

An experimental study of the influence of periphytic algae on invertebrate abundance in a Hong Kong stream

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SUMMARY

1. Small cages (294 cm²) containing unglazed clay quarry tiles were used to investigate the influence of periphytic algae on macroinvertebrate abundance in a Hong Kong stream. Algal biomass was manipulated by shading cages with plastic sheets. Individual cages were assigned to one of three treatment groups: unshaded, shaded and deeply shaded. Invertebrate densities and algal biomass within cages were monitored after 23, 37 and 65 days.
2. Multiple-regression analysis revealed that algal biomass, invertebrate morphospecies richness and total abundance declined with greater shading intensity. The responses of individual invertebrate taxa varied: some (especially Trichoptera) were unaffected by shading, whereas grazers (Baetidae, Psephenidae and Elmidae) declined as shading increased.
3. Significant regressions of the densities of individual taxa upon algal and detrital standing stocks in cages had positive slopes, but algal biomass increased during the study while detrital standing stocks declined. Abundance of invertebrates declined or remained rather stable over time. Density increases resulting from a positive association with algae were apparently offset by declines in abundance correlated with reductions in detritus.
4. Declines in algal biomass were associated with greater shading to which animals may respond directly. To uncouple the link between scarcity of algae and reduction of light intensity, the plastic covers on two groups of cages (deeply shaded and unshaded) which had been placed in the stream for 28 days were reversed so that cages which had been shaded became unshaded and vice versa. The cages were recovered on day 33. Only Coleoptera demonstrated a positive association with algae inside cages; no relationship between population densities and algal biomass or light intensity was apparent for other taxa. However, the design may have been confounded by deposition of sediment in the cages (due to declining stream discharge) which reduced population densities of colonizers.
5. This study documents changes in invertebrate abundance and morphospecies richness in response periphyton and detritus standing stocks within patches. Summation of such responses may account for observed variations in benthic communities among Hong Kong streams which differ in the extent of shading by riparian vegetation.

Introduction

The question of what determines the distribution and abundance of stream animals is related to the wider enquiry as to the factors determining community structure in nature. Stream biologists have emphasized the interplay between (relatively) deterministic biotic interactions and stochastic disturbances in this regard. They conclude that most lotic habitats are influenced by a combination of both processes, although biotic interactions tend to be more important at times of stable stream flow (e.g. Lake & Barmuta, 1986; Hildrew & Townsend, 1987; Statzner, 1987; Power *et al.*, 1988; Poff & Ward, 1989). Inter-stream differences in the abundance and composition of benthic invertebrate communities may therefore reflect discharge regime, but water chemistry or riparian vegetation will also have some influence. On a smaller scale, differences among patches within streams result from such factors as sediment characteristics, current speed and the presence of algae or detritus (e.g. Minshall, 1984).

There is evidence that periphytic algal biomass (or epilithon) can limit grazers in temperate streams and may lead to competition for food (Lamberti & Resh, 1983; McAuliffe, 1984a,b; Hawkins & Furnish, 1987; Feminella & Resh, 1990). Artificial shading of individual stream reaches in New Zealand and North America (Townsend, 1981; Fuller, Roelofs & Fry, 1986) have also resulted in lower densities and growth rates of some benthic invertebrates. By contrast, experimental investigations of the influence of resource availability on tropical stream invertebrates are scarce (Minshall, 1988) and may have biased perception of the importance of allochthonous detritus in streams (Minshall, 1978). This paper documents the effects of three levels of shading on the small (patch) scale of abundance of benthic invertebrates in a Hong Kong stream. The study was designed to demonstrate whether taxon-specific changes in abundance occurred in response to varying amounts of shading and algal standing stocks in individual patches. If present, such responses could account for reach- or catchment-level shifts in community composition associated with changes in riparian vegetation and shading in Hong Kong (Dudgeon, 1988, 1989).

Materials and Methods

Study site

The investigation was carried out in a first-order, headwater section of Kwun Yum Shan stream near Shek Kong, New Territories, Hong Kong, which drained a small, uninhabited valley (altitude 200 m) supporting mixed, evergreen, secondary forest. The stream waters were soft and slightly acidic (pH 6.4–6.7; conductivity 33.1–34.0 $\mu\text{S cm}^{-1}$), which is typical of unpolluted hillstreams in Hong Kong. Kwun Yum Shan stream is spring-fed and permanent. However, the experiments were carried out between 3 October and 12 December 1989 during the early part of the cool, dry season when discharge was declining. Weekly maximum–minimum water temperatures ranged from 15–21°C (minimum values) to 17–23°C (maximum values); the overall median temperature was 20.0°C. The stream had a stepped profile comprising a series of pools (<6 m² surface area, <30 cm deep) situated at the base of small waterfalls that were separated by short, shallow (<10 cm deep) riffles and runs. The stream bed in riffles and runs comprised small boulders (generally <50 cm longest dimension), sand and gravel. Despite its small size, the stream supported a diverse benthic fauna (Appendix 1) dominated by insects.

