on total invertebrate abundance by size-class

Total abundance of invertebrates was significantly affected by the fish treatment (split-plot ANOVA) (Table 1), with a significant interaction between fish treatment and substrate type (Fig. 5; Table 1). As expected, different size-classes of invertebrates responded differently to the presence of fish, but the effects were substrate specific (Table 2). There was a significant fish by invertebrate size interaction on tile but no significant fish effects or interaction on gravel (split-plot ANOVA) (Table 2). Enclosures are treated as blocks, and the significant enclosure effect indicates differences in invertebrate abundance between enclosures; the highly significant size effect (Table 2) simply indicates that abundance of invertebrates differs greatly among size-classes, i.e., invertebrates were more abundant in the smaller size-classes.

Fish predation on tiles in riffles increased the abundance of the smaller and intermediate invertebrate size-classes (Fig. 5). On tiles in pools, the smallest size-class was also more abundant in the presence of fish, although the effect size was smaller than in riffles. When considered by size-class, the PI index was positive for small and medium sizes and negative for the largest size-class on tiles. The PI index was also generally larger in riffles than in pools on both substrata, and fish predation effects were also generally smaller on gravel than on tile. The only apparent effect of fish on total invertebrate abundance on gravel substrate was a statistically nonsignificant increase in abundance of the smallest size-class in riffles.

Forty-nine percent of the variance in total invertebrate abundance on tile was due to the fish treatment ($F_{1,4} = 14.3$, $P = 0.02$) whereas none of the variance on gravel was accounted for by fish predation ($F_{1,4} = 0.39$, $P = 0.57$). In contrast, 59% of the variance in invertebrate abundance on gravel was due to correlation with organic matter abundance

Fig. 5. PI index (± 1 SD) for total invertebrate abundance in three size-classes, small (<3 mm), medium (≥ 3 mm, <6 mm), and large (≥ 6 mm), on tile and gravel substrate in pool ($n = 2$) and riffle ($n = 3$) habitat. Open bars represent riffles and solid bars represent pools.
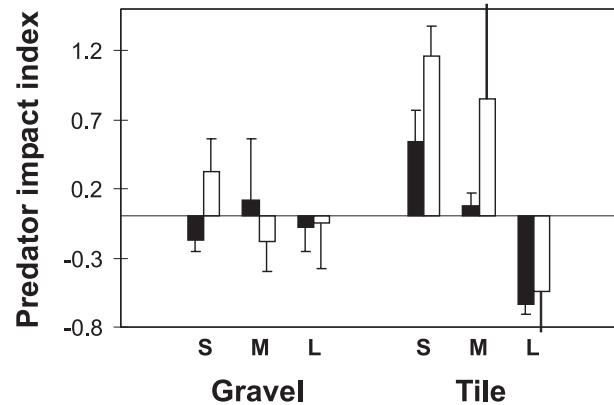
(measured as ash-free dry weight) both within (12%; $F_{1,43} = 19.0$, $P < 0.001$) and between (47%; $F_{443} = 72.7$, $P < 0.001$) enclosures. A much smaller but significant proportion of variance in abundance on tile was also correlated with organic matter both within (6%; $F_{1,33} = 11.7$, $P = 0.005$) and between (17%; $F_{1,33} = 33.9$, $P < 0.001$) enclosures.

