The effect of vertebrate predation on lotic macroinvertebrate communities in Québec, Canada

Seth R. Reice[1]

Department of Biology, University of North Carolina, Chapel Hill, NC, U.S.A. 27514

AND

Robert L. Edwards

Curriculum in Ecology, University of North Carolina, Chapel Hill, NC, U.S.A. 27514

Received October 29, 1985

Reice, S. R., and R. L. Edwards. 1986. The effect of vertebrate predation on lotic macroinvertebrate communities in Québec, Canada. Can. J. Zool. **64**: 1930–1936.

To test the role of vertebrate predation on benthic community structure, experiments were performed in two third-order streams in northern Québec, Canada. Predators were either enclosed in or excluded from replicate benthic cages (20 × 30 × 10 cm). Ruisseau du Cran Carré (RCC) has a normal complement of fish, while Low Hope Creek (LHC) is fishless. In June 1983, two species of fish were manipulated (one fish per cage, five replicate cages per treatment) in RCC, while the salamander *Eurycea bislineata* was manipulated in LHC. In August 1983, brook trout fry were manipulated in both streams. It was anticipated that the fauna in LHC, having had no previous contact with fish, would be more susceptible to fish predation than the fauna of RCC. Gut analysis revealed that fish did feed in the cages. However, neither fish predation nor salamander predation had significant effects on prey communities in either stream in June. Community parameters (species richness and diversity, and total numbers of individuals) were not influenced by the presence or absence of fish or salamanders. In August, three-quarters of the taxa were more abundant without trout than with trout. However, few individual taxa were significantly affected by the fish. This effect was similar in both streams. By enclosing fish in a fishless stream, this experiment was designed to enhance the possible effects of fish predation on the lotic macrobenthic community. This work strengthens the idea that brook trout are not major structuring agents of the macrobenthic communities of small streams.

Reice, S. R., et R. L. Edwards. 1986. The effect of vertebrate predation on lotic macroinvertebrate communities in Québec, Canada. Can. J. Zool. **64**: 1930–1936.

Des expériences en deux ruisseaux d'ordre 3 du nord du Québec, Canada, ont permis de mettre à l'épreuve le rôle de la prédation de vertébrés sur la structure des communautés benthiques. Au cours des expériences, certaines cages benthiques (20 × 30 × 10 cm) contenaient des prédateurs, d'autres n'en contenaient pas. Le ruisseau du Cran carré (RCC) contient une quantité normale de poissons, alors que le ruisseau Low Hope Creek (LHC) n'en contient pas du tout. En juin 1983, les populations de deux espèces de poissons ont été manipulées (un poisson par cage, cinq cages par expérience) dans le ruisseau RCC, alors que les populations de salamandres *Eurycea bislineata* ont été manipulées dans les deux ruisseaux. En août 1983, les populations d'alevins d'ombles de fontaines ont été manipulées dans les deux ruisseaux. Il semblait probable que la faune de LHC, qui n'avait pas eu de contact préalable avec des poissons, soit une meilleure cible pour les prédateurs que la faune de RCC. L'analyse des contenus stomacaux a révélé que les poissons se nourrissaient effectivement dans les cages. Cependant, ni la prédation par les poissons, ni la prédation par les salamandres n'ont eu d'effet significatif sur les communautés de proies dans l'un ou l'autre ruisseaux en juin. Les paramètres reliés à la communauté (richesse, diversité et nombre total d'individus) n'ont pas été influencés par la présence ou l'absence de poissons ou de salamandres. En août, les trois-quarts des taxons se sont avérés globalement plus abondants en l'absence des ombles qu'en leur présence. Cependant, peu de taxons ont été affectés significativement par la présence des poissons. Le même phénomène s'est produit dans les deux ruisseaux. L'introduction de poissons dans un ruisseau sans poissons a permis d'étudier les effets possibles de la prédation des poissons sur la communauté macrobenthique lotique. Les résultats de ces expériences corroborent l'hypothèse selon laquelle l'omble de fontaine ne constitue pas un agent important de structuration des communautés macrobenthiques dans les petits ruisseaux.

[Traduit par la revue]

Introduction

The role of predators in regulation of community structure has been a major issue in ecology since Paine's (1966) landmark paper. Predation has been demonstrated to be a major determinant of community structure in many aquatic ecosystems including the rocky intertidal zone, planktonic and benthic communities in lakes, and freshwater microcosms (Neill 1975). Recent studies in ponds have shown the importance of fish predators to the benthic community (Gilinsky 1984; Morin 1984a, 1984b; Crowder and Cooper 1982; Hall et al. 1970). In ponds the bluegill sunfish, *Lepomis macrochirus*, functions as a structuring agent by size-selective and habitat-specific predation. Changes in fish density (Gilinsky 1984) or habitat complexity (Crowder and Cooper 1982) have major effects on the abundance of different taxa and the structure of the benthic community.