Experimental manipulations of the effects of shading

The experimental units were plastic cages of 294 cm² basal area (21 × 14 × 7.5 cm) and 4-mm mesh size containing three, 9.9 × 9.9 cm, unglazed clay quarry tiles. The tiles were positioned in each cage so that two tiles lay flat on the floor of the cage, while the third rested on top of (and partially covered) the lower pair. The periphyton developing on such tiles (mainly diatoms) was assumed to be essentially the same as that on natural rocks (Lamberti & Resh, 1985). The upper surface of each cage was covered entirely by 0.5-mm-thick plastic sheets fixed in place by metal clips. Each cage was covered by either a single sheet of green plastic (=shaded treatment), two sheets of green plastic (=deep-shaded treatment) or a single sheet of clear plastic (=unshaded treatment). Green rather than black plastic, as has been used by other workers (Townsend, 1981; Fuller, Roelofs & Fry, 1988), was chosen because it permitted manipulation of the degree of shading by using either

one or two sheets. The pattern of absorbance of light by these sheets when placed in a Beckman DU-70 spectrophotometer cell is shown in Fig. 1, and confirms treatment rankings in terms of shading intensity.

Cages were positioned in shallow riffles in the stream so that the upper edges of each cage (and associated plastic sheets) were above the water surface. On October 3 1989, forty-eight cages (sixteen of each treatment) were placed in the stream. They were placed in five short riffles which appeared similar with respect to substrate and current, and treatments were randomized. The cages were collected 23, 37 or 65 days later. Six replicates of each treatment were taken on day 23, and five replicates of each on days 37 and 65. Cages were recovered by placing a fine-meshed (250 μm) net downstream of the cage and sweeping it forward to enclose the cage while at the same time lifting the cage clear of the substrate and removing it from the stream. Any animals which may have been dislodged by this manoeuvre were washed by the current into the net. Care was taken to avoid disturbing the bottom sediments during cage recovery; nevertheless, some animals located beneath the cage on the substrate surface may have been included in collections. Samples were preserved with 10% neutral formalin in the field and returned to the laboratory for processing.

Animals and associated detritus (mostly leaf frag-

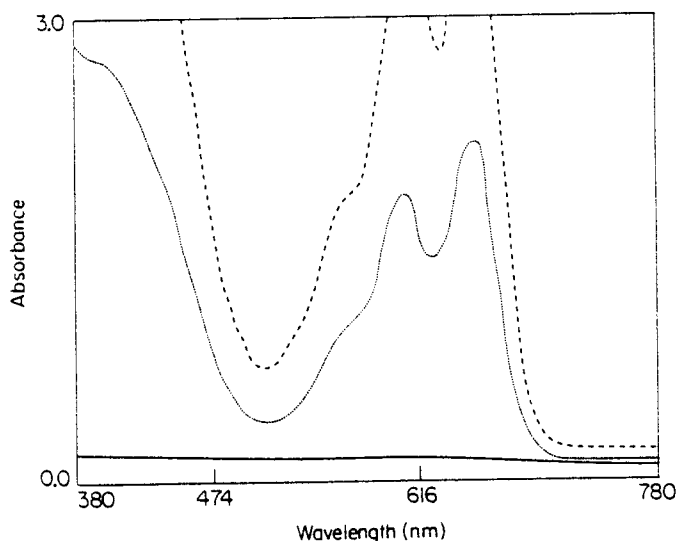


Fig. 1 Absorbance spectra of plastic sheets (clear plastic (—), single sheet of green plastic (---), double sheet of green plastic (-.-.-)) used in this experiment. Only wavelengths within the approximate limits of photosynthetically active radiation (PAR) are shown.

ments 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 and counted. Detritus was oven-dried at 70°C and weighed to the nearest 0.01 g. Periphyton was removed from the uppermost tile in each cage using a stiff brush and a small amount of water, and was concentrated on a glass-fibre filter (Whatman GF/F). The filters were deep-frozen for 30 min (to rupture algal cells) and photosynthetic pigments were extracted in darkness at 5°C for 1 h using 90% acetone. The concentration of chlorophyll *a* (corrected for phaeopigments) was obtained from spectrophotometer readings at 665 nm before and after acidification (Wetzel & Westlake, 1974) and used as an indication of algal biomass. Chlorophyll *a* has been used as an indicator of algal biomass in recent studies of interactions between stream invertebrates and periphyton (Vaughn, 1986; Richards & Minshall, 1988).

While the use of multiple cages rather than a single dark canopy (e.g. Towns, 1981; Fuller *et al.*, 1986) improves the experimental design of shading studies, it does introduce a cage effect. For example, current velocities inside the cages were generally less than 5 cm s^{-1} , approximately half those outside. In order to determine whether taxa colonizing cages were representative of the benthic community, twelve 25 \times 25-cm samples were taken using a modified Surber sampler procedure on 21 September 1989, prior to the start of experiments. Mesh size used was 220 μm . Samples were preserved with 5% formalin in the field. Invertebrates were hand-picked from stream debris under a stereomicroscope in the laboratory, identified and counted.