Predation effects on individual taxa by habitat and substrate

The proportion of variation in invertebrate abundance that was explained by fish predation was highest for those taxa that appeared to be partly or largely herbivorous, either as grazers (*Ameletus*, *Baetis*) or collector-gatherers on upper substrate surfaces (Orthocladiinae) (Fig. 6). Fish predation had a significant impact on density (evaluated using a sequential Bonferroni correction) only for those taxa marked with an asterisk in Fig. 6: *Ameletus* (split-plot ANOVA, Table 3) and *Zapada* (split-plot ANOVA, $F_{1,4} = 84.4$, $P = 0.008$, $n = 20$) on tile and gravel and orthoclads on tile ($F_{1,4} = 27.8$, $P = 0.006$, $n = 10$). Most other taxa had a relatively minor proportion of variation in abundance accounted for by the presence of fish. PI was negative for larger-bodied mayflies such as *Ameletus* and *Baetis* (Fig. 7) but tended to be positive for smaller taxa such as *Zapada* (Plecoptera: Nemouridae) and orthoclad chironomids, indicating a substantial increase in abundance in fish treatments. Although reduction of *Baetis* density by fish ($P = 0.08$ in all habitats, $P = 0.04$ in riffles) was not significant at a Bonferroni-adjusted level of significance, this is possibly due in part to a lack of statistical power rather than to an absence of predator impact, since density of both *Baetis* and *Ameletus* was significantly reduced in a replicated predation experiment the following year (Rosenfeld 1997*a*). In contrast with *Baetis* and *Ameletus*, heptageniid density (primarily *Cinygmula*) was not strongly affected by the presence of fish. As previously observed by Allan et al. (1986), slight observer movement stimulated an escape response in grazing heptageniids (J. Rosenfeld, personal observation) whereas *Ameletus* has a much higher tolerance to visual stimulation.

Table 2. Results of split-plot ANOVA for the effect of fish predation and enclosure on total invertebrate abundance (log transformed) on tile and gravel substrate.

Substrate	Source	df	SS	MS	F	P
Tile						
Main effect	Enclosure	4	1.090	0.273	5.77	0.06
	Fish	1	0.234	0.234	4.95	0.09
	Main plot error[a]	4	0.189	0.047	2.23	0.11
Subplot effect	Size	2	7.508	3.754	176.97	0.0001**
	Fish × size	2	0.396	0.198	9.34	0.002**
	Subplot error[b]	16	0.339	0.0212		
Gravel						
Main effect	Enclosure	4	0.391	0.098	10.48	0.022*
	Fish	1	0.000	0.000	0	0.99
	Main plot error[a]	4	0.037	0.009	0.26	0.9
Subplot effect	Size	2	5.527	2.764	76.28	0.0001**
	Fish × size	2	0.012	0.006	0.16	0.85
	Subplot error[b]	16	0.580	0.036		

Note: *Significant at $\alpha = 0.05$; **significant at $\alpha = 0.01$.
[a]Main plot error = (enclosure × fish).
[b]Subplot error = enclosure × substrate + enclosure × fish × substrate).

Table 3. Results of split-plot ANOVA for the effect of fish predation on abundance of *Ameletus* (log transformed).

Effect	Source	df	SS	MS	F	P
Main	Enclosure	4	0.647	0.162	7.16	0.041*
	Fish	1	0.787	0.787	34.82	0.004**
	Main plot error[a]	4	0.090	0.023	0.87	0.52
Subplot	Substrate	1	0.176	0.176	6.8	0.03*
	Fish × substrate	1	0.087	0.087	3.38	0.1
	Subplot error[b]	8	0.207	0.026		

Note: *Significant at $\alpha = 0.05$; **significant at $\alpha = 0.01$.
[a]Main plot error = (enclosure × fish).
[b]Subplot error = enclosure × substrate + enclosure × fish × substrate).

The relative proportion of variance in invertebrate abundance explained by fish predation was consistently higher on tile substrate than on gravel (Fig. 6), but the taxa most influenced by fish predation were the same on both substrata. In general, the PI index tended to be higher on tile substrate than on gravel (ANOVA for substrate effects on PI indices for all taxa, $F_{1,7} = 6.7$, $P = 0.036$). PI was significantly higher in riffles than in pools for tile substrate (ANOVA, $F_{1,7} = 7.0$, $P = 0.033$) (Fig. 7), but there was no significant habitat effect for gravel.

