

## Resource Enhancement of Grazing Mayfly Nymphs by Retreat-building Caddisfly Larvae in a Sandbed Stream

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### Abstract

Over the summer–autumn low-flow period in the sandy upper and middle reaches of the Creightons Creek system of northern Victoria, Australia, several different macroscopically visible substrate patch types form on the streambed. Exploratory multivariate analyses revealed a distinct macroinvertebrate fauna associated with each patch type. The major patch types were the thalweg, or pathway of main flow, in which the substrate consisted of constantly shifting fine sand, and adjacent stable patches of coarser sand, covered with larval retreats of the hydropsychid caddisfly *Cheumatopsyche* sp. (Trichoptera:Hydropsychidae). Although thalweg and *Cheumatopsyche* patches contained a similar interstitial macroinvertebrate fauna, the former lacked a surface-dwelling, or epibenthic, fauna. The silken retreats of *Cheumatopsyche* larvae entrained algal filaments and detritus, food of the grazing mayfly nymph *Baetis* sp. *Baetis* nymphs recolonized plots containing *Cheumatopsyche* retreats in higher numbers than plots in which *Cheumatopsyche* retreats and their entrained detritus had previously been scoured away. Given the widespread distribution of the *Cheumatopsyche* patch type in the system during the low-flow period, it is hypothesized that the indirect interaction between these two species may constitute a significant pathway in the energy budget of the stream.

*Extra keywords:* lowland stream, indirect interactions, Ephemeroptera, Trichoptera, multidimensional scaling, experiment.

### Introduction

The effects of indirect interactions between species can outweigh direct effects and may in some instances control community structure (Vandermeer *et al.* 1985; Miller and Kerfoot 1987). Although exploitative competition is probably the most thoroughly studied of all indirect interactions (Schoener 1983; Yodzis 1988), there are many examples of facilitation—a form of indirect mutualism (Vandermeer 1980) where one species, through its effect on an intermediary species or on the physical environment, benefits another. A typical example of this type of interaction is that reported by Gallagher *et al.* (1983), who found that tube building by polychaetes and crustaceans on intertidal sandflats facilitated the recruitment of other benthic invertebrates.

In comparison with other types of ecological systems, however, less is known about facilitation effects in streams. Power (1990a) found that grazing by armoured catfish in a Panamanian stream facilitated the growth of their own algal food source by clearing off smothering sediments. Diamond (1986) showed that hydropsychid caddisfly larvae facilitated the presence of other macroinvertebrate taxa in a stony stream, although in this instance the mechanism responsible for the facilitation effect was not ascertained.

The present study investigated the presence of a facilitation effect between hydropsychid caddisfly larvae and grazing mayfly nymphs in a soft-bottomed lowland stream. Over the summer–autumn low-flow period in sandy lowland streams of north-central Victoria, several different substrate patch types form on the streambed. One of the most extensive of these patch types is covered with larval retreats of the hydropsychid caddisfly *Cheumatopsyche* sp. (Trichoptera:Hydropsychidae). Like most hydropsychids, *Cheumatopsyche* larvae construct retreats over which they weave silk nets to filter detritus and prey from the water column. Algal filaments and discarded silk trail behind capture nets and drape over the substrate entraining fine particulate matter. As a result, the surface of *Cheumatopsyche* patches is covered in a thin layer of fine detritus. It was predicted, therefore, that the net construction activities of *Cheumatopsyche* larvae enhanced food resources for grazing macroinvertebrates by providing attachment sites for algae and entraining detritus. This paper provides a description of the substrate patches and records a removal experiment to test the hypothesis that retreat building by *Cheumatopsyche* larvae facilitates colonization by nymphs of the grazing mayfly *Baetis* sp. (Ephemeroptera:Baetidae) by enhancing the abundance of their food resource.

