

The effects of spate-induced disturbance, predation and environmental complexity on macroinvertebrates in a tropical stream

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SUMMARY

1. The combined effects of fish predation, substrate complexity and flow on benthic macroinvertebrates inhabiting riffles was investigated in a Hong Kong stream. Predation was manipulated using fish inclusion/exclusion cages containing complex (= many refuges) or simple (= few refuges) substrates. Experiments were undertaken during the winter dry season, when disturbance due to flow events was minimal, and repeated during the summer monsoon, when the stream experienced spates of varying intensity and duration.
2. Predation by the fish, *Oreonectes platycephalus*, significantly reduced the abundance of macroinvertebrates, especially chironomids and mayflies. Because chironomids (mostly Chironominae) were the dominant cage colonists, there was also a reduction in total macroinvertebrate density.
3. Predator impacts were significantly lessened during the wet season, when macroinvertebrate densities increased considerably, but significant reductions in the densities of vulnerable taxa and total macroinvertebrate abundance were nevertheless apparent.
4. Substrate complexity (the presence of prey refuges) had no significant effect on the ability of predators to reduce prey abundance.
5. Detritus accumulated in cages during the latter part of the study, and densities of most taxa were correlated with detrital standing stocks.
6. The results of this experiment indicate that biotic interactions such as predation may be suppressed during periods of spate-induced disturbance, although they can still influence benthic communities significantly. However, the effects of predation are highly taxon specific and may vary among streams in response to changes in predator and prey species composition, or the severity and duration of spates.

Introduction

The question of what affects the distribution and abundance of benthic invertebrates has been, and remains, a central concern of stream ecologists (Hynes, 1970). Considerable research has been devoted to the question of whether and to what extent vertebrate predators (especially fish) influence benthic communities, but the results differ depending on circumstances. In some streams, predators had little or no effect on the benthos (Allan, 1982, 1983; Flecker & Allan, 1984; Culp, 1986; Reice & Edwards, 1986),

whereas in others a significant influence was detected on at least some prey taxa (Flecker, 1984; Healey, 1984; Gilliam, Fraser & Sabat, 1989; Schofield, Townsend & Hildrew, 1988; Schlosser & Ebel, 1989; Dudgeon, 1991; Flecker, 1992). These contrasting results can be attributed to a variety of factors, including experimental design which can affect prey exchange in cage experiments (Cooper, Walde & Peckarsky, 1990; Lancaster, Hildrew & Townsend, 1991). Impacts also depend critically on the feeding mode of the fish involved (Flecker, 1992), and upon habitat conditions (Schlosser & Ebel, 1989). The presence of prey refuges,

which will depend upon substrate characteristics, ameliorates the impact of freshwater predators (Sih, 1987; Fuller & Rand, 1990; but see Flecker & Allan, 1984), whereas flood events and increasing environmental harshness can override the effect of predators on benthic prey, or prevent them from depleting prey significantly (Lancaster, 1990; Peckarsky, Horn & Statzner, 1990; but see Walde, 1986). Evidently, a hierarchy of factors influence stream invertebrate populations, with flood events acting in a density-independent manner to reset benthic densities, thereby outweighing predator effects (Peckarsky, 1985; Lancaster, 1990). Accordingly, the influence of predation on community structure may change over time (Thorp, 1986). While there is no overall consensus among stream ecologists, it is possible that the variability or predictability of flow regimes (and, hence, the intensity of disturbance) governs whether biotic or abiotic factors are more important as determinants of community structure in streams (e.g. Hildrew & Townsend 1987; Power *et al.*, 1988; Resh *et al.*, 1988; Poff & Ward, 1989; but see Rader & Ward, 1989). Moreover, it is clear that our explanatory power will be increased if we take explicit account of the interactions between these factors (Schlosser & Ebel, 1989; Hart, 1992).