The relative proportion of variance in abundance of individual taxa that was explained by variance in organic matter within and between enclosures differed among taxa. Detritivores (e.g., tipulids, Tanytarsini chironomids) tended to have a positive relationship with organic matter both within and between enclosures (Fig. 6), although some detritivores (e.g., *Despaxia* sp.) had no significant relationship with the abundance of organic matter at either scale. In general, more of the variance in abundance of most species on gravel substrate was explained by variance in organic matter than by the presence of fish. In contrast, variance in abundance of most taxa on tiles was poorly explained by variance in organic matter, with the exception of Tanytarsini and Tanypodinae chironomids (Fig. 6). Variance in abundance of algivorous inv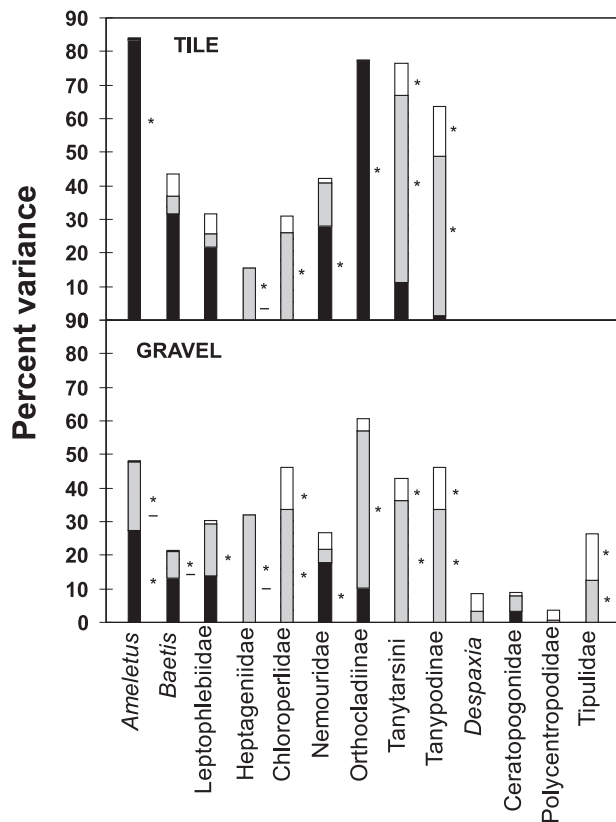ertebrates was largely unrelated to variance in organic matter within enclosures but was sometimes negatively related to variance in organic matter between enclosures for several taxa (*Ameletus*, *Baetis*, and heptageniids) (Fig. 6), indicating a negative association between these grazers and depositional habitats.

Discussion

As predicted, predator effects on different taxa appeared to be strongly related to their feeding habits. Invertebrates that appeared to function as epibenthic grazers or herbivores (large-bodied *Ameletus* and *Baetis*) experienced the largest impact of fish predation. Although absence of a fish effect on heptageniid mayflies suggests differential adaptation of some mayfly taxa to fish predation, decreased grazer density appeared to cause an increase in algal biomass (trophic cascade) in the presence of fish in riffles but not in pools. At the same time, there was an increase in the total abundance of smaller invertebrates in the fish treatments, primarily orthoclad chironomids, which was most pronounced in riffle habitat and on tile substrate.
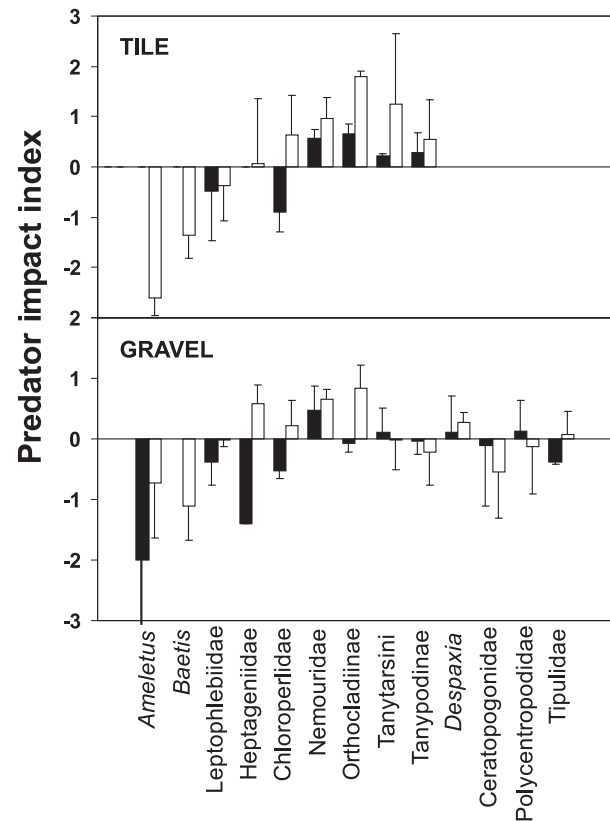
The increase in abundance of smaller invertebrates in the presence of fish suggests competitive release through predation effects on larger grazers. In separate grazing experiments with *Ameletus* in experimental troughs in Mayfly Creek (Rosenfeld 1997b), total invertebrate and orthoclad abundance increased in control treatments without large mayflies and declined in the presence of large grazers, presumably through a combination of exploitative competition for algae and direct consumption of small-instar chironomids. The significant increase in abundance of nemourid stoneflies in the presence of fish suggests the same indirect effect. The possibility that *Zapada* (classified by Merritt and Cummins (1984) as a shredder) are partly herbivorous or otherwise dependent on algal carbon is supported by their much higher densities in riffles than in pools (854 ± 404 versus 279 ± 166·m^{-2}, respectively) and by previous reports of strong algal isotopic signatures for nemourid stoneflies (Rosenfeld and Roff 1992).