## Materials and Methods

### Study Site

Creightons Creek is a low-gradient stream system draining the south-western arm of the Strathbogie Ranges of north-central Victoria. Large quantities of erosion-derived sand, resulting from agricultural activities in the upper part of the catchment, have blocked the mid reaches of Creightons Creek, forcing all flow down a former anabranch, Branjee Creek (see O'Connor 1991; O'Connor and Lake 1993). The study site was on Branjee Creek, immediately upstream of the Longwood–Pranjip Road (145°26'E, 36°45'S, National Map 7924, grid ref. CV 577336). At the time of this study, March 1988, the stream at this site was clear, broad (about 5 m wide) and shallow, with a bed composed of coarse to fine sand. Mean water depth and velocity ( $\pm 95\%$  C.I.) during the study were  $5.5 \pm 4.2$  cm and  $10.0 \pm 6.3$  cm  $\cdot$  s<sup>-1</sup>, respectively. Much of the original riparian vegetation had been cleared, or had been undercut by bank erosion and had toppled into the stream; however, some riparian trees remained (e.g. river red gum, *Eucalyptus camaldulensis*, and grey box, *E. microcarpa*). Dense stands of the macrophytes *Bulboschoenus medianus* and *Typha orientalis* were present along the stream margins.

### Substrate Patch Description

During the summer–autumn low-flow period in Branjee Creek, seven different types of submerged substrate patches were macroscopically visible on the streambed (Fig. 1). At low discharge, most water flowed down the middle of the stream in a sinuous pathway, referred to by hydrologists as the 'thalweg' (Morisawa 1968). The substrate of the thalweg consisted of unstable, constantly shifting sand. Adjacent to the thalweg were large patches of stabilized sand covered with larval retreats of the caddisfly, *Cheumatopsyche* sp. (Melbourne Water Board voucher MWB4). Other patches included leaf and bark litter, emergent reeds, small silty backwaters, stream-margin silt channels, and mats of blue-green algae in the thalweg (Fig. 1).

On 6 March, single samples from four separate patches of each type were collected to record the macroinvertebrate fauna of the patches. All samples from one patch type were considered as replicates. Each patch type, except for reeds and leaf litter, was sampled by pressing a 30-cm long PVC tube (15 cm diameter) 10 cm into the sand and sliding a metal disc underneath to seal the base. The resultant core was then slipped into a 250- $\mu$ m mesh net with an aperture of 25  $\times$  25 cm. Reed and leaf-litter patches were sampled by single scoops (approximately 1 s) of the same net. Invertebrates and organic matter were elutriated from sand in the field, and preserved in 2% formaldehyde for later sorting and identification.

Microhabitat information on each patch type included depth, current velocity (measured at 0.6 of the depth), and fine organic matter (<2 mm) content of each sample. Velocity was measured in the field with a Nixon Company (model 403) current meter. Organic-matter dry weight was measured in the laboratory after the removal of macroinvertebrates. Dry weight was measured as weight loss after ignition at 550°C. Macroinvertebrates were identified to described species where possible. Some

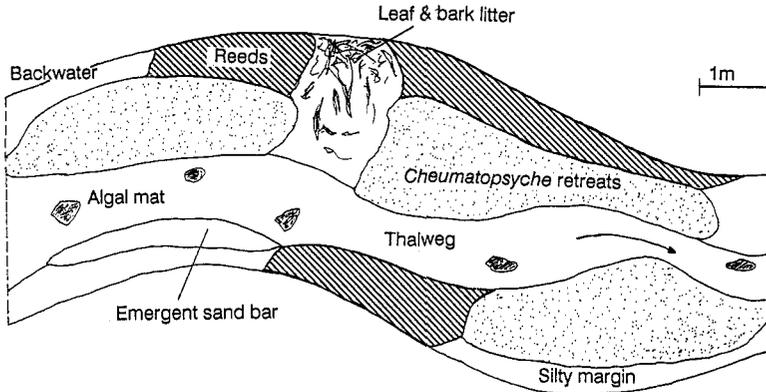


Fig. 1. Substrate patch types in Branjee Creek during the summer–autumn low flow period. Emergent sand bars were not sampled in this study.

specimens collected were as yet undescribed species or species for which larvae could not be matched conclusively with described adults. In most cases these taxa were matched to voucher specimens held at either the State Water Laboratory of Victoria (SV), the Museum of Victoria (MV) or the Melbourne Water Board Laboratories (MWB).

