

THE EFFECT OF FISH PREDATION ON BENTHIC COMMUNITY
STRUCTURE IN STREAMS

by

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ABSTRACT

The conditions under which fish have a large impact on benthic invertebrate community structure in streams are poorly defined. To better understand the mechanisms by which fish affect lotic invertebrate community structure, a series of experiments were performed in a fishless and fish-bearing stream in the University of British Columbia Malcolm Knapp Research Forest in the Coast Mountains of British Columbia.

The first experiment examined the effect of predation by prickly sculpin (*Cottus asper*) and coho parr (*Onchorhynchus kisutch*) on invertebrates associated with tile and gravel substrate placed in enclosures installed in pools and riffles in fishless Mayfly Creek. Effects of fish were most pronounced on tile substrate and in riffle habitat, and least pronounced on gravel substrate in pool habitat. Fish predation resulted in decreased density of larger-bodied (>6mm) herbivores (primarily the mayflies *Ameletus* and *Baetis*) and increased abundance of smaller (< 3mm) herbivorous invertebrates (primarily Orthoclaadiinae chironomids and nemourid stoneflies) and algae. The effects of fish predation in riffles in fish-bearing Jacobs Creek were similar to those observed in Mayfly Creek, except that there was no increase in algal biomass in the presence of fish.

The indirect increase in algal biomass and density of small herbivores observed under fish predation was reproduced in experimental stream channels by excluding large invertebrate herbivores (tailed frog tadpoles (*Ascaphus*) and *Ameletus*), confirming that

direct effects of fish on large-bodied grazers released algae and smaller herbivores from competitively dominant grazers.

Manipulation of coho densities in upper enclosure sections in a fourth experiment indicated that upstream predation could have a small but measurable indirect effect on algal biomass in downstream patches.

The abundance of detritivores in Mayfly and Jacobs Creek appear to be largely controlled by bottom-up forces (resource limitation), while herbivores are more strongly influenced by top-down effects (fish predation). A model for effects of fish predation on invertebrate community structure is proposed which predicts stronger predation effects in algal-based food chains than detrital-based food chains, both of which occur at a hierarchy of spatial scales in streams.

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CHAPTER 1

Introduction

Community structure is determined by both the abiotic environment, which constrains the suite of species that are adapted to living in a particular habitat (Hutchinson 1957, Southwood 1977, 1988, Grime 1974), and the species assemblage itself, which determines whether the community is structured by predation or resource limitation (competition; Connell 1975, Fretwell 1977, 1987, Hairston et al. 1960, Power 1992a, Hunter and Price 1992). The abiotic environment affects organisms at two time scales, first by constraining the adaptations of organisms over evolutionary (geologic) time (Southwood 1977, 1988), and secondly by the influence of environmental structure on the interactions of organisms in ecological time. In particular, the structure of the environment can have pervasive effects on predator-prey interactions (Sih et al. 1985, Menge and Olson 1990, Power 1992b). Habitat structure affects predator search efficiency (Crowder and Cooper 1982, Diehl 1988), the availability of refuges for prey (Brusven and Rose 1981, Fraser and Ceri 1982, Wilzbach et al. 1986), and the patch dynamics of predator-prey interactions (Huffaker 1958, Pringle 1988).

Stream ecosystems are structurally complex, with an abiotic environment that varies greatly over small spatial scales (Cooper et al. 1997), and rapidly over short temporal ones (i.e. during spates; Resh et al. 1988). Despite a frequent disturbance

regime, biotic process frequently play a large role in shaping community structure in streams (see references in Allan 1995). In particular, the effects of fish predation on invertebrate community structure have been intensively studied (see reviews in Power 1992b, Wooster 1994, Allan 1995, Dahl and Greenberg 1996). Early studies of fish predation on invertebrates typically detected only weak (Allan 1982, Reice 1983, Culp 1986, Reice and Edwards 1986, Flecker and Allan 1984) or moderate effects (Flecker 1984, Schofield et al. 1988). Although recent studies have demonstrated large impacts of fish predation on invertebrate community and trophic structure (e.g. Power 1990a, 1992b, Bechara et al. 1992, Flecker 1992a), substantial unexplained variation remains in the strength of fish effects between streams (Wooster 1994). This contrasts with structurally less complex systems such as lakes, where general rules surrounding the impact of fish on zooplankton and indirect effects on lower trophic levels are comparatively well understood (Carpenter et al. 1985, 1987, McQueen et al. 1986, Persson et al. 1988, McQueen 1990, Mazumder 1994). Variation among streams may be related to differences in disturbance regimes that prevent structuring of communities by biological processes (Townsend 1989), differences in fish community composition (Flecker 1992a, Dahl and Greenberg 1996), and differences in the complex structure of stream habitats which mediate predation effects (Sih et al. 1985, Power 1992b).

The physical stream environment can be characterized as a complex pattern of erosional and depositional habitats nested at a hierarchy of spatial scales (Frissel et al. 1986, Hawkins et al. 1993, Rosenfeld and Hudson 1997). At the microhabitat scale, the

surface of rock substrates in riffles are erosional with a current velocity sufficient to prevent settling of suspended particulates, unlike the interstices between gravel and cobble which are depositional. At the larger pool-riffle scale, riffles tend to be erosional and pools depositional. At the drainage basin scale, headwaters are erosional and lower reaches are depositional (Huet 1959). This pattern of erosional and depositional habitats serves as the templet for most biological processes in streams, constraining the spatial distribution of both invertebrates, fish, and carbon resources (Angermeir and Karr 1983, Statzner et al. 1989, Angradi 1996, Rosenfeld and Hudson 1997). In particular, detrital carbon tends to accumulate in depositional habitats and periphyton (algae) tends to grow on hard erosional substrata at both the microhabitat and pool-riffle scales.

Stream ecosystems have several additional unique features that influence the relationship between the habitat templet and fish predation effects on invertebrates. The first is that aquatic invertebrates fall into functional feeding groups associated with discrete habitats that influence their vulnerability to fish predation. Functional group classification is based on the way invertebrates forage and the resources they consume (Cummins 1974). Grazers consume algae, detritivores (filter-feeders in erosional habitats and collector-gatherers and shredders in depositional habitats) feed on detritus, and predators prey on other invertebrates. Functional feeding groups may differ in their risk of predation depending on whether the resources they consume are associated with habitats that are more or less exposed to fish predation. In particular, herbivorous

invertebrates are constrained to foraging on algae on the upper surfaces of rocks, leading to the prediction that direct and indirect predation effects should be greatest in habitats with an algal carbon base (i.e. rocks in riffles).

The second distinguishing feature of streams influencing predator-prey interactions is the heterogeneous nature of stream habitats and the associated large fluxes of mobile prey between patches (Townsend 1989), typically invertebrates drifting in a downstream direction in the water column (Hynes 1970). The strength of predation effects on the benthos in any particular patch will depend on the flux of prey migrating into the patch, which will tend to "swamp out" the effects of local predation (Cooper et al. 1990, Sih and Wooster 1994). Because fish predation in a patch can influence emigration rates out of a patch into a patch downstream, predator impact in any given patch will be highly dependent on the influence of fish predation on flux rates from upstream patches, as well as the background rate of migration, which may differ between habitat types. If this is the case, then predation effects should be less pronounced in riffles because of the potential for elevated invertebrate drift rates in fast-water habitats, an opposite prediction to that based on the available carbon base and the vulnerability of different functional groups in pool and riffle habitats.

Fish predation should also structure the invertebrate community at two discrete spatial scales - at a small scale between patches with and without fish *within* a fish-bearing stream, subject to the constraints described above, and at a larger scale *between* streams with and without fish. Most studies of fish predation in streams have been at

the smaller scale within a fish-bearing stream, and the role of fish in structuring differences in the invertebrate community between fishless and fish-bearing streams has been surprisingly neglected. It remains unclear whether the impacts of fish predation on invertebrate community structure within a stream are similar in nature and magnitude to differences in community structure at a larger scale between streams with and without fish.

Few studies have systematically considered the effect of fish predation on invertebrate community structure at a hierarchy of scales in streams. To better understand the role of physical habitat structure on fish predation effects in streams, a series of experiments were performed in two streams in the University of British Columbia Malcolm Knapp Research Forest in the Coast Mountains of British Columbia. Predation effects were contrasted at three separate spatial scales - between different microhabitats (substrates) within a channel unit (pool or riffle), between different channel units within a stream, and between streams with and without fish.

The first experiment (described in Chapter 2) examined the effect of differences in the carbon base of different habitats on predator versus resource control of community structure and the vulnerability of different invertebrate taxa at microhabitat and pool-riffle scales. Fish enclosures were installed in a previously fishless stream, and the impact of fish predation was documented on tile and gravel substrates nested within pool and riffle habitats. A series of smaller experiments (described in Chapter 3) were performed to clarify the direct and indirect mechanisms of the effects of fish

predation observed in the first experiment. The third experiment (described in Chapter 4) addressed the effects of fish predation in upstream patches on the expression of predation effects in habitats downstream. Predictions were that the effects of fish predation would be greater than in the first experiment if changes in prey flux rates were more important than differences in the vulnerability of different functional groups of invertebrates associated with different habitats.

The final experiment (described in Chapter 5) repeated the first fish predation experiment in a nearby fish-bearing stream, so as to contrast the effects of fish predation between streams with and without fish. Expectations were that fish predation should have larger effects on the naive invertebrate community in a fishless stream, and that differences in community structure between a fishless and fish-bearing stream should be similar to differences in community structure resulting from fish predation within a single stream.

CHAPTER II

The effects of habitat and fish predation on invertebrate community structure

INTRODUCTION

Understanding the factors that limit populations and control community structure is one of the fundamental goals of ecology. Although several recent studies have clearly demonstrated strong effects of fish predation on invertebrate community structure in streams (e.g. Power 1990a, 1992b, Bechara et al. 1992, Flecker 1992a), many other studies have found at best weak effects of fish predation (Allan 1982, Reice 1983, Culp 1986, Reice and Edwards 1986, Flecker and Allan 1984), and much of the variance in predator impacts in streams is unexplained. Consequently, the specific conditions under which invertebrate populations in streams are limited by fish predation remain poorly defined.

The degree to which community structure is controlled by predation versus resources (Hairston et al. 1960, Fretwell 1977, McQueen et al. 1986) will depend on a variety of biotic and abiotic factors (Hunter and Price 1992). Low diversity and limited differentiation within a trophic level will cause trophic organization to approximate linear food chains rather than webs, increasing the probability of a trophic cascade (Strong 1992). The carbon base of the food chain (detrital carbon vs. living plant tissue) will also influence the degree to which predators control trophic level and community structure (Weigert and Owen 1971), as will the attributes (e.g. size, intrinsic rate of growth) of the primary producer trophic level (Power 1992a, Strong 1992, Hairston and Hairston 1993).

Although the above generalizations are derived from comparisons of trophic dynamics in aquatic and terrestrial ecosystems, they may also apply at a smaller spatial scale within an ecosystem. Specifically, differences in the carbon base and associated food chains of patches within a stream may lead to differences in the impact of local predation in a spatially heterogeneous environment. Failure to adequately characterize the relationship between habitat structure, carbon resource availability, and predation may be largely responsible for our inability to clearly understand predator impacts in streams.

Community structure and the effects of predation are strongly influenced by the physical habitat structure of the environment (Huffaker 1958, Connell 1975, Sih et al. 1985, Menge and Olson 1990). The physical structure of the stream habitat will directly control the distribution of algal and detrital carbon resources on which prey depend (Rosenfeld and Hudson 1997). The physical habitat in streams will further influence predator-prey interactions by directly constraining the distribution of predator and prey (Peckarsky et al. 1990), by modifying predator foraging efficiency (e.g. Wilzbach et al. 1986, Brusven and Rose 1981), and by constraining the distribution of refuges. For example, predator limitation is enhanced when prey are constrained to foraging on resources in locations that are vulnerable to predation, such as aquatic invertebrates grazing on algae on the upper surfaces of rocks (Kohler and McPeck 1989, Bechara et al. 1992).

In addition to being habitat-dependent, the role and effect of fish predators in aquatic systems is also strongly scale-dependent (Neill 1994). Differences in the effects of predation may be apparent between different substrates in a pool (microhabitat), between

pools and riffles in a stream, and between streams with and without fish. Thorpe (1986) postulated that fish predation may have its greatest effect at this larger spatial scale, structuring differences between the invertebrate community in lakes or streams with and without fish predators. Predation within a particular stream or lake may have a smaller impact on community structure, since vulnerable taxa will have been eliminated, and the invertebrate community should be adapted to co-existing with predators. Most studies of fish effects in streams have been at the smaller scale, where variation in environmental factors can be controlled, but where fish effects are likely to be smaller, or expressed as differences in behavioural responses to predation risk (Dodson et al. 1994, Scrimgeour et al. 1994a) rather than as radical changes in species composition.

An alternative approach to studying the effects of fish predation in a fish-bearing stream 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 (Thorpe 1986, 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.

The experiment described in this chapter examines the impact of fish predation on invertebrate community structure in a previously fishless stream. The general goals were to understand how physical structure at a hierarchy of scales modifies the effects of fish

predation on invertebrate community structure. Specific hypothesis tested were i) that differences in the carbon base of the food chain are associated with physical habitat structure at different scales (microhabitat vs. pool/riffle), ii) that local predator impact is modified by the carbon base of the food chain and associated invertebrate functional feeding groups, and iii) that the relative limitation of invertebrate abundance by fish predation versus detrital resources is also strongly habitat dependent. Predictions are that the greatest impact of fish predation on community structure and trophic processes should be in habitats dominated by herbivorous invertebrates grazing on algal carbon, whereas community structure in habitats dominated by detritivores should be primarily resource controlled.

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 (Feller 1977, Stockner and Shortreed 1978). Mayfly Creek flows through second growth forest with a partially open canopy dominated by western red cedar (*Thuja plicata* Linnaeus), western hemlock (*Tsuga heterophylla* Sargent)

and douglas fir (*Pseudotsuga menziesii* Britton), 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 fish migration. 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 1992).

METHODS

Experimental design

Experimental units consisted of five enclosures placed in separate channel units (three in riffles, two in pools). Enclosures were constructed of a wooden frame supported by 19mm 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, 1 m high, and were divided internally into a larger upstream section and two lower sections (Fig. 1). Each lower section was 2m long and 1m wide. The upper sections of enclosures were in pools and the lower sections were either in slow riffles, where current velocity

averaged $16.4 \pm 1.8 \text{ cm s}^{-1}$ (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 ($4.9 \pm 1.2 \text{ cm s}^{-1}$ (range 2-7 cm s^{-1})). Velocities were measured once during baseflow at 4 points along transects across lower enclosure sections using a Marsh-McBirney Model 2000 flow meter.

Lower enclosure sections were used for fish treatments and controls. Upper enclosure sections were stocked with fish to prevent predation effects in lower sections from being swamped by high immigration rates of prey from fishless areas upstream (Cooper et al. 1990, Sih and Wooster 1994). This was of special concern in fishless Mayfly Creek, where ambient drift rates are likely to be higher than in a fish-bearing stream (Flecker 1992b).

Four 15 x 15 cm unglazed ceramic tiles and five gravel baskets were placed in each lower enclosure section as artificial substrata for colonization by algae and invertebrates. Gravel baskets were 30 cm long, 20 cm wide, and 5 cm deep, made of 6.5 mm mesh hardware cloth, and were buried flush with the streambed in each lower enclosure section. Baskets were filled with approximately 2.5 litres of 4-7 cm diameter river washed gravel; an additional litre of sand and fine gravel was added to partially fill gravel interstices.

One lower section of each enclosure was stocked with coho (*Onchorhynchus kisutch*) parr (mean length 50.2 ± 6.5 mm standard deviation, mean weight 1.6 ± 0.6 g standard deviation) and prickly sculpin (*Cottus asper*; mean length 72.8 ± 9.8 mm standard

deviation, mean weight 4.3 ± 1.9 g standard deviation) at a density of 2 and 1 fish per 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 per m^2 . Average coho and sculpin weight in all enclosure sections combined increased by 95% and 13%, respectively, during

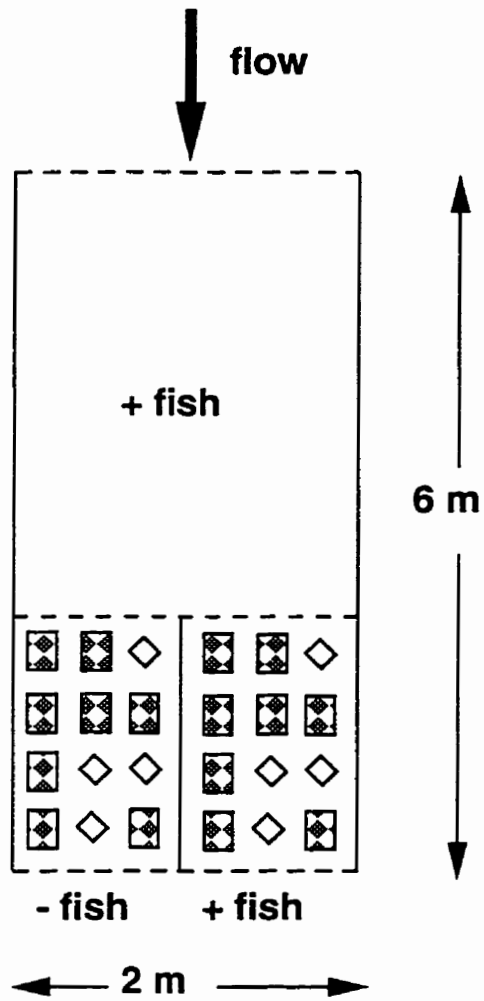


Fig. 1 Design of experimental enclosures. Stippled rectangles represent gravel baskets, diamonds represent tiles, and broken lines denote permeable mesh.

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 (Rosenfeld, unpublished data). Coho and sculpin used during the experiment were collected from the Allouette River downstream in the same drainage by electrofishing or baited minnow traps.

Fish were stocked during May 18-20, 1993, one 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 after running to the ocean. Fish were collected from enclosures by electroshocking at the end of the experiment. Voltage was turned up to 700 V and the entire enclosure thoroughly shocked to ensure complete fish mortality.

Visual counts of mayflies on tiles were made during the day at two to four day intervals throughout the experiment. Enclosures were carefully approached so as to minimize disturbance of grazing mayflies, and the number of mayflies observed on tiles in lower enclosure sections with and without fish was recorded.

Tiles and gravel baskets were sampled from Aug. 26 to Aug. 31, 101 days after fish introduction, by carefully lifting each substrate off the stream bottom into a 150 μm mesh

Surber sampler held immediately downstream. Invertebrates were rinsed off of tiles into a bucket using a wash bottle and brush, and the contents of the Surber sampler were then backwashed into the same bucket. Contents of gravel baskets were emptied into a 10 litre basin, agitated, and water in the basin was repeatedly decanted into a 150 μm net until the gravel was clean of organic matter and invertebrates. Invertebrates and detritus from gravel and tile baskets were filtered through 150 μm mesh sieves, and 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 (Roff & Hopcroft 1986).

Chlorophyll *a* was measured only on gravel substrate. 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. Chlorophyll *a* fluorescence was measured the next day using a Turner Designs model 10-005 R fluorometer. Chlorophyll concentrations

were calculated using formulae described in Strickland & Parsons (1972). Chlorophyll abundance was corrected for the upper surface area of each stone (measured by tracing outlines on paper), and is expressed as mg m^{-2} .

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 pre-ashed aluminium boat at 75 C, and then combusting samples in a muffle furnace for 4 h at 550 C.

Data analysis

Data analysis was performed using PC SAS version 6.03 (SAS Institute, 1989). Invertebrate abundance data were ($\log+1$) transformed, proportional data were arcsine-square root transformed, and Predator Impact indices (described below) were square root transformed to normalize distributions and equalize variances. All fish effects were analyzed as a paired t-test ($n=5$) by substrate, or as a split-plot design with enclosures as blocks, fish presence as the main effect, and substrate as a subplot ($n=20$; Snedecor and Cochran 1989), with a sequential Bonferroni correction for evaluating the significance of fish effects on individual taxa (Sokal and Rohlf 1997). The effect of fish predation was analyzed as a randomized block design without replication ($n=10$) when invertebrate densities were analyzed separately on tile and gravel substrate (Sokal and Rohlf 1997). Visual counts of mayfly abundance on tiles were analyzed using repeated measures ANOVA. Invertebrate-organic matter relationships were evaluated using ANCOVA,

with organic matter as the covariate. Untransformed data were used for ANCOVA of total invertebrate - organic matter relationships, in order to simplify interpretation of results.

Because differences in densities between taxa lead to biases in objectively scaling predation effects, a modification of the Predator Impact (PI) index described by Cooper et al. (1990) was used to assess predation effects on total invertebrate abundance, as well as for the most abundant individual taxa. 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 with an increase or decrease in prey abundance in the presence of predators. 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. Other indices, such as percent change in abundance, are directionally biased in that an increase in density has no theoretical upper limit, whereas a decrease in density is limited to a maximum of 100% (i.e. when prey density approaches zero in the predator treatment). For example, a fourfold (+400%) increase in prey in the presence of predators has a PI value of $\ln(4/1) = 1.39$, equivalent in absolute value to a fourfold (-75%) decrease in prey density ($PI = \ln(1/4) = -1.39$). One of the disadvantages of the PI index is that when prey are completely eliminated from predator treatments the ratio of N_p/N_c is zero, and the index cannot be calculated.

Differences in community structure between combined substrate and habitat types were evaluated using principle components analysis. The correlation matrix was used as this removes the influence of invertebrate abundance and has been demonstrated to give the most consistent results in ordination (Jackson 1993).

The contribution of fish predation as a source of variation for total invertebrate abundance and abundance of individual taxa on different substrate types was calculated using variance components as described by Sokal and Rohlf (1997). The correlation of invertebrate abundance with organic matter, for all invertebrates and taxa individually, was also partitioned into within and between enclosure components for gravel and tile separately using sequential sums of squares

Research in aquatic systems has demonstrated that large-bodied invertebrate taxa are more vulnerable to fish predation (Allan 1978, Zaret 1980, Culp and Scrimgeour 1993; Scrimgeour et al. 1994b). To test for differences in predation effects as a function of prey size, invertebrates were divided into small (<3mm), medium ($\geq 3\text{mm}, < 6\text{mm}$) and large ($\geq 6\text{mm}$) size classes based on total length. These size class divisions roughly correspond to < 0.1 mg, 0.1 - 1.0 mg, and >1.0 mg weight classes, based on length-weight regressions from Smock (1980). These biomass classes were identified by Allan (1981) as being approximately representative of the vulnerability of invertebrates to drift-foraging fish. Invertebrates less than 0.1 mg show a lower vulnerability to fish predation and propensity for diurnal drift periodicity, whereas those greater than 1 mg are preferentially selected by fish and tend to drift primarily at night (Allan 1984). The effect of fish predation on

total abundance of invertebrates in different size classes was analyzed as a split-plot design with enclosures as blocks, fish presence as the main effect, and size as a repeated measure (subplot) within a plot (total n=30) for tile and gravel separately (Steel and Torrie 1980, Snedecor and Cochran 1989).

RESULTS

Fish effects on mayfly counts and chlorophyll *a*

The impacts of fish on mayflies and algae were generally consistent with the expectation of greater fish effects in habitats dominated by herbivorous invertebrates. The number of mayflies observed grazing on tile surfaces was significantly higher in the absence of fish (repeated measures ANOVA, Table 1) in both pool and riffle habitat. Mayflies were also significantly more abundant in riffles (n=3) than in pools (n=2), and there was also a significant interaction between habitat type and fish effects (Table 1, see Fig. 2), with the reduction in mayfly abundance being most pronounced in riffles. Chlorophyll *a* was significantly higher on gravel substrate in riffles with fish (Fig. 3; paired t-test, $t_2 = 4.41$, $p = 0.05$), 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 within enclosures was also significantly lower in the absence of fish in riffles (Fig. 3; paired t-test, $t_2 = 6.1$, $p = 0.03$) but not in pools (paired t-test, $t_1 = -0.96$, $p = 0.52$).

Source	df	SS	MS	F	P
Fish presence	1	20.7	20.7	32.5	0.001**
Habitat	1	7.7	7.7	12.0	0.013*
Fish presence * habitat	1	6.0	6.0	9.4	0.022*
Error	6	3.8	0.6		

Table 1. Results of repeated measures analysis of variance of the numbers of mayflies (all species combined) observed grazing on upper tile surfaces (* indicates significance at the 0.05 level, ** indicates significance at the 0.01 level).

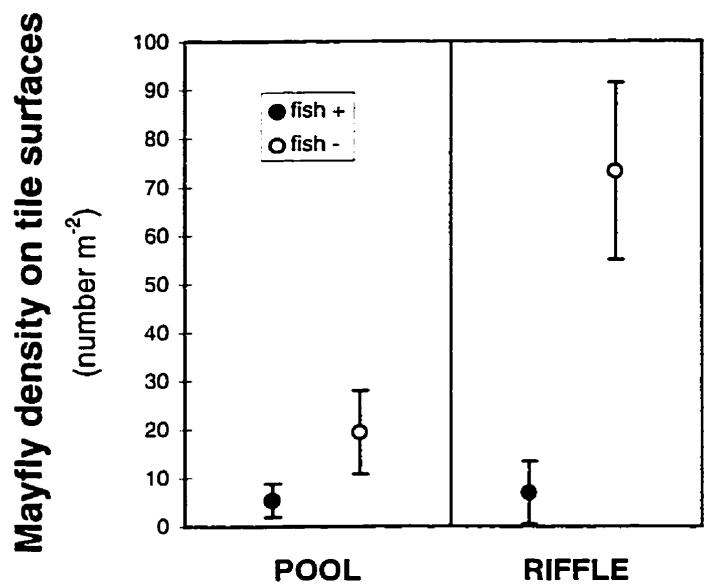


Fig. 2 Mean density of mayflies (no. m⁻² + 1SD for all species combined) observed foraging on tiles in lower enclosure sections in the presence and absence of fish.