When similar questions are posed about the role of vertebrate predation in streams (see Allan 1983; Healey 1984), the answers are quite different. Reice (1983) manipulated patches of substrate in New Hope Creek, NC, U.S.A., to either permit or restrict access of fish. The two substrate types (cobbles and pebbles) produced radically different communities. However, the communities on the same type of substrate, with or without fish, were nearly identical. Allan (1982) removed trout from a 1200-m reach of a Colorado, U.S.A., mountain stream and compared the structure of the benthic community to upstream and downstream unmanipulated segments. He could not detect significant differences in the communities because of high variability among samples. In an 18-month study of the role of fish predation in second-order streams (S. R. Reice, unpub-

---

[1]Author to whom all correspondence should be addressed.

TABLE 1. Physical and biological characteristics of study streams

	Ruisseau de Cran Carré	Low Hope Creek
Temperature, °C	11–20	14–23
Current, m/s	0.07–0.80	0.09–0.58
Width, m	3.75±0.87*	3.9±0.14*
Cage depth, cm		
Low water	1–10	4–14
High water	20–30	14–24
Vertebrate predators		
Salamander	*Eurycea bislineata*	*E. bislineata*
Fish	*Salvelinus fontinalis*	
	Pungitius pungitius	

*Mean ± SE.

lished data), minor species-specific responses were detected, but no broad community changes. Griffith (1981), as cited in Allan (1983), introduced trout to a fishless headwater stream. Of nine tested insect species, three decreased and two increased relative to control abundances. The effects of fish predation on stream benthos remains obscure.

These experiments were designed to test the effects of fish by comparing a stream that has never had a fish population with a stream with fish. It is possible that an invertebrate community that has not been subject to fish predation would respond more to fish than a community with previous exposure to fish. Perhaps the lack of significant numerical responses by the benthos in Reice's (1983) and Allan's (1982) work was due to coadaptation of the fish and their prey. In a fishless stream, added fish could have a greater impact. Further, it was our intention to concentrate the effect of fish by confining them in small cages. Peckarsky and Dodson (1980) demonstrated that an invertebrate predator had pronounced effects when placed in similar cages. A lingering problem from previous work is that fish may have been too sparse to have a significant effect on the overall community structure. To address this issue, we manipulated the presence or absence of vertebrate predators in benthic cages. The null hypothesis was that there would be no difference between predator and no-predator cages. The alternative hypothesis was that benthic invertebrates will be reduced in the presence of predators. Furthermore, we hypothesize that the effect of fish predation will differ between streams with and without resident fish populations.

Experimental design

Study area

The experiments were carried out in two third-order streams located near the Matamek Research Station. The area is approximately 25 km east of Sept Îles, Québec, on the north shore of the Gulf of St. Lawrence. The general characteristics of this area have been described previously (Naiman 1983). Both streams flow through boreal forest, with numerous beaver meadows and small lakes in their catchment basins. One of the study sites was Low Hope Creek (LHC), approximately 100 m upstream from its mouth on Lac Mechant. The stream lies above a glacial escarpment, where postglacial colonization of fishes has not occurred (Power et al. 1973). It has salamanders (*Eurycea bislineata*, the northern two-lined salamander) but no fish. The other stream site is in Ruisseau du Cran Carré (RCC), approximately 400 m upstream from Highway 138. RCC has two species of fish (see Table 1). These two sites have similar substrates (cobbles underlain by pebbles, gravel, and sand), widths, depths, and current velocities (Table 1). Sphagnum and aquatic mosses are abundant on the stream banks and on large rocks in both streams, but alder is more

common in the riparian vegetation of RCC. In August, filamentous algae were abundant in LHC and sparce in RCC (personal observation).

In addition, a site directly above the second falls of the fifth-order Matamek River was used to collect brook trout fry (*Salvelinus fontinalis*) and to investigate the effect of caging on their feeding behavior. The river is approximately 40 m wide with depths ranging from 0.2 to >2 m. The substrate is primarily cobbles, boulders, and rock outcrop. A shallow area near the north bank was similar in substrate, depth, and current to the third-order stream sites. Alder is the most abundant riparian vegetation along the Matamek River shoreline.