The similarity of the macroinvertebrate fauna among patch types was measured using hybrid multidimensional scaling (HMDS) which has been shown by Minchin (1987), Faith *et al.* (1987) and Minchin (personal communication) to be superior to the commonly used ordination method of detrended correspondence analysis. Prior to ordination, species occurring in fewer than two samples were deleted and abundances of remaining species were  $\log(x+1)$  transformed. The log-transformed species data were standardized by dividing the abundance of each species in each sample by the maximum abundance attained by that species in any sample. These transformations and standardizations prevented very abundant species from dominating the ordination (Bowman and Minchin 1987). Compositional dissimilarity between each pair of samples was computed using the Bray–Curtis coefficient (Greig-Smith 1983). Vectors of maximum linear correlation of the three sample variables (depth, velocity, and organic matter) were plotted in HMDS ordination space and the significance of each variable tested by comparison with 99 random permutations of the same variable (Faith and Norris 1989; Minchin 1990a). The maximum correlation of a sample variable was judged significant ( $P < 0.05$ ) if it was greater in absolute magnitude than at least 95 of the random permutations. Data entry, transformations, standardizations and HMDS procedures were performed using the computer programs DECODA and MDS (Minchin 1990a, 1990b).

#### Facilitation Experiment

Preliminary field observations indicated that the macroinvertebrate fauna of *Cheumatopsyche* patches could be separated into two groups: sediment-surface-dwelling or epibenthic species; and interstitial species. The most abundant epibenthic grazer in *Cheumatopsyche* patches was the conspicuous mayfly nymph, *Baetis* sp. (Museum of Victoria voucher MV4). Three other common epibenthic grazer species were also present: a conoesucid caddis larva, *?Costora* sp., a leptophlebiid mayfly nymph, *Nousia ?fuscula*, and naidid oligochaetes. However, because of the cryptic daylight behaviour of *Nousia*, and the difficulty in observing tiny *?Costora* and naidids with the naked eye, the facilitation hypothesis was tested using only *Baetis*. Other epibenthic grazer species were too rare for use in experimental manipulations.

To test the facilitation hypothesis, 60 circular plots of 20 cm diameter in *Cheumatopsyche* patches were selected on 22 March with no more than one plot per patch. To avoid changing the current velocity, each plot was marked by hammering in wooden stakes 30 cm clear of either side of the plot centre. A piece of masking tape on a monofilament nylon line strung between the two stakes marked the centre of each plot. Using random number tables, 10 plots were allocated to each of six treatments (Table 1). In the first treatment, all *Cheumatopsyche* retreats were manually scoured away. This procedure also removed the fine-sediment matrix surrounding retreats and all other macroinvertebrates.

**Table 1. Treatments for the facilitation experiment**

The Scour 48 h, Removal 48 h, and Scare treatments were initiated and then left for 48 h prior to sampling. Scour 0 h and Removal 0 h treatments were initiated and sampled immediately. All treatments were sampled on the same day. For each treatment,  $n=10$

Treatment	Procedure
Scour 48 h	All species and sediment matrix scoured away
Removal 48 h	<i>Cheumatopsyche</i> larvae and their retreats picked out
Scare	<i>Baetis</i> nymphs scared away
Control	
Scour 0 h	As for Scour 48 h
Removal 0 h	As for Removal 48 h

In the second treatment, *Cheumatopsyche* larvae were picked out of their retreats with fine forceps. About 25% of the larvae hung onto their retreats while being removed, thus dislodging the retreat as well. However, in such instances the fine-sediment matrix around the retreats remained intact and the total area of dislodged retreats made up less than 5% of the plot area. The removal activity also caused *Baetis* nymphs to flee the disturbed area. For the third treatment, the *Cheumatopsyche* removal activity was simulated without removing any *Cheumatopsyche* larvae. This had the effect of scaring away *Baetis* nymphs in the same fashion as the previous treatment while leaving *Cheumatopsyche* larvae and their retreats intact. After 48 h, the first three treatments and a previously undisturbed 'control' treatment, were sampled using the PVC tube and metal disc described above. The first two treatments were also repeated and sampled immediately to assess their initial effectiveness. These treatments enabled the examination of the recolonization of *Baetis* on (i) plots with normal densities of *Cheumatopsyche* larvae and retreats, (ii) plots with retreats only, and (iii) plots without larvae or retreats.