Statistical analysis

Multiple regression analysis was employed to test the hypothesis that shading treatment and/or time in the stream affected the numbers of animals colonizing cages. Treatments were quantitative and therefore multiple regression of numbers of colonists against shading level (1 = unshaded, 2 = shaded, 3 = deeply shaded) and time in stream (23, 37 and 65 days) was appropriate (Perry, 1986; Schultz, 1989). Chlorophyll *a* and detrital standing stocks were included as independent variables in these regressions, as both factors could have had direct effects

on colonizer abundance and need not have changed systematically over time or across shading treatments. Stepwise multiple regressions of colonizer abundance (Y) on various combinations of the four independent variables (X_{1-4}) were calculated according to Walpole & Myers (1978), and the coefficient of determination (i.e. 100% r^2) was used to indicate the proportion of the variation in Y that could be accounted for by the linear relationship with the independent variables. The aim was to obtain a minimum of unexplained residual variance in terms of the smallest number of independent variables, by removing those which did not reduce a significant ($P < 0.05$) independent portion of the variation in colonizer abundance (i.e. where t values for the partial regression coefficient were insignificant). Because these calculations assume a bivariate normal distribution of variables, data were log-transformed prior to analysis, thereby also minimizing difficulties associated with regressions of curved functions of Y on X . Analysis was carried out on counts of total number of animals per cage, the number of taxa (=morphospecies) per cage, and the abundance of those individual taxa (orders, families, subfamilies or species) which were relatively common ($\geq 5\%$ of total individuals collected). Three cages with exceptionally low densities of animals (< 30 individuals per cage; one replicate in each treatment) were not included in the statistical analysis.

Confounding variable

A criticism that could be levelled at the present investigation is that two factors are involved. A decline in algal standing stock by shading is accompanied by a reduction in light intensity to which animals may respond directly. Thus it is not clear whether differences in macroinvertebrate population densities among shading treatments can be directly attributed to reduced algal biomass. To separate the effects of light intensity and algae, twelve cages (six unshaded and six deep-shade treatments) were placed in the stream on 7 November; after 28 days the covers on the cages were switched so that cages that had accumulated a relatively high algal biomass became deeply shaded and those with a low algal biomass became unshaded. By this procedure, the link between high-light intensity and greater algal biomass was uncoupled. Animal colonization was

allowed to continue for 5 days before the cages were removed from the stream and returned to the laboratory for processing. Differences in invertebrate abundance and algal standing stocks between treatments were analysed by one-way ANOVA on log-transformed data.

Results

Experimental manipulations of the effects of shading

Multiple regression analysis revealed that algal biomass differed significantly among treatments ($t = 3.62$, $P = 0.0008$) and increased over time ($t = 3.69$, $P = 0.0006$; overall model $F_{2,42} = 13.35$, $P < 0.0001$) (Fig. 2). This confirmed the expectation that a lower algal biomass was associated with a greater degree of shading. Accumulated detritus in cages, in contrast, did not vary significantly among treatments and decreased significantly over time ($F_{1,43} = 7.99$, $P = 0.007$).

A total of fifty-two morphospecies were recovered from cages during the study, compared to seventy-six morphospecies taken in benthic samples from

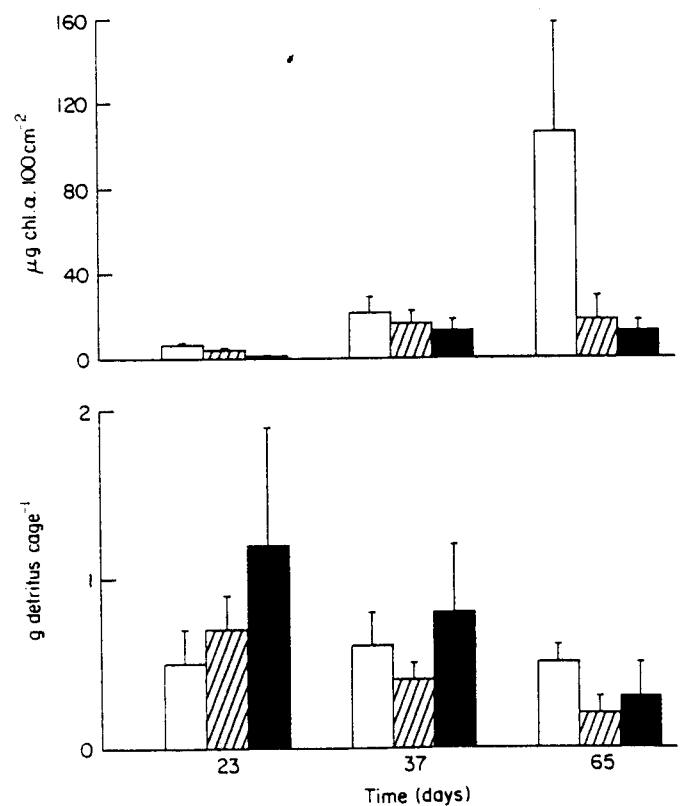


Fig. 2 Mean (\pm SEM) algal biomass and detrital standing stocks in cages in Kwun Yum Shan stream under three shading regimes. □, unshaded; ▨, shaded; ■, deeply shaded.

Kwun Yum Shan Stream immediately before the investigation (Appendix 1). The results of multiple regression analysis upon the abundance of various taxa of cage colonizers are summarized in Table 1. In all cases of significant models, correlation coefficients (r) or the slope of the regression line of colonizer abundance on chlorophyll a biomass and detritus standing stocks were positive; r values for regressions of abundance on treatment and time were negative (i.e. there were fewest animals in the deeply shaded cages towards the end of the experiment). Overall, shading treatment affected the numbers of individuals and taxa colonizing cages (Fig. 3), but detrital and algal biomass were also significant predictor variables in best-fit regression models (Table 1).