Methods

To test whether stream macroinvertebrates would respond to the presence of a vertebrate predator, we manipulated predator presence or absence in benthic cages. The cages were of similar design to the modified Peckarsky cages (see Fig. 5.6 in Peckarsky, 1984). The cages were 20 × 30 cm by 10 cm deep. The cages had 3 mm opening mesh side panels (30 × 10 cm) to permit migration of aquatic invertebrates, while confining or excluding vertebrates. Large invertebrates with head capsules ≥3.0 mm were restricted by the 3-mm baffle. Nearly all benthic species passed easily (see Peckarsky and Dodson, 1980). The tops, bottoms, and end panels were 0.8 mm mesh. The cages were set into the substratum so that the top of the cage was flush with the surface of the stream bed. Peckarsky's (1985) discussion of cage effects addresses the use, limitations, and advantages of this type of cage. Walde and Davis (1984) review the problems with enclosure–exclosure experiments in streams.

The experimental protocol was as follows. Twenty cages were filled with rounded, cobble-sized rocks (diameter, ~10 cm) freshly collected from the stream bed. Approximately 50% of the cage volume was filled with cobbles, thus leaving space for fish to swim. Cages were left open (i.e., top removed) for colonization, and remained open for 2.5 weeks. Then five cages were sampled. These were designated I for initial community. The remaining 15 cages were searched for vertebrate predators which might have colonized. The search was conducted with the cage in the water and caused minimal disturbance, since the rocks were gently lifted, then replaced. No fish were found, but some small salamanders were removed. Then, if it was a predator cage (P), one vertebrate predator was stocked per cage. The tops were affixed to create the predator inclusion treatment. In five other cages, tops were affixed to exclude vertebrate predators (no-predator (NP) cages). The final five cages were left open (and designated O) to allow free movement of all animals, including vertebrate predators.

The complete design was run twice. Preliminary trials with native predators from each stream were conducted in June 1983. Adult northern two-lined salamanders (*Eurycea bislineata*) were collected and used in LHC, while brook trout (*Salvelinus fontinalis*) and nine-spined sticklebacks (*Pungitius pungitius*) were used in RCC. In round 1 experiments, fish and salamanders were collected the day of the experiments. Holding time was less than 30 min for the fish, and less than 5 min for the salamanders. The predator inclusion–exclusion lasted 8 days before the June experiment was terminated. The relatively short duration was to insure that conditions in the cages did not change significantly during the experiment and that the behavior of the predators did not become aberrant due to prolonged confinement. Note that Peckarsky's (1985) experiments ran 3–7 days when manipulating stoneflies.

The main experiments were run in August. We used brook trout fry collected from the Matamek River as a standard predator. Fish were collected the night before the experiments were initiated in RCC and LHC. They were transferred to the lab in buckets, weighed on the morning of the experiment, and transported to the streams in individual chambers in a bucket of water. The transfer took 1.5 h (RCC) or 2.5 h (LHC). Fish were never out of water, were handled only with nets, and were active when added to and removed from the cages. The predator manipulation lasted 12 days. The increase from 8 to 12 days was due to weather delays which prevented us from reaching LHC by float plane until day 12. Predator densities were close to normal for *Eurycea* and two to five times normal for fish (in RCC). Fish densities were

determined by seining and electroshock (R. Morin, personal communication).

The sample collection procedure was standardized, with the aim of collecting all animals with head capsule diameter >0.25 mm present at the end of the experiment. Cages were lifted from the water in a 0.25 mm mesh sample receiver. All cobbles in a cage were hand-scrubbed in a bucket in stream water. Material on the inside of the cage and receiver was washed into the bucket. All particulate matter that was retained by a No. 60 Tyler Series seive (250 μm) was preserved in 70% alcohol. An animal-specific stain (Biebrich scarlet and eosin B in water (1:1:100, by weight)) was added to the samples. Owing to the large amount of particulate detritus in the samples, they were separated into a coarse and a fine fraction by seiving through a 1-mm mesh. The entire coarse (>1 mm mesh) fraction was picked under a dissecting microscope (6×). The fine fraction was subsampled on a weight basis and one-quarter was picked as above. Subsampling was necessary because of manpower limitations. Animals and gut contents of enclosed predators were identified to the lowest feasible taxonomic level (usually genus).

Analysis was performed on each experiment separately, comparing the four treatments (I,P,NP, and O). Comparisons of total numbers and species richness were made using the a priori, single degree of freedom, orthogonal contrasts test (ONEWAY program, Statistical Package for the Social Sciences 1985, see Sokal and Rohlf (1981) for discussion). This test avoids the experiment-wise error associated with Duncan's multiple-range test when comparing all pairs of means. This test is the most powerful test for multiple comparisons given planned contrasts. The three single degree of freedom contrasts were (*i*) initial samples (I) vs. later samples (O,P,NP), (*ii*) open (O) vs. closed treatments (O vs. P,NP), (*iii*) vertebrate predators present (P) vs. absent (NP).