To assess whether *Cheumatopsyche* retreats were enhancing the food resource of *Baetis* nymphs, five 1-cm deep substrate samples were collected in both thalweg and *Cheumatopsyche* patches and preserved in 2% formaldehyde. In the laboratory, sand was separated from organic matter by elutriation, and subsamples of the organic matter were mounted on slides, beneath glass coverslips, for microscopic examination. The diet of *Baetis* was compared with the availability of its putative food source by mounting the gut contents of 10 specimens from *Cheumatopsyche* patches. A microscope eye-piece with a  $10 \times 10$  graticular grid was used to separate organic matter from sediments and to sort *Baetis* gut contents into five categories: vascular plant material, fine amorphous detritus, filamentous algae, diatoms, and animal material. The abundance of each category was calculated as the percentage of grid cells in which that category was the dominant organic-matter type. This procedure provided an approximate but satisfactory guide to the relative abundance of each organic-matter type.

Before linear models were used to test the facilitation hypothesis, the data were tested for normality using the probability plots contained in the SYSTAT statistical software package (Wilkinson 1989). Where the data were not normally distributed they were  $\log(x+1)$  transformed and re-tested to see if the transformation had been successful. For analyses of variance on *Cheumatopsyche* and *Baetis* densities returning significant  $F$ -values, multiple comparisons (Ryan's  $Q$ -test, Day and Quinn 1989) were used to compare treatments. As *Cheumatopsyche* removal treatments involved only minor disturbance to the substrate surface with no disturbance to deeper strata, treatment effects were expected to differ between epibenthic and interstitial species. Therefore, effects of scouring treatments on other common species were investigated by separating epibenthic and interstitial species and performing separate pairwise multivariate analyses of variance (MANOVA) contrasts between these treatments and controls for both groups. As the control treatment was used in more than one analysis, the Type-I error rate was maintained at  $P < 0.05$  by the Dunn-Sidak procedure (Sokal and Rohlf 1981).

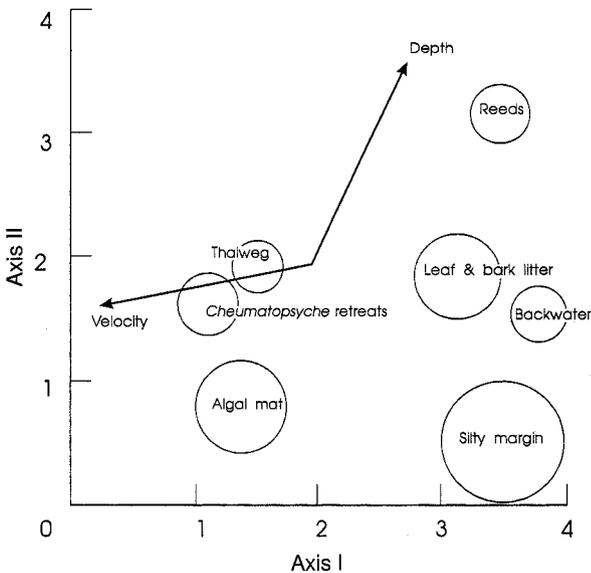
## Results

### Substrate Patch Description

A two-dimensional solution was retained for the HMDS ordination of the substrate-patch macroinvertebrate fauna, because the three-dimensional solution resulted in only a small

decrease in stress (from 0.18 for 2 dimensions to 0.15 for 3 dimensions). The main distinction on the velocity vector was between the high-velocity *Cheumatopsyche*, thalweg, and algal mat patches, and the remaining low-velocity depositional patches (Fig. 2). Variation amongst depositional habitats was related to water depth, as evidenced by their correlation with the depth vector. The fauna of depositional patches was characterized by silt-tolerant taxa such as tubificid oligochaetes and chironomids (Table 2).