Taxon-specific responses to shading treatment were found, and the effects of shading were apparent on mayflies, Plecoptera, Psephenidae (*Mataopsephus*) and other beetles (mostly Elmidae) (Figs 4 & 5). Algal biomass was included in best-fit regression models as a significant predictor of the abundance of mayflies (as well as some Diptera) but not beetles (Table 1). In contrast, *Diplectrona* (Hydropsychidae) and other caddisflies such as philopotamids (*Chimarra*) and the shredder *Anisocentropus maculatus* Ulmer (Calamoceratidae) were unaffected by shading treatment

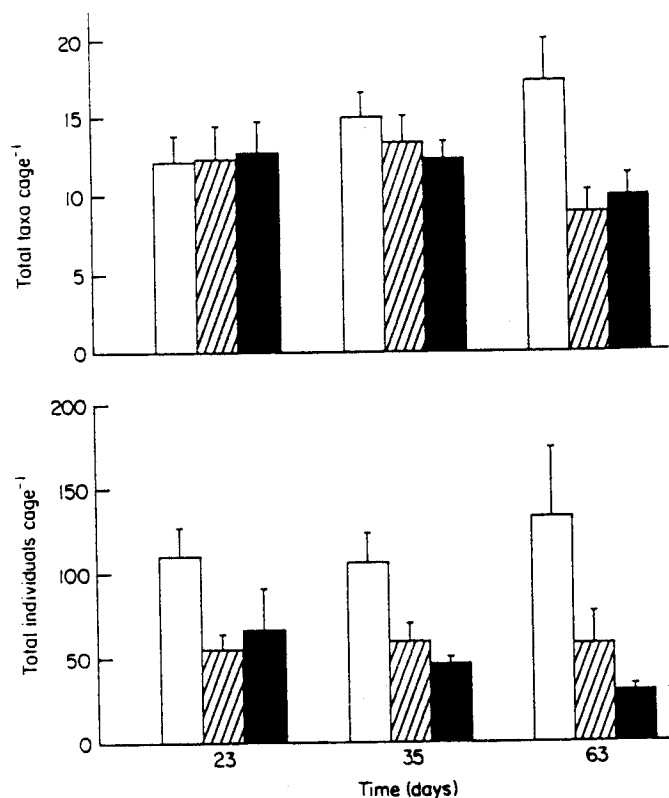


Fig. 3 Total number of invertebrate taxa (= morphospecies) and individuals colonizing cages in Kwun Yum Shan stream under three shading regimes; data were collected on three occasions during the 65-day investigation. □, unshaded; ▨, shaded; ■, deeply shaded.

Table 1 Results of multivariate regression analysis of macroinvertebrate abundance (Y) on shading treatment, time, chlorophyll a concentration and detrital biomass (X_{1-4}). The significance of partial regression coefficients in best-fit models is indicated as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

	Treatment	Time	Chl. a	Detritus	Overall model			
					100 $r^2\%$	F	df	P
<i>Indobaetis</i>	***	***	***	—	70.0	31.83	3,41	<0.0001
Other mayflies	***	—	—	—	26.3	15.33	1,43	0.0003
All mayflies	***	***	***	*	69.8	23.08	4,40	<0.0001
Plecoptera	*	—	—	**	27.5	7.95	2,42	0.0012
<i>Diplectrona</i>	—	—	—	**	21.3	11.67	1,43	0.001
Other caddisflies	—	—	—	***	33.8	21.93	1,43	<0.0001
All caddisflies	—	—	—	***	31.8	20.05	1,43	0.0001
Orthoclaudiinae	**	—	—	***	34.5	11.05	2,42	0.0001
Chironominae	—	***	—	**	46.6	18.30	2,42	<0.0001
Other Diptera	—	—	—	*	13.3	6.59	1,43	0.014
All Diptera	—	***	—	**	50.6	13.97	2,42	<0.0001
<i>Mataopsephus</i>	**	—	—	—	17.0	8.80	1,43	0.005
Other beetles	***	—	—	—	32.2	20.44	1,43	<0.0001
All beetles	*	—	—	**	33.8	10.73	2,42	0.0002
<i>Neocaridina</i>	—	***	—	—	39.9	28.58	1,43	<0.0001
Total taxa	*	—	*	**	39.4	8.9	3,41	0.0001
Total individuals	***	—	*	***	64.7	25.03	3,41	<0.0001