A $\ln(N+1)$ transformation of the community data was used to homogenize variances. Total densities of each species (five samples pooled) were compared in P and NP cages. The proportion of the total number of species reduced in P was tested with the Fisher sign test (Siegel 1956). The Wilcoxon rank sum test (Hollander and Wolfe 1973) was used to test individual species population sizes from P and NP cages. This test was used to deal with problems of large variances.

Brook trout (*Salvelinus fontinalis*) fry were the principle predators in this study. We used fish of standard length (SL) = 4.36 ± 0.09 cm ($\bar{x}$ ± SE). Many authors have shown that brook trout of that size feed on aquatic insects (Carlander 1969; Smith 1961). The trout fry reside in the sediments and feed in and on the rocks and in the water column. Allan (1981) demonstrated that larger trout feed principally from the drift. Williams (1981) showed that the first diet of postemergent brook trout (SL = 25.1 mm) in the Matamek River is primarily small- to medium-sized invertebrates (especially simuliid larvae) from the tops of rocks. O'Connor and Power (1976) working in small streams in the Matamek River watershed (quite similar and near to LHC and RCC) showed that brook trout fed on the benthos. Nine-spined sticklebacks are known as feeders on benthic invertebrates (Carlander 1969; Thompson 1985). *Eurycea bislineata* adults feed on benthic invertebrates when in streams (Hamilton 1932). *Eurycea* adults respire through the skin and buccal cavity, and are often found in streams.

To check the validity of the fish experiments, the feeding behavior of trout fry in cages was compared with unenclosed fry in the Matamek River site in July 1984. Five open cages placed near the riverbank at depths of 30–60 cm were filled with cobbles directly from the river bottom. Colonization occurred for 6 days, then five trout fry which had been caught and weighed the night before were placed in the cages at 1000 h. The cages were collected 30 h later. Unenclosed trout fry were collected from the same area at the same time. All fish were weighed and preserved in 70% alcohol. Guts were dissected out, gut fullness estimated volumetrically, and stomach contents were identified to the family level when possible.

Results

Gut content analysis of predators

Round 1. Preliminary

In RCC, *Pungitius pungitius* (the nine-spined stickleback)

guts contained more than twice as many prey ($x = 56.50$, SE = 3.53, $n = 2$) as did brook trout (*Salvelinus fontinalis*), which averaged 18.33 prey items per gut (SE = 5.36, $n = 3$). The differences were significant ($P(t)$ (probability of t-test) ≤ 0.01). Both species took principally Chironomidae with some *Simulium* sp. Several other prey items were rare.

In LHC, *Eurycea bislineata*, the northern two-lined salamander, basically did not feed (at least in the 24 h prior to sampling). Only one of five salamanders had any prey organisms in their guts, and it had a single mayfly.

Round 2

Only *Salvelinus fontinalis* individuals were used in this round. Brook trout fry in LHC ate nearly six times more prey ($\bar{x} = 104.2$, SE = 8.9, $n = 5$) than in RCC ($\bar{x} = 17.4$, SE = 4.57, $n = 5$). There were nearly six times more individuals in the I cages in LHC ($\bar{x} = 3089.4$) than RCC ($\bar{x} = 524.5$). The differences were highly significant ($P(t) ≤ 0.01$). Most of this difference was based on consumption of Chironomidae ($\bar{x}_{RCC} = 11.8$, while $\bar{x}_{LHC} = 59.4$). Note that Chironomids were 34% more abundant in I cages in LHC ($\bar{x} = 831.20$) than RCC ($\bar{x} = 617.6$). Chydoridae were also common prey in LHC ($\bar{x} = 27.4$) and were absent in RCC. *Salvelinus fontinalis* had a broader diet in RCC (12 families) than in LHC (6 families). The faunal composition in both streams was similar. There were 62 taxa in LHC and 65 in RCC. All prey taken were aquatic.

Feeding of Salvelinus fontinalis in and out of cages

In the summer 1984 test of brook trout fry feeding, we found that the mean number (± 1 SE) of prey consumed by brook trout was higher but more variable for free-ranging individuals ($\bar{x} = 20.6 ± 8.33$ (SE)) than for caged individuals (($\bar{x} = 6.6 ± 1.83$ (SE)). These values are statistically indistinguishable ($P(t) > 0.05$). In all the fry sampled, chironomid larvae were the numerically dominant prey (from 54 to 90% of the prey taken). This is comparable with the August 1983 experiments in which Chironomidae represented 57% of prey taken in LHC and 68% of prey taken in RCC. Brook trout fry that were outside cages took a substantial fraction (22% by numbers) of their prey from winged insects which fell into the stream. The biomass represented by these terrestrial adults approached 80% of the total biomass they consumed. Trout in cages took no terrestrial prey. Guts of fish in cages averaged one-quarter or less full, while guts of fish outside cages averaged more than three-quarters full. Thus total biomass consumed by *Salvelinus fontinalis* outside the cages was significantly greater than consumed by those inside the cages ($P(W) ≤ 0.01$), mainly due to the consumption of larger, terrestrial items.