The present study considers the combined effects of fish predation, substrate complexity and flow on benthic macroinvertebrates inhabiting riffles in a Hong Kong stream. Previous experimental work in the same stream has shown that the fish reduced benthos densities in pools (Dudgeon, 1991), but invertebrate densities tend to be relatively low in such sites in Hong Kong streams and elsewhere (e.g. Hynes, 1970; Logan & Brooker, 1983). Predation in riffles was manipulated using fish inclusion/exclusion cages containing complex (= many prey refuges) or simple (= few prey refuges) substrates. Work was carried out during the winter dry season, when disturbance associated with flow events was minimal, and was repeated during the summer monsoon when the stream experienced spates of varying intensity and duration. A particular aim of the study was to determine whether spate-induced disturbance during the monsoon reduced the intensity of predation impacts (if any) on benthic macroinvertebrates.

Materials and Methods

Study site

The investigation was undertaken in a first-order headwater section of Kwun Yum Shan Stream near Shek Kong, New Territories, Hong Kong. The stream is permanent and spring-fed, and drains a small uninhabited valley (altitude 200 m) supporting mixed, evergreen, secondary forest. The stream waters are soft and slightly acidic, and therefore typical of unpolluted hillstreams in Hong Kong. Dudgeon (1991) and Dudgeon & Chan (1992) have presented additional information of Kwun Yum Shan Stream including the composition of the diverse benthic macroinvertebrate community (see Appendix 1 in Dudgeon & Chan, 1992). The predatory loach, *Oreonectes platycephalus* Günther (Cobitidae), is the only fish that occurs in Kwun Yum Shan Stream (Dudgeon, 1991).

Fieldwork began in May 1990 but rainstorms in late May and again in June gave rise to spates which disrupted two attempts to begin the experiments, thereby indicating the extent of wet-season disturbance. However, data were obtained from experiments carried out during a 6 week period in the summer wet season (June to August 1990) and a 4 week period in the winter dry season (February to March). These periods coincided with high and low rainfall respectively, and stream discharge peaked during the summer study period when flow volumes were ten times greater than during the dry season (Fig. 1). Minimum–maximum water temperatures were 22.5–25.0°C in summer and 14–20°C during winter.

The study reach was approximately 90 m long, and comprised mainly shallow (<10 cm deep) riffles and runs which were rarely more than 40 cm wide. It was completely shaded by a continuous canopy of riparian trees above the stream bed. The substrate comprised small boulders (generally <50 cm longest dimension). The study reach was divided into two approximately equal sections by a small, 2.5 m high waterfall, but there was no apparent difference between the benthic fauna above and below the falls.

Experimental manipulations

The experimental units were plastic cages of 294 cm² basal area (21 × 14 × 7.5 cm) and 4 mm mesh, containing three 9.9 × 9.9 cm unglazed clay quarry tiles (see