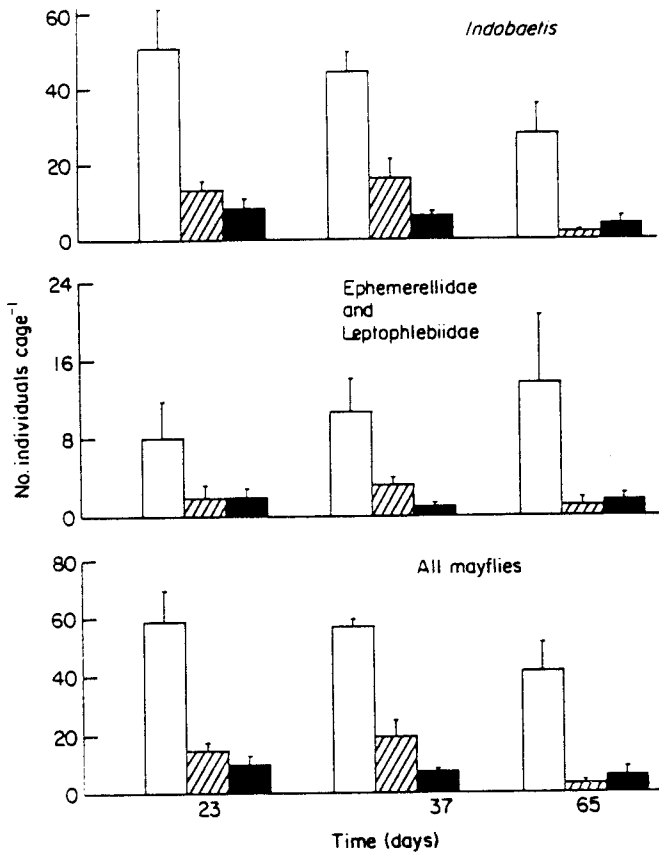


Fig. 4 The number of mayflies colonizing cages in Kwun Yum Shan stream under three shading regimes; data were collected on three occasions during the 65-day investigation. □, unshaded; ▨, shaded; ■, deeply shaded.

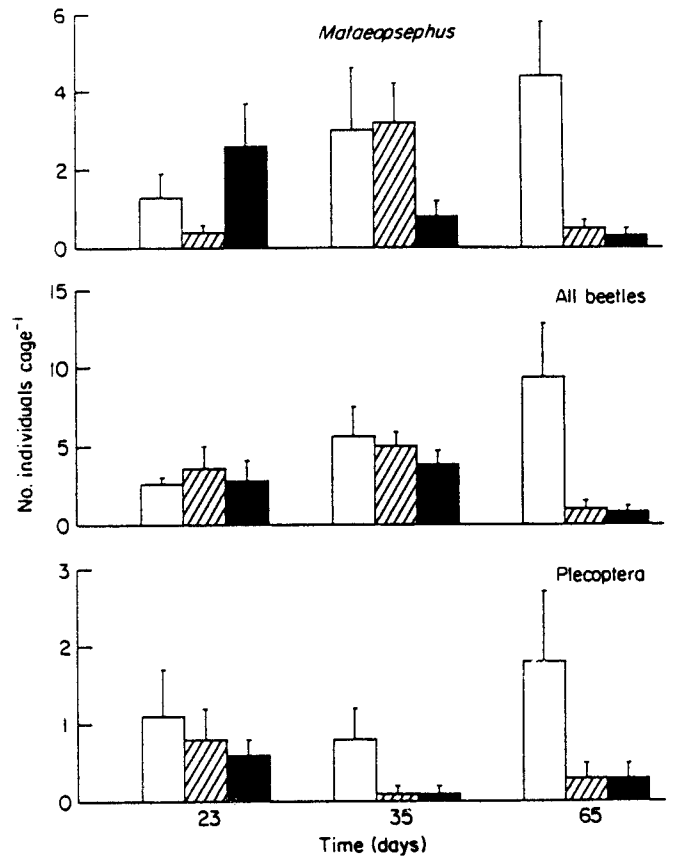


Fig. 5 The number of Coleoptera and Plecoptera colonizing cages in Kwun Yum Shan stream under three shading regimes; data were collected on three occasions during the 65-day investigation. □, unshaded; ▨, shaded; ■, deeply shaded.

(Fig. 6), and their abundance was related to standing stocks of detritus in cages (Table 1). Detritus was also an important predictor variable for chironomids and other Diptera (mostly Tipulidae).

As the aim of this study was to investigate the importance of algae as a determinant of the distribution and abundance of macroinvertebrates in Kwun Yum Shan stream, a bivariate regression analysis of the abundance of individual taxa inside each cage versus the algal standing stock in that cage ($n = 45$) was undertaken. The analysis was repeated using detritus as the independent variable, because the multivariate analysis had highlighted its possible influence on macroinvertebrate abundance. The results indicated that numbers of taxa and the abundance of all taxa tested (with the exception of the shrimp *Neocaridina serrata* (Stimpson)) were significantly and positively affected by either algae, or detritus and sometimes both (Table 2).

Confounding variable

To uncouple the link between scarcity of algae and reduction of light intensity, the plastic covers on two groups of cages (deeply shaded and unshaded) which had been placed in the stream for 28 days were reversed so that cages which had been shaded became unshaded and vice versa. One-way ANOVA revealed no significant differences in the numbers of animals colonizing cages in the two treatment groups ($F_{1,10} < 1.89$, $P > 0.19$) except for Coleoptera. *Mataeopsephus* ($F_{1,10} = 5.50$, $P = 0.040$), other beetles (mostly Elmidae) ($F_{1,10} = 22.86$, $P = 0.0007$), and all beetles combined ($F_{1,10} = 21.96$, $P = 0.0009$) were more numerous in cages which had been unshaded for 28 days and then deeply shaded for a further 5 days prior to recovery from the stream (Fig. 7). These cages had higher algal standing stocks ($9.5 \pm 3.9 \mu\text{g } 100 \text{ cm}^{-2}$) than the group treated in the converse