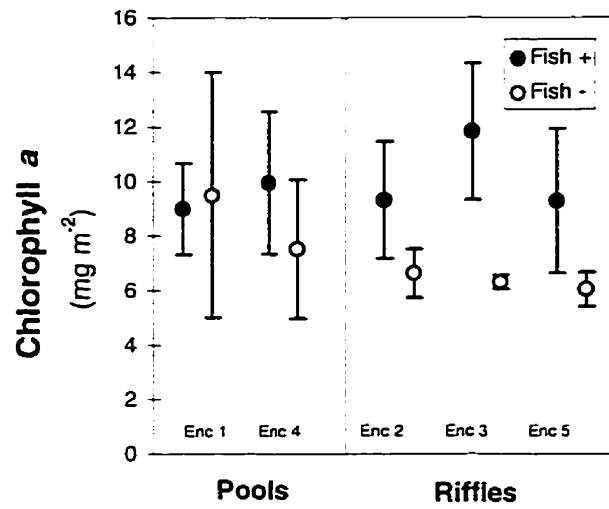


Fig. 3 Chlorophyll a concentration (mg m^{-2} , + 1SD) on gravel substrate in individual pool and riffle enclosures in the presence and absence of fish.

Tadpoles of the tailed frog *Ascaphus truei* were also relatively abundant grazers in Mayfly creek, although they occurred at much lower densities than small invertebrates (average of 4–6 individuals m⁻², Rosenfeld unpublished data). Tadpoles were observed grazing on natural and artificial substrates on both sides of enclosures, and there was no significant difference in density between fish treatments and controls. However, the low power associated with the small number of *Ascaphus* collected on substrates at the end of the experiment makes it difficult to determine whether there was an effect of fish on *Ascaphus* density.

Invertebrate community structure and organic matter relationships

More taxa were collected on gravel than on tile substrate at the end of the experiment (see Fig. 4). The most abundant invertebrates on both substrates were chironomids. Detritivorous invertebrates such as the stonefly *Despaxia* sp. (Leuctridae) and tipulids were more abundant in gravel than on tile. Mayflies were more abundant in riffles than in pools on both substrate types, and Orthocladiinae chironomids tended to be more abundant on tile substrate, while Tanytarsini (detritivorous chironomids) were most abundant on gravel and in pools. In general, herbivorous invertebrates tended to be more abundant on gravel and in pools. In general, herbivorous invertebrates tended to be more abundant in riffles and on tiles, and detritivores were more abundant in pools and in gravel.

A combined ordination of substrate samples (n=50 for gravel, n=40 for tile) in species space demonstrated that the invertebrate communities on different substrate and

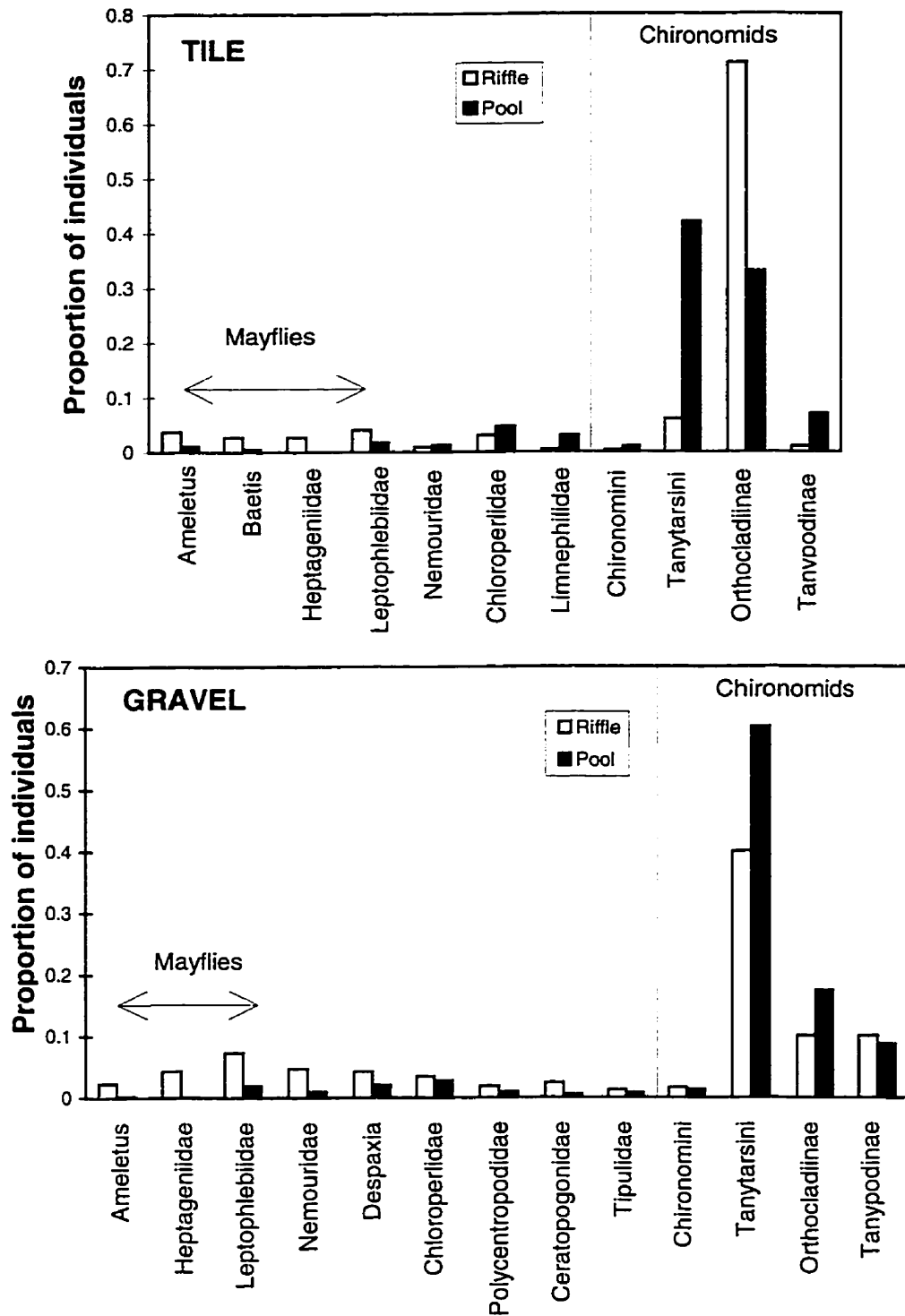


Fig. 4 Relative proportions of different taxa (by number) in pool and riffle habitat on tile and gravel substrate at the end of the predation experiment. Only those taxonomic groups contributing to at least 1% of the total invertebrate community on a substrate are included.

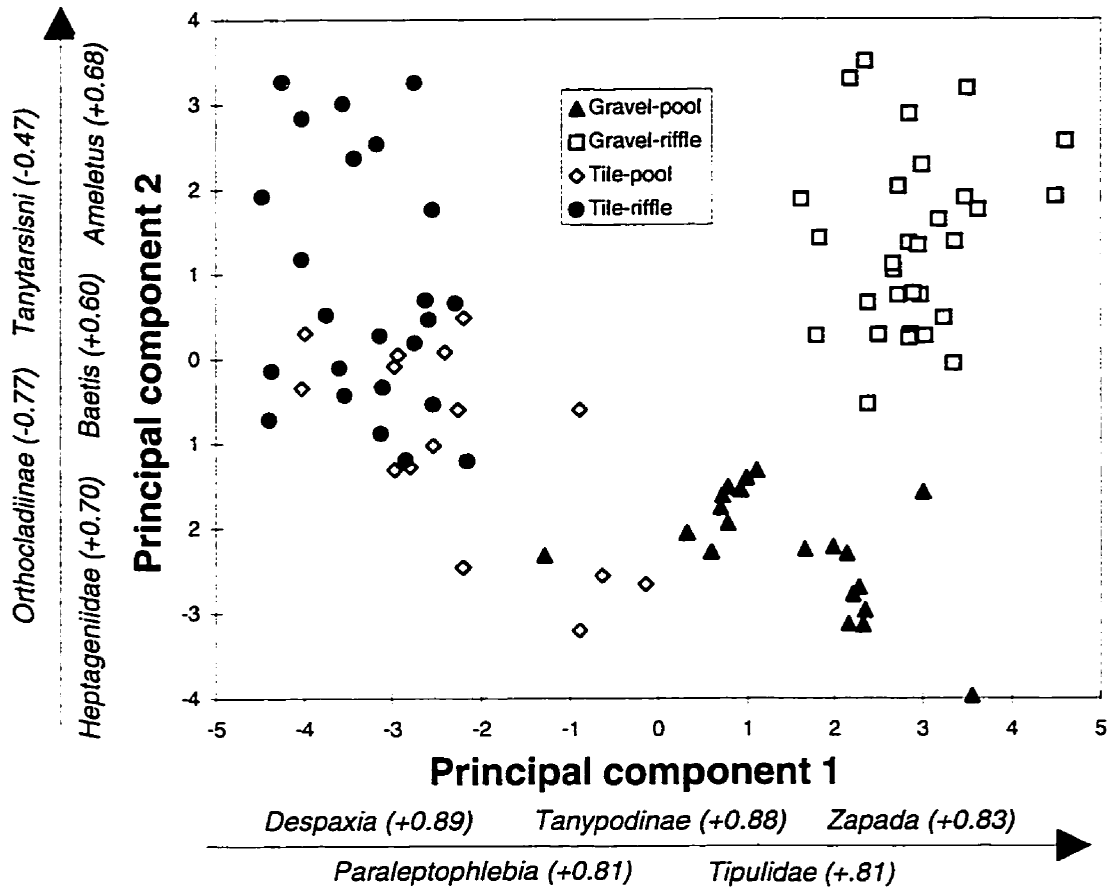


Fig. 5 Ordination of the four substrate-habitat combinations in species space (using only those taxa contributing to at least 1% of the invertebrate community). N=50 for gravel, n=40 for tile. Those taxa with the highest correlations of density with principal component score (correlation coefficient in parenthesis) are labelled on the axes.

habitat types separate reasonably well (Fig. 5), although tile substrate in pools tended to overlap both with tile in riffles and gravel in pools. The first principal component (PC1) explained 46.7 % of the variation in the data set, and the second principal component explained an additional 19.6%. There is a positive correlation between PC1 and the abundance of several taxa, most of which are detritivores (e.g. *Despaxia* sp., *Zapada* sp., *Paraaleptophlebia* sp., and Tipulidae); PC1 appears to be an axis representing detritivore abundance, and separates tile from gravel substrate. PC2 is positively correlated with the abundance of mayflies and negatively correlated with the abundance of chironomids, and appears to be an axis separating pools from riffles.

The proportion of the subfamily Orthocladiinae in the chironomid community was not significantly affected by the presence of fish (split plot ANOVA, $F_{1,1} = 34$, $p = 0.11$). However, habitat (split plot ANOVA, $F_{1,1} = 198$, $p = 0.045$) and substrate (split plot ANOVA, $F_{1,14} = 53.5$, $p < 0.0001$) exerted a much more significant influence on chironomid community structure (Fig. 6), with orthoclads being most abundant on tiles in riffles, whereas tanytarsini were dominant in gravel substrate. These observations suggest that orthoclads are primarily herbivores associated with an algal resource in erosional habitats, whereas tanytarsini are associated with detrital carbon in interstitial or depositional habitats.

A significant positive relationship was observed between total invertebrate abundance on tiles and organic matter (see Fig. 7; ANCOVA, $F_{1,7} = 30.1$, $p = 0.001$, total $n=10$ fish for treatment means), suggesting limitation of invertebrate abundance by

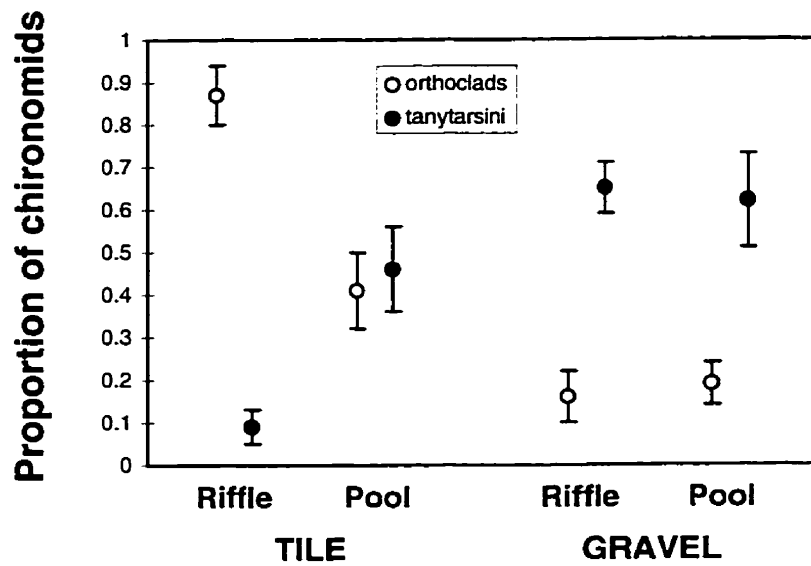


Fig. 6 Relative proportions (+ 1SD) of orthoclad and tanytarsini chironomids on tile and gravel substrate in pools and riffles. N=2 for pool, n=3 for riffles.

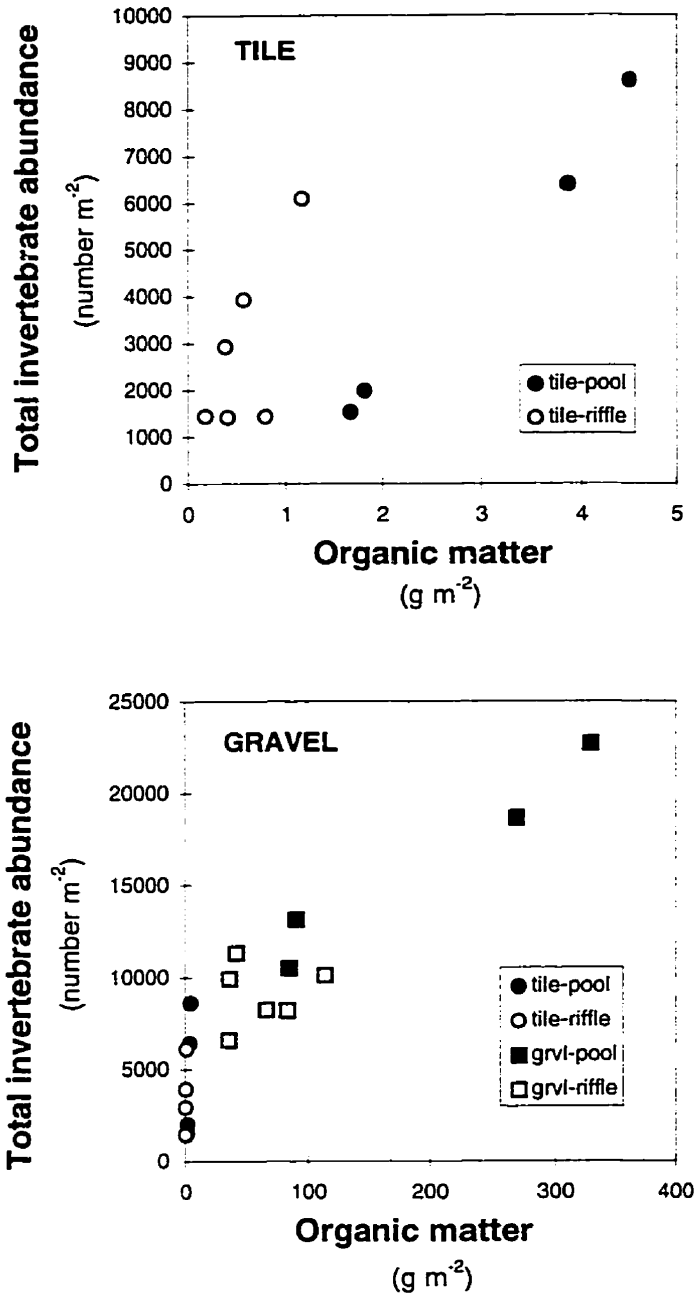


Fig. 7 Relationship between total invertebrate abundance and organic matter on tile and gravel in pool and riffle habitats. Points represent enclosure side means (n=10). The regression equation for tile is $N=2520(\text{organic})-4240(\text{habitat})+1400$, where habitat = 0 for riffle and 1 for pool. The regression equation for total invertebrate abundance on gravel is $N=46.4(\text{organic})+6600$.

detrital carbon. There was also a significant difference in intercept for pools and riffles (ANCOVA, $F_{1,7} = 10.0$, $P = 0.016$), 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 as well, but the slope of the relationship is significantly less than that for tile (t-test with unequal variances, Welch's approximate $t_s = 17.04$, $P < 0.01$), and there is no significant habitat effect (Fig. 7), indicating substantial differences in invertebrate abundance-organic matter relationships between substrate types.

The ratio of total invertebrate abundance to organic matter, a rough index of food quality (Fig. 8), was significantly different between the four combinations of substrate and habitat (ANOVA of log-transformed ratios, $F_{3,7} = 184$, $p = 0.0001$ for substrate effects, $F_{3,7} = 10.6$, $p = 0.014$ for habitat effects, $n=10$ for treatment means), suggesting large differences in food quality between habitats. Over 90 percent of the total variation in organic matter abundance on individual substrates was between substrate type (tile vs. gravel, ANOVA, $F_{1,88} = 86.3$, $p = 0.0001$), and the remainder was due to variation between pool and riffle habitats.

The fish treatment had no effect on the abundance of organic matter on gravel substrate, but caused a small but significant increase in organic matter biomass on tiles (ANOVA, $F_{1,5} = 11$, $p = 0.03$, total $n=10$ for treatment means); mean organic matter on tiles averaged 1.7 g m^{-2} in the fish treatment and 1.4 g m^{-2} in the control.

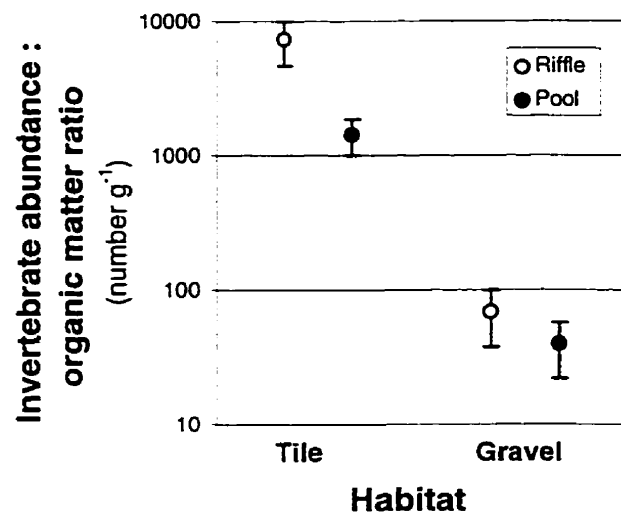


Fig. 8. Ratio of total invertebrate abundance to organic carbon biomass (a rough index of food quality) on tile and gravel substrate in pools and riffles (n=2 for pools, n=3 for riffles, error bars represent + 1SD).

Predation effects on total invertebrate abundance by size class

Total abundance of invertebrates was significantly affected by the fish treatment (split plot ANOVA, Table 2), with a significant interaction between fish treatment and substrate type (Fig. 9; Table 2). As expected, different size classes of invertebrate responded differently to the presence of fish, but the effects were substrate-specific. There was a significant fish treatment and fish by invertebrate size interaction on tile substrate, but no significant fish effects or interaction on gravel (split plot ANOVA, Table 3). Enclosures are treated as blocks, and a significant size effect (Table 3) simply indicates that abundance of invertebrates differs among size classes across treatments and control. Fish predation on tiles in riffles increased the abundance of the smaller and intermediate invertebrate size classes (Fig. 9); variance in abundance also tended to be higher when fish were present. On tiles in pools, the smallest size class was also more abundant in the presence of fish, although the effect size is smaller than in riffles and the difference is not significant. Fish predation effects in general appeared to be smaller on gravel than on tile. The only apparent effect of fish on total invertebrate abundance on gravel substrate was a statistically non-significant increase in abundance and variance 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, whereas none of the variance on gravel was accounted for by fish

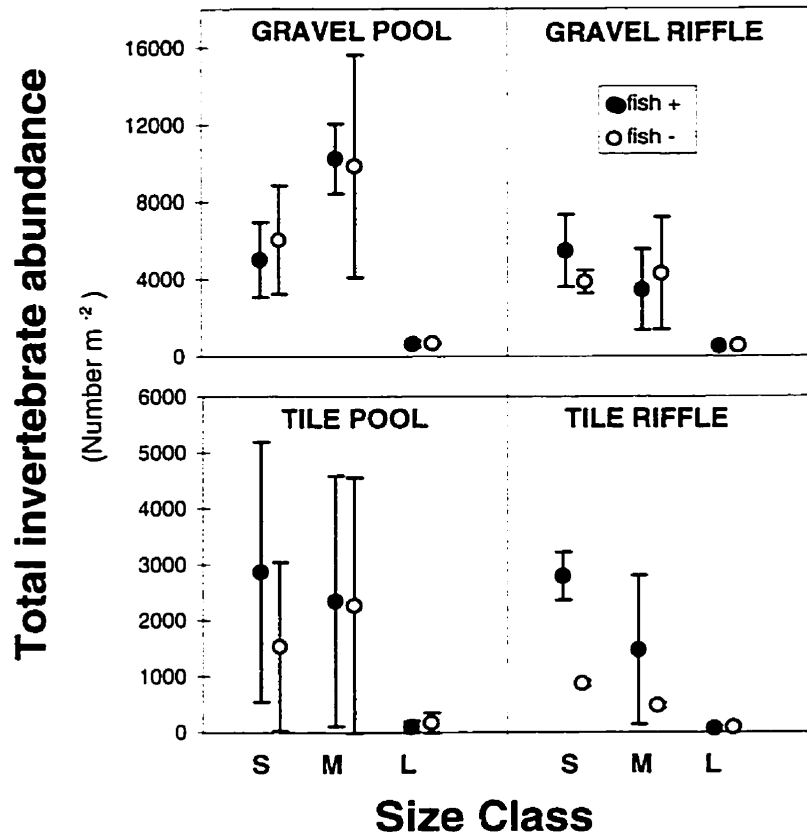


Fig. 9 Total invertebrate abundance (per m⁻², + 1SD) for all taxa combined, in 3 size classes (small < 4mm, 4mm > medium < 6mm, large > 6mm) in the presence and absence of fish on tile and gravel substrate in pool and riffle habitat (n=2 for pools, n=3 for riffles).

	Source	df	SS	MS	F	P
Main effect	enclosure	4	0.52	0.13	13.2	0.014*
	fish	1	0.18	0.18	18.0	0.013*
	main plot error (enc*fish)	4	0.04	0.01	0.6	0.68
Subplot effect	substrate	1	1.82	1.82	107.6	0.0001**
	fish*substrate	1	0.12	0.12	7.3	0.03*
	subplot error (enc*substrate + enc*fish*substrate)	8	0.14	0.02		

Table 2. Results of split-plot analysis of variance for the effect of fish predation and substrate type on total invertebrate abundance (log-transformed); * indicates significance at $\alpha = 0.05$, ** indicates significance at $\alpha = 0.01$.

Substrate	Source	df	SS	MS	F	P
Tile						
Main effect	enclosure	4	1.09	0.27	5.8	0.06
	fish	1	0.23	0.23	5.0	0.09
	main plot error (enc*fish)	4	0.19	0.05	2.2	0.11
Subplot effect	size	2	7.51	3.75	178.6	0.0001**
	fish*size	2	0.40	0.20	9.4	0.002**
	subplot error (enc*size + enc*fish*size)	16	0.34	0.021		
Gravel						
Main effect	enclosure	4	0.39	0.10	10.5	0.022*
	fish	1	0.00	0.00	0.0	0.99
	main plot error (enc*fish)	4	0.04	0.01	0.3	0.90
Subplot effect	size	2	5.52	2.76	76.8	0.0001**
	fish*size	2	0.01	0.006	0.2	0.85
	subplot error (enc*size + enc*fish*size)	16	0.58	0.036		

Table 3. Results of split-plot analysis of variance for the effect of fish predation and enclosure on total invertebrate abundance (log-transformed) on tile and gravel substrate; * indicates significance at $\alpha = 0.05$, ** indicates significance at $\alpha = 0.01$.

predation (Fig. 10). In contrast, a large proportion of the variance in invertebrate abundance on gravel was due to correlation with organic matter abundance (measured as ash-free dry weight) both within and between enclosures (Fig. 10). A smaller but significant proportion of variance in abundance on tile was also correlated with organic matter.

The predator impact index for total numbers of invertebrates was highest on tiles in riffles, and lowest on gravel substrate (Fig. 11). 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 higher in riffles than in pools on both substrata.

Predation effects on individual taxa by habitat and substrate

Fish effects on absolute densities of prey are presented for only four of thirteen taxa to minimize redundancy. In order to evaluate whether predation effects differed by invertebrate functional feeding group, taxa were selected that were representative of the general effects of fish predation on different functional groups, and also occurred on both tile and gravel so that predation effects could be evaluated by substrate type. *Ameletus* sp. was chosen as a representative large herbivore, the chironomid subfamily Orthocladiinae was chosen as a representative small herbivorous collector-gatherer, Tanytarsini was chosen as a representative small detritivorous gatherer, and *Suwallia* sp. (Chloroperlidae) was chosen as a representative small predator. In general, fish predation effects were greatest on herbivorous invertebrates. Fish greatly reduced the abundance of medium

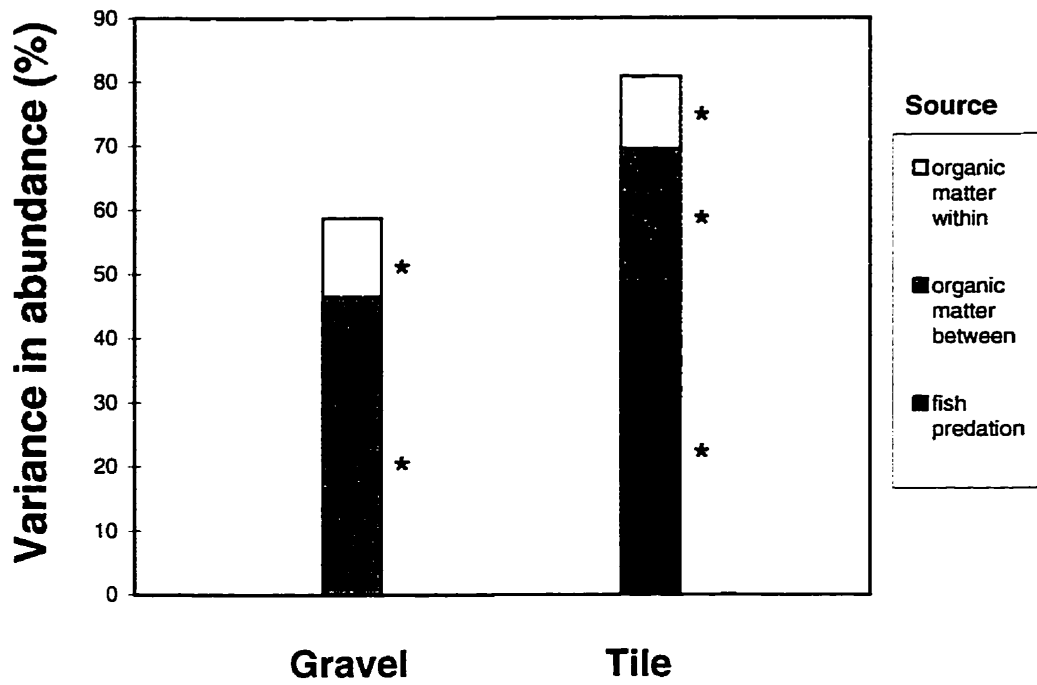


Fig. 10. Components of variance in total invertebrate abundance on tile and gravel substrate (pool and riffle habitats combined) related to variance in fish predation effects and variance in organic matter within and between enclosures. Asterisks indicate significance at $p = 0.05$.