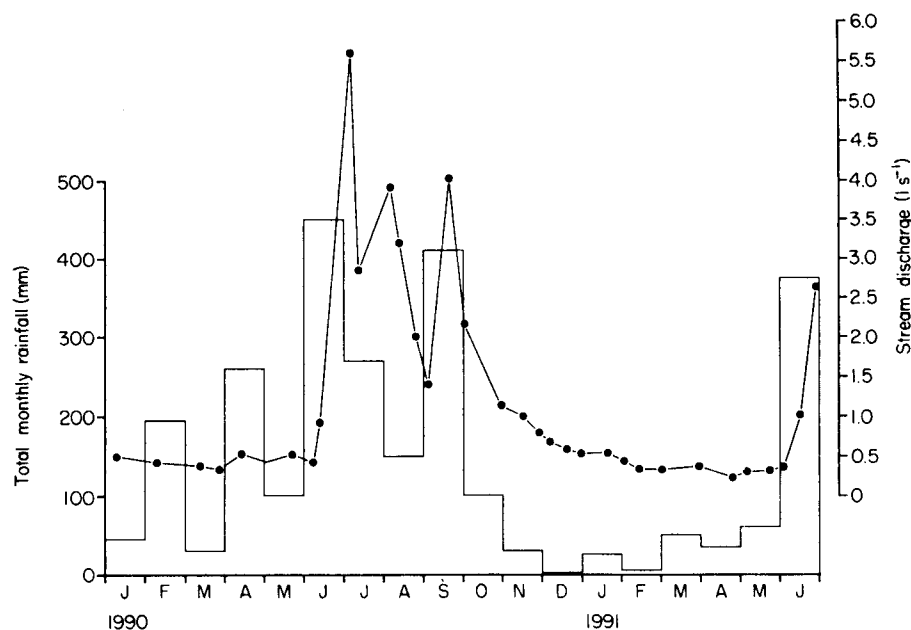


Fig. 1 Total monthly rainfall histogram (mm) and stream discharge (l s^{-1}) between January 1990 and June 1991.

Dudgeon & Chan, 1992). Cages were positioned in shallow riffles, with the narrow side facing the current, and fixed in place using steel pegs such that the upper edges of each cage were above the water surface. Four treatments were established: closed cages (predator exclusion) with simple (= few prey refuges) substrate; closed cages with complex (= many prey refuges) substrate; open cages (predator access) with simple substrate; and open cages with complex substrate. Access by predatory fish was allowed for half of the cages by removing the mesh panels on the downstream end; predator exclusion cages were complete. The cage design was similar to that used by Flecker (1984), and permitted fish to attain natural densities inside the open cages. Previous work in Kwun Yum Shan Stream has shown that a diverse array of benthic taxa colonize closed cages (Dudgeon & Chan, 1992). Fish were frequently seen entering open cages, but were never observed inside closed cages.

In treatments providing a simple colonization surface for invertebrates, the tiles were positioned so that two tiles lay side by side on the floor of the cage, while the third rested on top of (and partially covered) the lower pair. In treatments providing a complex colonization surface, three clay tiles were shattered into fragments (approximately $4\text{--}12\text{ cm}^2$) with a hammer before being added to the cages. The precise

surface area of the shattered fragments was probably in excess of that of the intact tiles (because of the edge effect) and, although the difference would not have been large, it could have led to greater numbers of invertebrate colonists in the 'complex' treatment.

Approximately half the cages were recovered after 2 weeks in the stream, and the rest after 4 weeks. Throughout these periods, detritus was removed routinely from the outside of the cages to maintain a free flow of water (current speed approximately 5 cm s^{-1}) through the cages. This rate of flow was approximately half that prevailing outside the cage. The experiment was repeated in the summer wet season and winter dry season.

The wet season experiments commenced on 26 June 1990 when fourteen cages of each treatment ($n = 56$) were placed in the stream. They were positioned in riffles which appeared similar with respect to substrate and current, and treatments were randomized. The cages were recovered 4 weeks later but, due to washout during spates, only five cages remained in three of the treatments and twelve cages in the fourth treatment (simple substrate, open cages). A second set of nine cages of each treatment ($n = 36$) was placed in the stream on 25 July 1990 and recovered 2 weeks later. At that time, six cages remained in three of the treatments, and five cages in the fourth treatment (simple substrate, closed cages). Rainfall

was slightly above normal (448.1 *v* 431.8 mm) in June, but 15% below the normal figure in July (268.0 *v* 316.8 mm).

The dry season experiments began on 11 February 1991 when sixteen cages ($n = 64$) were placed in the stream. Six of each treatment were recovered 2 weeks later, and a further six cages of three treatments and seven cages of one treatment (simple substrate, open cages) were recovered on 11 March after 4 weeks in the stream. Fifteen cages were stranded due to low flow volume during the dry season, and were excluded from the study. A combined total of ninety-nine cages was recovered from the stream during the dry and wet seasons, and provided the data that were analysed.