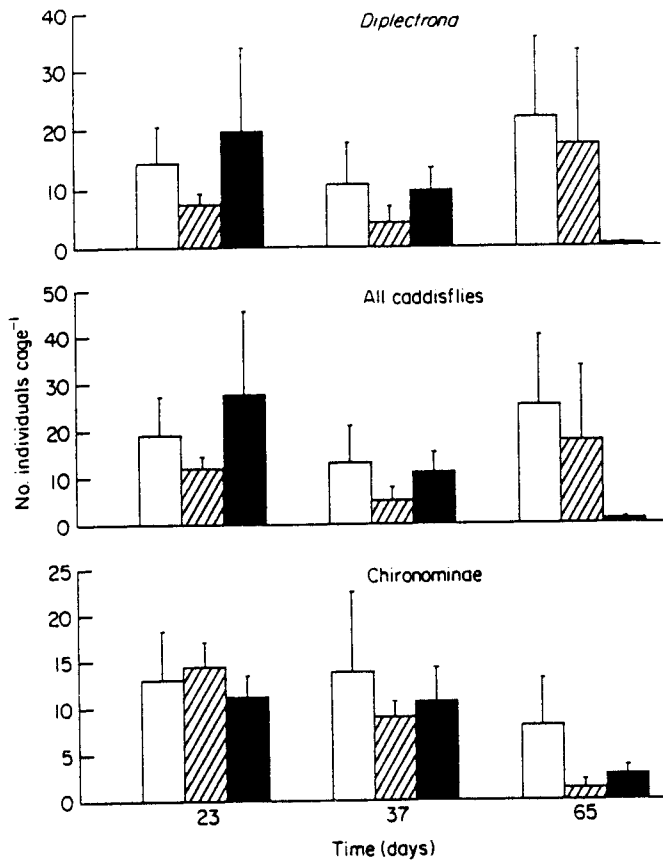


Fig. 6 The number of Trichoptera and Chironominae (Diptera: Chironomidae) colonizing cages in Kwun Yum Shan stream under three shading regimes; data were collected on three occasions during the 65-day investigation. □, unshaded; ▨, shaded; ■, deeply shaded.

fashion ($1.4 \pm 0.7 \mu\text{g } 100 \text{ cm}^{-2}$) ($F_{1,10} = 20.98$, $P = 0.001$). No significant difference was observed in the standing stocks of detritus between the two groups of cages (1.2 ± 0.1 and $1.4 \pm 0.1 \text{ g DW cage}^{-1}$). The importance of algae in enhancing the abundance of Coleoptera was shown from regression analysis of total numbers of beetles per cage (both treatment

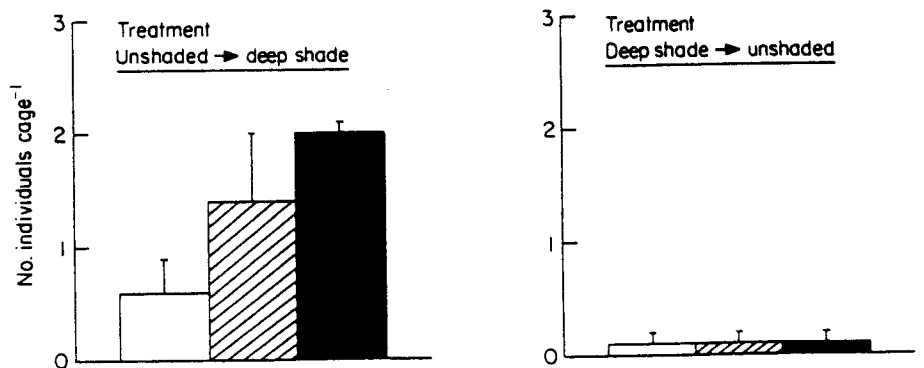
Table 2 Results of bivariate regression of macroinvertebrate abundance on chlorophyll *a* or detrital biomass in cages during the confounding variable experiment. The significance of the regressions and the *r* values presented are indicated as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

	Independent variables			
	Chl. <i>a</i>		Detritus	
<i>Indobaetis</i>	*	0.368	*	0.336
Other mayflies	*	0.368	—	—
All mayflies	**	0.390	*	0.339
Plecoptera	—	—	**	0.413
<i>Diplectrona</i>	—	—	**	0.462
Other caddisflies	—	—	***	0.581
All caddisflies	—	—	***	0.564
Orthocladiinae	*	0.353	**	0.451
Chironominae	—	—	***	0.553
Other Diptera	*	0.365	—	—
All Diptera	—	—	***	0.506
<i>Mataeopsephus</i>	*	0.320	—	—
Other beetles	—	—	***	0.568
All beetles	—	—	***	0.485
<i>Neocaridina</i>	—	—	—	—
Total taxa	**	0.395	**	0.401
Total individuals	**	0.379	***	0.487

groups combined) upon algal standing stocks ($r = 0.814$, $F_{1,10} = 19.67$, $P = 0.0001$).

The lack of any inter-treatment difference among most groups of macroinvertebrates may have been a consequence of declining stream discharge during the latter part of the investigation, culminating in flow becoming interstitial in parts of the stream during January 1990 (Dudgeon, 1991). Declining flows led to deposition of a fine film of sediment on the surface of tiles within cages shortly after the plastic covers had been switched between treatments.