A major distinction between *Cheumatopsyche* and thalweg patches was the depauperate epibenthic fauna of the latter (Table 2). It was evident that epibenthic species found the constantly shifting sand of the thalweg an unsuitable habitat. Interstitial species, however, such as nymphs of the mayfly *Tasmanocaenis tillyardi*, and larvae of the chironomid *Corynoneura australiensis* and *Microchironomus* sp., showed little variation in density between the two patch types. Conspicuous mats of the cyanobacterium *Schizothrix* near *friessi* appeared to provide refuge for some epibenthic species in the thalweg, such as algal-grazing larvae of the chironomid *Cricotopus annuliventris*, whose burrows riddled algal mats.



**Fig. 2.** Hybrid multidimensional scaling ordination of the macro-invertebrate fauna of each substrate patch type. The radius of each circle is the mean distance of replicate samples from the centroid. Larger circles reflect greater within-patch heterogeneity. Ordination axes are scaled in half-change units (i.e. samples one half-change unit apart are approximately 50% similar). Arrows: directions of significant maximum linear correlation for velocity and depth. The vector for organic matter did not show a significant linear correlation and is not shown.

### Facilitation Experiment

The low numbers of *Baetis* in 0-h removal plots showed that the *Cheumatopsyche* removal procedure caused most of them to flee the perturbed area (Fig. 3; note the logarithmic ordinate axis). Numbers of *Cheumatopsyche* larvae were also significantly reduced by removal with forceps and by scouring (Fig. 3, Table 3). After 48 h, there appeared to be some recolonization by *Cheumatopsyche* but their densities in removal plots were still lower than in control plots. Plots scoured clean of *Cheumatopsyche* larvae and their retreats 48 h prior to sampling contained fewer *Baetis* than plots from which *Baetis* had previously been scared away (both scare and 48 h removal) and control plots. This showed that *Cheumatopsyche* larvae facilitated the presence of *Baetis*. Furthermore, *Baetis* densities were the same in scare plots, 48-h removal plots, and controls. This indicated that *Baetis* recolonized plots with equivalent densities of *Cheumatopsyche* retreats, regardless of whether or not the retreats contained larvae. It was therefore the physical presence of the *Cheumatopsyche* retreats, rather than the larvae themselves, which facilitated the presence of *Baetis* nymphs.

**Table 2. Ordered condensed table of the 35 most abundant species in Branjee Creek**

Mean abundance of each taxon in each habitat type  $\log(x+1)$  transformed, standardized so that maximum mean abundance in any habitat equals 1.0, and rounded into five classes with upper limits of 0.2, 0.4, 0.6, 0.8, and 1.0. Habitats ordered by mean score on the velocity vector in HMDS space, with velocity increasing from left to right. Species ordered by weighted average score on the same velocity vector, with score increasing down the table. BW, backwater; RE, reeds; SC, silt side-channel; LL, leaf litter; TH, thalweg; CH, *Cheumatopsyche* retreats; AM, algal mats. (L), larvae; (e), epibenthic; (i), interstitial; -, species absent