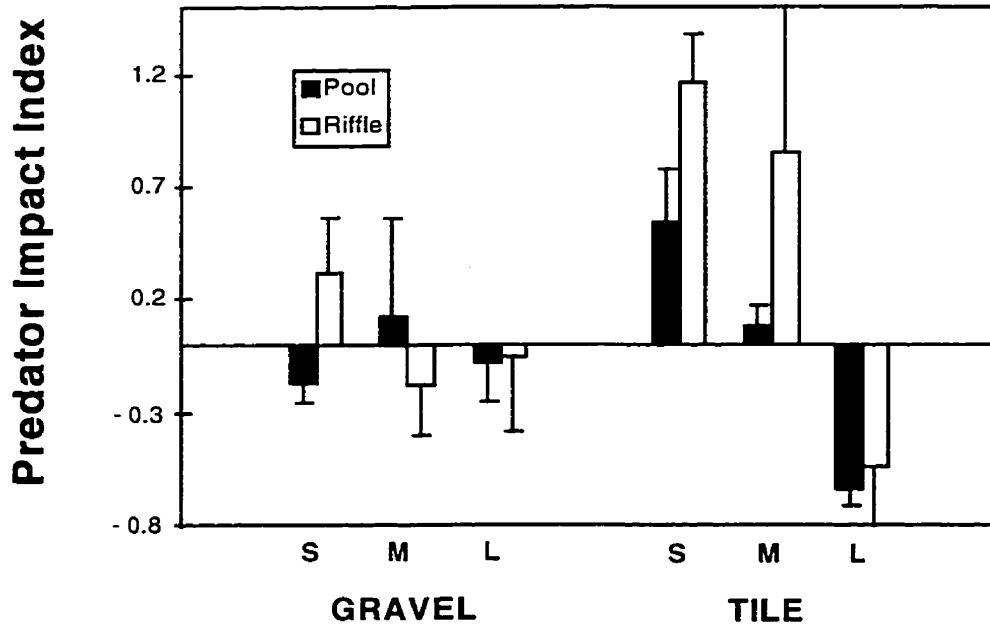


Fig. 11. Predator impact index (+ 1 SD) for total invertebrate abundance in 3 size classes (small < 3mm, 3mm > medium < 6mm, large > 6mm) on tile and gravel substrate in pool and riffle habitat (n=2 for pools, n=3 for riffles).

and large *Ameletus* sp. on tile substrate in both pools and riffles (Fig. 12, Table 4). In contrast, the abundance of small and medium orthoclad chironomids on tiles increased in the presence of fish, primarily in riffles ($F_{1,4} = 27.8$, $P = 0.006$, $n=10$). The smallest size class in pools also expressed a non-significant increase, as well as a pronounced decrease in variation on tiles when fish were absent (Fig. 12). Abundance of Tanytarsini chironomids on tiles was also slightly reduced in the presence of fish, although the difference was not significant. There was no consistent or interpretable effect of fish predation on *Suwallia* sp. on tile substrate in either habitat. Patterns of fish effects were similar on gravel substrate, but the effect sizes were generally smaller (Fig. 12). *Ameletus* abundance was reduced in the presence of fish, but to a lesser degree than for tile. Orthoclad abundance was higher in the presence of fish for the smallest size class, with no effect on the medium size class. There was no apparent effect of fish predation on the density of tanytarsini chironomids or *Suwallia* sp..

In general, the predator impact index tended to be higher on tile substrate (Fig. 13) than on gravel (Fig. 14; 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 (Fig. 13; ANOVA, $F_{1,7} = 7.0$, $P = 0.033$), but there was no significant habitat effect for gravel (Fig. 14).

Predator impact tended to be negative for larger-bodied mayflies such as *Ameletus*, *Baetis*, and *Paraleptophlebia*. In contrast, PI tended to be positive for smaller taxa such as *Zapada* (Plecoptera:Nemouridae) and chironomids, in particular orthoclad chironomids.

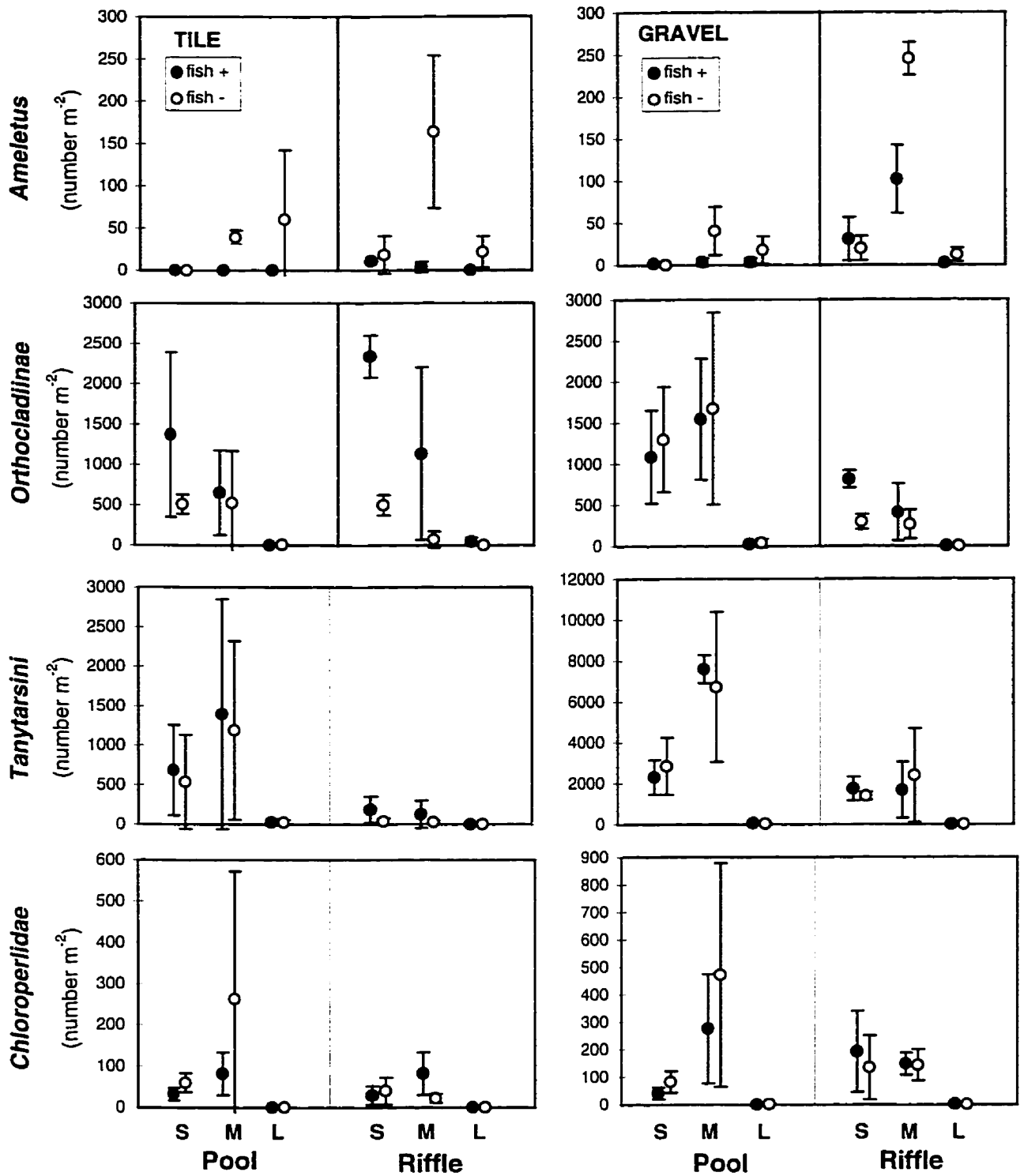


Fig. 12. Densities (+ 1SD) of a large grazer (*Ameletus* sp.), small herbivorous chironomids (Orthoclaadiinae), small detritivorous chironomids (Tanytarsini), and intermediate-sized predators (Chloroperlidae) in the presence and absence of fish on tile and gravel substrate in pool and riffle habitat.

	Source	df	SS	MS	F	P
Main effect	enclosure	4	0.65	0.16	7.2	0.041*
	fish	1	0.79	0.79	34.8	0.004**
	main plot error (enc*fish)	4	0.09	0.023	0.9	0.52
Subplot effect	substrate	1	0.18	0.18	6.8	0.03*
	fish*substrate	1	0.09	0.09	3.4	0.10
	subplot error (enc*substrate + enc*fish*substrate)	8	0.21	0.026		

Table 4. Results of split plot analysis of variance for the effect of fish predation on abundance of *Ameletus* (log-transformed); * indicates significance at $\alpha = 0.05$, ** indicates significance at $\alpha = 0.01$.

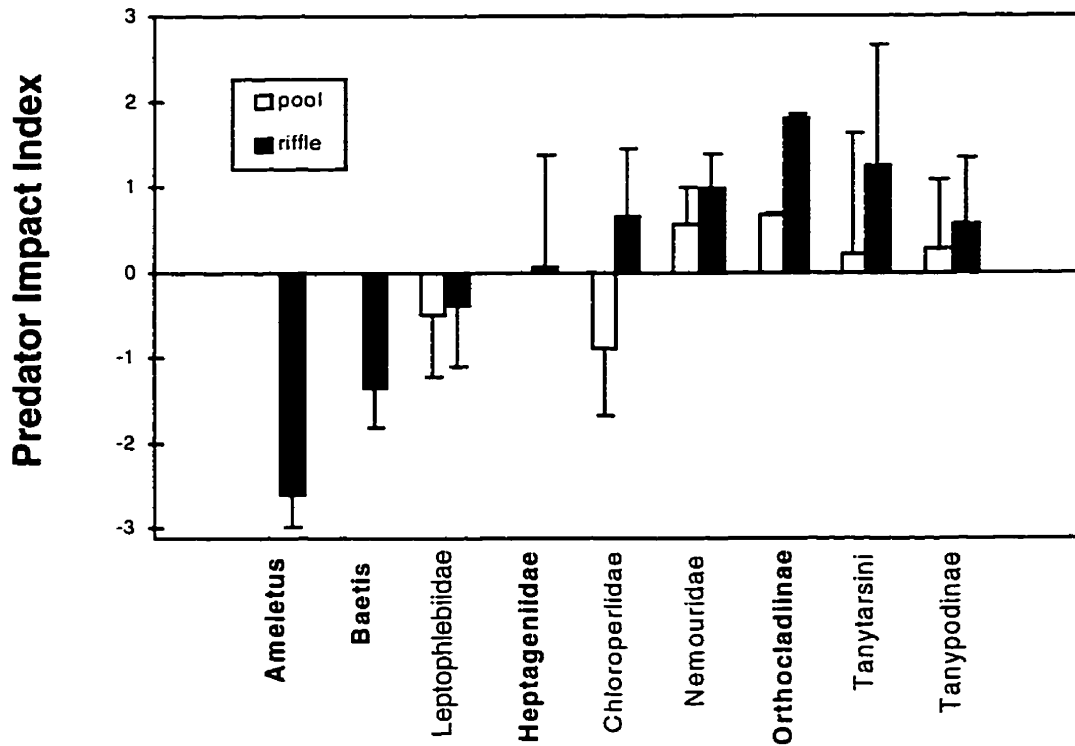


Fig. 13. Predator impact index (+ 1 SD) for the most common invertebrate taxa on tile substrate in pool and riffle habitat (n=2 for pools, n=3 for riffles).

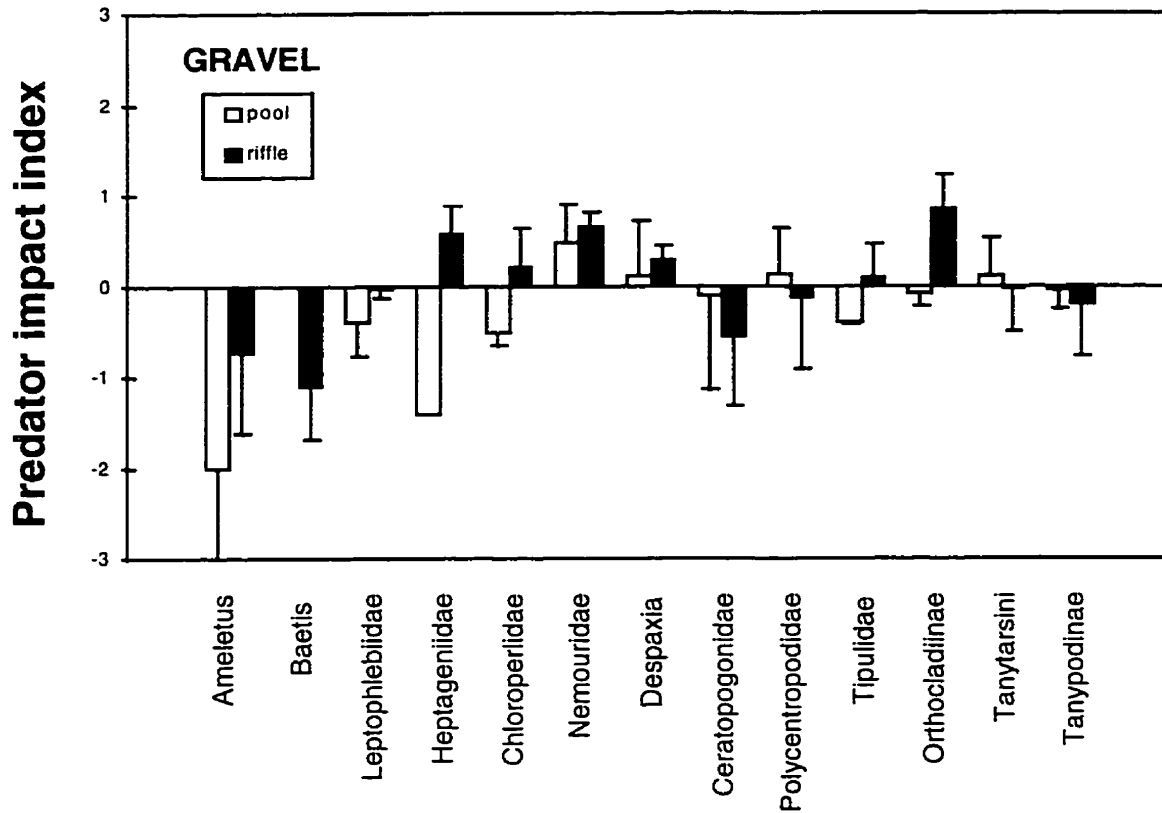


Fig. 14. Predator impact index (+ 1 SD) for the most common invertebrate taxa on gravel substrate in pool and riffle habitat (n=2 for pools, n=3 for riffles).

PI indices appear to be highest for those taxa that are partly or largely herbivorous, either as grazers (*Ameletus*, *Baetis*) or collector-gatherers on upper substrate surfaces (Orthocladiinae). Fish predation had a significant impact on density (evaluated using a sequential Bonferroni correction (Sokal and Rohlf 1997)) only for those taxa marked with an asterisk in Figs. 15 and 16 - *Ameletus*, *Zapada* and orthoclads on tile, and *Ameletus* and *Zapada* on gravel. PI appears to be a more sensitive indicator of fish effects than absolute density, probably because the ratio of predator treatment over control standardizes for differences in density between habitats. The relative proportion of variance in invertebrate abundance explained by fish predation was consistently higher on tile substrate (Fig. 15) than on gravel (Fig. 16), but the taxa most influenced by fish predation are the same on both substrata. The relative proportion of variance in abundance of individual taxa that was correlated with variance in organic matter within and between enclosures differed among taxa. Detritivores (e.g. tipulids, tanytarsini chironomids) tended to have positive correlations with organic matter both within and between enclosures, although some detritivores (e.g. *Despaxia* sp.) had no significant correlation with the abundance of organic matter at either scale. Abundance of algivorous invertebrates was uncorrelated with organic matter within enclosures, but sometimes weakly negatively correlated with organic matter between enclosures (Fig. 15).

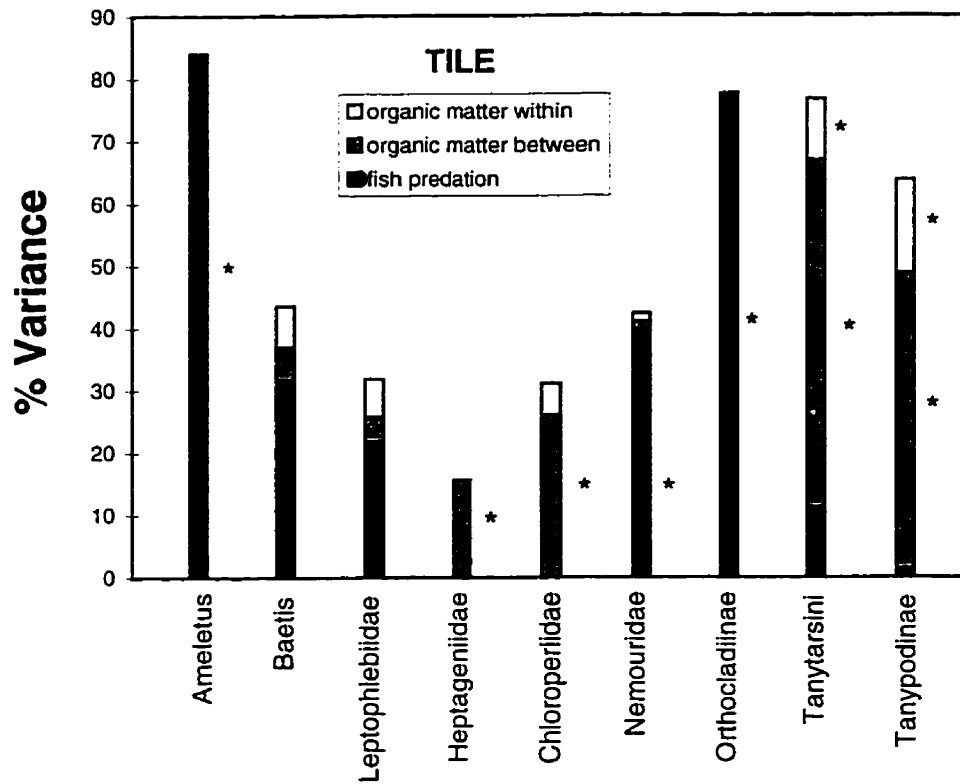


Fig. 15. Components of variance in total invertebrate abundance on tile substrate (pool and riffle habitats combined) related to variance in fish predation effects and variance in organic matter within and between enclosures. Asterisks indicate significance of organic matter at $p = 0.05$ with a sequential Bonferroni adjustment.

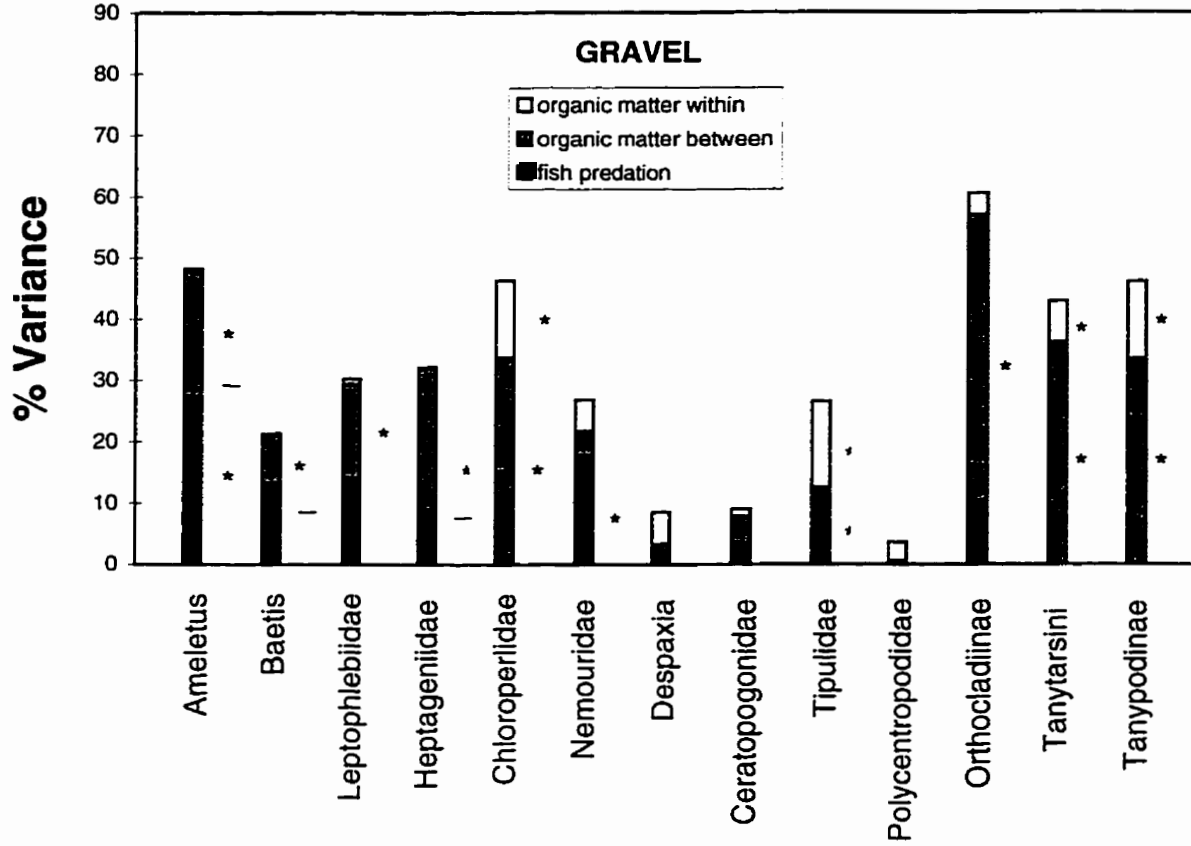


Fig. 16. Components of variance in total invertebrate abundance on gravel substrate (pool and riffle habitats combined) related to variance in fish predation effects and variance in organic matter within and between enclosures. Asterisks indicate significance of organic matter at $p = 0.05$ with a sequential Bonferroni adjustment. Negative signs below asterisks indicate a negative relationship between organic matter and abundance of a taxa.

DISCUSSION

The distribution of invertebrates and carbon resources in Mayfly Creek supports the hypothesis that the carbon base available to invertebrates differs both between pools and riffles and between substrate microhabitats, leading to habitat-specific differences in invertebrate abundance and community structure. Both pools and gravel were depositional habitats relative to riffles and tile, because of slower current velocities in pools and interstitial crevices in gravel. Greater detrital accumulations in pools and gravel substrate were reflected in a more diverse invertebrate community that included detritivores and other taxa that were absent or reduced on tiles and in riffles (e.g. the shredding stonefly *Despaxia*, tanytarsini chironomids, tipulids, and ceratopogonids; Fig 4). In contrast, the greater proportional abundance of mayflies (*Ameletus*, *Baetis*, *Paraleptophlebia*, and heptageniids (primarily *Cinygmula*)) and orthoclad chironomids on tiles and in riffles (Fig. 4 and 6) indicates a strong association with algal carbon in more erosional habitats.

The association of different invertebrate assemblages with different habitats and carbon resources is captured by the discrete ordination of different habitat-substrate combinations in species-space (Fig. 5). The first principal component (PC1) is correlated with the abundance of detritivorous taxa and separates tile from gravel along an axis of increasing detrital abundance in the two microhabitats. The second principal component (PC2) separates algal-based riffles from more detrital-based pools, and is positively

correlated with the abundance of grazing mayflies, and negatively correlated with chironomid abundance. PC2 probably also incorporates an element of biotic interaction, since the negative correlation between grazing mayflies and orthoclad chironomids is partly a result of exploitative competition (discussed below).

The effects of fish on total invertebrate abundance, individual taxa, and algal biomass were also strongly related to habitat and the associated carbon base of the food chain. Predator impacts were most pronounced on tile substrate in riffles, where algae is the dominant carbon source. The presence of fish significantly reduced the abundance of mayflies grazing on tiles, resulting in a trophic cascade to the primary producer trophic level in riffles, but not in pools (Fig. 3). Spatial variation in chlorophyll within riffle enclosures was also greatly reduced in the absence of fish, confirming that in the absence of predation risk grazers tend towards an ideal free distribution and reduce the patchiness of their resource (e.g. Power 1983). Lack of an indirect fish effect on chlorophyll in pools was probably due to a combination of lower grazing pressure and lower algal productivity. Although chlorophyll abundance was similar in pools and riffles, higher grazer density in riffles suggests a higher rate of primary production, assuming that mayfly density scales directly to algal production rather than biomass, as has been demonstrated for other herbivores (e.g. grazing catfish; Power 1983).

The observed trophic cascade is consistent with other studies that have clearly demonstrated indirect effects of predation on algal biomass in streams. Decreased grazing by herbivorous fish under increased risk of predation from birds (Power et al.

1989) or predatory fish (Power et al. 1985) resulted in dramatic increases in biomass of algae. In north temperate streams, where herbivorous fish are less common and invertebrates are frequently the primary algivores, a similar increase in algal biomass under fish predation has been observed for brook char (Bechara et al. 1992) in Quebec, and with native galaxids and introduced brown trout in New Zealand (Flecker and Townsend 1994, McIntosh and Townsend 1996).