A cage was recovered by placing a fine-meshed (250 μm) net behind it and carefully removing the anchoring pegs. The net was then swept forward to enclose the cage while the cage was lifted clear of the bottom sediments and removed from the stream. Any animals which may have been dislodged by these activities were washed by the current into the net. The fact that fish were frequently taken along with the open cages testifies to the effectiveness of this collecting procedure. Care was taken to avoid disturbing bottom sediments during cage recovery; nevertheless, some animals hiding beneath cages may have been included in collections. Samples were preserved in the field with 10% neutral formalin and returned to the laboratory for processing.

Animals and associated detritus (mostly leaf fragments and bark) were rinsed gently from cages and tile surfaces and preserved in 70% ethanol. Animals were hand picked from the detritus at $\times 15$ magnification, identified to the lowest possible taxon (genus for most groups, families or subfamilies for Diptera except for the chironomid *Corynoneura*), and counted. Detritus was oven dried at 70°C and weighed to the nearest 0.01 g.

Data analysis

Data analysis was carried out on counts of individual taxa in each cage, and the number of taxa (= morphospecies) per cage. Most taxa were relatively rare and were combined into broader taxonomic groupings (order or family) unless they comprised $\geq 1.0\%$ of the total number of invertebrates counted. Abundance data were $\log(x + 1)$ transformed to

ensure homogeneity of treatment means and variances. Three-way ANOVA was used to investigate the effects of season (dry *v* wet season), substrate (complex *v* simple) and predation (open *v* closed cages) on benthic invertebrate abundance. Data from 2 and 4 week colonization periods were analysed separately. Because these comparisons were decided a priori an experiment-wise alpha value of 0.05 was chosen. Regression analysis was used to investigate the relationship between detrital standing stocks and cage colonists, and one-way ANOVA was used to compare wet and dry season abundance of animals colonizing cages.

Results

Dipterans were the major colonists of cages in Kwun Yum Shan Stream, comprising 79.9% of all individuals counted. Most were Chironomidae (74% of individuals), especially Chironominae which comprised 60.8% of the colonists. Other abundant chironomid taxa were *Corynoneura* (7.4%) and Tanypodinae (1.4%); Simuliidae (*Simulium* spp., 4.6%) constituted most of the remaining Diptera. Among other groups of colonizers, the thiarid snail *Brotia hainanensis* (Brot) made up 6.3% of the total. The relative abundances of major insect taxa were as follows: Ephemeroptera, 8.6% (including Baetidae, 6.5%) and Trichoptera, 6.5% (including Hydropsychidae, 1.4%). Coleoptera and Plecoptera comprised fewer than 1% of cage colonists.

Three-way ANOVA of the effects of treatment variables (season, predation and complexity), calculated separately for 2 and 4 week data sets, are shown in Table 1. The results were striking in several aspects. Firstly, in only one instance (Ephemeroptera, 4 weeks) out of twenty-six sets of faunal data tested, did substrate complexity significantly affect abundance. Secondly, in only a single case (Baetidae, 4 weeks) was there a significant interaction between the treatment factors. Thirdly, whereas Hydropsychidae, Simuliidae and *B. hainanensis* were unaffected by predators on Weeks 2 and 4, densities of Ephemeroptera (including Baetidae), Diptera (Chironomidae and Chironominae only) and total individuals were reduced significantly in predator treatments. The abundance of Trichoptera, *Corynoneura* and Tanypodinae and the number of morphospecies were reduced significantly by predators on Week 2 only. Fourthly,

Table 1 Three-way ANOVA of the densities of macroinvertebrates colonizing cages after 2 and 4 weeks in Kwun Yum Shan Stream: the significance of individual factors and their interactions are shown; d.f. in all cases = 1,39. Factor A = season, Factor B = predation, Factor C = complexity; - NS, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