Species		Habitat						
		BW	RE	SC	LL	TH	CH	AM
<i>Chironomus alternans</i> group	Diptera, Chironomidae	5	2	-	4	-	-	-
<i>Microvelia distincta</i>	Hemiptera, Veliidae	-	5	1	3	-	-	-
<i>Procladius paludicola</i>	Diptera, Chironomidae	5	3	3	3	-	-	-
<i>Triplectides ciuskus</i>	Trichoptera, Leptoceridae	-	5	-	1	-	-	1
<i>Limnodrilus hoffmeisteri</i>	Oligochaeta, Tubificidae	4	5	3	5	-	-	-
<i>Ilyocryptus</i> sp.	Cladocera, Macrothricidae	2	2	5	-	-	-	-
<i>Polypedilum oresitrophus</i>	Diptera, Chironomidae	-	5	-	5	-	-	2
<i>Tanytarsus</i> spp.	Diptera, Chironomidae	4	3	5	5	3	1	-
<i>Polypedilum tonnoiri</i>	Diptera, Chironomidae	1	2	5	3	-	-	-
<i>Eucyclops</i> spp.	Copepoda, Cyclopoida	5	4	5	4	5	1	2
<i>Macrocyclus albidus</i>	Copepoda, Cyclopoida	4	4	1	5	2	3	1
<i>Chaetogaster</i> spp.	Oligochaeta, Naididae	5	1	-	3	-	4	-
<i>Micronecta annae illiesi</i>	Hemiptera, Corixidae	4	4	5	4	4	2	3
<i>Lumbriculus variegatus</i>	Oligochaeta, Lumbriculidae	3	1	5	5	2	3	2
<i>Physa acuta</i>	Gastropoda, Physidae	4	2	1	5	2	3	4
<i>Hydra</i> sp.	Hydroida, Anthomedusae	-	3	-	5	4	4	2
<i>Ablabesmyia notabilis</i>	Diptera, Chironomidae	-	-	-	5	-	4	-
Naididae spp.	Oligochaeta, Naididae (e)	2	2	5	3	4	5	3
<i>Sternopriscus mundanus</i>	Coleoptera, Dytiscidae (i)	-	2	-	-	5	1	-
<i>Tasmanocaenis tillyardi</i>	Ephemeroptera, Caenidae (i)	5	3	2	4	5	5	3
<i>Ecnomus continentalis</i>	Trichoptera, Ecnomidae (e)	3	3	2	5	4	5	2
<i>Austrogomphus</i> sp.	Odonata, Gomphidae (i)	-	1	4	-	5	5	-
<i>Ferrissia petterdi</i>	Gastropoda, Ancyliidae (e)	2	3	2	4	3	5	5
<i>Austrolimnius</i> MV L62E (L)	Coleoptera, Elmidae (e)	3	-	-	1	4	5	1
<i>Corynoneura australiensis</i>	Diptera, Chironomidae (i)	1	2	3	4	5	5	3
<i>Cura pinguis</i>	Tricladida, Dugesidae (e)	1	1	1	3	2	5	4
<i>Rheotanytarsus</i> MV4	Diptera, Chironomidae (e)	-	1	2	3	4	5	3
<i>Nousia ?fuscula</i>	Ephemeroptera, Leptophlebiidae (e)	-	1	1	2	4	5	4
<i>Microchironomus</i> SV43	Diptera, Chironomidae (i)	-	-	-	-	5	5	3
? <i>Prostoma</i> sp.	Enopla, Hoplonemertea (i)	2	1	-	-	5	5	1
<i>Baetis</i> MV4	Ephemeroptera, Baetidae (e)	1	2	2	2	3	5	3
? <i>Costora</i> sp.	Trichoptera, Conoesucidae (e)	1	-	1	1	3	5	2
<i>Cheumatopsyche</i> MWB4	Trichoptera, Hydropsychidae (3)	-	-	1	1	2	5	3
<i>Corticacarus</i> spp.	Hydracarina, Hygrobatidae (e)	-	-	-	-	2	5	1
<i>Cricotopus annuliventris</i>	Diptera, Chironomidae	-	-	-	1	-	3	5

The samples of the surface centimetre of the thalweg patch type contained little organic matter other than some fine detritus (mean dry weight of organic matter,  $0.01 (\pm 0.01$  95% C.I.)  $\text{mg cm}^{-2}$ ). In contrast, samples from *Cheumatopsyche* patches contained significant quantities of organic matter (mean dry weight of organic matter,  $0.30 (\pm 0.20$  95% C.I.)  $\text{mg cm}^{-2}$ ). About 80% of this material consisted of fine amorphous detritus, less than 1% was diatoms and animal material, and the remainder comprised equal amounts of filamentous algae and vascular plant material. By comparison, gut contents of *Baetis* were about 95% fine amorphous detritus and about 4% filamentous algae, with other