Benthic community responses

The 2.5-week colonization interval was sufficient to establish the macroinvertebrate community in the cages. This is demonstrated by the fact that in three experiments no significant differences between initial (I) cages sampled at 2.5 weeks and open controls (O) sampled 8 or 12 days later (see Table 2). In both RCC experiments the means did not change appreciably. In LHC round 1, the means increased from I to O, but the variances were very high. In LHC round 2, I densities were significantly higher than NP, P, and O cages ($P(t) ≤ 0.003$).

Low Hope Creek, round 1, June 1983

In this experiment the indigenous salamanders, *Eurycea bislineata*, were manipulated. The total number of individuals and species was significantly greater ($P(t) < 0.05$, Table 2) in the O treatment relative to P and NP. This shows that immigration via drift continued during the study (i.e., top entry

TABLE 2. Summary statistics

	Initial (I), $\bar{x} \pm$ SE	Open (O), $\bar{x} \pm$ SE	Predator (P), $\bar{x} \pm$ SE	No predator (NP), $\bar{x} \pm$ SE	Contrasts		
					I vs. O,OP,NP	N vs. P,NP	P vs. NP
Low Hope Creek I							
Total no. of individuals	1144.4±276.1	2852.4±456.6	1518.6±226.7	1288.8±227.1	ns	P=0.002	ns
Total no. of species	18.2±3.0	20.4±1.3	18.0±1.2	15.8±1.7	ns	P=0.004	ns
Species diversity*	1.13	0.741	0.50	0.74			
Low Hope Creek II							
Total no. of individuals	3089.4±474.5	1200.2±308.2	1253.4±351.6	1780.4±451.6	P=0.003	ns	ns
Total no. of species	20.2±1.34	21.2±1.7	18.6±1.43	23.4±3.0	ns	ns	ns
Species diversity*	0.891	1.502	1.415	1.234			
Ruisseau du Cran Carré I							
Total no. of individuals	905.8±223.9	998.2±245.5	1185.6±316.9	1075.2±73.3	ns	ns	ns
Total no. of species	24.6±30.89	21.6±3.6	21.0±1.16	21.0±1.34	ns	ns	ns
Species diversity*	1.51	1.48	1.26	1.27			
Ruisseau du Cran Carré II							
Total no. of individuals	524.5±140.0	647.0±181.7	409.6±64.2	708.4±98.3	ns	ns	P=0.038
Total no. of species	28.0±5.2	25.0±1.9	27.6±2.5	32.0±3.5	ns	ns	ns
Species diversity*	2.33	2.41	2.35	2.31			

*H' (base e), all samples pooled.

TABLE 3. Effect of predators on all taxa via sign test

	Number of taxa			
	Increased with predators present	Decreased with predators present	Z score	P(Z)
Round 1				
Ruisseau du Cran Carré (mixed fish)	27	28	0	0.50 ns
Low Hope Creek (*Eurycea bislineata*)	17	15	0.177	0.431 ns
Round 2				
Ruisseau du Cran Carré (*Salvelinus fontinalis*)	16	49	−3.969	0.00005
Low Hope Creek (*Salvelinus fontinalis*)	18	44	−3.175	0.0075

in O, side entry in all cages). The closed cages (P + NP) had approximately half the number of individuals in open cages. This is due mainly to higher numbers of Chironomidae in O cages. Diversity peaked in the I treatment (Table 2). Analysis by the sign test (Table 3) showed that there was no overall pattern of taxonomic response to salamanders (Table 3). No taxa or community parameters (Tables 2 and 4) showed a significant effect due to predation by *Eurycea bislineata* (P vs. NP cages).

Ruisseau du Cran Carré, round 1, June 1983

Pungitius pungitius (three) and *Salvelinus fontinalis* (two) were used as the fish predators in this experiment. None of the community parameters responded to the treatment (Table 2). Variations in N (number of individuals), S (number of species), and H' (species diversity) were minor and insignificant. Out of 16 common taxa, only *Baetis* larvae and *Promoresia* larvae were significantly reduced by fish (see Table 4). The sign test showed no significant pattern of fish-induced population reductions (Table 3).