	A	B	C	A × B	A × C	B × C	A × B × C
2 weeks							
<i>Brotia hainanensis</i>	***	-	-	-	-	-	-
Ephemeroptera	-	**	-	-	-	-	-
Baetidae	-	*	-	-	-	-	-
Trichoptera	***	*	-	-	-	-	-
Hydropsychidae	***	-	-	-	-	-	-
Diptera	***	**	-	-	-	-	-
Chironomidae	**	**	-	-	-	-	-
Chironominae	***	*	-	-	-	-	-
<i>Corynoneura</i>	-	***	-	-	-	-	-
Tanypodinae	-	***	-	-	-	-	-
Simuliidae	-	-	-	-	-	-	-
Total individuals	***	**	-	-	-	-	-
No. morphospecies	-	**	-	-	-	-	-
Detritus (g cage ⁻¹)	-	-	-	-	-	-	-
4 weeks							
<i>Brotia hainanensis</i>	*	-	-	-	-	-	-
Ephemeroptera	***	*	*	-	-	-	-
Baetidae	-	**	-	*	-	-	-
Trichoptera	***	-	-	-	-	-	-
Hydropsychidae	***	-	-	-	-	-	-
Diptera	***	**	-	-	-	-	-
Chironomidae	***	**	-	-	-	-	-
Chironominae	***	**	-	-	-	-	-
<i>Corynoneura</i>	*	-	-	-	-	-	-
Tanypodinae	***	-	-	-	-	-	-
Simuliidae	*	-	-	-	-	-	-
Total individuals	***	**	-	-	*	-	-
No. morphospecies	***	-	-	-	-	-	-
Detritus (g cage ⁻¹)	-	**	-	-	-	-	-

significant seasonal differences in the number of morphospecies, and the abundance of most taxa (except Ephemeroptera, *Corynoneura*, Tanypodinae and Simuliidae), were apparent on Weeks 2 and 4.

Because of the minor influence of substrate complexity and general lack of interaction effects between treatments on macroinvertebrate abundance, only data relating to the effects of season and predation on the abundance of cage colonizers are presented in Table 2. From this table it is clear that in all cases where significant differences associated with season and/or predators were detected, densities were reduced in the presence of predators and were generally lower during the dry season. The data also show that reductions in colonizer density in the presence of fish occurred in both the dry and wet seasons, and there were no significant interactions between the effects of season and predation (Table 1).

Although predation significantly reduced prey abundance in both seasons, the amount of the reduction—i.e. the predator impact—appeared to be less during the wet season. Predator impact can be inferred by the negative natural logarithm of the ratio of mean prey density in open cages to that in the closed cages, with a larger ratio indicating a greater impact. This index removes the potentially confounding influence of prey density on the magnitude of predation, and scales positively with predation impact (Peckarsky *et al.*, 1990). Only those taxa with densities significantly influenced by predators (see Table 1) are considered here. Impacts were higher in the dry than the wet season (Table 3), and were apparent both for total densities of colonizers and densities of individual taxa. The only exception to this generalization occurred in Week 4 when Tanypodinae was more severely impacted by pred-