1376

Can. J. Fish. Aquat. Sci. Vol. 57, 2000

Fig. 6. Components of variance of total invertebrate abundance on tile and gravel substrate (pool and riffle habitats combined) related to fish predation (solid bars) and variance in organic matter within (open bars) and between (stippled bars) enclosures. Asterisks indicate significance at α = 0.05 with a sequential Bonferroni adjustment. Negative signs below asterisks indicate a negative relationship between organic matter and abundance of taxa.

Fig. 7. PI index (±1 SD) for the most common invertebrate taxa on tile and gravel substrate in pool (*n* = 2) and riffle (*n* = 3) habitat. Open bars represent riffles and solid bars represent pools.

In contrast with the strong effects of fish predation in the primarily algal-based grazing food chain of Mayfly Creek, variance in abundance of detritivores such as Tanytarsini chironomids and tipulids was not significantly influenced by fish predation but was closely related to variance in abundance of their detrital carbon resource. Organic detritus and its associated microflora constitute a carbon resource for many invertebrate taxa in streams, and a general positive relationship between detrital carbon and invertebrate abundance is well documented (e.g., Rabeni and Minshall 1977; Culp et al. 1983). A positive correlation of detritivores with detritus is not unequivocal evidence of resource limitation but is consistent with resource limitation, given that experimental additions of detritus to streams have clearly demonstrated increases in abundance of detritivores (Culp et al. 1983; Richardson 1991). The steeper slope of the invertebrate abundance – organic matter relationship on tile relative to gravel suggests that organic carbon on gravel was lower-quality food relative to that on tile substrate (in terms of fewer invertebrates per gram of organic matter). Lower food quality on gravel is consistent with a lower proportion of periphyton on gravel and higher proportion of coarse particulate organic carbon trapped in gravel interstices, since algal carbon tends to be a higher-quality food resource than

woody detritus (Andersen and Cummins 1979; Cummins and Klug 1979).

Consistent with observations in Mayfly Creek, fish effects in algal-based food chains in previous studies commonly result in decreased abundance (e.g., Bechara et al. 1992; Flecker and Townsend 1994; Forrester et al. 1999) or activity (Power 1992*b*; McIntosh and Townsend 1996) of large-bodied herbivores, leading to increased algal biomass and often increased abundance of small epibenthic herbivores. Excretion of nutrients by fish is an alternative hypothesis for increased algal biomass in the presence of fish, but the observed trophic dynamics are most parsimoniously explained by direct fish effects on large grazers. Nevertheless, the role of both predators and herbivores in nutrient cycling in streams is poorly understood and clearly deserves further study. Increased chironomid abundance in the presence of fish has been observed during previous fish predation experiments in both streams (Bechara et al. 1992; Forrester et al. 1999) and lakes (Crowder and Cooper 1982) and appears to be an indirect effect of size-selective fish predation on larger-bodied herbivores. This is supported by independent grazing experiments, which have shown that large grazers reduce the abundance of smaller epibenthic herbivores (e.g., Harvey and Hill 1991; Lamberti et al. 1992; Wooton et al. 1996), primarily chironomids. The generality of this indirect effect of fish predation is supported by a recent metaanalysis of predation effects in streams, which found that chirono-

mids were the only taxa to significantly increase in abundance in the presence of drift-feeding fish (Englund et al. 1999).