Low Hope Creek, round 2, August 1983

We introduced brook trout fry from the Matamek River

(*Salvelinus fontinalis*) into the predator cages. Presence of young trout reduced the populations of 71% of the taxa, producing a highly significant effect (P = 0.007, sign test, see Table 3). The rank sum test (Table 4) shows that only *Oxyethira* sp. was significantly reduced in the presence of fish (out of 14 common taxa). However, the mean number of large invertebrate predators was reduced from 18.60 in the no-fish cages to only 7.60 in the fish cages (ns). No community parameter was affected by fish (P vs. NP, Table 2). Therefore, many species had reduced density in the presence of trout fry (by as little as one individual), but only one was reduced significantly.

Ruisseau du Cran Carré, round 2, August 1983

Again, brook trout fry from the Matamek River were manipulated. This experiment parallels LHC round 2. The total number of individuals was significantly reduced by the trout (P(t) ≤ 0.05). The cages without fish averaged 708.4 ± 98.3 ($x \pm$ SE) individuals. With trout this was reduced to 409.6 ± 64.2 (Table 2). Neither species richness nor diversity was affected. The sign test showed 75% of the 65 taxa responding were reduced in the presence of the fish (P << 0.001, Table 3).

TABLE 4. Mean abundances of common taxa

(A) Low Hope Creek

	Round 1, June			Round 2, August		
Taxon	With Eurycea	Without Eurycea	P(W)	With Salvelinus	Without Salvelinus	P(W)
Baetis sp.	0.6	0	ns	5.2	4.4	ns
Chelifera	0.4	0.4	ns	5.2	3.6	ns
Chironomid larvae	1385.6	1108.0	ns	824.4	325.2	ns
Chironomid pupae	20.4	37.4	ns	30.4	51.0	ns
Chydoridae	0	0	ns	12.8	61.8	ns
Eurylophella doris	10.0	16.2	ns	15.2	25.0	ns
Habrophlebia sp.	3.4	0.6	ns	0	0	ns
Hydracarina	37.2	40.8	ns	50.8	64.4	ns
Isoperla sp.	2.8	2.8	ns	0.2	3.0	ns
Leuctra sp.	15.6	14.0	ns	1.0	1.0	ns
Oligochaeta	4.4	25.6	ns	131.6	103.8	ns
Oxyethira sp.	1.2	0.2	ns	4.6	20.2	$P \leq 0.05$
Promoresia larvae	0.8	0	ns	10.0	4.6	ns
Psilotreta sp.	0.8	0.6	ns	2.4	3.0	ns
Rhyacophila sp.	0.2	0.2	ns	0.0	1.0	ns
Simulium sp.	9.0	9.2	ns	0	0.6	ns

(B) Ruisseau du Cran Carré

	Round 1, June			Round 2, August		
Taxon	With mixed fish	Without mixed Fish	P(W)	With Salvelinus	Without Salvelinus	P(W)
Baetis sp.	3.2	13.4	$P<0.05$	5.6	9.6	ns
Chironomid larvae	866.0	795.4	ns	178.4	341.6	ns
Chironomid pupae	54.2	35.4	ns	11.2	9.0	ns
Choroperlidae	0	0.4	ns	21.2	32.0	ns
Eurylophella doris	2.0	6.0	ns	2.0	2.6	ns
Heleidae	5.0	6.2	ns	8.6	20.4	ns
Habropsyche sp.	0.4	0.4	ns	15.2	30.5	ns
Hydracarina	23.6	24.8	ns	13.8	22.6	ns
Isoperla sp.	0.2	0.6	ns	2.6	5.6	ns
Isotomidae	0.8	1.4	ns	3.8	11.6	ns
Leptophlebiidae	0	0	ns	1.2	3.0	ns
Leuctra sp.	6.2	6.6	ns	43.6	46.2	ns
Limnephilidae	0	0	ns	6.4	4.8	ns
Oligochaeta	4.6	6.2	ns	10.8	27.6	ns
Polycentropus sp.	0.8	0.4	ns	2.2	3.4	ns
Promoresia larvae	12.8	22.2	$P \leq 0.05$	18.8	25.6	ns
Promoresia adults	4.4	1.4	ns	0.2	1.2	ns
Rhyacophilia sp.	1.8	3.0	ns	11.8	15.8	ns
Serratella sp.	0	0	ns	0.2	3.2	ns
Simulium sp.	40.6	9.8	ns	1.4	2.2	ns
Sphaerium sp.	0	0.2	ns	0.6	3.0	$P \leq 0.05$
Taeniopteryx sp.	0	1.6	ns	5.4	8.4	ns

NOTE: $W = \sum_{i=1}^{n} R$, where R = rank of all P (predator cages) among all P and NP cages.