Predation effects on benthic invertebrates by fish in streams appear to fall into two main classes, either direct (a decrease in abundance through predation) or indirect, typically an increase in abundance in the presence of insectivorous fish (Fig. 11). Larger taxa or size classes of invertebrates are most vulnerable to direct effects (Allan 1983, Flecker and Allan 1984, Bannon and Ringler 1986, Schofield et al. 1988), whereas indirect effects appear to be most pronounced for smaller taxa. The observed increase in abundance of smaller invertebrates in the presence of fish in Mayfly Creek appears to be an indirect effect of predation on large-bodied grazers, which releases smaller grazing invertebrates from exploitative competition. Experiments with *Ameletus* and *Ascaphus* directed at understanding these indirect mechanisms are described in detail in Chapter 3. Fish absence also influences spatial variation in abundance of smaller invertebrates; increased grazing in the control treatments reduced the variance in abundance of smaller invertebrates on both tile and gravel in riffle habitats (Fig. 9), similar to the reduced variation in chlorophyll (Fig. 2).

The overall pattern of fish effects by substrate and habitat indicate that different mechanisms limited invertebrate abundance in different habitats. The strength of predation effects appear to have been broadly related to the relative abundances of autochthonous and allochthonous carbon in different habitats. Both direct and indirect effects of predation were most pronounced on tiles and in riffles where algal carbon constituted a higher proportion of the carbon base of the food chain. Fish effects on total invertebrate abundance were minimal in gravel substrate and pools where detrital carbon constitutes a higher proportion of available carbon. This is supported by partitioning the variance of total invertebrate abundance into components (Fig. 10), which show that 23.6% of the variance in abundance on tiles and 58.8% of the variance in riffles is accounted for by a correlation with detrital carbon. Unfortunately, partitioning of variance components by pool and riffle habitat was not possible because of the low number of habitat replicates.

While grazers of algae in erosional habitats are most strongly affected by fish predation, there was a significant relationship between total invertebrate abundance on both tile and gravel substrate (Fig. 7), suggesting some degree of resource limitation. Organic detritus and its associated microflora constitute a carbon resource for many taxa of invertebrates in streams, and the general positive relationship between organic detritus and invertebrate abundance is well documented (Egglisshaw 1964, 1968 , Rabeni and Minshall 1977, Culp et al. 1983). The negative correlation of grazing mayflies with the abundance of mean organic matter between enclosures (Fig. 15) probably indicates a

preference for erosional habitats with more abundant epilithic algae, rather than direct avoidance of pool habitats with more abundant detritus. Abundance of detritivores such as tanytarsini chironomids, however, are positively correlated with organic matter both within and between enclosures (Figs. 15 and 16), indicating that organic matter is a direct carbon resource.

The relationship between total invertebrate abundance and organic carbon are markedly different on tile and gravel substrate (Fig. 7), and likely relate to differences in the relative contributions of algae and detritus to their respective carbon bases. The rate of increase in invertebrate abundance per unit organic matter is similar between pools and riffles, but the different intercepts indicate that tile in riffles support a higher invertebrate density at very low levels of organic matter. One plausible interpretation is that the greater invertebrate abundance on tiles in riffles is supported by a higher algal production which contributes little to total organic biomass, and that increases in organic carbon on tiles are largely due to deposition of fine particulate organic matter (FPOM) of allochthonous origin, particularly in pools. In contrast, gravel substrate appears to support similar invertebrate biomass per unit organic matter in both pools and riffles.

Although invertebrates are far more abundant in gravel substrate, the slope of the organic carbon - invertebrate abundance relationship is much lower than on tile. This indicates lower overall food quality in gravel substrate relative to tile, where food quality is defined as the biomass of consumers supported by a given biomass of resource. Lower food quality in gravel relative to tile may be related to a higher proportion of coarse

particulate organic matter (CPOM) in gravel substrate; generally speaking, FPOM is of higher food quality, presumably because of a greater surface area:volume ratio for microbial colonization (Peters et al. 1989). However, a general decrease in transfer efficiency as resource abundance increases is also a common pattern in ecology (Ashenden 1986, Downing et al. 1990), particularly if factors other than resources become limiting to consumers (Power 1992a), and the slope of the invertebrate abundance - organic carbon relationship may decline with increasing benthic organic biomass regardless of any real changes in food quality.

Food quality can also be related to the relative contributions of algae and detritus to the carbon base in different habitats. Food quality of resources in streams tends to be related to the origin of the carbon (Barlocher and Kendrick 1975, Ward and Cummins 1979). Generally speaking, food quality is higher for autochthonous carbon than for allochthonous (terrestrial) carbon (Anderson and Cummins 1979, Hawkins et al. 1982). This is based on experiments that have demonstrated higher growth and survival on autochthonous carbon (e.g. Bird and Kaushik 1984), as well as differences in structural and chemical qualities of aquatic and terrestrial organic matter. Autochthonous carbon tends to have lower C:N ratios (Cummins and Klug 1979), primarily because terrestrial detritus (e.g. leaves, twigs) has a higher proportion of structural carbon (cellulose and lignins; Triska et al. 1975). Invertebrates in headwater streams with abundant detritus also tend to respond positively to increases in primary production (Wallace and Gurtz 1986, Hawkins et al. 1982, Behmer and Hawkins 1986). This is consistent with the highest

ratio of invertebrate abundance : organic carbon ashfree dry weight being on riffles in tiles (Fig. 8), with a largely algal carbon base. Tiles in pools tended to accumulate more particulate organic carbon, but not as much as gravel, whose interstices trapped an order of magnitude more detritus and had the lowest apparent food quality.

Throughout this analysis, invertebrate density (abundance) has been used as the response variable to predation. Use of density rather than biomass tends to bias observed trends towards effects on more abundant (typically smaller) size classes, and therefore tends to overemphasize the indirect effects of predation. In contrast, use of biomass biases effects towards the direct effects of predation on larger invertebrates, which contribute less to total invertebrate abundance but disproportionately more to total biomass. In terms of production, smaller invertebrates tend to have higher P/B ratios (Morin and Bourassa 1992) so that average expected impacts of predation on production should be intermediate between those observed for abundance and density.

Vulnerability of different taxa appeared to be strongly related to their functional feeding group. Grazing or herbivorous invertebrates experienced the largest impact of fish predation. *Ameletus* sp. was the taxa of large-bodied grazer most strikingly affected by fish predation (Figs. 13 and 14) on both substrate types. Reduction in density was greater on tile than gravel, presumably because interstitial refuges in gravel decreased vulnerability to predation. *Baetis*, another large-bodied grazer, showed a similar response to fish predation (Fig. 13). 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 probably due in part to a lack of statistical power rather than an absence of predator impact, since density of both *Baetis* and *Ameletus* were significantly reduced in replicated predation experiments the following year (Rosenfeld 1997b, Chapter 4). In contrast with *Baetis* and *Ameletus*, heptageniid density (primarily *Cinygmula*) was not strongly affected by the presence of fish. Slight observer movement would stimulate an escape response in heptageniids grazing on tiles, whereas *Ameletus* had a much higher tolerance to visual stimulation (J. Rosenfeld, personal observation), suggesting that heptageniids in Mayfly Creek are more strongly adapted to fish predation than either *Ameletus* or *Baetis*.

Larvae of the tailed frog *Ascaphus truei* were observed foraging in enclosures both with and without fish, but densities of *Ascaphus* on substrates collected at the end of the experiment were too low to draw meaningful conclusions concerning fish predation effects on *Ascaphus* abundance. Although coho parr used in the study were too small to consume *Ascaphus*, the sculpin used in the experiment had a sufficiently wide gape, and both trout and sculpin have been shown to reduce the abundance of *Ascaphus* in other studies (Feminella and Hawkins 1994). Grazing by *Ascaphus* has been shown to produce indirect effects on total invertebrate abundance (Lamberti et al. 1992, Rosenfeld 1997a) identical to those described for *Ameletus* (Rosenfeld 1997a, Chapter 3), so that part of the observed indirect effect of fish predation on both algal biomass and smaller grazers may well have been due to direct predation on *Ascaphus*. However, Lamberti et al. (1992) found no significant effects of *Ascaphus* on either chlorophyll a, algal biomass, or total

invertebrate abundance at tadpole densities below 8 m⁻². Since densities of *Ascaphus* in fishless sections of enclosures in subsequent experiments in Mayfly Creek averaged 4-6 m⁻² (J.S. Rosenfeld, unpublished data), predator-induced changes in grazing pressure by *Ascaphus* were unlikely to have been primarily responsible for the observed indirect effects of fish on algae and smaller invertebrates.

The decline in abundance of large-bodied grazers was mirrored by an increase in abundance of orthoclad chironomids, which was also most pronounced in riffles and on tile substrate, reflecting the general association of both orthoclads and grazing mayflies with algal carbon in erosional habitats. In contrast, with herbivorous invertebrates, detritivores such as tanytarsini chironomids and tipulids which are primarily associated with depositional habitats showed no significant change in density in the presence of fish (Fig. 12), but had high correlations with the abundance of their detrital carbon resource (Figs. 15 and 16). Predatory chloroperlid stoneflies (primarily *Suwallia* spp.) and predatory Tanypodinae chironomids also appeared largely unaffected by the presence of fish on both tile and gravel substrate (Figs. 12, 13, and 14), but were strongly correlated with organic matter both within and between enclosures (Figs. 15 and 16), suggesting bottom-up control of both predators and prey (Tanytarsini chironomids). Although larger predatory stoneflies have been shown to decrease in abundance in the presence of fish (Feltmate and Williams 1989), both chloroperlid stoneflies and tanypode chironomids are smaller invertebrate predators, with presumably a reduced risk of fish predation. Because numbers of large predatory stoneflies (primarily *Doroneuria*, *Acroneuria*, and

Isoperla) collected at final sampling were too low to estimate densities with any confidence, the experiment yielded little insight into predation effects on these larger predatory taxa.

Nemourid stoneflies in the genus *Zapada* were the only other taxon to show a significant response to the presence of fish. *Zapada*, 99% of which were in the smallest size class, also increased in abundance in the fish treatment, suggesting that fish effects were due to the same indirect mechanism that resulted in increased orthoclad density. The possibility that *Zapada* 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). Although Merritt and Cummins (1984) classify *Zapada* as collector-gatherers, this does not necessarily preclude a dependence on algal carbon, and limited stable carbon isotope analysis of nemourids in a forested headwater stream in Ontario demonstrated a strong algal isotope signature (Rosenfeld and Roff 1992), suggesting a substantial dependence on algal carbon.

It appears that both the functional role and the size of an invertebrate influence its vulnerability to fish predation. Detritivores appear to be less vulnerable to predation, possibly because detrital resources tend to be trapped in interstices that provide a refuge from fish, or detritus itself may constitute a refuge from predation. The role of substrate complexity in decreasing predator impact by creation of interstitial refuges has been experimentally demonstrated in a number of stream studies (e.g. Brusven and Rose 1981, Cooper 1984, Wilzbach et al. 1986). As interstitial refuges increase, both detrital

accumulations and detritivorous invertebrates should become more abundant, and relative predator impacts on the invertebrate community should decline, as was observed on gravel substrate relative to tile. The greatest impact of fish on invertebrate detritivores in streams was demonstrated by Gilliam et al. (1989), who observed strong effects of fish predation on detritivores in spatially homogenous sediment in experimental streams.

Clearly, all invertebrate taxa or life stages do not always fall into discrete functional feeding groups. Many taxa are omnivorous, and most show distinct ontogenetic shifts in trophic level consumption, with smaller instars typically being detritivores regardless of the functional role of larger larvae. Regardless, invertebrates that consume algae on upper substrate surfaces should be at higher risk of fish predation than interstitial detritivores, whether they are obligate herbivores or opportunistic ones.

The fish predation experiment in Mayfly Creek clearly demonstrated that habitat structure at the pool-riffle and microhabitat (substrate) scale controls the contribution of algae and detritus to the local carbon base, which subsequently influences both invertebrate community structure and the impact of fish predation in different habitats. Large-bodied herbivores in erosional habitats appear to be most vulnerable to fish predation, presumably because herbivores are constrained to forage on periphyton on the upper surfaces of rocks. The increase in abundance of smaller herbivores in the presence of fish appears to be a direct consequence of decreased density or grazing activity of larger competitively dominant herbivores. The experiments described in the following

chapter verify this indirect mechanism of fish on smaller invertebrates by documenting the direct impact of larger grazers on small epibenthic herbivores.

CHAPTER III

Mechanisms of indirect fish effects: large grazer impacts on small herbivores and algae

INTRODUCTION

The competitive ability of organisms is often mediated by body size (e.g. Brooks and Dodson 1965, Gliwicz 1990). Although larger aquatic invertebrates tend to be more vulnerable to fish predation (Allan 1978, Culp and Scrimgeour 1993; Scrimgeour et al. 1994b, Chapter 2), they often appear to be more efficient short-term competitors for resources. Lamberti et al. (1992) demonstrated that grazing by tailed-frog larvae (*Ascaphus truei*) and a large caddisfly (*Dicosmoecus gilvipes*) reduced abundance of smaller invertebrates in experimental channels. Bechara et al. (1992) also found that an increase in large-bodied grazing invertebrates led to a decrease in both chlorophyll *a* and the biomass of smaller grazing chironomids in experimental streams. Similar observations have been made for benthic invertebrate grazers in lakes; both Crowder and Cooper (1982) and Gilinsky (1984) found a decrease in the abundance of smaller grazing chironomids when density and activity of larger grazing benthic invertebrates increased in fish enclosures. These observations collectively suggest that there is a competitive asymmetry between large grazers and small epibenthic herbivores, presumably because of the mechanical advantage of larger herbivores, and their ability to dislodge or even consume smaller epibenthic invertebrates (Bechara et al. 1992).

A significant increase in algal and chironomid biomass was observed in the presence of fish in the enclosure experiment described in Chapter 2. Large grazing mayflies were reduced in the presence of fish, suggesting that the increase in algal biomass and chironomid abundance was due to a release from competition by larger grazing mayflies. To evaluate whether a reduction in grazing by large herbivores increases the abundance of algae and small herbivores, I performed a set of grazing experiments using the dominant grazers present in Mayfly Creek, mayflies in the genus *Ameletus* (maximum size collected 8 mm, final instar), and larvae of the tailed frog, *Ascaphus truei* (30-45mm, 0.3-0.5 g). *Ameletus* is a widely distributed genus of mayflies (Edmunds et al. 1976, Merritt and Cummins 1984). Tadpoles of the tailed frog have mouthparts modified as a sucking disc that aids in clinging to rocks and scraping algae, and typically occur in steep gradient streams throughout the Pacific Northwest United States and Canada (Hawkins et al. 1988). Both taxa have been shown to be effective grazers capable of reducing algal abundance in streams (Hill and Knight 1987, Lamberti et al. 1992).

The first experiment was performed in streamside troughs fully exposed to sunlight, and was replicated in a second experiment using instream troughs to evaluate the consistency of grazing effects under more natural light conditions. Objectives of the experiments were i) to determine whether size affected competitive dominance of grazing invertebrates, further confirming the generality of this effect in streams, and ii) to assess whether a competitive asymmetry between large and small grazers could account for the

observed increase in small herbivores and algae in the presence of fish in Mayfly Creek. Predictions were that both chlorophyll *a* and abundance of epibenthic chironomids would decrease in the presence of *Ascaphus* and *Ameletus*.

SITE DESCRIPTION

Refer to site description in Chapter 2.

METHODS

Experiments were performed from June to August 1994 during the summer low flow period. For the first set of experiments, four 2 m long, 10 cm deep, 20 cm wide plexiglass troughs were placed in a clearing on the streambank exposed to full sunlight. Troughs were fed by streamwater diverted into a header box to stabilize flow. Discharge in each trough averaged approximately 1 l s^{-1} . Streamwater entering the troughs was filtered through a 0.475 mm mesh to exclude larger grazers and detritus, but permit colonization of troughs by small invertebrates. Troughs were divided transversely into three 40 cm sections using 0.475 mm mesh screens to prevent the exchange of large invertebrates between sections. Screens were cleaned on a regular basis to maintain current velocity within the range of $6 - 9 \text{ cm s}^{-1}$ (measured using a Marsh-McBirney Model 2000 flow meter) Four 7.5 by 15 cm unglazed ceramic tiles were placed in each trough

section. Four grazer treatments were randomly assigned to the twelve sections in three replicates each. Grazer treatments consisted of *Ameletus sp.* alone, *Ascaphus* alone, both *Ameletus* and *Ascaphus* together, and a control treatment with no grazers. *Ameletus* were stocked at a density of 172 m⁻² (4 per tile), which was comparable to the upper range of densities of *Ameletus* observed on ceramic tiles placed in Mayfly Creek (Chapter 2), and slightly less than the ambient density used by Hill and Knight (1987) in grazing experiments with *Ameletus* in a California stream. *Ascaphus* were stocked at 21 m⁻² which was the lowest density possible (one tadpole per section). This density was high, but within the upper range of densities observed in Mayfly Creek and streams in Washington (Hawkins et al. 1988, Lamberti et al. 1992). The densities of *Ameletus* and *Ascaphus* in the combined treatment were the same as the densities used in the individual treatments.

The length of individual mayflies was estimated live at the beginning and end of the experiment by measuring their length when placed on a 1.15 mm Nitex grid over a black background in a 40 mm petri dish. *Ascaphus* weight was measured to the nearest 0.01 g at the beginning and end of the experiment using an Ohaus model CT-200 electronic balance.

To pre-empt emergence of adult mayflies, the experiment was ended when larvae began to develop black wingpads 13 days after mayflies were stocked. Tiles were removed, and periphyton and invertebrates were rinsed off into a beaker using a wash bottle. The upper tile surface was then scrubbed with a brush to remove any attached algae. The volume of the resultant slurry was recorded, and two replicate 0.8 ml samples

were removed for chlorophyll *a* analysis using a 1 ml syringe, added to 7.2 ml of 100% acetone to achieve a final concentration of 90% acetone, and placed on ice in the dark. Filtration of the extract was unnecessary because the concentration of solids was extremely low. Chlorophyll *a* was measured the next day using a Turner Designs model 10-005 R fluorometer, and chlorophyll *a* concentrations were calculated using the equations described in Strickland and Parsons (1972). After sampling for chlorophyll, the remaining slurry was passed through a 150 mm screen. Invertebrates and detritus retained on the screen were preserved in 5% formalin. Invertebrate samples were later sorted in the lab, identified to genus (with the exception of chironomids, which were identified to subfamily), and counted.

Because the streamside troughs developed filamentous algae that was somewhat atypical of the algal community in Mayfly Creek, a second experiment was carried out under more natural light and temperature conditions using instream troughs embedded in the streams channel. Only the *Ameletus* and control treatments were successfully replicated using instream troughs because tadpoles would not actively graze in the troughs for unknown reasons. Troughs were 40 cm long, 10 cm deep, 20 cm wide, and lined with three unglazed 15 cm by 15 cm ceramic tiles. Space and time constraints precluded placement of all troughs in the same riffle at the same time. Two experimental blocks of four troughs each were placed in each of two separate riffles 5 days apart, and two sets of grazer and control treatments were randomly assigned within each riffle. Densities of mayflies (394 m^{-2} , 9 mayflies per tile) were higher than in the first experiment.

Effective densities of mayflies were lower than stocking densities in both experiments, since mayflies were frequently observed foraging on the front screens of the troughs. Observed mayfly densities on tiles never exceeded 54 m^{-2} in the instream troughs (mean density $25 \pm 15 \text{ m}^{-2}$ for 11 observations on separate days), despite much higher stocking densities. Consequently, estimates of grazers effects in these experiments are likely to be conservative.

All instream troughs were sampled simultaneously when a summer spate threatened to destroy the experiment 8 and 13 days after stocking of grazers in the different riffles. Although tiles were recovered from the troughs, some mayflies escaped when the water level rose above the trough sides immediately prior to sampling. Tiles were sampled for chlorophyll *a*, mayflies, and other invertebrates as in the first experiment.

Where necessary, data were log transformed to equalize variances. Treatment effects were evaluated with analysis of variance using PC SAS (SAS Institute Inc., 1989).

RESULTS

Average initial and final mayfly lengths in the first experiment were 4.2 and 5.1 mm, respectively. Recovery of mayfly larvae at the end of the experiment averaged 66%; loss of mayflies was due to mortality or emergence. Average initial *Ascapthus* weight was 0.42 g, and average growth was 3% during the 13 day experiment, with no mortality.

Positive growth rates for both herbivores suggests that grazer density was within a range that did not exceed available food supply.

All grazer treatments reduced chlorophyll *a* on ceramic tiles relative to the control treatment (Fig. 17), although only the *Ameletus* and combined grazer treatment were significantly different from the control ($F_{3,11} = 7.5$, $p = 0.01$, ANOVA, post-hoc Tukey test $p < 0.05$). There was no difference between grazer treatments (Tukey test, $p > 0.05$ for all grazer comparisons), although chlorophyll *a* was lowest in the combined grazer treatment (Fig. 17). Chironomid abundance on ceramic tiles was reduced approximately one third in grazer treatments relative to controls (Fig. 17), but there was no significant difference in chironomid density among the four treatments ($F_{3,11} = 1.7$, $p = 0.24$, ANOVA). However, chironomid density in all grazer treatments combined ($n=9$) was significantly lower than density in controls ($n=3$; $t_{10} = 2.6$, $p = 0.03$, t-test). There was also a significant positive correlation between chironomid abundance and chlorophyll *a* across all treatments ($n=12$, $p = 0.001$, $R^2=0.69$). On average 71% of chironomids on tiles were in the subfamily Orthocladiinae, classified as collector-gatherers and scrapers by Merritt and Cummins (1984).

Because some mayflies were lost from the instream trough experiment when the water level in the stream rose above the trough sides, the proportion of mayflies surviving until the end of the second experiment could not be estimated. As with the first experiment, the presence of *Ameletus* reduced both chlorophyll *a* and numbers of chironomids relative to controls ($F_{1,7} = 45.5$ for chlorophyll, $F_{1,7} = 38.5$ for chironomids, $p <$

0.001 for log-transformed data; Fig. 18). Both chlorophyll *a* concentrations and chironomid densities were lower in the instream trough treatments than the streambank experiment, probably because the streamside troughs were in an unshaded clearing, whereas the instream troughs were much more heavily shaded.

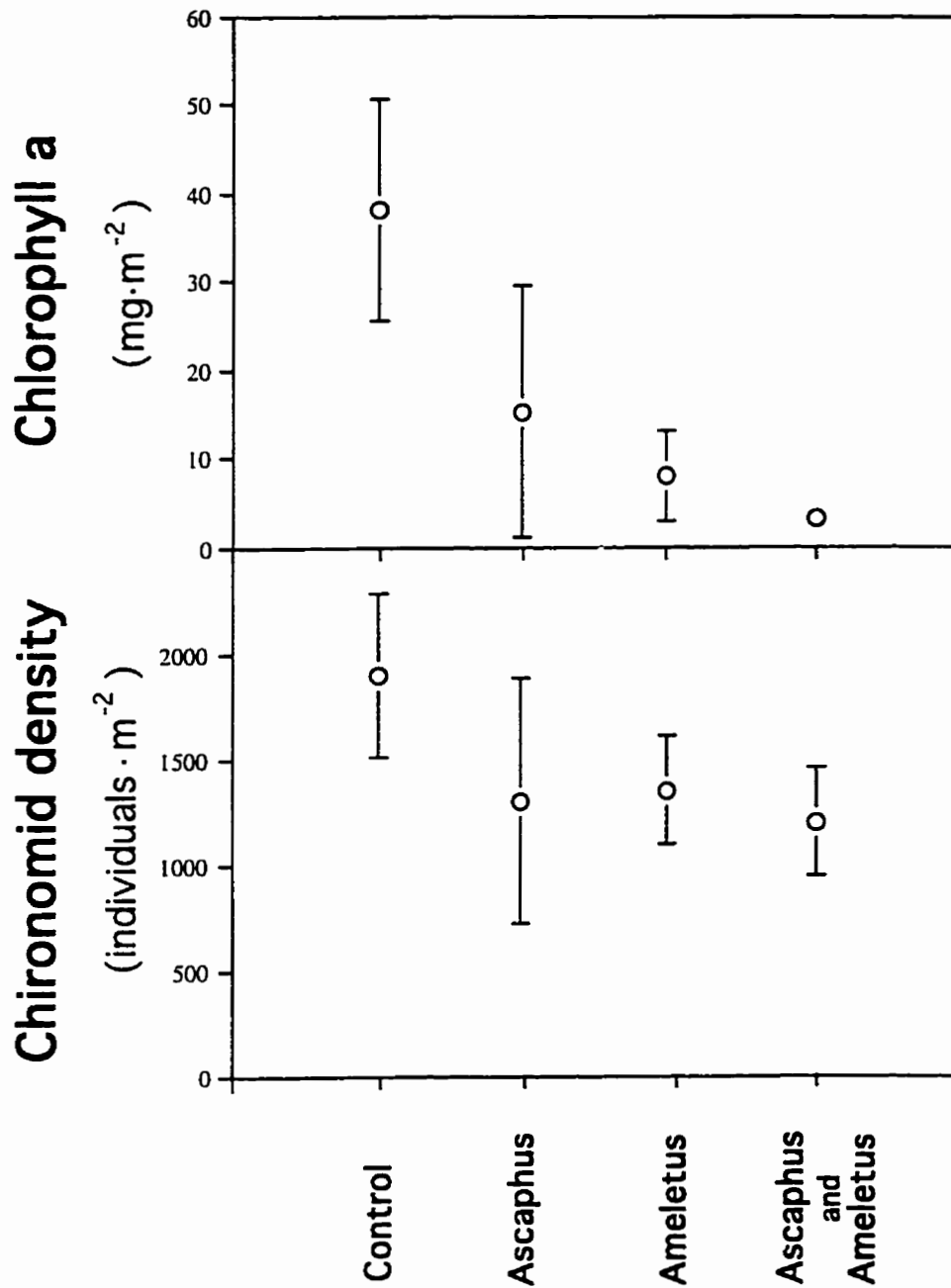


Fig. 17 Chlorophyll a concentrations and chironomid density (m⁻²) at the end of the first grazing experiment. Treatments are no grazers, *Ascaphus* only, *Ameletus* only, and both *Ascaphus* and *Ameletus* combined. Error bars represent one standard deviation above and below the mean.