	Wet season		Dry season	
	-F	+F	-F	+F
2 weeks				
<i>Brotia hainanensis</i>	8.2 ± 2.7	23.5 ± 5.2	5.1 ± 1.2	3.5 ± 1.2
Ephemeroptera	16.1 ± 3.1	9.7 ± 1.5	21.5 ± 6.2	7.6 ± 1.7
Baetidae	10.8 ± 2.1	7.2 ± 1.2	17.5 ± 5.3	6.1 ± 1.6
Trichoptera	9.2 ± 2.5	4.3 ± 1.5	1.9 ± 0.7	0.3 ± 0.1
Hydropsychidae	6.2 ± 1.7	2.8 ± 1.2	0.5 ± 0.2	0.1 ± 0.1
Diptera	213.5 ± 36.7	146.9 ± 40.0	124.4 ± 28.8	32.0 ± 5.1
Chironomidae	194.0 ± 34.1	134.6 ± 34.5	118.7 ± 27.7	30.4 ± 5.0
Chironominae	172.0 ± 31.2	124.1 ± 33.2	74.8 ± 17.2	22.3 ± 4.2
Corynoneura	17.5 ± 3.8	7.4 ± 1.9	18.0 ± 3.9	4.3 ± 1.0
Tanypodinae	2.0 ± 1.9	1.2 ± 0.6	3.9 ± 1.0	1.7 ± 0.4
Simuliidae	16.6 ± 5.6	11.4 ± 5.6	2.0 ± 1.1	0.1 ± 0.1
Total individuals	251.2 ± 40.7	188.2 ± 40.8	158.6 ± 33.9	45.9 ± 6.7
No. morphospecies	15.8 ± 1.3	12.6 ± 1.4	14.2 ± 1.3	9.8 ± 0.9
Detritus (g cage ⁻¹)	1.1 ± 0.5	0.6 ± 0.1	1.3 ± 0.1	0.7 ± 0.1
4 weeks				
<i>Brotia hainanensis</i>	10.5 ± 3.2	11.8 ± 2.5	18.4 ± 3.7	15.0 ± 2.8
Ephemeroptera	38.8 ± 8.5	31.0 ± 4.1	27.1 ± 5.5	6.7 ± 1.2
Baetidae	20.1 ± 4.4	16.0 ± 2.3	23.5 ± 5.0	2.9 ± 0.8
Trichoptera	18.0 ± 4.8	10.9 ± 2.3	1.1 ± 0.4	0.3 ± 0.2
Hydropsychidae	10.1 ± 2.9	5.2 ± 1.7	0.1 ± 0.1	0.0
Diptera	466.3 ± 115.2	228.7 ± 33.4	103.5 ± 26.2	24.3 ± 10.5
Chironomidae	442.7 ± 107.3	213.2 ± 29.4	97.5 ± 24.4	22.0 ± 9.9
Chironominae	339.9 ± 93.9	142.1 ± 23.4	68.2 ± 17.0	14.6 ± 7.5
Corynoneura	41.2 ± 14.2	71.5 ± 44.8	11.2 ± 3.5	1.3 ± 0.5
Tanypodinae	15.1 ± 4.3	10.0 ± 2.3	3.2 ± 1.0	2.7 ± 0.8
Simuliidae	14.9 ± 5.7	11.7 ± 5.7	1.1 ± 1.1	0.1 ± 0.1
Total individuals	564.0 ± 134.9	312.2 ± 40.6	160.5 ± 26.5	54.8 ± 11.8
No. morphospecies	25.4 ± 3.2	20.7 ± 1.5	13.8 ± 1.1	11.5 ± 1.2
Detritus (g cage ⁻¹)	2.7 ± 0.5	1.4 ± 0.2	2.6 ± 0.3	1.0 ± 0.2

Table 2 The influence of season and predation on the densities (mean no. cage⁻¹ ± SEM) of fauna colonizing cages after 2 and 4 weeks in Kwun Yum Shan Stream: +F = fish access; -F = fish excluded. The significance of inter-treatment differences is shown in Table 1

ators in the wet than the dry season. To assess predator impacts between seasons, one-tailed Wilcoxon signed-rank tests were undertaken on the 2 and 4 week data sets; in both cases, impacts were significantly greater ($P < 0.01$) during the dry season. However, no significant differences in predator impacts were detected between weeks within the same season.

Significant differences in the amounts of detritus were apparent among some treatments, with more detritus in closed cages on Week 4 (Table 1). Because of this systematic, inter-treatment difference, detritus had the potential to act as a confounding variable in Week 4 of the present investigation. Regression analysis was used to determine if there was a significant relationship between detrital standing stocks and the abundance of colonists in cages. Data from all treatments were combined for this analysis

($n = 99$), using detritus as the independent variable. Total individuals, total morphospecies, and the densities of all but two of the individual taxa were positively related to detrital standing stocks in cages (Table 4). These relationships held when the analysis was repeated to include only those cages that had been in the stream for 4 weeks (significant for all taxa except *Brotia hainanensis*, where $r > 0.48$, $r^2\% > 23.6$, $F > 7.14$, $P < 0.014$). Despite the possible confounding effects of detritus on Week 4, no difference was found between predation impacts on Weeks 2 and 4 during either the wet or dry seasons (see above).