These overall patterns did not translate into significant reductions of specific taxa. Only *Sphaerium* sp. showed a significant effect due to fish (Table 4, $P(t) \leq 0.029$), out of 20 common taxa.

Discussion

The principle goal of this study was to test the effect of fish on benthic populations and community structure. The first round was preliminary. The salamander, *Eurycea bislineata*, appar-

ently did not feed in the 24 h prior to sampling, although they normally do feed in the benthos. Only Oligochetes were depressed in the presence of salamanders. This may be due to the presence or activity of the salamanders in the cages. Peckarsky and Dodson (1980) have shown that a stonefly's presence in a cage was sufficient to alter the distribution of its prey, even when it was not free to feed. Peckarsky (1985) showed variation in total community response to insect predators. If the predator was free, the total density was often reduced

relative to controls. The effect of confined predators was intermediate. The fish used in round 1 in RCC had little effect. This may be due to cold water in June and reduced feeding activity by fish. We will therefore focus on the patterns of benthic responses to trout fry in round 2.

Allan (1982) argued that prey organisms in streams should be well adapted to fish predation, that fish have influenced body size, cryptic coloration, and behavior (particularly nocturnal activity patterns). The effect of trout fry did not change between the normal stream (RCC) with resident fish and the fishless stream (LHC). In LHC the fauna was naive with respect to fish, yet the trout rarely caused significant changes in population sizes of individual species' populations of benthic invertebrates. Fish had a greater impact in RCC as was evidenced by the significant effect on total N (Table 2). Trout did take six times more prey individuals in LHC than RCC in August. Note, however, that there were three times more individuals in LHC than RCC in August. The grand mean number of individuals per cage for LHC was 1850.9, while in RCC it was 572.4. This difference was not apparent in June. The percent reduction in P vs. NP cages was 42% in RCC and only 30% in LHC. Therefore, the prey were probably not more vulnerable in LHC.

It is unlikely that these prey taxa are reproductively isolated from conspecifics in other streams below the glacial escarpment. Streams with indigenous fish populations are only 10 km away. The taxa identified are ubiquitous in Québec. So, no genetically based differences in invertebrate behavior should be expected. In fact, no pattern of differences in benthic population responses to fish predation were observed between the two streams.

In the experiments, the Wilcoxon ranked sum test showed a reduction of *Baetis* sp. and *Promoresia* sp. in RCC, round 1, and *Oxyethira* sp. in LHC, round 2. Given the number of taxa tested (75 total), one should expect this frequency (0.04) of significant differences by chance alone when $\alpha = 0.05$. Clearly very few taxa were reduced significantly by fish feeding. This suite of responses is similar to the effects of predaceous stoneflies (Peckarsky 1985). Note that the effects of stonefly predation were eliminated by siltation.

In part, this lack of significant fish effects is due to high variances in abundances of the taxa (see discussion by Allan, 1982, 1983). However, the magnitudes of the variances strongly suggest that other factors influenced the abundnce of these taxa far more than fish did. Such factors might include patchy distribution of food or current velocity (since the substrates were identical). Fish predation did not produce measurable effects on benthic population sizes, even while it caused general reductions in overall abundances.

Trout did feed in the cages. The numbers of prey taken per trout in LHC (round 2) averaged 104.2, while in RCC (round 2) the mean was only 17.4 individuals. The total number of individuals in P cages for round 2 in LHC was 1253.4 ± 351.6 ($\bar{x}$ ± SE), while in RCC it was 409.6 ± 64.2 ($\bar{x}$ ± SE). That means that the RHC gut contents represented 8.3% of the numbers of individuals present in the cages. In RCC the fish gut contents represented only 4.2% of the individuals present. These are relatively small fractions of potential prey consumed. This sort of analysis requires far greater knowledge of gut residence time and population turnover rates.

The trout were at higher than normal densities and were confined to a single patch of prey. They did not have the option of terrestrial prey items. Therefore, these estimates of the fraction of the fauna consumed may indicate the natural or even enhanced feeding level of trout fry on the benthos. The fish did

not significantly reduce most population sizes. This is probably due to insect immigration (through the 3 mm mesh side panels) exceeding the sum of fish feeding and insect emigration. If immigration is great enough to swamp out the effect of fish predation, then that establishes the relative importance of these factors in lotic macrobenthic communities.

The general effect (sign test) that most taxa were reduced somewhat by the trout feeding demonstrates that trout are consuming the fauna. Peckarsky (1985) found a similar effect for stonefly predation. However, the generalist feeding tendencies of the fish and the great availability of prey organisms combine to minimize the effect of trout on individual benthic taxa. The continual immigration of individuals into the cages further mitigates the effect of trout on benthic prey. This does not imply that all fish will have such modest effects on the benthos. Use of exclusively benthic feeding fish like suckers (Castomidae) could produce dramatically different results. Trout fry are just not very efficient benthic predators (A. Sheldon, personal communication).