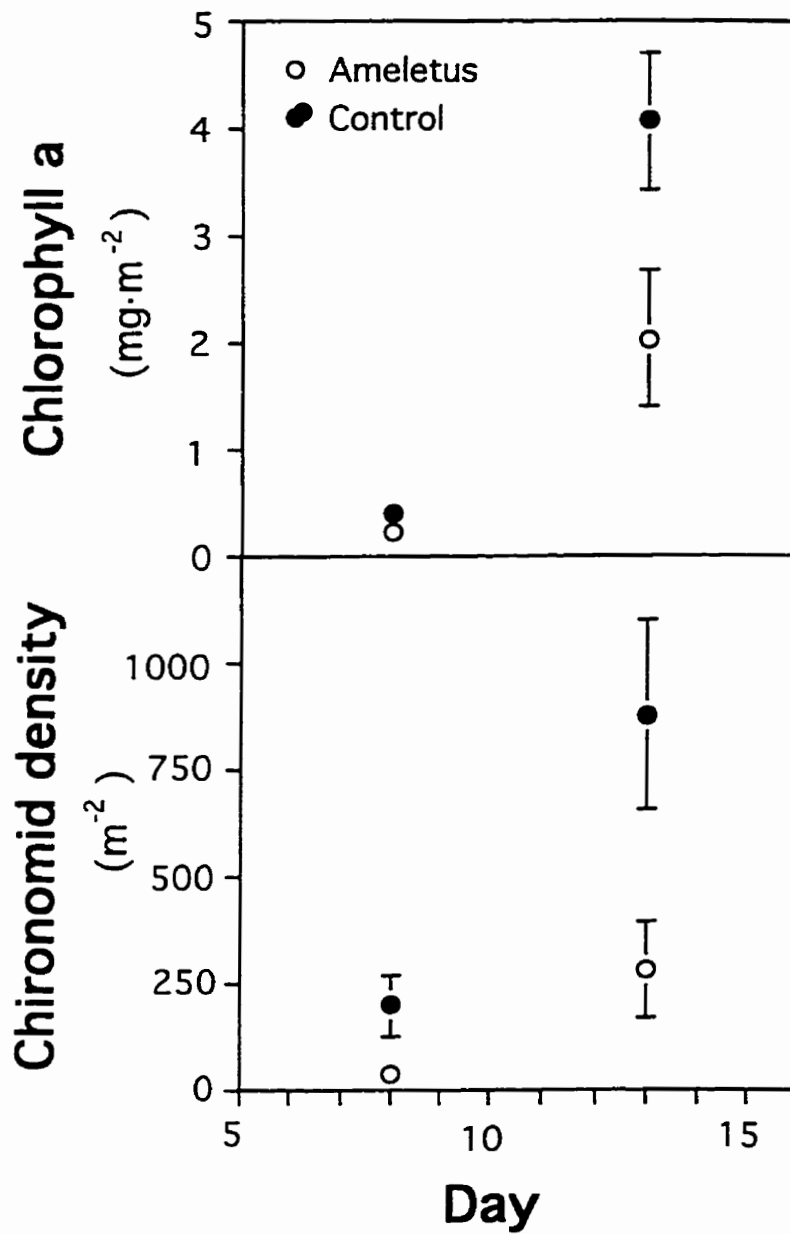


Fig. 18 Chlorophyll a concentrations and chironomid density (m⁻²) in control (dark circles) and *Ameletus* (open circles) treatments after 8 and 13 days. Error bars represent one standard deviation above and below the mean.

DISCUSSION

Both experiments demonstrate that the presence of larger invertebrate herbivores reduces the abundance of smaller sessile epibenthic invertebrates, primarily chironomids in the subfamily Orthocladiinae. This effect of larger grazers on smaller invertebrates appears to be both consistent and rapid. Large-bodied grazer taxa had similar effects, despite substantial phylogenetic and morphological differences (e.g. an arthropod vs. a vertebrate), and a reduction in chironomid numbers by mayfly grazing was evident within eight days. The generality of large grazer effects on smaller epibenthic herbivores is supported by previous observations of increased chironomid abundance following the reduction of large grazer activity in lakes (Crowder and Cooper 1982, Gilinsky 1984) and streams (Lamberti et al. 1992, Bechara et al. 1992, Power 1992b). Although the generalized effects of larger grazers appear to be similar in most of these experiments, it is conceivable that different herbivore instars or taxa vary in their effects on smaller epibenthic invertebrates. This did not appear to be the case in the present experiments, although relatively low replication limits the power to detect differences in grazer effects. The precise mechanism whereby larger grazers affect smaller invertebrates is unclear. Large grazers may reduce chironomid abundance by resource depletion (exploitative competition), displacement of chironomids during grazing (interference competition), or direct consumption (predation). These mechanisms are not mutually exclusive, and may vary with grazer taxa. The role of incidental or deliberate predation is supported by the

presence of chironomid larvae in the guts of grazing limnephilid caddisflies examined by Bechara et al. (1992). However, examination of guts of twenty *Ameletus* from my experiments revealed no chironomid remains, suggesting displacement of chironomids or resource competition as the primary mechanisms of competitive dominance in *Ameletus*.

The increase in abundance of smaller epibenthic invertebrates in control treatments without larger grazers clearly supports the hypothesis that the higher density of small invertebrates in the fish treatment (Chapter 2) was due to the observed decrease in abundance of large herbivores.

CHAPTER IV

Effects of fish patchiness at a small scale: The influence of upstream fish predation on fish effects in downstream patches

INTRODUCTION

One of the distinguishing features of flowing waters is the patchy or heterogeneous nature of the stream habitat (Pringle et al., 1988, Hildrew and Giller 1994). Patches are areas with relatively homogenous internal conditions that differ from adjacent areas or patches, leading to discontinuity in habitat at a hierarchy of spatial scales (Frissel et al. 1986, Statzner et al. 1988, Hawkins et al. 1993). In addition to a high degree of patchiness, streams are characterized by extremely high rates of movement of organisms between patches (Townsend and Hildrew 1976, Townsend 1989), which is facilitated by the ability of many aquatic invertebrates to drift in the water column (Waters 1972, Kohler 1985). The rate of exchange of individuals between patches may have a large influence on community structure (Townsend 1989, Frid and Townsend 1989, Lancaster et al. 1991), and the outcome of biological processes within a patch may be strongly influenced by biological process in adjoining patches when immigration rates are large (Pulliam 1988, Cooper et al. 1990).

In a review of predation experiments in streams, Cooper et al. (1990) found predator enclosures made of small mesh were more likely to reveal predation effects, presumably because smaller mesh artificially reduced movement rates of prey into and out of enclosures. The influence of prey exchange (dispersal between patches) on predation effects was further demonstrated by experimentally manipulating mesh size in enclosures (Cooper et al. 1990). Sih and Wooster (1994) subsequently modelled predation and exchange rates between stream patches. They confirmed that high exchange rates can "swamp out" local predation effects, whereas low exchange rates intensify them, unless prey alter their dispersal rate in the presence of predators (e.g. drift out of predator patches).

Although the source of variation in immigration rate considered by Cooper et al. (1990) was an experimental artefact of mesh size, it is probable that immigration rate between patches varies in the natural stream environment, and might similarly influence the expression of predation effects on the benthos. Fish predation or foraging activity is one natural factor that may modify exchange rates between patches (Forrester 1994b). Predation on drifting or benthic invertebrates may reduce the immigration rate of invertebrates into downstream patches by direct mortality. Alternatively, foraging by fish may generate visual, tactile or chemical cues that cause invertebrates to drift (Culp et al. 1991, Dodson et al. 1994, Scrimgeour et al. 1994a Scrimgeour et al. 1994b), effectively increasing immigration rates into downstream patches. Increased drift of aquatic invertebrates as a response to foraging by fish has been demonstrated for a

variety of lotic invertebrates (Kohler and McPeck 1989, Scrimgeour et al. 1994a), particularly highly mobile mayfly taxa such as *Baetis spp.* (Forrester 1994a). In either case, alteration of immigration rates of invertebrates as a consequence of fish predation in upstream patches may influence the expression of predation effects on the benthos downstream.

The experiments described in this chapter had two objectives. The first was to test whether the abundance of fish in upstream patches (at the pool-riffle or channel width scale) could influence the strength of fish predation effects on the benthos downstream. This was evaluated by manipulating the density of coho salmon fry (*Oncorhynchus kisutch* Walbaum) in the upper sections of enclosures used in the first experiment (Chapter 2), and monitoring the abundance of grazing mayflies and their algal resource on artificial substrata downstream. The second objective was to investigate the mechanisms whereby fish affect grazing mayflies in the study stream (e.g. direct predation vs. induced behavioural changes from mechanical or chemical cues), so as to interpret the generality of the observed fish effects. The relative significance of mechanical vs. chemical cues in inducing behavioural responses in mayflies was evaluated in separate experiments in plexiglass bankside troughs.

STUDY SITE

Refer to site description in Chapter 2.

METHODS

Experimental and sampling design

Fish predation experiment

The experiment was performed in the three riffle enclosures used in the first experiment (Chapter 2). Most details of the experimental methodology were identical to those described in Chapter 2, and only methods that differ from those previously described are included below.

The upper sections of enclosures were in pools and the lower sections were in slow riffles where current velocity averaged $11.3 \pm 3.1 \text{ cm s}^{-1}$ (range 4-22 cm s^{-1}), sufficient to prevent deposition of fine particulate organic matter on upper substratum surfaces. Eight 15 x 15 cm unglazed ceramic tiles were placed in each lower enclosure section as artificial substrata for colonization by algae and invertebrates (Fig. 19). Six clusters of five pieces of natural stream gravel (3-4 cm diameter) were also placed in each lower section for colonization by algae. One of the lower sections of each enclosure was randomly chosen, and coho parr (mean length $53.3 \pm 5 \text{ mm SD}$, mean weight $1.68 \pm 0.46 \text{ g SD}$) were stocked at an ambient density of 2 m^{-2} , and the other lower section remained unstocked as a fishless control. The upper section of each enclosure section was stocked with coho at one of three randomly assigned densities: no fish, ambient fish density (2 coho m^{-2}), and high fish density (5.25 coho m^{-2}). Coho

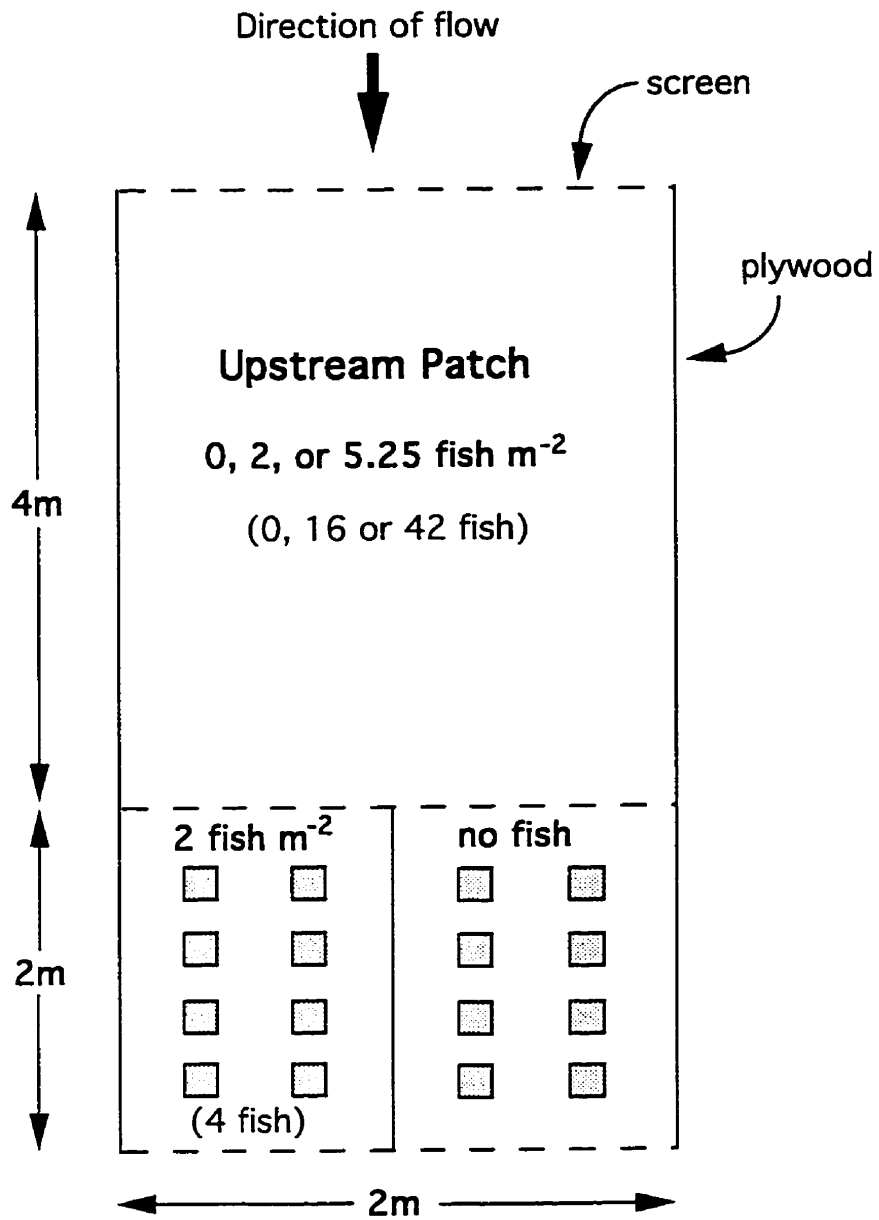


Fig. 19 Design of experimental enclosures used for the fish predation experiment. Squares represent tiles, and broken lines denote permeable mesh.

used during the experiment were collected from the nearby Allouette River by electrofishing or baited minnow traps.

To replicate the upstream density treatments, two sequential trials were run in the three riffle enclosures between early June and early September 1994, with three treatments in each trial. At the end of the first trial, eight weeks after fish were stocked, tile and gravel substrates were removed for invertebrate sampling and chlorophyll analysis, and then replaced in enclosures. Upper fish density treatments were then reassigned to a different enclosure for the second trial, and fish were removed from the upper section of each enclosure and transferred as a group to the upper section of a different enclosure. Fish in lower enclosure sections were not exchanged between runs. Tile and gravel substrates were then resampled for chlorophyll and invertebrates at the end of the second trial.

Visual counts of mayflies on tiles were made at two to three day intervals throughout the experiment. Enclosures were carefully approached so as to minimize disturbance of grazing mayflies, and the number of mayflies observed on tiles in lower enclosure sections with and without fish was recorded. Night counts were also made between midnight and 04:00 on five nights during each sequential trial of the experiment. Mayflies were observed using a narrow beam flashlight with a red filter. Some mayflies (< 10%) were observed to react to red light during night observations. Although exposure to red light may influence the subsequent short-term behaviour of

mayflies (Heise, 1992), it probably had little effect on their initial detection during night counts, and potential biases were similar across treatments.

Tiles were sampled at the end of each trial by carefully lifting them off the stream bottom into a 150 μm mesh net held immediately downstream. Periphyton and invertebrates were rinsed off tiles into a beaker using a wash bottle. The upper tile surface was then scrubbed with a brush to remove attached algae. The volume of the resultant slurry was recorded and two replicate 0.8 ml samples were removed for chlorophyll *a* analysis using a 1 ml syringe, added to 7.2 ml of 100% acetone to achieve a final concentration of 90% acetone, and placed on ice in the dark. Chlorophyll *a* concentrations were measured the next day using a Turner Designs model 10-005 R fluorometer. After sampling for chlorophyll, the remaining slurry was passed through a 150 μm screen. Invertebrates and detritus retained on the screen were preserved in 5% formalin. Invertebrate samples were later sorted in the laboratory, identified to genus using Merritt and Cummins (1984), with the exception of chironomids which were identified to subfamily, and then counted and measured using a digitizing system (Roff and Hopcroft 1986). Chlorophyll *a* on gravel substrate was measured by extracting chlorophyll from individual pieces of gravel in a known volume of 90% acetone in a 250 ml glass jar. Storage and measurement for chlorophyll on gravel then followed the same protocol as for chlorophyll on tiles. Chlorophyll concentrations were calculated using formulae described in Strickland and Parsons (1972).

Mayfly behaviour experiments

Ameletus sp. was the most abundant grazing mayfly in the upper reach of Mayfly Creek, although *Baetis* sp. was also common. Experiments were performed with coho parr and *Ameletus* to distinguish between the effects of chemical and mechanical cues in modifying *Ameletus* behaviour. Four 2 m long, 20 cm wide, 10 cm deep plexiglass troughs were mounted on the streambank and fed with water from a header box to stabilize flow. Channels were divided transversely into three 40 cm long sections using 0.475 mm mesh screen to prevent movement of late instar mayflies. Discharge in the channels was approximately 1 l s⁻¹, and current velocity was maintained in the range of 4-7 cm s⁻¹.

For the chemical cue experiment, four 7.5 x 15 cm unglazed ceramic tiles were placed in the upper and lower sections of each channel, and a short piece of PVC pipe was placed in the centre section to provide cover for fish. Eleven *Ameletus* nymphs were placed in each of the upper and lower channel sections, and a single coho parr was introduced into each centre section. Numbers of mayflies on exposed upper surfaces of tiles in sections above and below fish were recorded three times over a 24 h interval prior to and after fish introduction.

To test for the additional effects of mechanical cues from coho juveniles, the same experimental setup was used, except that fish were directly introduced into lower channel sections containing mayfly nymphs. Small (4 x 8 cm) canopies were placed in

lower sections to provide cover for fish. Coho remained under these shelters swimming slowly to hold position, and occasionally moving beyond them to explore the channel. Fish were introduced into channels in the late morning, and mayfly abundance on exposed tile surfaces in upper control and treated sections was monitored at roughly 2 h intervals for 12 h following fish introduction.

Data analysis

Data were analyzed using PC SAS (SAS Institute Inc., 1989). There was no significant effect of trial on chlorophyll *a* or invertebrate abundance, nor was there an interaction between trial and either fish presence or upstream density treatments. Trials were therefore treated as replicates in all analysis. Effects of fish presence and upstream density on visual counts of mayfly abundance on tiles during the day and night from the first experiment were analyzed using repeated measures ANOVA, with upstream fish density as a covariate (continuous variable). The significance of fish presence and upstream density were evaluated using the fish presence*upstream density interaction mean square as the error term.. Count data were $\sqrt{(x+0.5)}$ transformed to equalize variance (Sokal and Rohlf, 1997). Effects of fish presence and upstream density on chlorophyll *a* on tile and gravel were analyzed using ANCOVA with upstream density as the covariate. Numbers of mayflies on tiles at final sampling were non-normally distributed, and were analyzed using a Wilcoxon two-sample test with normal

approximation. Fish effects from the chemical and hydrodynamic cue experiments were analysed using a repeated measures ANOVA.

Because invertebrate densities on tiles were much lower than in the first predation experiment (Chapter 2), invertebrates were divided into two size classes (small, < 5 mm, and large, > 5mm) rather than three. Preliminary analysis with invertebrates in three size classes resulted in much lower numbers per size class, severely limiting statistical power.

RESULTS

Fish predation experiment

Average fish weight in upper and lower enclosure sections increased by 68% at ambient densities and 35% at high densities (upper sections only) over the course of the experiment; growth rates were consistently higher in upper enclosure sections.

Although the presence of fish in lower enclosure sections significantly reduced the number of mayflies observed on tiles (repeated measures ANOVA, Table 5; see Fig. 20), there was no significant effect of upstream fish density on mayfly numbers observed on tiles. However, there was also a significant interaction between fish presence and time of day (day vs. night); reduction in mayfly abundance on tiles was much greater during the day than at night (Fig. 20).

Source	df	SS	MS	F	P
Fish presence	1	23.4	23.4	489	0.029*
Upstream density	1	0.17	0.17	3.5	0.31
Upstream density * fish presence	1	0.05	0.05	0.03	0.86
Time of day	1	4.3	4.3	2.8	0.11
Fish presence * time of day	1	16.8	16.8	10.8	0.004**
Error	19	28.0	1.6		

Table 5. Results of repeated measures analysis of variance of the numbers of mayflies (all species combined) observed grazing on upper tile surfaces (* indicates significance at the 0.05 level, ** indicates significance at the 0.01 level). The fish presence*upstream fish density interaction is used as the error term to test for fish presence and upstream density effects.

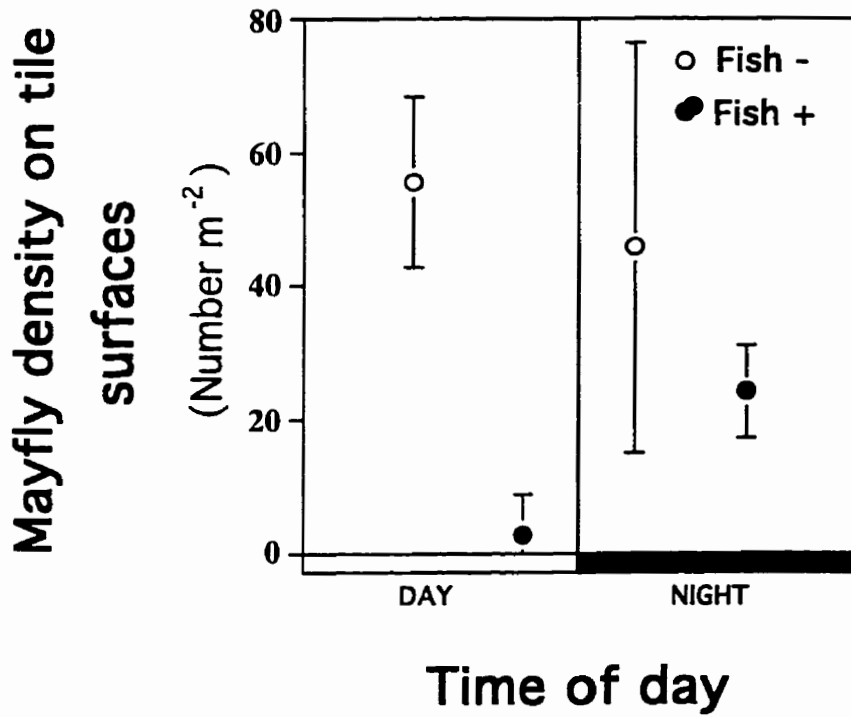


Fig. 20 Mean density (± 1 SD) of mayflies (number m^{-2} for all species combined) observed foraging on tiles in lower enclosure sections during the day and night in the presence (fish +) and absence (fish -) of fish.

Densities of large (>5 mm) nymphs of both *Ameletus sp.* and *Baetis sp.* on tiles at final sampling were significantly lower in the presence of fish than in fishless controls (Wilcoxon 2-sample test; Table 6), but there was no difference between treatments for smaller (<5mm) mayflies. There was no significant effect of upstream fish density on the abundance of either size class or species of mayfly.

There was no detectable effect of either upstream fish density or fish presence on chlorophyll *a* on gravel substrate (ANCOVA, Table 7; see Fig. 21a). In contrast, chlorophyll *a* on tiles was significantly higher in the presence of fish, and increased with increasing fish density in upstream enclosure sections (ANCOVA, Table 7; Fig. 21b). There was no significant effect of upstream fish density (ANCOVA, $F_{3,5} = 0.7$, $p = 0.6$) or fish presence in lower enclosure sections (ANCOVA, $F_{1,5} = 4.7$, $p = 0.08$) on abundance of chironomids on tiles, although average chironomid abundance was higher in the lower fish treatments (mean density $1350 \pm 1100 \text{ m}^{-2}$ SD) than in the control sections (mean density $570 \pm 170 \text{ m}^{-2}$ SD).

Mayfly behaviour experiments

There was no detectable difference in the number of mayflies foraging on exposed tile surfaces above and below channel sections containing coho (repeated measures ANOVA, $F_{1,4} = 0.01$, $p = 0.92$), although mayflies tended to be slightly less abundant in the lower treatment sections following fish addition (Fig. 22). In the second behavioural experiment where fish were present in the same compartment as mayflies,

	Fish Present	Fish Absent	P
<i>Ameletus</i>			
Large (> 5mm)	3.1 ± 7.1	21.8 ± 8.0	0.007**
Small (< 5mm)	38.7 ± 20.9	41.3 ± 53.3	0.87
<i>Baetis</i>			
Large (> 5mm)	0	19.6 ± 20.4	0.001**
Small (< 5mm)	16.4 ± 6.7	35.1 ± 28.4	0.18

Table 6. Densities (number m⁻² ± 1 SD) of large (> 5mm) and small (<5mm) *Ameletus sp.* and *Baetis sp.* on unglazed ceramic tiles at final sampling of lower enclosure sections (n=6 for both trials combined).

Substrate	Source	df	SS	MS	F	P
Gravel						
	Fish presence	1	0.08	0.08	0.09	0.78
	Upstream fish density	1	0.07	0.07	0.07	0.79
	Error	9	8.75	0.97		
Tile						
	Fish presence	1	4.96	4.96	14.3	0.004**
	Upstream fish density	1	3.32	3.32	9.6	0.013*
	Error	9	3.12	0.35		

Table 7. Results of analysis of covariance of the effect of upstream fish density and fish presence on chlorophyll *a* on tile and gravel substratum for both trials combined (n=12; * indicates significance at the 0.05 level, ** indicates significance at the 0.01 level).