Discussion

Species richness and the abundance of animals colonizing cages were relatively high during the wet season, when increased discharge favoured the estab-

Table 3 Seasonal differences in predation impacts on the densities of fauna colonizing cages after 2 and 4 weeks in Kwun Yum Shan Stream. Impact was measured by the negative natural logarithm of the ratio of prey density in open cages to that in closed cages (where larger ratios represent greater impacts). Only those taxa with densities significantly influenced by predators (see Table 1) are included

	Wet season 2 weeks	Dry season 2 weeks	Wet season 4 weeks	Dry season 4 weeks
Ephemeroptera	0.51	1.04	0.22	1.40
Baetidae	0.41	1.05	0.23	2.09
Trichoptera	0.76	1.90	0.50	1.30
Diptera	0.37	1.36	0.71	1.45
Chironomidae	0.37	1.36	0.73	1.49
Chironominae	0.33	1.21	0.87	1.54
<i>Corynoneura</i>	0.86	1.43	-0.56	2.15
Tanypodinae	0.51	0.83	0.41	0.17
Total individuals	0.29	1.24	0.59	1.07

Table 4 Regression analysis of the relationship between detrital standing stocks and the abundance of colonists in cages. Data from all treatments were combined for this analysis ($n = 99$) using detritus as the independent variable. ** $P \leq 0.01$, *** $P \leq 0.001$

	r	$r^2\%$	F	P
<i>Brotia hainanensis</i>	—	—	—	NS
Ephemeroptera	0.52	27.0	35.9	***
Baetidae	0.39	15.1	17.3	***
Trichoptera	0.51	26.1	34.2	***
Hydropsychidae	0.38	14.7	16.8	***
Diptera	0.58	33.6	49.2	***
Chironomidae	0.58	33.3	48.5	***
Chironominae	0.54	29.5	40.5	***
<i>Corynoneura</i>	—	—	—	NS
Tanypodinae	0.50	25.3	32.9	***
Simuliidae	0.32	10.5	11.4	**
Total individuals	0.60	36.5	55.8	***
No. morphospecies	0.59	35.1	52.5	***

ishment of rheophilic species such as Hydropsychidae, and led to an increase in the densities of most other abundant taxa. Schlosser & Ebel (1989) reported similar trends in invertebrate abundance, associated with inter-year flow fluctuations, in a headwater stream in the United States, and a seasonal change in benthos abundance is typical of small, headwater streams in Hong Kong. Only 3% of the Territory's annual rainfall occurs during the driest months (December–February) when stream flows are often reduced to a trickle, or may disappear into the bottom

sediments (Dudgeon, 1992). Under these circumstances, predators and their prey are brought into close contact in the remaining habitable areas of the stream, and it is therefore not surprising that predator impacts were more intense in the dry season.

The results of this study showed that marked reductions of prey densities—especially mayflies and Chironomidae—were caused by predatory fish in a Hong Kong stream, in contrast to some studies undertaken in temperate running waters (Allan, 1982, 1983; Flecker & Allan, 1984; Culp, 1986; Reice & Edwards, 1986). Other investigations have detected a significant influence on at least some benthic prey taxa (Healey, 1984; Gilliam *et al.*, 1989; Schofield *et al.*, 1988; Schlosser & Ebel, 1989), and it is notable that some of these effects are most apparent for chironomids and mayflies. Dudgeon (1991) showed that *Oreonectes platycephalus* greatly reduced the abundance of mayflies in stream pools but had no effect on chironomids, despite the fact that they are part of the predator's diet (D. Dudgeon, unpublished observations), whereas Flecker (1984) found that *Cottus* spp. (Cottidae) depressed chironomid densities in an Appalachian stream where they comprised 85% of the total benthic fauna. The dominance of chironomids in the present study ensured that a decline in their abundance reduced a total macroinvertebrate densities, as occurred also in Flecker's (1984) investigation. Because the impact of fish on prey is often highly taxon dependent (Thorp, 1986), predation may have an important impact on community structure if the numerically dominant species are vulnerable to predation. Accordingly, the importance of predation as a structuring mechanism for benthic communities will vary in response to (among other factors) the specific composition of the benthic community.