Although all three effects (decreased large grazer abundance, increased algal biomass, and abundance of small herbivores) do not consistently occur in all predation experiments, they recur frequently enough to indicate some generality to the underlying mechanisms in simple three-link (sensu Fretwell 1987) algal-based food chains in streams. Interestingly, these effects of fish predation in algal-based food chains at the within-stream scale are also apparent between streams that differ in predation intensity. Comparison of two New Zealand streams that differ in the effectiveness of their fish predators (brown trout versus native galaxis) shows a similar pattern: increased algal biomass and chironomid abundance in the presence of the more effective predator (brown trout; Huryn 1998). There is also some evidence that this pattern appears across a wider landscape scale between fishless and fish-bearing streams. A comparison of benthic community structure between Mayfly Creek and a nearby fish-bearing stream demonstrated greater abundance of algae and small epibenthic invertebrates in the fish-bearing stream (Rosenfeld 2000). Similarly, Harvey (1993), in a broad survey of Utah streams, found fish-bearing streams to have fewer large grazers and increased abundance of small epibenthic herbivores relative to fishless ones. Although Power (1990) also observed strong effects of fish predation in a four-link (sensu Fretwell 1987) algal-based food chain, the presence of an effective invertebrate predator trophic level resulted in a decrease in algal biomass in the presence of fish rather than the increase observed in Mayfly Creek and elsewhere.

As expected, predation effects were greatest on simple substrates (tiles) with minimal refuges. The role of substrate complexity in decreasing predator impact by providing interstitial refuges has been experimentally demonstrated in a number of stream studies (e.g., Brusven and Rose 1981; but see Dahl and Greenberg (1998) for contrasting results). Power (1992*b*) also found that predation effects in algal-based food chains were most pronounced in simple boulder–bedrock habitats and minimal in gravel habitats with abundant interstitial refuges. However, the presence of refuges is confounded by the carbon base of the food chain available to invertebrates on a substrate. Interstitial spaces provide refuges for surface grazers but also accumulate detritus and detritivores, so that as refuges increase, the average carbon base of the food chain on a substrate shifts from algal to detrital. While carbon base and availabilty of refuges appear confounded, they probably function separately to influence vulnerability of invertebrates to fish. Predation effects were greater in riffles than in pools in Mayfly Creek, independent of substrate type and the availability of refuges, which is consistent with the hypothesis that predation effects are most pronounced when the carbon base of a substrate is predominantly algal rather than detrital.

As a consequence of deposition in gravel interstices, detrital carbon was roughly two orders of magnitude higher on gravel substrate than on tile. At the channel unit scale, detrital carbon was also on average three to five times higher in pools than in riffles. In contrast, algal biomass differed little between pools and riffles; subsequent chlorophyll *a* extraction on tile substrate also indicated little difference in algal

Fig. 8. Schematic illustrating the relationship between habitat type, carbon source, and the predicted strength of trophic interactions in streams.
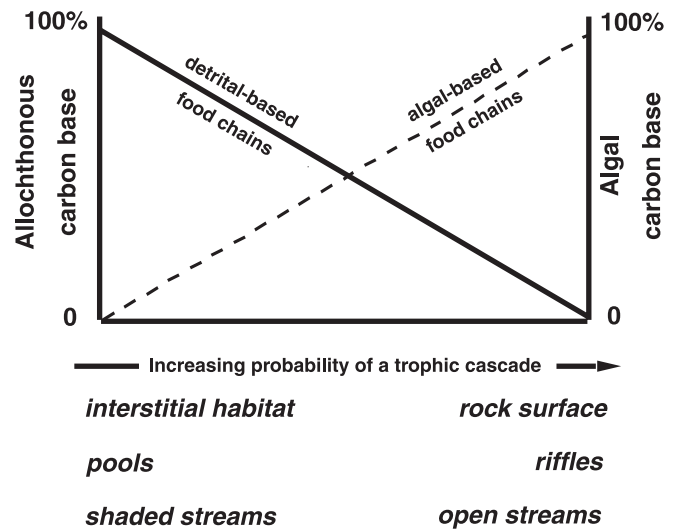
biomass between gravel and tile (Rosenfeld 1997*a*), although algal biomass on tile was not directly measured in this study. This pattern of algal and detrital carbon distribution indicates accumulation of detritus with increasing substrate complexity and decreasing current velocity and a consequent reduction in the relative contribution of algal carbon to the local carbon base. If trophic cascades are more pronounced in algal-based food chains, then the local effects of fish predation on the entire benthic community should become weaker as predation effects in the epibenthos are diluted (Bechara et al. 1993) by inclusion of interstitial detritus and less vulnerable detritivores (Fig. 8). At a larger spatial scale, one might hypothesize that predation effects on the entire benthic community may become more pronounced as light limitation decreases, and increases in algal production shift the food base away from interstitial detritus towards epibenthic production, causing a greater proportion of the invertebrate community to become exposed to fish predation (Fig. 8).