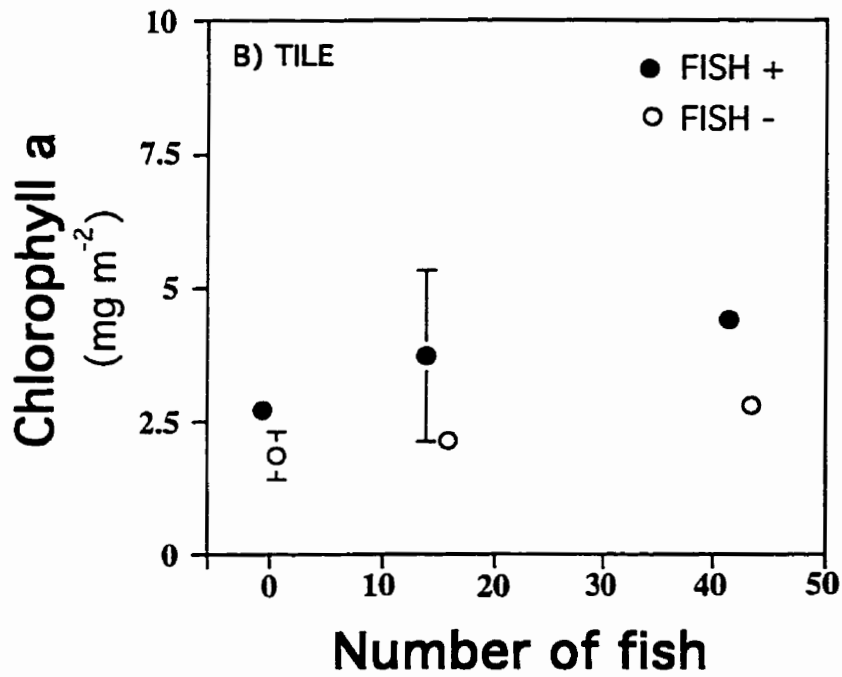
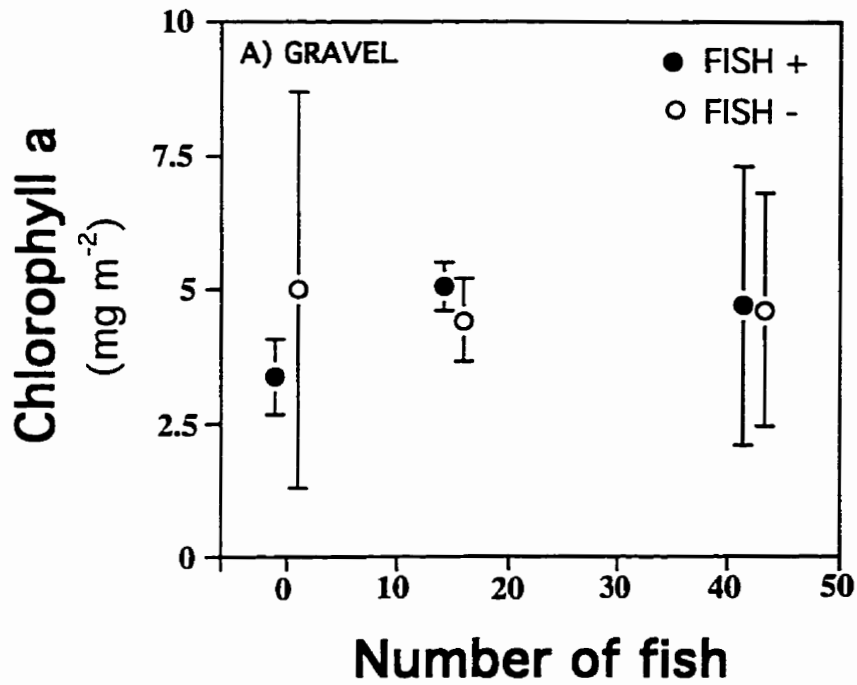


Fig. 21 Chlorophyll *a* (mg m⁻² ± 1 SD) on gravel (a) and tile substrate (b) in lower enclosure sections with (fish +) and without (fish -) fish (n=6) as a function of the number of fish in upstream patches. Where error bars are absent they are contained within the point.

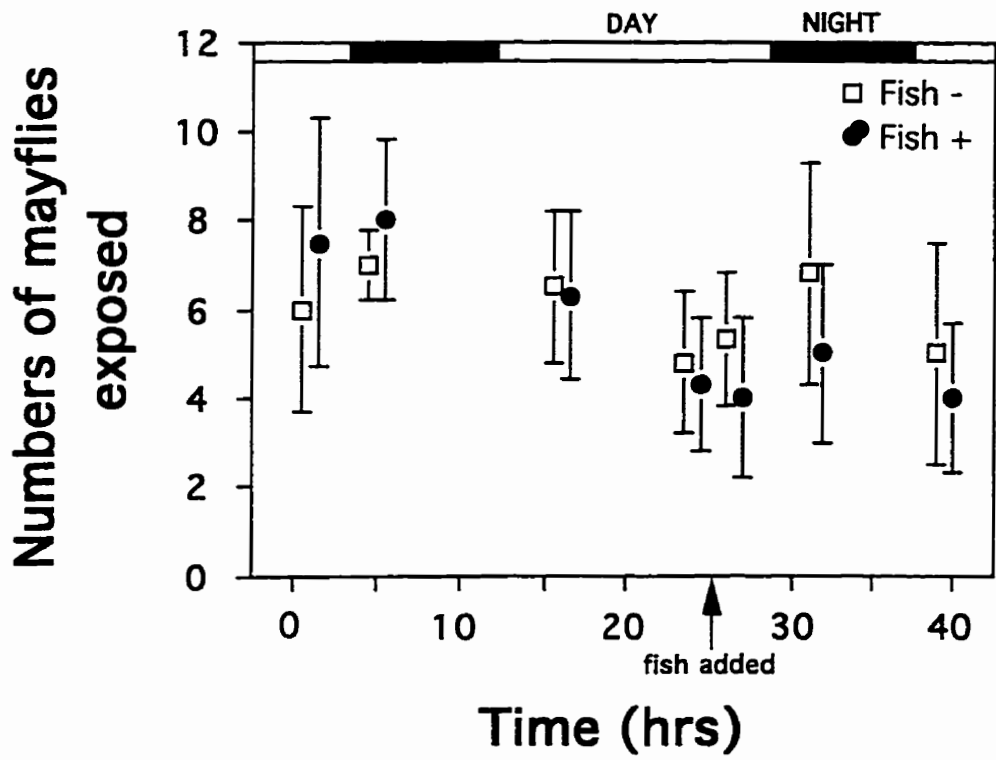


Fig. 22 Number of mayflies (± 1 SD) grazing on exposed tile surfaces in plexiglass channel sections over time in experimental treatments exposed to chemical cues below coho parr (fish +, n=4), and control treatments above coho parr (fish -, n=4).

numbers of mayflies on exposed tile surfaces were significantly lower relative to fishless control sections (repeated measures ANOVA $F_{1,3} = 102.9$, $p = 0.01$, Fig. 23). There was no significant difference in total mayfly abundance between fish treatments and controls at the end of the second experiment, indicating that fish were not directly consuming mayflies during the experiment.

DISCUSSION

Although the enclosure experiment demonstrated a strong effect of fish presence on mayfly activity and density, especially for larger size classes, there was no detectable effect of upstream fish density on mayfly abundance. The only significant effect of upstream fish density was on algal biomass on tiles. This suggests that algal biomass may be a more sensitive indicator of mayfly grazing activity than more variable short-term behavioural observations or density estimates, possibly because algal biomass integrates grazing activity over time.

The increase in algal biomass on tiles with increasing fish density upstream suggests that reduced grazing pressure in downstream patches is associated with increased fish abundance in upstream patches. This effect may be due to direct predation by fish in upstream patches, which can potentially reduce the colonization of downstream patches by decreasing immigration rates. Alternatively, high densities of fish may induce elevated drift rates of mayflies, which cause them to leave the upstream

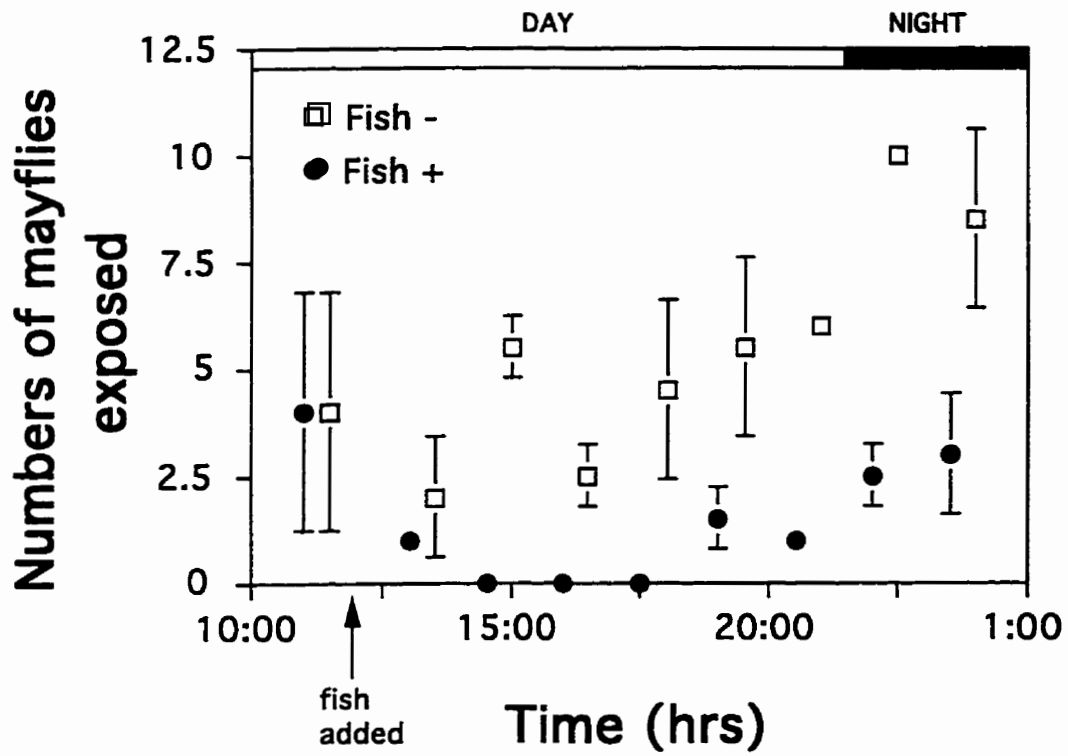


Fig. 23 Number of mayflies (± 1 SD) grazing on exposed tile surfaces in plexiglass channels sections over time in the presence (fish +, n=4) and absence (fish -, n=4) of fish.

patch (e.g. Forrester 1994b), and potentially drift out of the downstream patch. In this case, downstream effects of upstream predation may be related to the scale of the downstream patch and how far mayflies drift after encountering a predator. Mayflies drifting out of high density upstream patches, however, should still eventually accumulate in predator-free patches downstream and reduce algal biomass. The presence of mayflies in the guts of coho (Rosenfeld, unpublished data) suggests that direct predation is an important mechanism, but does not exclude the possibility of increased emigration from high density treatments. Drift from enclosures was not measured in this experiment, so the potential role of increased drift from fish enclosures cannot be evaluated.

Increased cycling and excretion of nutrients is an alternative mechanism for higher algal biomass in the presence of fish. However, decreased algal biomass in fishless controls is correlated with increased mayfly abundance on tiles, which is consistent with a mechanism of indirect fish effects on algal biomass through a trophic cascade (Carpenter et al. 1985) rather than increased nutrient cycling. Grazing experiments using *Ameletus* in Mayfly Creek (Rosenfeld 1997b, Chapter 3) and elsewhere (Hill and Knight 1987) have also demonstrated that *Ameletus* can greatly reduce algal biomass. Thus a mechanism involving fish effects on mayfly grazing appears to be a sufficient (but not exclusive) explanation for the observed increase in algal biomass in the presence of fish.

The lack of an effect of either fish presence or upstream density on gravel chlorophyll demonstrates the effectiveness of artificial tile substrata in reducing spatial variation in benthic effects (i.e. variation between 3-4 cm diameter gravel pieces). However, it also indicates that the observed indirect effects of fish predation on algae are comparatively minor relative to small scale spatial variation in algal biomass on natural substrata within an enclosure. Similarly, the lack of a downstream effect of upstream predation on chironomid abundance suggests a minor impact on the expression of predation effects in downstream patches. However, indirect effects of fish predation on chironomid abundance within lower enclosure sections were small relative to the first experiment (Chapter 2), suggesting weaker general effects of fish predation. This was probably partly due to the absence of sculpin from the predator treatments; this mechanism is discussed in greater detail in Appendix 1.

Densities of fish used in this experiment (2 - 5.25 coho m⁻²) were low relative to many previous fish predation experiments (e.g. Culp 1986, 0-48 coho m⁻²; Bechara et al. 1992, 6.6 fish m⁻²; Power 1990, 10 fish m⁻²). The appropriate density of fish to use in a predation experiment is difficult to determine; strong effects can usually be generated if high enough densities of predators are used, but the results may not be ecologically meaningful. In general, positive fish growth is one indication that fish density is not excessive relative to invertebrate production. Positive growth of juveniles over a short time frame, however, does not guarantee survival and reproduction of adults, and

growth rates may also have been enhanced in this particular experiment by the naiveté of the invertebrate community in a fishless stream.

The observed effects of fish predation in Mayfly Creek may have been exaggerated because the invertebrate community was not behaviourally adapted to the presence of fish. The behavioural experiments were intended to elucidate the mechanisms whereby fish affect mayfly activity, so as to evaluate the relevance of the observed predation effects in Mayfly Creek to fish predation effects in other streams. The chemical cue experiment shows that chemical cues from coho fry are not in themselves sufficient to induce a change in *Ameletus* grazing behaviour. This is supported by the lack of a detectable effect of fish presence in upstream patches on the number of *Ameletus* foraging in downstream controls, although there are more subtle aspects of foraging behaviour (e.g. rate of movement between and within patches) that may not be captured by simple counts of exposed mayflies. The mechanical cue experiment demonstrates that hydrodynamic or visual cues from coho, in addition to or independent of chemical cues, cause *Ameletus* nymphs to hide. Increased grazing of mayflies on upper tile surfaces during the night in the presence of fish also suggests a flexible behavioural response in *Ameletus* to hydrodynamic cues from fish. Similar flexible behavioural responses to the presence of fish have been observed for mayflies from both fishless streams and streams with fish present (Cowan and Peckarsky 1994, Douglas et al. 1994, McIntosh and Townsend 1994).

Sensitivity of mayfly nymphs to both chemical and mechanical cues has been demonstrated for a variety of mayfly species (Peckarsky 1980, Peckarsky and Penton 1989, Culp et al. 1991). Prey responses, and the combination of chemical and mechanical stimuli required to initiate them, tend to be extremely taxon-specific. For instance, Scrimgeour et al. (1994a) found that *Ephemerella* and *Paraleptophlebia* nymphs responded to chemical stimuli from longnose dace (*Rhinichthys cataractae* Valenciennes), whereas *Baetis* nymphs required mechanical stimuli in addition to chemical cues. While chemical cues do not always appear to induce behavioural responses in terms of drift and presence on exposed surfaces (e.g. Cowan and Peckarsky 1994), hydrodynamic stimuli consistently appear to stimulate some form of anti-predator response (e.g. Scrimgeour et al. 1994a). Thus the observed requirement of *Ameletus* for hydrodynamic stimuli is similar to the response of some species of mayfly nymphs from streams with fish. This suggests that similar effects of upstream fish density on predation effects downstream may also occur in streams where the prey community is adapted to fish predation.

This study demonstrates that the intensity of fish predation in upstream patches appears to have indirect effects on the abundance of algae in downstream patches, although there were no detectable effects on the abundance of mayflies. The ability of *Ameletus* to alter their behaviour in the presence of fish suggest that the results are not simply an artefact of predation on a maladapted prey community; nevertheless, the influence of upstream predation on the expression of predation effects in downstream

patches needs to be further evaluated in streams where the invertebrate community is adapted to fish

CHAPTER V

Effects of fish patchiness at a large scale: contrasting effects of fish predation in a fishless and fish-bearing stream

INTRODUCTION

The effects of fish predation on invertebrate community and trophic structure may be apparent at two spatial scales - both *within* a fish-bearing stream or lake, and *between* lakes or streams with and without fish. At the larger spatial scale, fish predation will operate to select for differences in invertebrate community structure between fishless and fish-bearing waterbodies (Zaret 1980, Neill 1994). In fish-bearing streams, predation will eliminate the most vulnerable invertebrate species, and there will be selection for taxa with either fixed or flexible adaptations to fish; if there is a cost to these adaptations, then these taxa will be at a competitive disadvantage in streams without fish, where they will be reduced or absent. At the smaller spatial scale within a fish-bearing stream invertebrates may also differ in their vulnerability to fish predation, and invertebrate community structure should differ between patches with high and low predation risk.

The relative magnitude of predator impacts at these two spatial scales is unclear, primarily due to a lack of comparative studies of fish predation between streams with and without fish (with several notable exceptions, e.g. Harvey 1993, Crowl et al. 1997). If invertebrates in fish-bearing streams are indeed better adapted to fish predation than

invertebrates in fishless streams, then predator impacts in ecological time should be greatest on a naive invertebrate community following introduction of predators to a fishless stream.

Fish predation has been observed to have three general effects on invertebrate community and trophic structure in north temperate streams. The first is a reduction in abundance of larger-bodied invertebrates (Flecker and Allan 1984, Bechara et al. 1992, Harvey 1993, Chapters 2 and 4), which typically are most vulnerable to fish predation because they are preferentially selected as prey items (Allan 1981, 1984, Bannon and Ringler 1986, Scrimgeour et al. 1994a). These larger-bodied invertebrates commonly include grazers of algae, which either decrease in abundance (Bechara et al. 1992, Rosenfeld 1997a, Chapter 2 and 4) or reduce their foraging activity (Scrimgeour et al. 1994b, Rosenfeld 1997a, Chapter 4) when fish are present. The second common (but less consistent) effect of fish predation is an increase in abundance of smaller epibenthic invertebrates, primarily chironomids, in the presence of fish (Bechara et al. 1992, Rosenfeld 1997b, Chapter 3); this a direct consequence of reduced grazing activity by larger, competitively dominant grazers (Crowder and Cooper 1982, Gilinsky 1984, Bechara et al 1992, Rosenfeld 1997b). The third frequently observed effect is an increase in the abundance of algae in the presence of fish (Bechara et al. 1992, Flecker and Townsend 1994, McIntosh and Townsend 1996, Rosenfeld 1997a, Chapters 2 and 4), again as a consequence of reduced grazing activity by larger herbivores.

This chapter describes the results of an experiment designed to compare the effect of fish predation in a fish-bearing stream to the effects of fish in a nearby fishless system (Mayfly Creek, described in Chapter 2). Since previous studies have clearly demonstrated that fish presence exerts a strong influence on invertebrate community structure (e.g. Zaret 1980, Harvey 1993), it is assumed that differences in community structure between the streams were at least partly due to fish predation. This assumption is supported by the observation that *Ameletus*, which was far more abundant in fishless Mayfly Creek, appears to be poorly adapted to fish predation (pers. obs., Chapter 2 pp. 48), and that mayfly grazing activity on upper rock surfaces during daylight was much higher in Mayfly Creek than in the fish-bearing stream (pers. obs.). The objectives of the experiment were i) to determine whether the mechanisms of fish predation were similar in a fishless and a fish-bearing stream, which is necessary to validate extrapolation of predation effects in fishless Mayfly Creek to fish-bearing streams, and ii) to determine whether the effects of fish predation on invertebrate community structure in ecological time *within* a fish-bearing system were similar to the effects of fish predation at a larger spatial scale *between* a fishless and a fish-bearing stream. Predictions were i) that the reduction in large grazer abundance and corresponding increase in algae and smaller invertebrates in the presence of fish would be greater in the fishless system, and ii) that the fish-bearing stream would have lower average abundance of large grazers, and higher abundance of small grazers and algae.

STUDY SITE

Experiments were conducted in the upper fishless reaches of Mayfly Creek, and fish-bearing Jacobs Creek 300 m above its confluence with the North Allouette River. Mayfly Creek is a second order stream with a minimum summer wetted width of 2-5 m and baseflow of 30 l s^{-1} . Jacobs Creek is a somewhat larger third-order stream, with a minimum summer width of 3-8 m and baseflow approximately five times Mayfly Creek discharge. Reach gradients where enclosures were installed average 1% in both streams, and substrate is dominated by gravel, cobble, and sand. Both streams are cool enough to support salmonids, although Jacobs Creek tends to be warmer during the summer.

Refer to Chapter 1 for a more detailed site description.

METHODS

Experimental design

Five enclosures were installed in the upper fishless reaches of Mayfly Creek during the summer of 1993; the results of this study have been described in detail in Chapter 2, and only selected aspects will be considered here for comparison with fish effects in Jacobs Creek. Two identical enclosures were subsequently installed the following year (1994) in Jacobs Creek, a fish-bearing stream with both stream-resident cutthroat trout and lake-resident juvenile cutthroat rearing in the stream during the summer months. Experiments were conducted from May to August during summer low flow conditions in

Mayfly Creek in 1993 and Jacobs Creek in 1994. Although enclosures were placed in both pools and riffles in fishless Mayfly Creek, enclosures in Jacobs Creek were placed in riffles or slow runs because of limited site availability. To control for the effect of habitat on fish predation, comparisons of fish effects between streams are between riffle/run habitat only. Because most details of the experimental methodology were identical to those described in Chapter 2, only methods that differ are included below.

The upper sections of enclosures were in pools or runs and the lower sections were in slow riffles or runs, where current velocity averaged $16 \pm 2 \text{ cm s}^{-1}$ (range 11-22 cm s^{-1}) in Mayfly Creek and $9 \pm 2 \text{ cm s}^{-1}$ (range 3-14 cm s^{-1}) in Jacobs Creek, sufficient to prevent deposition of fine particulate organic matter on upper substratum surfaces. Four 15 x 15 cm unglazed ceramic tiles were placed in each lower enclosure section as artificial substrata for colonization by algae and invertebrates. Clusters of five pieces of natural stream gravel (3-4 cm diameter) were also placed in each lower section for colonization by algae.

One lower section of each enclosure was stocked with coho (*Onchorhynchus kisutch*) parr (mean length 52 mm, mean weight 1.6 g) and prickly sculpin (*Cottus asper*; mean length 73 mm, mean weight 4.3 g) at a density of 2 and 1 fish per 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, although final density of coho in upper sections averaged between 2 and 3 fish m^2 because of partial restocking following fish escapes in both Mayfly and Jacobs Creek.

Average coho and sculpin weight increased by 95% and 13%, respectively, in Mayfly Creek, and 129% and 40% in Jacobs Creek during the course of the experiment, with a range in final weight of 1.2 - 9.8 g for coho and 2.6 - 9.3 g for sculpin. Positive growth suggests that fish densities were not excessive for the productivity of either system. The appropriate ambient density of fish was determined by electrofishing reaches in nearby streams of similar size and water chemistry (Rosenfeld, unpublished data). Coho and sculpin used during the experiment were collected from the Allouette River downstream in the same drainage by electrofishing or baited minnow traps.

Fish were stocked in Mayfly Creek during May 18-20, 1993, one week after substrates were placed in enclosures. Fish were stocked in Jacobs Creek from June 4-5 1994. Experiments were terminated at the end of August in both years. Tiles were sampled as described in Chapter 2, lengths of invertebrates were later measured in the laboratory using a digitizing system (Roff & Hopcroft, 1986).

Chlorophyll *a* in both Mayfly and Jacobs Creek was measured only on gravel substrate, as described in Chapter 2.

Data analysis

To test for differences in predation effects as a function of prey size and to allow comparison with the Mayfly Creek predation experiment (Chapter 2), invertebrates were divided into small (<3mm), medium (\geq 3mm,<6mm) and large (\geq 6mm) size classes based on total length.

Data analysis was performed using PC SAS version 6.03 (SAS Institute, 1989). Invertebrate abundance data were log transformed to normalize distributions and equalize variance. All fish effects were analyzed as a nested ANOVA of tile means per enclosure side using a combined data set from both streams (total n=10, n=6 from Mayfly Creek, n=4 from Jacobs Creek), treating enclosures as blocks nested within streams. Predation effects were analyzed for total invertebrate abundance, and for four representative taxa common to both streams. Two-tailed tests were used for testing fish effects in Mayfly Creek, and one-tailed tests were used for testing hypothesis in Jacobs Creek, where there were directional expectations based on the experiments in Mayfly Creek the previous year. The prediction of greater impact of fish predation in fishless Mayfly Creek was evaluated by testing for interaction between fish and stream effects (ANOVA) using a combined data set from both creeks; one-tailed tests were also used for testing interactions because of directional predictions.

Predator impact indices were used to evaluate the relative magnitude of predation effects for the three size classes of invertebrates, as described in Chapter 2.

RESULTS

The effects of fish predation were generally larger in the fishless stream than the fish-bearing one. Both the mean and variance in chlorophyll *a* increased in the presence of fish in fishless Mayfly Creek (paired t-test, $t_1 = 4.41$, $p = 0.05$ for means, $t_2 = 6.1$, $p=0.03$ for variance), but there was no significant effect of fish on chlorophyll in Jacobs Creek

(Fig. 24). As predicted, there was a significant interaction between stream and fish effects on chlorophyll ($F_{1,3} = 6.95$, $p = 0.04$), and average chlorophyll concentrations were higher in the fish-bearing stream.

As expected, smaller invertebrates (all taxa combined) increased in abundance in the presence of fish (positive Predator Impact) in both Mayfly and Jacobs Creek, with the relative increase in abundance being largest in Mayfly Creek (Fig. 25 and 26; significant interaction between stream and small invertebrate density $F_{1,3} = 8.2$, $p = 0.03$). There was no apparent effect of fish predation on intermediate-sized (3-6mm) invertebrates in Jacobs Creek, although intermediate-sized invertebrates tended to be more abundant in fish treatments in Mayfly Creek. Larger invertebrates (all taxa combined) tended to be less abundant (negative Predator Impact) in the presence of fish in both streams, but the fish effect was not significant ($F_{1,3} = 3.1$, $p = 0.09$), and there was no significant interaction between fish effects and stream ($F_{1,3} = 0.05$, $p = 0.42$). While predator impact indices tended to be higher in fishless Mayfly Creek for small and intermediate size classes, predator impact for larger size classes was similar in both streams (Fig. 26).

Average absolute density of smaller invertebrates was greater in Jacobs Creek (4220 individuals m^{-2}) than in Mayfly Creek (1830 individuals m^{-2} , $F_{1,4} = 28.3$, $p = 0.006$; Fig. 25). In contrast, average density of larger invertebrates tended to be slightly lower in Jacobs Creek (45 individuals m^{-2} vs. 74 individuals m^{-2} in Mayfly Creek), although the difference was not significant. The overall size distribution of invertebrates in Jacobs Creek appears to be skewed towards smaller size classes than in Mayfly Creek (Fig. 27).

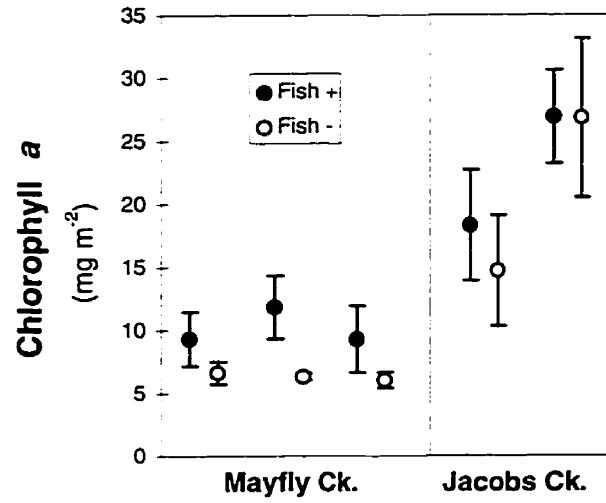


Fig. 24 Chlorophyll a concentration (mg m^{-2} , + 1SD) on gravel substrate in individual enclosures in the presence and absence of fish in Mayfly and Jacobs Creek.