Although predator impacts appeared to be more severe during the dry season, impacts did occur during the wet season. This was despite the fact that the stream experienced greater, spate-induced disturbance at this time. The reduced predator impact in the wet season could be taken as support for the view that biotic factors are less important as determinants of community structure during times of abiotic disturbance in streams (Peckarsky, 1985; Hildrew & Townsend 1987; Power *et al.*, 1988; Resh *et al.*, 1988; Poff & Ward, 1989; Lancaster, 1990), but an effect of predators was still apparent. While biotic factors may be reduced in importance during periods of disturbance and high flow, it is clear that they can still

operate. In addition, although predator impacts inside cages appear to be reduced during the wet season, high flows at this time may be accompanied by increased mobility of invertebrates so that exchange rates between cages and the benthos are enhanced. This may have the effect of swamping predator impacts inside cages and could lead to an underestimate of predation intensity (Cooper *et al.*, 1991; Lancaster *et al.*, 1991).

A surprising result of the present study was that the presence of prey refugia did not reduce the impact of predators on benthic prey (cf. Sih, 1987; Fuller & Rand, 1990), especially larger invertebrates (Flecker & Allan, 1984). However, the apparent disparity depends upon the assumption that the relatively complex substrates provided secure refuges from predators. While the intact clay tiles that served as the 'simple' substrate offered few hiding places (and somewhat less surface area for settlement), the tile fragments that provided places of concealment in the 'complex' treatment could be moved aside (through a combination of pushing and butting movements) by well-grown *O. platycephalus* loaches (approximately 15 g fresh weight).

Accumulation of detritus in the closed cages on Week 4 gave rise to a possible confounding variable in the present investigation (see also Dudgeon, 1991), because of the positive relationship between macroinvertebrate densities and detrital standing stocks in cages (see also Egglishaw, 1964; Minshall & Minshall, 1977; Flecker, 1984). Peckarsky (1985) noted a similar confounding effect of siltation associated with predator inclusion/exclusion cages. Predation impacts that were detected during the present study did not differ significantly between Weeks 2 and 4 during the wet or dry season. This suggests that accumulations of detritus inside closed cages on Week 4 did not alter the effects of fish on macroinvertebrate densities. Nevertheless, differences in the amounts of detritus accumulating in open and closed cages point to a possible 'cage effect' that increased in importance as the study progressed. While the cage design used was the only practicable one if natural densities of fish were to be maintained inside open cages, it does raise the possibility that other, undetected differences may have arisen among treatments as the experiment proceeded.

Both season (acting through changes in stream flow volume) and predation affected the abundance of benthic invertebrates in Kwun Yum Shan stream.

Predation impacts were apparently reduced in summer when abiotic disturbance was greater, and were highly taxon specific. Substrate complexity did not reduce the ability of predators to reduce prey densities, but this effect may reflect distinctive foraging attributes of *O. platycephalus*. Abiotic factors, such as flow, may have a dominant influence upon the abundance of macrobenthos in Kwun Yum Shan Stream. Predation also plays a role, however, and the distribution of food (such as periphyton) results in small-scale, inter-patch differences in population densities (Dudgeon & Chan, 1992). These responses are taxon specific and, depending upon the particular predator and prey communities in the study stream, may be influenced also by the intensity of spate-induced disturbances. It remains to be seen, therefore, whether the findings reported herein will apply to other streams, or even to the same stream in a year where variation in the magnitude of the monsoonal rains alters the duration or intensity of spates.

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