Algal- and detrital-based food chains are a useful construct for understanding trophic interactions in streams and have additional features beyond differences in the vulnerability of primary consumers that will influence consumer–resource dynamics. Feedback between invertebrate consumers and their periphyton resource should be strong in algal-based food chains because grazers have the potential to reduce both the biomass and the production of the primary producer trophic level (e.g., Lamberti and Moore 1984). Detritivorous food chains, however, are donor controlled (Richardson 1993; Polis and Strong 1996). Detritivores have the potential to reduce the biomass of their detrital resource, but they can have no effect on its rate of production, which is determined by allochthonous inputs from the riparian zone or detrital production from algal-based food chains. A better understanding of the linkages between parallel algal- and detrital-based food chains is critical, since food chains are rarely independent and "multichannel omnivory" (e.g., feeding on both algae and detritus) may influence the strength of

1378

Can. J. Fish. Aquat. Sci. Vol. 57, 2000

trophic interactions in a focal food chain (Polis and Strong 1996). This is especially true in open systems such as streams, where the effects of fish predation in algal-based food chains may be enhanced by a predator trophic level that is subsidized through inputs of aquatic invertebrates from detrital-based food chains or by terrestrial invertebrates falling onto the stream surface.

Although trophic cascades appear to be rare in aquatic detrital food chains (Polis and Strong 1996), invertebrate predators may be able to forage more effectively in interstices and detritus than fish, with the potential for a trophic cascade (e.g., Oberndorfer et al. 1984). Detritivores may also in some instances be significantly affected by fish predation; in particular, freshwater gammarids (e.g., Friberg et al. 1994) and isopods (Holomuzki and Hatchett 1994) appear to both be vulnerable to fish predation and have the potential to measurably affect detrital abundance (Short and Holomuzki 1992). Consequently, their presence may significantly alter overall fish–invertebrate–resource dynamics. Similarly, the presence of algivorous or detritivorous fish in tropical streams (Flecker 1992) may have more pervasive effects on benthic community structure than the direct effects of generalized insectivores more typical of north temperate streams with histories of recent glaciation.

Physical habitat structure clearly has a pivotal influence on biotic processes in streams, ranging from community structure to production processes (Huryn and Wallace 1987). The present study indicates that variation in the strength of fish effects can also be constructively understood within the context of the physical stream habitat and its influence on the local carbon base in streams.

Acknowledgements

References

Allan, J.D. 1978. Trout predation and the size composition of stream drift. Limnol. Oceanogr. 23: 1231–1237.

Allan, J.D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Can. J. Fish. Aquat. Sci. 38: 184–192.

Allan, J.D. 1982. The effects of reduction in trout density on the invertebrate community in a mountain stream. Ecology, 63: 1444–1455.

Allan, J.D. 1984. The size composition of invertebrate drift in a Rocky Mountain stream. Oikos, 42: 68–76.

Allan, J.D., Flecker, A.S., and McClintock, N.L. 1986. Diel epibenthic activity of mayfly nymphs, and its non-concordance with drift. Limnol. Oceanogr. 31: 1057–1065.