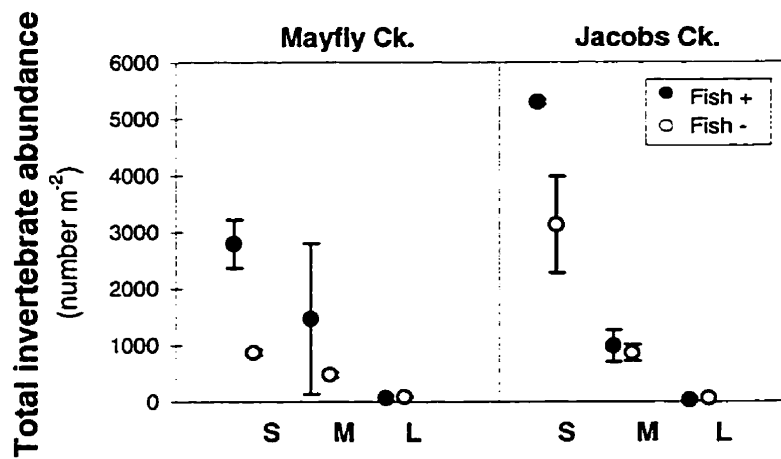


Fig. 25 Total invertebrate abundance (per m⁻², + 1SD) for all taxa combined, in 3 size classes (small < 3mm, 3mm > medium < 6mm, large > 6mm) in the presence and absence of fish in Mayfly (n=3) and Jacobs Creek (n=2).

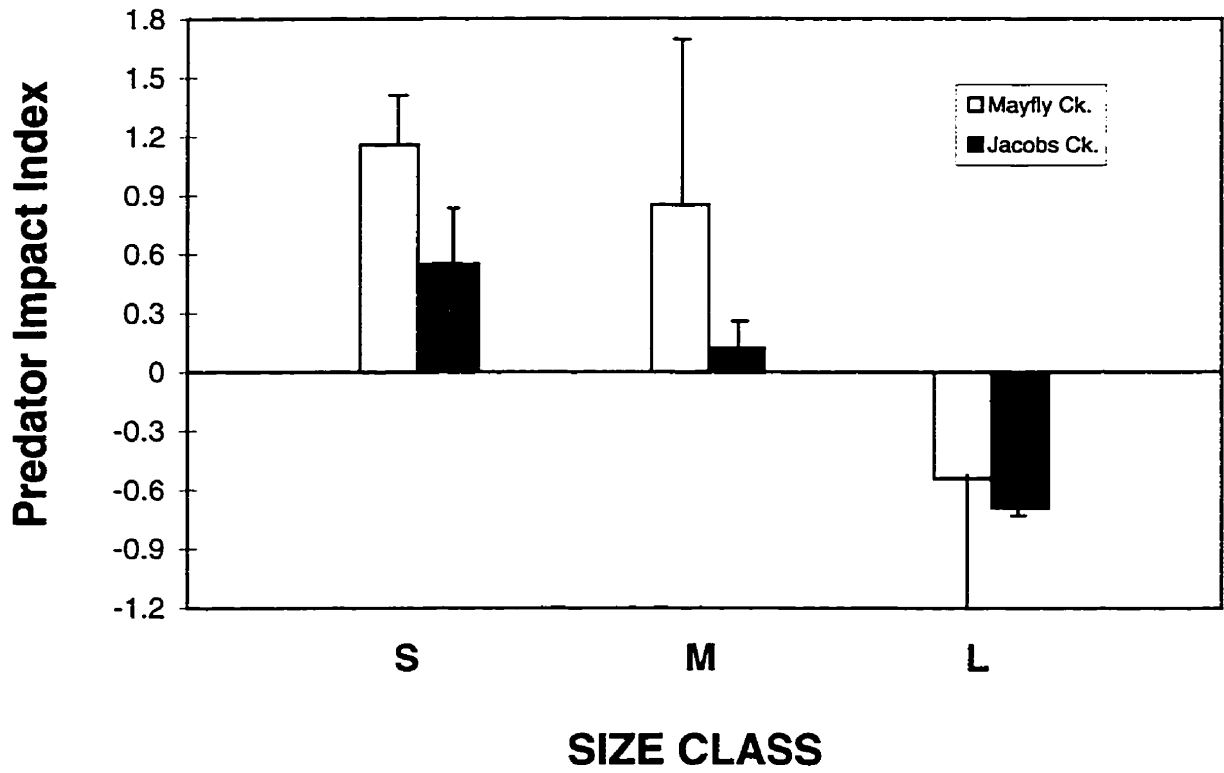


Fig. 26 Predator impact index (+ 1 SD) on total invertebrate abundance in 3 size classes (small < 3mm, 3mm > medium < 6mm, large > 6mm) in Mayfly and Jacobs Creek.

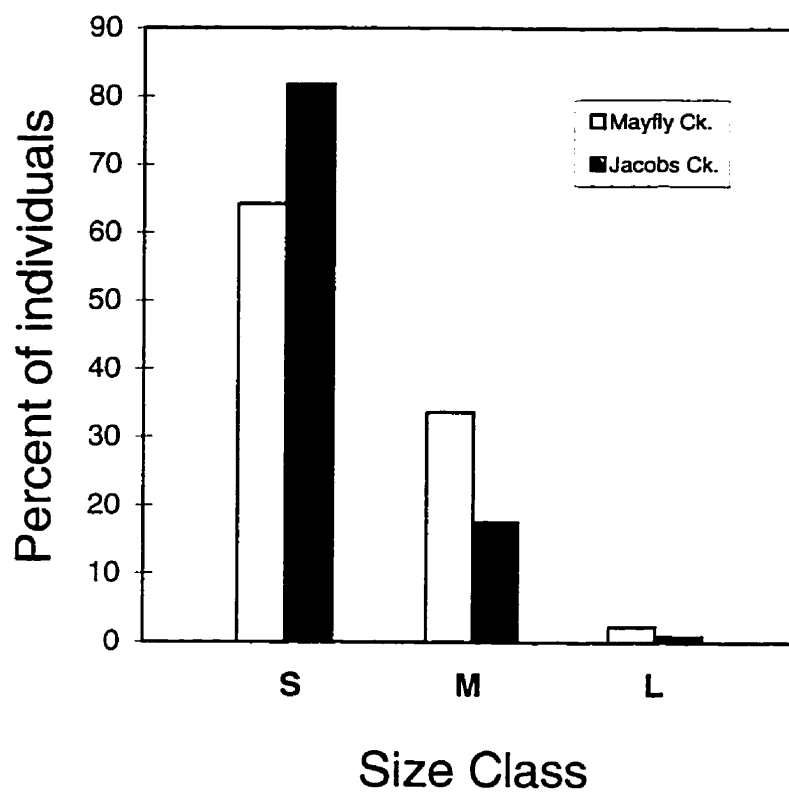


Fig. 27 Proportional abundance of invertebrates in different size classes (small < 3mm, 3mm > medium < 6mm, large > 6mm) in Mayfly and Jacobs Creek.

Higher absolute and relative densities of smaller invertebrates and lower densities of larger taxa in Jacobs Creek is consistent with the hypothesis that predator effects are similar both between and within streams. Predation effects on individual taxa indicate that the direct effect of fish predation on larger grazing invertebrates is similar between the two streams, as is the indirect increase in abundance of small herbivores in the presence of fish. For simplicity, only taxa common to both streams are considered: the mayflies *Ameletus sp.*, *Baetis sp.*, and *Paraleptophlebia sp.*, and chironomids in the subfamily Orthoclaadiinae. These taxa (with the exception of *Paraleptophlebia*) represent the most abundant invertebrates common to both streams that are likely to function as herbivores (Merritt and Cummins 1984), and collectively account for 75% and 81% of all individuals collected in Jacobs and Mayfly Creek, respectively.

Although *Ameletus* was the most abundant mayfly on tiles in Mayfly Creek, they were rare in Jacobs Creek, where *Baetis* was the dominant mayfly grazer (Fig 28). *Ameletus* density was significantly reduced in the presence of fish in both streams ($F_{1,3} = 12.1$, $p=0.04$), and there was a significant interaction between stream and fish effects on total *Ameletus* abundance (all size classes combined; $F_{1,3} = 32.0$, $p=0.005$). *Baetis* were also significantly reduced in the presence of fish ($F_{1,3} = 48.2$, $p=0.006$) for both streams combined (Fig. 28), but there was no interaction between fish effects and stream ($F_{1,3} = 0.16$, $p=0.35$). Although *Paraleptophlebia* were less abundant in both streams in the presence of fish, the reduction was not significant ($F_{1,3} = 5.8$, $p=0.01$). Orthoclaadiinae chironomids were significantly more abundant in the presence of fish in both streams ($F_{1,3}$

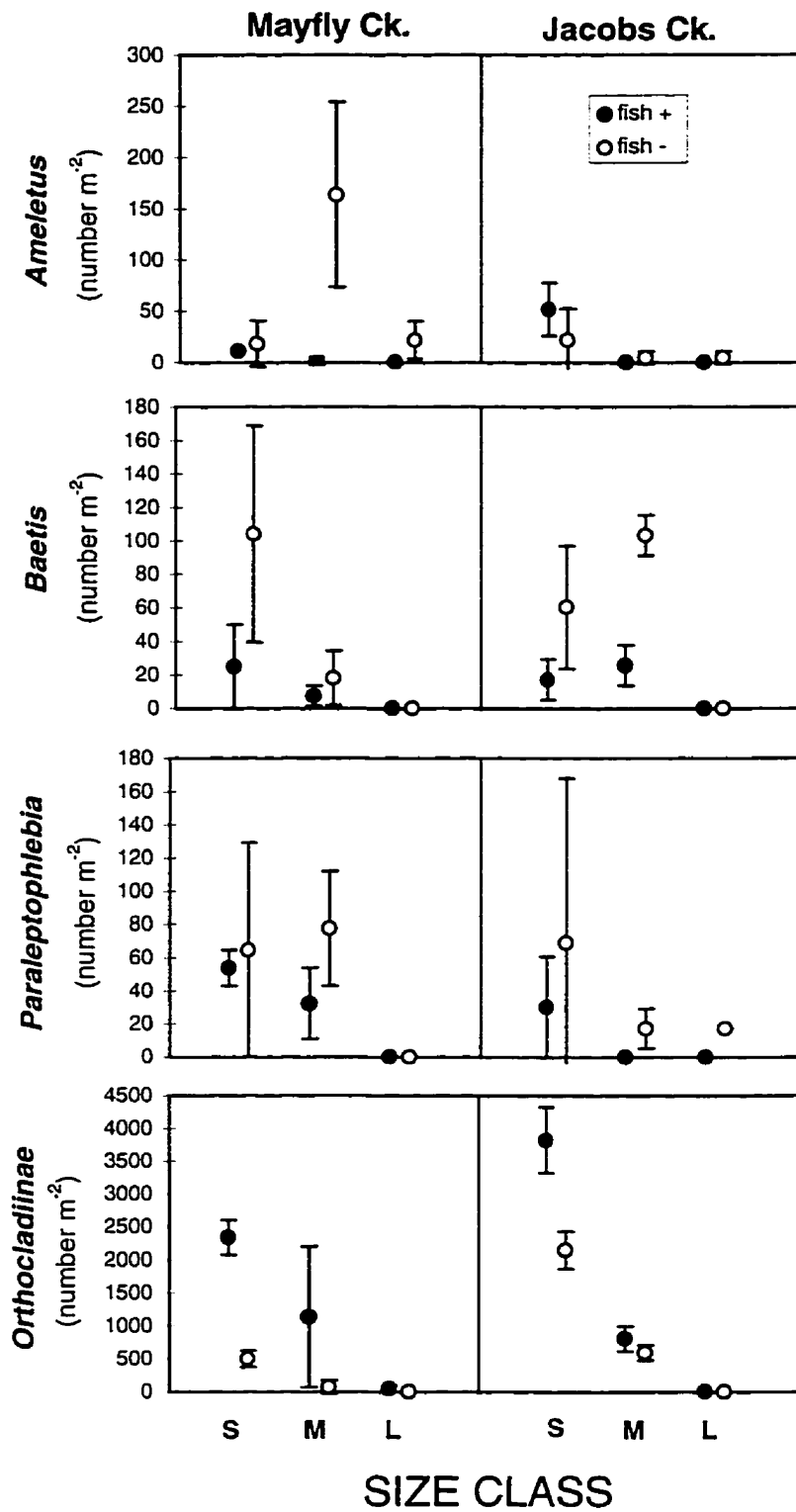


Fig. 28 Densities (+ 1SD) *Ameletus* sp., *Baetis* sp., *Paraleptophlebia* sp., and Orthoclaadiinae chironomids in the presence and absence of fish in Mayfly (n=3) and Jacobs Creek (n=2).

= 435, $p = 0.0002$), with fish effects being most pronounced in the smallest size class (Fig. 28), and the effects of fish predation being greatest in fishless Mayfly Creek (significant stream by fish interaction, $F_{1,3} = 127$, $p=0.001$).

DISCUSSION

Fish predation in ecological time affected the naive invertebrate community in a fishless and fish-bearing stream in very similar ways. In both cases there appears to be a general decrease in the abundance of larger invertebrate taxa, particularly grazers, in the presence of fish. There is a pronounced reduction in the abundance of larger grazers, primarily *Ameletus* mayflies in fishless Mayfly Creek and *Baetis* in Jacobs Creek. There is a corresponding increase in abundance of smaller invertebrates (primarily orthoclad chironomids) in the presence of fish in both streams, presumably as a result of reduced abundance and grazing activity by larger grazers (Rosenfeld 1997b, Chapter 3).

One of the hypotheses tested in this final experiment was that fish effects in ecological time would be more pronounced on the naive invertebrate community in a fishless stream than on the adapted community in a fish-bearing stream. The relative increase in smaller invertebrates was indeed more pronounced in fishless Mayfly Creek. There was also no strong effect of fish presence on chlorophyll in Jacobs Creek, indicating a weaker cascade of predation effects to lower trophic levels in the fish-bearing stream. Grazers at a watershed scale in fish-bearing Jacobs Creek may already be at lower

densities or have lower grazing activity, so that the proportional reduction in grazing in the presence of fish is less than in Mayfly Creek. However, relative predator impacts on larger taxa within each stream appear to be similar, suggesting that larger taxa may be equally vulnerable to fish predation in both streams. Although the advent of fish predation in a previously fishless stream represents an ecologically rare event associated with fish colonization or introductions of exotics by humans (Neill 1994), the greater impact of fish predation in a fishless stream supports the hypothesis that differential adaptation to fish predation takes place at a large spatial scale.

The effects of fish predation at a larger spatial scale (i.e. between drainages with and without fish) appears to be similar to the effect of fish predation in ecological time within a single stream. Algal biomass is higher in the fish-bearing drainage (Jacobs Creek), the absolute density of small epibenthic invertebrates is higher, the density of larger invertebrates is lower, and there is a general shift in the relative size-distribution towards smaller size classes (Fig. 27). Although the similarity of fish predation effects at the within-and between-drainage basin scales is supported by the Mayfly Creek - Jacobs Creek comparison, it is also clearly an unreplicated experiment. However, a similar pattern has been observed in one of the few studies to explicitly compare invertebrate community structure in multiple fishless and fish-bearing streams (Harvey 1993). Harvey (1993) found that densities of larger invertebrates were also generally higher in the fishless streams, whereas densities of smaller epibenthic chironomids and elmids beetle larvae tended to be higher in the fish-bearing streams. This suggests that the same

mechanisms underlying fish predation effects at both within and between stream spatial scales - size-selective predation on larger invertebrates, including grazers, thereby releasing smaller epibenthic herbivores and algae, leading to a general shift towards a smaller size-class distribution.

One of the basic predictions of trophic-level models (Hairston et al. 1960, Fretwell 1977) is that ecosystems with a predator trophic level will have reduced herbivore populations, resulting in increased plant biomass, whereas systems without predators will be dominated by herbivores and plant biomass will be depressed. While these processes have been demonstrated fairly convincingly within a single stream (e.g. Power 1990a, 1992b, Bechara et al. 1992), clear differences in trophic structure (i.e. grazer and primary producer biomass) have not been demonstrated between streams with and without fish. Detection of differences in trophic structure between fishless and fish-bearing streams is complicated by the fact that nutrient status and presence of fish are often confounded. Fishless streams are typically higher gradient lower-order systems where falls present barriers to fish colonization, and are also typically nutrient-poor, and might be expected to have lower algal biomass irrespective of fish presence.

It remains unclear to what degree the lower chlorophyll levels in fishless Mayfly Creek are a result of heavy grazing by herbivores versus lower nutrient levels. Conversely, it is also unclear to what extent the higher chlorophyll levels in fish-bearing Jacobs Creek are the result of reduced grazing pressure versus increased nutrients, or growth of unpalatable filamentous algae along a trophic gradient (Leibold 1989). In an

exhaustive synthesis of fish effects in freshwater pelagic lake communities, Mazumder (1994) compared algal biomass in functionally "fishless" lakes (2-link systems, *sensu* Fretwell (1987)) with low fish density, and fish-bearing lakes (3-link systems) with high fish density. His analysis provided strong evidence for both nutrient (bottom-up) and predator (top-down) control of phytoplankton biomass along a trophic gradient. A carefully planned survey of invertebrate community structure and algal biomass along a trophic gradient in a set of fishless and fish-bearing streams might similarly help resolve the relative roles of nutrients, grazers, and predators in controlling algal biomass in streams. It would also permit testing of some of the basic predictions of food-chain theory (Fretwell 1977, 1988, Oksanen 1980, Mazumder 1994) as applied to streams, e.g. that primary producer biomass is on average lower and herbivore biomass higher in fishless streams.

CHAPTER 6

General Discussion

Two central themes have been emphasized throughout this thesis. The first is the strong relationship between habitat structure and the effects of fish predation. This permits the development of a general model, presented below, for the effects of fish predation in north temperate streams based on the habitat-specific effects observed in Mayfly and Jacobs Creek. This is followed by a consideration of the generality of this model, particularly its relevance to the effects of fish predation in streams dominated by functional guilds of fish other than insectivores. The second theme involves the spatially hierarchic nature of habitat and predation effects, ranging from the microhabitat scale within fish-bearing streams to a larger-scale contrast between streams with and without fish. The partitioning of the effects of fish predation at the within- and between-streams scales is considered in the last section of the following discussion.

A model for the effects of fish predation in north temperate streams

The experiments described in this thesis demonstrate that both resource distribution and the effects of fish predation are strongly linked to habitat, at both pool-riffle and microhabitat (substrate) scales. The abundance of organic detritus is higher in depositional habitats such as pools and gravel interstices, whereas the abundance of

grazers (and presumably their algal resource) is higher in riffles and on tile substrate (Chapter 2). Predation effects are also similarly related to habitat, and are most pronounced in riffles and on tile substrate (erosional habitats). Thus the strength of predation effects appear to be closely linked to the distribution of autochthonous and allochthonous carbon, which is in turn controlled by stream habitat structure. The spatial arrangement of patches suitable for fish can also influence the strength of fish effects, since fish density in upstream patches can have a measurable effect on predator impact immediately downstream (Chapter 4). However, the carbon base of the food chain had a much stronger influence on the magnitude of predator impact than changes in immigration rates associated with predation in adjacent patches. Given the apparent influence of the carbon base on fish effects, it is useful to consider predation impacts in terms of detrital-based and algal-based food chains (Heal and McLean 1975).

Predator impacts and trophic interactions are likely to be stronger in algal-based food chains (Fig. 29) for several reasons. Both the direct and indirect effects of fish predation on invertebrates should be more pronounced because of the greater vulnerability of herbivores constrained to foraging on the upper surfaces of rocks (relative to detritivores foraging in interstitial refuges). Feedback between invertebrate consumers and their periphyton resource should also be stronger in algal-based food chains, because grazers have the potential to reduce both the biomass (e.g. Hill and Knight 1987) and rate of production of the primary producer trophic level (Lamberti and Moore 1984). Detritivorous food-chains, however, are donor-controlled.

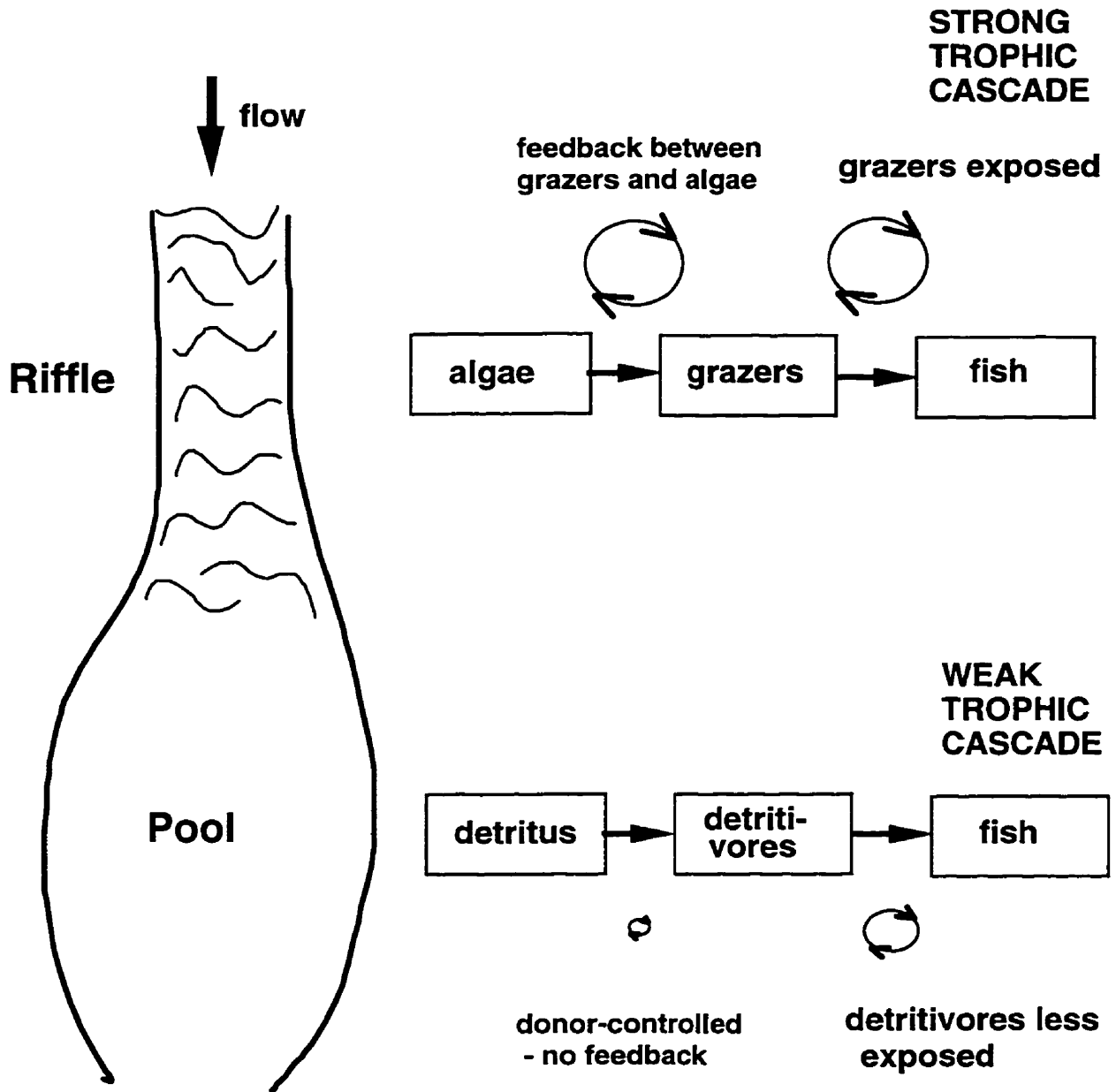


Fig. 29 Model for fish predation effects in algal- and detrital-based food chains. Arrows indicate direction of energy flow, circles indicate strength of trophic interactions.

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.

Algal and detrital-based food chains, and the associated strengths of predator impact, also occur at a hierarchy of scales in streams (Fig. 30). At the microhabitat scale, algal-based food chains occur on the upper surfaces of rocks, and detrital-based food chains are associated with organic accumulations in substrate interstices. At the pool-riffle scale, riffles tend to be more algal-based than pools. At the drainage basin scale, forested headwater streams tend to be more detrital-based, and the proportional contribution of algal carbon increases downstream as a stream increases in width and canopy cover decreases (Vannote et al 1980). A model of predation effects in hierarchically nested algal and detrital food chains (Fig. 31) predicts that fish effects on the invertebrate community should be greatest in algal-based food chains at all of these scales.