These experiments show no differences in the responses of the benthic species or community between the fishless stream (LHC) and the stream with indigenous fish populations (RCC) to the manipulation of vertebrate predators. In these experiments fish were not effective agents in the control of either individual population sizes or overall community structure.

Acknowledgments

ALLAN, J. D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Can. J. Fish. Aquat. Sci. **38**: 184–193.

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

—— 1983. Predator–prey relationships in streams. *In* Stream ecology: application and testing of general ecological theory. *Edited by* J. R. Barnes and G. W. Minshall. Plenum Press, New York. pp. 191–229.

CARLANDER, K. D. 1969. Handbook of freshwater fishery biology. Vol. 1. The Iowa State University Press, Ames.

CROWDER, L. B., and W. E. COOPER. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology, **63**: 1802–1813.

GILINSKY, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology, **65**: 455–468.

GRIFFITH, R. W. 1981. The effect of trout predation on the abundance and production of stream insects. M.S. thesis, University of British Columbia, Vancouver.

HALL, D. J., W. E. COOPER, and E. E. WERNER. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. **15**: 839–928.

HAMILTON, W. J., JR. 1932. The food and feeding habits of some Eastern salamanders. Copeia, **2**: 83–86.

HEALEY, M. 1984. Fish predation on aquatic insects. *In* The ecology of aquatic insects. *Edited by* V. H. Rush and D. M. Rosenberg. Praeger Publishers, New York. pp. 255–288.

HOLLANDER, M., and D. A. WOLFE. 1973. Nonparametric statistical methods. John Wiley & Sons, New York.

MORIN, P. J. 1984a. Odonate guild composition: experiments with colonization history and fish predation. Ecology, 65: 1866–1873.

—————— 1984b. The impact of fish exclusion on the abundance and species composition of larval odonates: results of short term experiments in a North Carolina farm pond. Ecology, 65: 53–60.

NAIMAN, R. J. 1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. Ecol. Monogr. 53: 73–94.

NEILL, W. E. 1975. Experimental studies of microcrustacean competition, community composition and efficiency of foraging. Ecology, 56: 809–826.

O'CONNOR, J. F., and G. POWER. 1976. Production by brook trout (Salvelinus fontinalis) in four streams in the Matamek watershed, Quebec. J. Fish. Res. Board Can. 33: 6–18.

PAINE, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100: 65–75.

PECKARSKY, B. L. 1984. Sampling the stream benthos. In A manual on methods for assessment of secondary productivity in fresh waters. Edited by J. A. Downing and F. H. Rigler. IBP Handbook No. 17. 2nd ed. Blackwell Scientific Publications, Oxford and Edinburgh. pp. 131–160.

—————— 1985. Do predaceous stoneflies and siltation affect the structure of stream insect communities colonizing enclosures? Can. J. Zool. 63: 1519–1530.

PECKARSKY, B. L., and S. I. DODSON. 1980. Do stonefly predators influence benthic distributions in streams? Ecology, 61: 1275–1282.

POWER, G., G. F. POPE, and B. W. GOAD. 1973. Postglacial colonization of the Matamek River, Quebec, by fishes. J. Fish. Res. Board Can. 30: 1586–1589.

REICE, S. R. 1983. Predation and substratum: factors in lotic community structure. In Dynamics of lotic ecosystems. Edited by S. Bartell and T. Fontaine. Ann Arbor Science, Ann Arbor, MI. pp. 325–345.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Company, Inc., New York.

SMITH, M. W. 1961. Bottom fauna in a fertilized natural lake and its utilization by trout (Salvelinus fontinalis) as food. Verh. Int. Ver. Theor. Agnew. Limnol. 14: 722–726.

SOKAL, R. R., and F. J. ROHLF. 1981. Biometry. The principles and practice of statistics in biological research. 2nd ed. W. H. Freeman and Co., San Francisco.

THOMPSON, P. 1985. Thompson's guide to freshwater fishes. Houghton Mifflin Company, Boston.

WALDE, S. J., and R. W. DAVIES. 1984. Invertebrate predation and lotic prey communities: evaluation of in situ enclosure/exclosure experiments. Ecology, 65: 1206–1213.

WILLIAMS, D. D. 1981. The first diets of postemergent brook trout (Salvelinus fontinalis) and Atlantic salmon (Salmo salar) alevins in a Quebec river. Can. J. Fish. Aquat. Sci. 38: 765–771.