Fig. 7 The number of Coleoptera colonizing cages after 33 days in Kwun Yum Shan stream; the plastic covers on the two groups of cages (deeply shaded and unshaded) were reversed after the first 28 days so that cages which had been shaded became unshaded and vice versa. □, *Mataeopsephus*; ▨, other beetles (Hydrophilidae, Helodidae and Elmidae and Dryopidae); ■, all beetles.



The effects of sediment reduced the numbers of animals colonizing cages and may have lessened any treatment effect. Evidence of this reduction is apparent from total densities of cage colonizers. Cages that had been in the stream for 23 days (3–26 October 1989) contained between fifty-six and 110 animals per cage (= range of mean values for the three treatment groups; Fig. 2), but mean values for the two groups that had been in the stream for 33 days (28 + 5 days, 9 November to 12 December, 1989) were only 24.2 ± 8.3 and 24.6 ± 10.6 animals.

Discussion

Shading significantly reduced the rate of accumulation of algal biomass in cages and influenced the abundance of certain macroinvertebrate taxa. Some of these (Baetidae, Psephenidae, Elmidae) were algal grazers. In addition, species richness and total numbers of colonizers declined in shaded cages, demonstrating a local community-level effect of the experimental treatment. The abundance of Trichoptera did not change systematically among treatments but varied in response to detrital standing stocks in cages. This was true also of certain Diptera, and detritus standing stocks accounted for some of the inter-cage variation in species richness and total macroinvertebrate abundance.

Colonizer densities in cages did not increase over time, as a simple model of colonizer dynamics on introduced substrates (e.g. Sheldon, 1977) might have predicted. Indeed, taxa whose densities changed significantly (see Table 1) continued to decline over the study period. Variation in the abundance of some taxa was a consequence of positive correlations with algal and/or detrital standing stocks (e.g. mayflies and beetles in Table 1). While algae increased over the study and may have enhanced invertebrate abundance, detritus decreased at the same time and may have contributed to lower population densities. The relative strengths of responses to these variables could have determined whether populations remained fairly stable or declined over the period of the investigation.

Declines in detritus standing stocks inside cages may have resulted from the processing activities of shredders. However, it is also possible that the initially high rate of accumulation of detritus (up to day 23) was not maintained throughout the study

because stream discharge was declining. If so, flow conditions inside the cages may have changed during the investigation, and could have contributed to declines in the abundance of some taxa (*Indobaetis*, Chironominae, etc.).

The results of this experiment suggest that both algae and detritus are important determinants of macroinvertebrate abundance among patches in Kwun Yum Shan stream. However, evidence of the importance of algae is confounded by the fact that light intensity was reduced in patches with low algal biomass. Attempts at experimental manipulation to uncouple the link between light and algae were obscured by further declines in stream flow and deposition of fine sediment which reduced the numbers of colonizers in cages. Nevertheless, there was evidence that beetle abundance was greater in algae-rich patches (despite reduced light intensity) although no relationship between population densities and algal biomass or light intensity was apparent for other taxa.

Research in temperate streams has shown that periphytic algae can have an important effect on macroinvertebrate abundance, growth rate, production and community composition (e.g. Towns, 1981; Behmer & Hawkins, 1986; Fuller *et al.*, 1986; Vaughn, 1986; Richards & Minshall, 1988). The results of the present investigation are in general agreement with those of such studies in that total invertebrate abundance, species richness and the densities of some taxa were reduced by shading. Moreover, regression of population densities on algal biomass (Table 2) were positive for some taxa although not as frequent nor as strongly significant as the positive relationship between the abundance of individual taxa and detrital standing stocks. Other research in Hong Kong (Dudgeon, 1990) and elsewhere (reviewed by Minshall, 1984) suggests that detritus may not restrict the distribution or abundance of invertebrates in streams as it is present in excess and rarely limiting (but see Richardson, 1991). In the cages in Kwun Yum Shan, however, rather small amounts of detritus accumulated and it may have been a limiting resource (as substrate or food). For example, the standing stocks (mean \pm SEM) of detritus in cages on day 23 and day 65 were 27.56 ± 8.51 and 11.91 ± 2.72 g DW m⁻², respectively. At the beginning of the experiment, standing stocks of non-woody detritus in the stream were 57.76 ± 14.24 g DW m⁻² ($n = 12$; Dudgeon,

unpublished data) — more than twice the amount in cages on day 23 and almost five times that on day 65.

The influence of algae and detritus on macroinvertebrate distribution and abundance within streams is likely to be reflected in inter-stream (or inter-reach) variations in community structure where there are differences in riparian vegetation and hence in the relative importance of allochthonous and autochthonous food sources (e.g. Hawkins *et al.*, 1982, 1983). Riparian vegetation does influence macroinvertebrate community structure and functional organization in Hong Kong streams (Dudgeon, 1988; 1989) and the present study demonstrates that such differences may have their origin in taxon-specific responses to inter-patch differences in algal and detrital standing stocks.