Andersen, N.H., and Cummins, K.W. 1979. Influence of diet on the life histories of aquatic insects. J. Fish. Res. Board Can. 36: 335–342.

Bechara, J.A., Moreau, G., and Planas, D. 1992. Top-down effects of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. Can. J. Fish. Aquat. Sci. 49: 2093–2103.

Bechara, J.A., Moreau, G., and Hare, L. 1993. The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community: the role of spatial and size refugia. J. Anim. Ecol. 62: 451–464.

Brooks, J.L., and Dodson, S. 1965. Predation, body size, and competition of plankton. Science (Washington, D.C.), 150: 28–35.

Brusven, M.A., and Rose, S.T. 1981. Influence of substrate composition and suspended sediment on insect predation by the torrent sculpin, *Cottus rhotheus*. Can. J. Fish. Aquat. Sci. 38: 1444–1448.

Cooper, S.D., Walde, S.J., and Peckarsky, B.L. 1990. Prey exchange rates and the impact of predators on prey populations in streams. Ecology, 71: 1503–1514.

Crowder, L.B., and Cooper, W.E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology, 63: 894–908.

Culp, J.M. 1986. Experimental evidence that stream macroinvertebrate community structure is unaffected by different densities of coho salmon fry. J. North Am. Benthol. Soc. 5: 140–149.

Culp, J.M., Walde, S.J., and Davies, R.W. 1983. Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. Can. J. Fish. Aquat. Sci. 40: 1568–1574.

Cummins, K.W., and Klug, M.J. 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. 10: 147–172.

Dahl, D., and Greenberg, L. 1996. Impact on stream benthic prey by benthic vs. drift feeding predators: a meta-analysis. Oikos, 77: 177–181.

Dahl, J., and Greenberg, L.A. 1998. Effects of fish predation and habitat type on stream benthic communities. Hydrobiologia, 361: 67–76.

Englund, G. 1997. Importance of spatial scale and prey movements in predator caging experiments. Ecology, 78: 2316–2325.

Englund, G., Sarnelle, O., and Cooper, S.D. 1999. The importance of data selection criteria: meta-analyses of stream predation experiments. Ecology, 80: 1132–1141.

Flecker, A.S. 1992. Fish trophic guilds and the structure of a tropical stream: weak direct vs. strong indirect effects. Ecology, 73: 927–940.

Flecker, A.S., and Allan, J.D. 1984. The importance of predation, substrate, and spatial refugia in determining lotic insect distributions. Oecologia, 64: 306–313.

Flecker, A.S., and Townsend, C.R. 1994. Community-wide consequences of trout introduction in New Zealand streams. Ecol. Appl. 4: 798–807.

Forrester, G.E., Dudley, T.L., and Grimm, N.B. 1999. Trophic interactions in open systems: effects of predators and nutrients on stream food chains. Limnol. Oceanogr. 44: 1187–1197.

Fretwell, S.D. 1987. Food chain dynamics: the central theory of ecology? Oikos, 50: 291–301.

Friberg, N., Andersen, T.H., Hansen, H.O., Iversen, T.M., Jacobsen, D., Krojgaard, L., and Larsen, S.E. 1994. The effect of brown trout (*Salmo trutta* L.) on stream invertebrate drift, with special reference to *Gammarus pulex* L. Hydrobiologia, 294: 105–110.

Harvey, B.C. 1993. Benthic assemblages in Utah headwater streams with and without trout. Can. J. Zool. 71: 896–900.

Harvey, B.C., and Hill, W.R. 1991. Effects of snails and fish on benthic invertebrate assemblages in a headwater stream. J. North Am. Benthol. Soc. **10**: 263–270.

Holomuzki, J.R., and Hatchett, L.A. 1994. Predator avoidance costs and habituation to fish chemicals by a stream isopod. Freshwater Biol. **32**: 585–592.

Hunter, M.D., and Price, P.W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology, **73**: 724–732.

Huryn, A. 1998. Ecosystem-level evidence of top-town and bottom-up control of production in a grassland stream system. Oecologia, **115**: 173–183.

Huryn, A., and Wallace, B.J. 1987. Local geomorphology as a determinant of local macrofaunal production in a mountain stream. Ecology, **68**: 1932–1942.