Most experimental studies of predation effects on invertebrate community structure in north temperate streams are consistent with this model (e.g. Allan 1982, Reice 1983, Flecker and Allan 1984a, 1984b, Reice and Edwards 1986, Schofield et al. 1988, Bechara 1992, Power 1990a, 1992b). The majority of studies that have documented strong effects of fish predation on invertebrate community structure have been in unshaded streams where the primary carbon base is algae, or in algal-based food chains in streams with mixed carbon sources. The strong effects of fish in the Eel river,

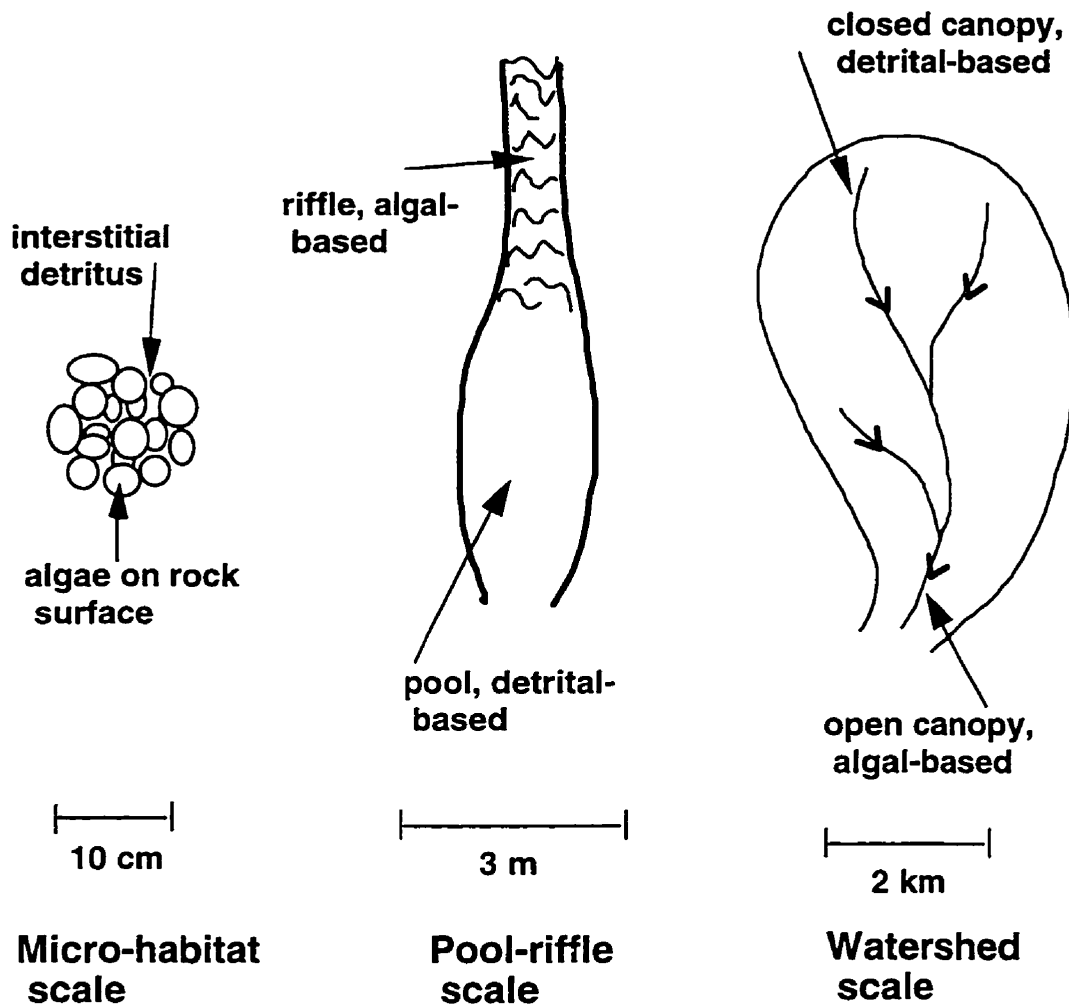


Fig. 30 Nesting of algal and detrital food chains at a hierarchy of spatial scales.

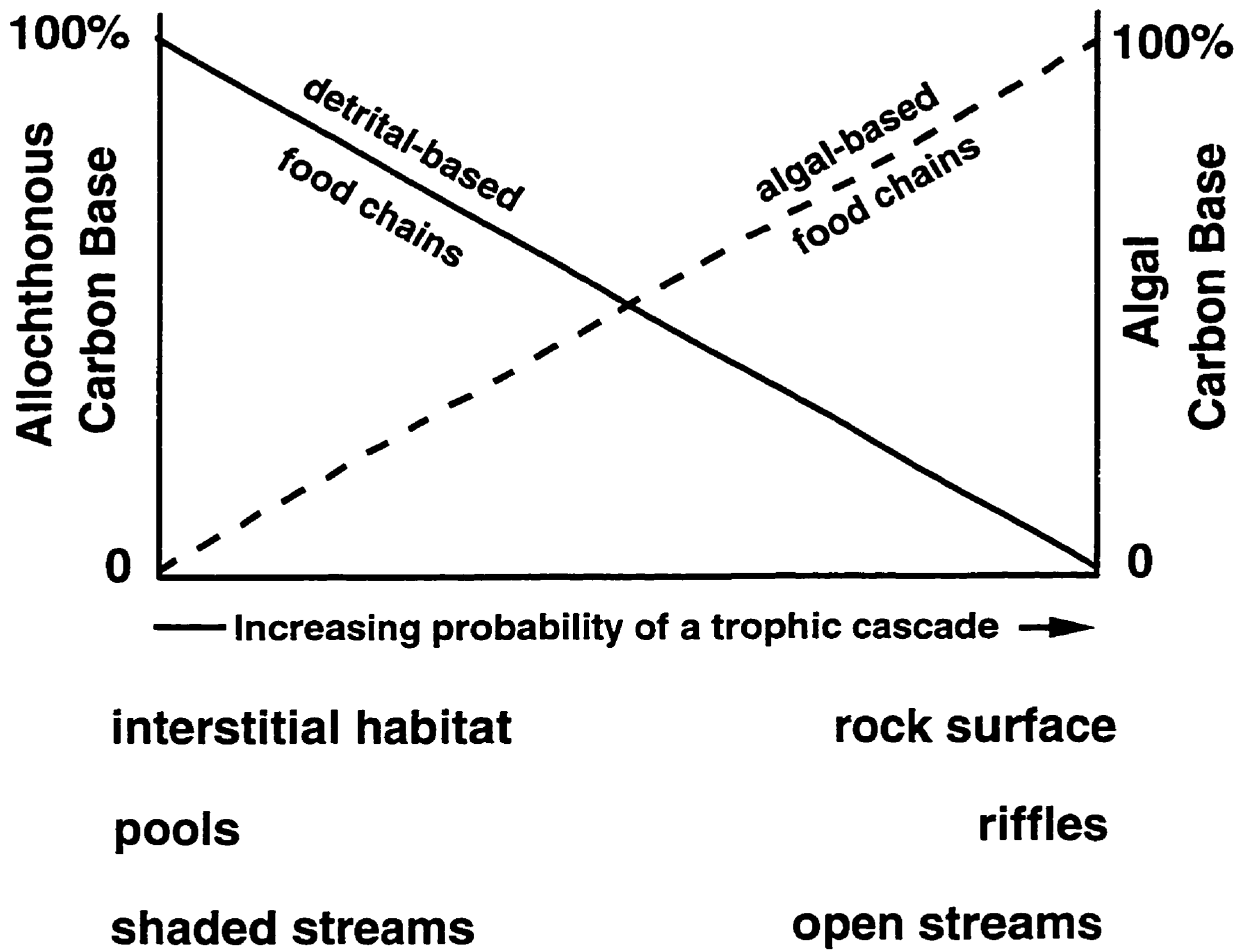


Fig. 31 Schematic illustrating the relationship between stream habitat type, carbon source, and the predicted strength of trophic interactions. Relationships are drawn as linear for illustrative purposes only.

California (Power 1990a, 1992b), were associated with filamentous algae, and were considerably more pronounced on simple boulder substrate than on gravel, although this was largely attributed to the availability of refuges rather than the available carbon base. Bechara (1992) also observed marked effects of fish predation on primarily algalivorous species. The very strong indirect effects of grazing fish observed by Gelwick and Matthews (1992) and Flecker (1992; discussed below) were also associated with algal-based food chains. In contrast, most of the studies that observed no (Allan 1982, Reice 1983, Reice and Edwards 1986) or weak effects of fish predation (Flecker and Allan 1984a, 1984b, Schofield et al. 1988) were associated with primarily detrital-based food chains in systems with a largely allochthonous carbon base. The observation of strong predation effects in pools in the Eel river (current velocity $< 5 \text{ cm s}^{-1}$; Power 1990a) further demonstrates that the dichotomy in carbon base between riffle and pool habitats decreases as the forest canopy opens in larger streams, and primary production becomes the dominant carbon source in both habitats.

Studies of predation effects in algal-based food chains have consistently observed either decreased density (Bechara et al. 1992, Flecker and Townsend 1994, Rosenfeld 1987b, Chapters 2 and 4) or grazing activity (Power 1992, McIntosh and Townsend 1996) of large-bodied herbivorous invertebrates. An indirect increase in chironomid density resulting from reduced activity of larger grazers, identical to that documented in this study (Chapter 3), was also observed by Bechara et al. (1992); Power (1992b) observed a similar increase in the density of chironomid tubes on upper cobble surfaces

in the presence of fish. Indirect increases in chironomid abundance in lakes have also been attributed to reduced grazing by larger invertebrates in the presence of fish (Crowder and Cooper 1982, Gilinsky 1984). Although indirect increases in small herbivore abundance under fish predation appear to be common, direct effects may override indirect effects if predation risk is high enough, and chironomid abundance may decline in the presence of fish (e.g. Hershey 1985, Flecker and Alan 1984b).

Trophic cascades leading to an increase in periphyton in the presence of insectivorous fish are also commonly observed in temperate streams (Bechara et al. 1992, Flecker and Townsend 1994, McIntosh and Townsend 1996, Rosenfeld 1997a, Chapters 2 and 4). The exception was an observed decrease in algal biomass in the presence of fish by Power (1990a, 1992b), which was due to the presence of a four-link food chain (fish-invertebrate predators-herbivorous chironomids-algae) based on filamentous algal turfs rather than a three-link food chain (*sensu* Fretwell 1977, 1987) based on non-filamentous periphyton

. The effects of carbon base and substrate-associated refuges are to some degree confounded, since complex substrata typically accumulate more interstitial detritus, while at the same time providing greater refugia from fish predation. Regardless of substrate type, the expectation of greater predator impact in algal-based food chains remains because of the necessary constraint that algae grow on upper substrate surfaces exposed to fish. Availability of refuges associated with different substrate types is

nevertheless a pervasive factor affecting prey vulnerability, and for a fixed carbon base predation effects should be most pronounced in simplified habitats.

Although experiments in streams generally demonstrate stronger effects of fish predation on herbivorous invertebrates, detritivores can in some instances be significantly affected by fish predation. In particular, freshwater gammarids (Friberg et al. 1994, Andersen et al. 1993, Williams and Moore 1982, 1985) and isopods (Holomuzki and Hatchett 1994) appear to be both 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.

The proposed model for fish predation effects in north temperate streams is based on experiments in a fishless stream, where the impact of fish predation is likely to be exaggerated because of the potential naiveté of the invertebrate community. Nevertheless, the observed effects are remarkably consistent with reported predator impacts in fish-bearing streams, as described above. The application of the model to fish-bearing streams is further validated by the observation of most of the predicted effects in Jacobs Creek (Chapter 5).

Predation effects and the functional role of fish

The simple model for the effects of fish predation presented above is clearly constrained to north temperate streams, which are dominated by generalist insectivores (such as salmonids or sculpins) rather than herbivores or detritivores. However, insectivorous fish dominate the fish fauna of only a subset of streams worldwide. An evaluation of the effects of fish predation on invertebrate community structure in general would be distorted if it focused solely on the effects of insectivorous fish. It is therefore worth considering how differences in functional roles and habitat preference by different species may alter the strength and distribution of the effects of fish predation.

Predation by insectivorous fish will have direct effects on larger invertebrate taxa or instars (Chapters 2 and 3, Allan 1981), and indirect effects on smaller taxa (Chapters 2 and 3, Bechara et al. 1992). Grazing and detritivorous fish, on the other hand, function more as competitors than predators, and can have strong effects on the invertebrate community either through interference competition, exploitative competition for resources, or incidental ingestion (Flecker 1992a). In general, the effects of herbivorous and detritivorous fish tend to be larger than the effects of insectivores, since herbivores and detritivores can have pervasive effects on resource availability (Power 1990b, Flecker 1992a, Flecker 1996). In south temperate and tropical streams, which support a higher diversity of taxa and functional guilds, the effects of fish on the invertebrate

community will be a more complex outcome of direct predation and competition for shared algal and detrital resources (Flecker 1992a, 1996, 1997).

The habitat preferences of predators will also influence the spatial distribution of fish effects in streams. Benthicly foraging insectivores appear to have a larger impact than fish that position themselves in the water-column and feed primarily on drift (Appendix 1, Dahl and Greenberg 1996). This is attributed to benthic insectivores feeding exclusively on aquatic prey (Dahl and Greenberg 1996), and foraging more effectively in substrate interstices that would otherwise provide a refuge from drift-feeding predators. If the fish species present in a stream prefer pools to riffles, as is typically the case for species that forage in the water-column, then predator impacts will be greatest in pools simply due to the absence of fish from riffle habitat. For instance, Schlosser and Ebel (1989) found that predation on invertebrates by creek chub (*Semotilus atromaculatus*) in experimental streams was greatest in pools, and least pronounced in the shallow (4-6 cm) fast-flowing experimental riffle habitats that creek chub did not use. In this case, riffles constitute a hydraulic refuge from fish predation, because the energetic costs of foraging in riffles are often excessive for non-benthic species (Facey and Grossman 1990). If, however, the fish community contains species capable of foraging in riffles (e.g. longnose dace; Scott and Crossman 1973, Culp 1989), then contrasting predator impacts in pool and riffle habitats may occur, as described in this study.

Fish effects within vs. between drainages

Thorpe (1986) and later Neill (1994) have emphasized the spatially hierarchic nature of predation risk in aquatic systems, and that both the magnitude and nature of the responses of the invertebrate community may be scale dependent. Risk of fish predation varies at two discrete scales, within a stream or lake system containing fish, and between streams or lakes with and without predators. Within a single system fish predation can operate to limit or regulate prey density in ecological time, while at a larger (biogeographic) spatial scale fish predation can create differences in invertebrate community structure between systems by extirpation of prey species lacking evolutionary adaptations to predation (Zaret 1980, Neill 1994). Thorpe (1986) argued that fish may have a weak regulatory role in lakes and streams with fish, implying that there is little effective variation in predation risk with varying fish density in fish-bearing waters, and that most of the variation in risk of predation (and therefore fish impact on prey) will be between systems with and without fish.

The enclosure experiments in Jacobs Creek and the literature review above clearly indicate that fish can have a considerable impact on invertebrate community structure in fish-bearing streams. This implies that risk of predation varies considerably within a stream, and invertebrates have been shown to exhibit adaptive responses to predation at the within-stream scale (e.g. Forrester 1994a, 1994b). Differences in invertebrate community structure between fishless and fish-bearing streams (Chapter 5, Harvey 1993) and the greater impact of fish predation in fishless Mayfly Creek indicate

that differences in predation risk at the larger scale also result in differences in community structure. The pattern of fish impact on the invertebrate community at the larger scale between streams with and without fish also appears to be similar to the effects of fish within a single stream (Chapter 5), supporting the conclusion that the nature (if not the magnitude) of the effects of fish predation on invertebrate community structure are similar at the within and between streams spatial scales.

The experiments described in this thesis support a general model for the effects of fish predation in north temperate streams, and demonstrate its application at both the within- and between-stream scales. However, the effects of predation by insectivorous fish need to be integrated into a more general model incorporating the effects of a suite of functional guilds of fish. Fish effects in streams also need to be tested systematically at a hierarchy of spatial scales of variation in predation risk (e.g. Crowl et al. 1997). Specifically, by examining: i) spatial changes in invertebrate community structure associated with variation in predation risk within a single stream ii) changes in community structure over space associated with variation in predation risk between different streams (e.g. Bowlby and Roff 1986), and iii) differences in prey community structure between streams with and without fish.

The focus in community ecology has shifted from simply demonstrating that predation and competition are important in structuring communities, to more clearly defining the conditions under which biological interactions play a significant role. Future research needs to focus on understanding the specific circumstances and spatial

scales at which predators structure prey communities, and to incorporate habitat structure as a critical factor constraining the outcome of biological processes.

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APPENDIX 1

Contrasting effects of drift *versus* benthic feeding fish (coho and sculpin)

Fish in streams typically differ in the vertical orientation of their foraging activity. Some species have unique adaptations to a benthic lifestyle and forage exclusively on benthic invertebrates; sculpin (*Cottus sp.*) and longnose dace (*Rhinichthys catatracte*) are typical benthic species with reduced air bladders and enlarged pectoral fins. Other species swim or maintain position in the water column, and forage largely on drifting aquatic invertebrates or invertebrates on the water surface. Juvenile salmonids and resident adults are typically drift-feeders (Hughes 1990), and the freshwater stages of species such as coho are strongly surface-oriented. More generalist species, such as many cyprinids, forage on the stream bottom as well as at the surface and throughout the water column (Scott and Crossman 1973).

A constant "redistribution" of invertebrates occurs in streams (Townsend 1989), largely through the process of downstream drift (Hynes 1970) where invertebrates deliberately enter the moving water column so as to avoid benthic predators (Walton 1980, Malmqvist and Sjostrom 1987, Culp et al. 1991) or seek out optimal resource patches (Kohler 1985). At any given time a fraction of the benthic community is drifting in the

water column, thereby increasing their vulnerability to drift-feeding fish while decreasing their risk of benthic predation.

Thus fish can affect benthic invertebrates by two major pathways, by direct predation on the benthos, and predation on the drifting fraction of the invertebrate community. Because drift- and benthic-feeding fish forage in different ways, the strength and nature of their effects may differ (Dahl and Greenberg 1996). Predation by benthic fish has direct effects on invertebrate community structure. Benthic fish also have a larger pool of invertebrates available to them because of their ability to forage interstitially in habitats that are refuges from drift-feeding fish. Predation on drifting invertebrates has less clearly defined effects on invertebrate community structure. If drifting invertebrates are weak and senescent individuals (Williams and Levens 1988) in a saturated habitat, then the effects of predation on drift may be compensatory and will have little effect on community structure. If, on the other hand, drifting invertebrates are important colonists of benthic habitats, then reduced drift may have strong effects on downstream invertebrate communities. High drift rates in streams may tend to swamp out the expression of predation effects (the "postage stamp" effect; Cooper et al. 1990, Sih and Wooster 1994); benthic predation effects are more likely to be expressed if predation on the drift reduces immigration from upstream (Chapter 5).

Both drift and benthic foraging fish were used in the 1993 enclosure experiment (Chapter 2), which was intended to simulate the potential impact of a generalized fish assemblage. Only coho were used in the 1994 enclosure experiment (Chapter 5), which

was intended to examine the effect of upstream predation on downstream fish effects. Contrasting the effects of a drift-feeding fish (1994 experiment) with the combined effects of a drift and benthic forager (1993 experiment) can give some insight into the differential effects of foraging on the drift vs. foraging on the benthos. However, there are several attributes of coho and prickly sculpin that complicate the simple contrast between benthic and drift-feeding fish. First, prickly sculpin are nocturnal foragers, while coho forage during the day. Secondly, sculpin have large gapes that enable them to consume *Ascapthus* larvae, while coho cannot. Given these qualifications, examining the contrasting effects of predation in the 1993 and 1994 experiments may give insight into the functional roles of benthic and drift-feeding fish.

In the 1993 experiment where both coho and sculpin were present there was a strong trophic cascade, resulting in a significant increase in algae (measured on gravel) and smaller invertebrates in the presence of fish. In the 1994 experiment where only coho were present, there was a significant increase in algae in the presence of fish on tile substrate, but not on gravel, which is the appropriate comparison with the 1993 experiment. There was also no significant effect of coho on abundance of smaller invertebrates. Clearly the presence of sculpin was a necessary (if not exclusive) condition for the large effects observed in 1993. It is not clear whether the presence of coho was essential as well; conceivably, overall effects of predation in 1993 may have been substantially less if upstream predation by coho does play a significant role in reducing immigration rates of drifting invertebrates (Chapter 5).

The presence of sculpin may have increased the effects of predation in the 1993 experiment over the 1994 experiment by three possible mechanisms: i) reduction in numbers of mayflies by predation or induction of mayfly drift, ii) reduction in *Ascapthus* abundance by direct predation, iii) behavioural inhibition of mayfly grazing during the night (sculpin are nocturnal foragers), or any combination of the above. Sculpin as benthic predators may have a larger impact on mayflies than coho (for the reasons discussed above), but it is also conceivable that the per capita magnitude of sculpin and coho effects are similar, and it is simply the increased predator density (four coho and two sculpin combined in 1993 versus four coho in 1994) that resulted in the stronger trophic cascade in the first experiment.

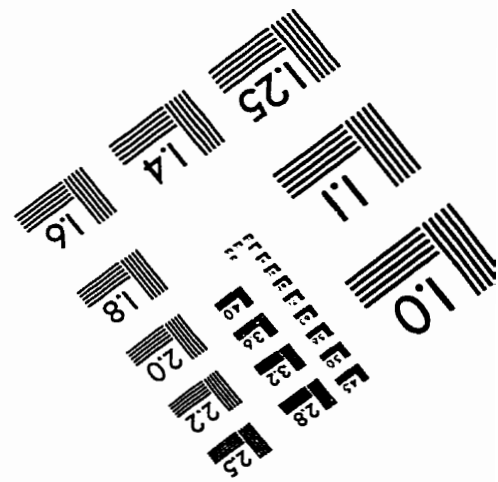
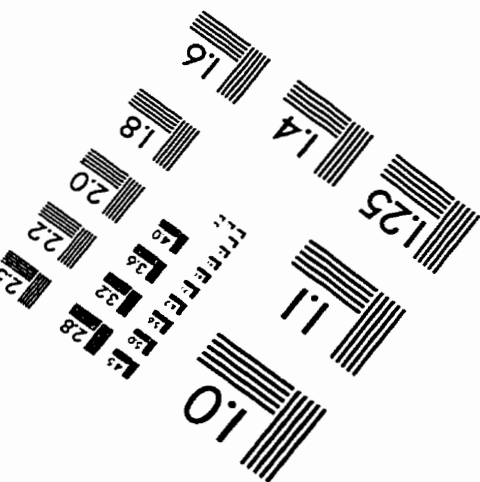
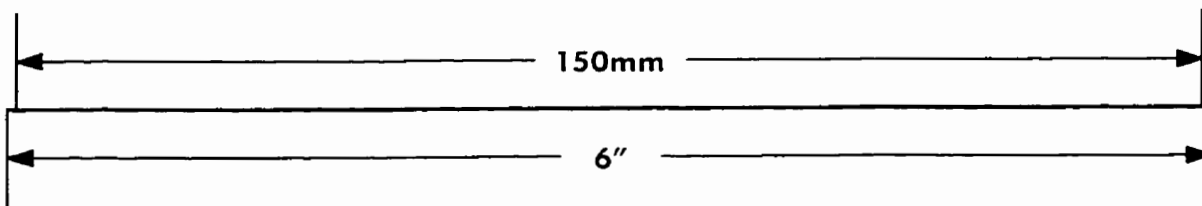
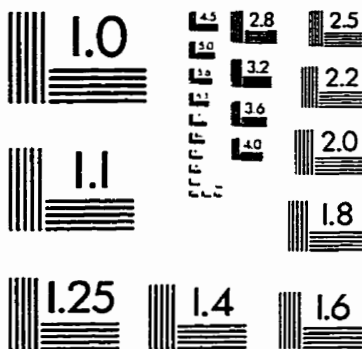
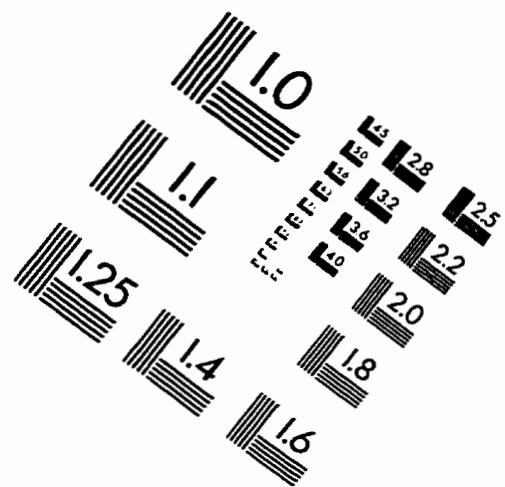
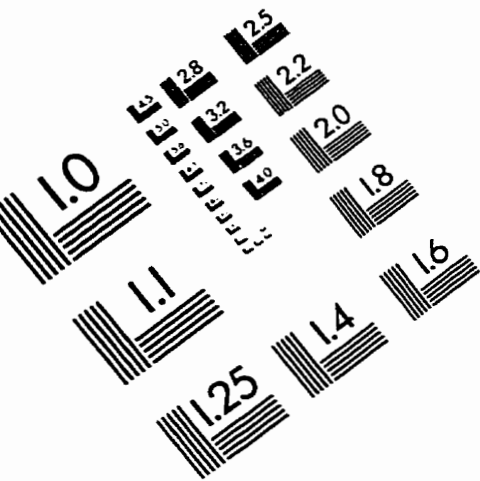
Ascapthus abundance was not adequately quantified in the 1993 enclosure experiments, so that it is impossible to assess whether sculpin reduced *Ascapthus* density. Densities of mayflies grazing at night were definitely higher in the absence of sculpin in 1994 than in 1993. However, I only did several cursory night observations to determine whether mayflies were grazing on tiles during 1993; when I observed almost no mayflies, night observations were not continued in the repeated systematic fashion used the following year, so that there is no statistical basis for comparing mayfly night abundances between years. Nevertheless, it appears that there was a substantial decrease in mayfly foraging activity at night in the 1993 experiment, and that the presence of sculpin was the likely cause.

Given the ambiguity of sculpin effects on *Ascaphus* and the largely anecdotal observations on nocturnal abundance of mayflies in 1993, it is difficult to convincingly discriminate between the three mechanisms of sculpin impact on community structure listed above. This is particularly true since the indirect effects of *Ascaphus* on algal biomass and small invertebrates are indistinguishable from those of *Ameletus* (Rosenfeld 1997b, Chapter 3). However, mean *Ascaphus* densities in control treatments were 4-6 m⁻² in 1994, and were probably similar in 1993 (when they were not measured accurately). Since Lamberti et al. (1992) found no effects of *Ascaphus* on either algae or invertebrates below densities of 8 m⁻², it seems unlikely that the increase in algae and invertebrates in the presence of fish was due exclusively to sculpin predation on *Ascaphus*. And since average *Ameletus* abundance in the presence of fish was lower in the 1993 experiment with both coho and sculpin (mean density \pm SD 14.2 \pm 6.0 m⁻³) than in 1994 (mean density \pm SD 41.8 \pm 28.0 m⁻³), and mayfly grazing at night was apparently lower in 1993, it is most likely that greater predator impact in 1993 was primarily due to sculpin effects on mayfly grazers.

The stronger effects on the invertebrate community of predation by sculpin relative to coho is consistent with the predictions of greater impact by benthic feeding fish (Dahl and Greenberg 1996). The expectation of greater effects of predation by benthic-feeding fish is based on the assumption that the stream bottom provides a spatial refuge from drift foragers, but not benthic foragers. However, this analysis suggests that a temporal refuge, where invertebrates forage nocturnally when fish are inactive, may be

equally if not more important than a spatial one for escaping predator control. The elimination of the temporal refuge offered by nocturnal grazing is more likely responsible for the enhanced effects of fish predation in the presence of sculpin than their ability to forage in spatial refuges from drift-feeding fish.

IMAGE EVALUATION TEST TARGET (QA-3)



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