Acknowledgments

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	Density	%	C
Gastropoda			
<i>Brotia hainanensis</i> (Brot)	≤0.3	* ≤0.1	*
Decapoda			
<i>Neocaridina serrata</i> (Stimpson)	≤0.3	≤0.1	*
Ephemeroptera			
<i>Baetiella</i> sp.	1.0 ± 0.4	0.4	—
<i>Baetis</i> spp. (3)	4.8 ± 1.6	2.0	* (2)
<i>Chopralla</i> sp.	0.5 ± 0.2	0.2	*
<i>Indobaetis</i> sp.	5.3 ± 1.4	2.2	*
<i>Pseudocloeon</i> spp. (2)	0.4 ± 0.2	0.2	* (1)
<i>Cinygmia</i> sp.	≤0.3	≤0.1	*
<i>Electrogena</i> sp.	—	—	*
<i>Paegniodes cupulatus</i> (Eaton)	≤0.3	≤0.1	—
<i>Choroterpes</i> sp.	2.5 ± 0.8	1.1	*
<i>Habrophlebiodes gilliesi</i> Peters	1.6 ± 0.6	0.7	*
<i>Isca (Isca) purpurea</i> Gillies	2.8 ± 0.3	1.2	*
<i>Ephemerellina</i> sp.	≤0.3	≤0.1	—
<i>Serratella</i> sp.	1.8 ± 1.4	0.8	*
Ephemerellid sp. indet.	≤0.3	≤0.1	*
<i>Ephemera (Ephemera)</i> spp. (2)	13.5 ± 3.7	5.7	*
Odonata			
<i>Euphaea decorata</i> Selys	0.8 ± 0.3	0.3	*
<i>Mnias mneme</i> Ris	—	—	*
<i>Protosticta taipokauensis</i>			
Asahina & Dudgeon	0.4 ± 0.2	0.2	—
<i>Heliogomphus scorpio</i> Ris	≤0.3	≤0.1	—
<i>Onychogomphus sinicus</i> Chao	≤0.3	≤0.1	—

Appendix 1

Densities of taxa in benthic samples from Kwun Yum Shan stream, (mean no. $0.065 \text{ m}^{-2} \pm 1$ SEM, $n = 12$) and their relative abundance (overall %). Taxa present in (*) or absent from (—) cages (C) are also shown. Figures in parentheses indicate the numbers of morphospecies distinguished within a genus or family

Appendix 1 (cont.)

		Density	%	C
Plecoptera				
<i>Amphinemura</i> sp.		0.8 ± 0.5	0.3	*
Neoperlinae	(3)	0.9 ± 0.2	0.4	* (2)
Heteroptera				
<i>Distotrephes heveli</i> Polhemus		0.6 ± 0.2	0.3	*
Trichoptera				
<i>Rhyacophila</i> sp.		≤ 0.3	≤ 0.1	*
<i>Agapetus</i> sp.		0.9 ± 0.5	0.4	*
<i>Chimarra</i> sp.		1.2 ± 0.4	0.5	*
cf. <i>Polycentropus</i> sp.		≤ 0.3	≤ 0.1	—
<i>Pseudoneureclipsis</i> spp.	(3)	0.4 ± 0.2	0.2	* (2)
<i>Cheumatopsyche</i> sp.		≤ 0.3	≤ 0.1	—
<i>Hydropsyche</i> sp.		≤ 0.3	≤ 0.1	—
<i>Diplectrona</i> sp.		5.0 ± 1.4	2.1	*
<i>Anisocentropus maculatus</i> Ulmer		0.8 ± 0.4	0.3	*
<i>Micrasema</i> sp.		≤ 0.3	≤ 0.1	—
<i>Psilotreta kwantungensis</i> Ulmer		2.0 ± 0.6	0.8	*
<i>Goerodes</i> sp.		≤ 0.3	≤ 0.1	—
Lepidoptera				
Pyrilidae	(2)	≤ 0.3	≤ 0.1	—
Coleoptera				
cf. <i>Hydrovatus</i> sp.		≤ 0.3	≤ 0.1	—
Hydrophilidae	(2)	8.1 ± 2.2	3.4	* (2)
cf. <i>Helodes</i> sp.	(2)	42.3 ± 8.9	17.9	*
<i>Eulichas</i> sp.		≤ 0.3	≤ 0.1	—
Ptilodactylidae sp. indet.		≤ 0.3	≤ 0.1	—
<i>Eubrianax</i> sp.		≤ 0.3	≤ 0.1	—
<i>Mataeopsephus</i> sp.		15.9 ± 3.5	6.7	*
Dryopidae	(2)	2.8 ± 1.1	1.2	* (2)
Elmidae	(3)	12.1 ± 2.2	5.1	* (2)
Diptera				
<i>Simulium</i> sp.		5.5 ± 2.5	2.3	*
Chironominae		21.8 ± 8.8	9.2	*
Orthocladiinae		28.5 ± 14.1	12.1	*
Tanypodinae		13.7 ± 4.1	5.8	*
<i>Bezzia</i> sp.		0.6 ± 0.3	0.3	—
Ceratopogonidae	(2)	0.5 ± 0.3	0.2	* (2)
Tipulidae	(4)	29.1 ± 5.6	12.3	* (2)
Dixidae		—	—	*
Psychodidae	(2)	2.0 ± 1.6	0.8	* (2)
Empididae	(3)	2.7 ± 0.9	1.1	* (2)
Statiomyidae	(2)	≤ 0.3	≤ 0.1	* (2)
Total taxa	76			52
Total density (no. 0.065 m ⁻²)		235.6 ± 41.2		