Kohler, S.L., and McPeek, M.A. 1989. Predation risk and the foraging behavior of competing stream insects. Ecology, **70**: 1811–1825.

Lamberti, G.A., and Moore, J.W. 1984. Aquatic insects as primary consumers. *In* The ecology of aquatic insects. *Edited by* V.H. Resh and D.M. Rosenberg. Prager Science, New York. pp. 164–195.

Lamberti, G.A., and Resh, V.A. 1985. Comparability of introduced tiles and natural substrates for sampling lotic bacteria, algae, and macroinvertebrates. Freshwater Biol. **15**: 21–30.

Lamberti, G.A., Gregory, S.V., Hawkins, C.P., Wildman, R.C., Ashkenas, L.R., and DeNicola, D.M. 1992. Plant–herbivore interactions in streams near Mount St. Helens. Freshwater Biol. **27**: 237–247.

McIntosh, A.R., and Townsend, C.R. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? Oecologia, **108**: 174–181.

Merritt, R.W., and Cummins, K.W. 1984. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.

Neill, W.E. 1994. Spatial and temporal scaling and the organization of limnetic communities. *In* Aquatic ecology: scale, pattern, and process. *Edited by* P.S. Giller, A.G. Hildrew, and D.G. Raffaelli. Blackwell Scientific Publications, Oxford, U.K. pp. 189–231.

Oberndorfer, R.Y., McArthur, J.V., Barnes, J.R., and Dixon, J. 1984. The effect of invertebrate predators on leaf litter processing in an alpine stream. Ecology, **65**: 1325–1331.

Polis, G.A., and Strong, D.R. 1996. Food web complexity and community dynamics. Am. Nat. **147**: 813–846.

Power, M.E. 1990. Effects of fish in river food webs. Science (Washington, D.C.), **250**: 811–814.

Power, M.E. 1992a. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology, **73**: 733–746.

Power, M.E. 1992b. Habitat heterogeneity and the functional significance of fish in river food webs. Ecology, **73**: 1675–1688.

Rabeni, C.F., and Minshall, G.W. 1977. Factors affecting the microdistribution of stream benthos. Oikos, **29**: 33–43.

Richardson, J.S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology, **72**: 873–887.

Richardson, J.S. 1993. Limits to productivity in streams: evidence from studies of macroinvertebrates. *In* Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. *Edited by* R.J. Gibson and R.E. Cutting. Can. Spec. Publ. Fish. Aquat. Sci. No. 118. pp. 9–15.

Rosenfeld, J.S. 1997a. The influence of upstream predation on the expression of fish effects in downstream patches. Freshwater Biol. **37**: 535–543.

Rosenfeld, J.S. 1997b. The effect of large macroinvertebrate herbivores on sessile epibenthos in a mountain stream. Hydrobiologia, **344**: 75–79.

Rosenfeld, J.S. 2000. Contrasting effects of fish predation in a fishless and fish-bearing stream. Arch. Hydrobiol. **147**: 129–142.

Rosenfeld, J.S., and Hudson, J.J. 1997. Primary production, bacterial production, and invertebrate biomass in pools and riffles in southern Ontario streams. Arch. Hydrobiol. **139**: 301–316.

Rosenfeld, J.S., and Roff, J.C. 1992. Examination of the carbon base in southern Ontario streams using stable isotopes. J. North Am. Benthol. Soc. **11**: 1–10.

Short, T.M., and Holomuzki, J.R. 1992. Indirect effects of fish on foraging behaviour and leaf processing by the isopod *Lirceus fontinalis*. Freshwater Biol. **27**: 91–97.

Smock, L.A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biol. **10**: 375–383.

Snedecor, G.W., and Cochran, W.G. 1989. Statistical methods. 8th ed. Iowa State University, Ames, Iowa.

Sokal, R.R., and Rohlf, F.J. 1997. Biometry. Freeman and Company, New York.

Wooster, D. 1994. Predator impacts on stream benthic prey. Oecologia, **99**: 7–15.

Wooton, J.T., Parker, M.S., and Power, M.E. 1996. Effects of disturbance in river food webs. Science (Washington, D.C.), **273**: 1558–1561.