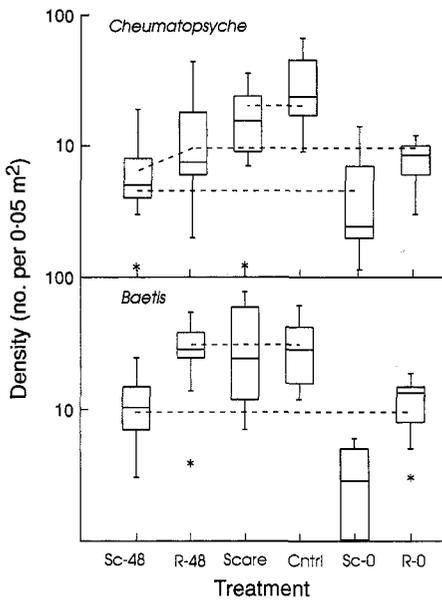


Fig. 3. Boxplots of *Cheumatopsyche* and *Baetis* densities for each facilitation experiment treatment: Sc-48, Scour 48 h; R-48, Removal 48 h; Scare; Cntrl, Control; Sc-0, Scour 0 h; R-0, Removal 0 h. Note the log scale on the y-axis. Boxes connected by or containing dashed lines indicate treatments that were not significantly different from each other (i.e.  $P > 0.05$ ), as determined by a multiple comparisons test (Ryan's Q-test, Day and Quinn 1989). Each box encloses the upper and lower fourth spread (fourth spread = mean - 0.6745  $\times$  s.d.). The central bar on each box is the median. Outlying values are greater in magnitude than 1.5 fourths, denoted by the lines extending from each box. Outlying samples (\*) were included in analyses of variance and multiple comparison procedures.

Table 3. One-factor ANOVA for facilitation experiment treatments for *Baetis* and *Cheumatopsyche*  
Both  $\log(x+1)$  transformed

Source	<i>Baetis</i>				<i>Cheumatopsyche</i>			
	SS	d.f.	F	P	SS	d.f.	F	P
Treatment	25.83	5	7.62	<0.0005	42.76	5	17.21	<0.0005
Error	36.61	54			26.83	54		

categories making up less than 1%. As *Baetis* densities were highest in *Cheumatopsyche* patches, it was apparent that they were grazing on the detritus and algae entrained on the substrate around *Cheumatopsyche* retreats.

Pairwise MANOVA contrasts between scour treatments and the control treatment showed that densities of both interstitial and epibenthic species (other than *Baetis* and *Cheumatopsyche*) were decreased by scouring (Table 4). In 0-h scour samples, the multi-

Table 4. Pairwise MANOVA contrasts between scour treatments and controls, and between *Cheumatopsyche* removal treatments and controls for epibenthic and interstitial species

The  $F$ -ratio is the multivariate  $F$ .  $F$ -ratios with a probability <0.013 have a Dunn-Sidak corrected probability of <0.05. Epibenthic species: *Ecnomus continentalis*, Naididae spp., *Nousia ?fuscula*, *Eucyclops* spp., *Tanytarsus* spp., and *?Costora* sp. Interstitial species: *Microchironomus* sp., *Tasmanocaenis tillyardi*, *Corynoneura australiensis*, Tubificidae spp., and Candonidae spp. For epibenthic species d.f. 6,49; for interstitial species d.f. 5,50. Taxonomic information in Table 2. \* Significant with Type-I error rate ( $\alpha$ ) <0.05

Contrast	Epibenthic species		Interstitial species	
	F	P	F	P
Scour 0 h v. Control	19.08	<0.0005*	32.72	<0.0005*
Scour 48 h v. Control	4.64	0.001*	5.15	<0.0005*
Removal 0 h v. Control	1.82	0.115	0.88	0.820
Removal 48 h v. Control	0.78	0.590	0.84	0.815

variate *F*-ratios were 32.72 and 19.08 for interstitial and epibenthic species respectively. After 48 h, however, this decreased to 5.15 and 4.64 respectively, showing that both species groups were rapidly recolonizing the disturbed area. In contrast, there was no significant effect of *Cheumatopsyche* removal on epibenthic or interstitial species either initially, or after 48 h; thus, *Baetis* was the only species to show a significant flight response to the removal treatments.

## Discussion

The facilitation hypothesis was supported in this study because densities of *Baetis* nymphs were higher when *Cheumatopsyche* larvae were present. The mechanism for this indirect effect appeared to be the entrainment of the detrital and algal food of *Baetis* by *Cheumatopsyche* retreats. However, other mechanisms may also have been involved. For example, nutrients from *Cheumatopsyche* excretions may have enhanced the growth of entrained algae around their retreats thereby indirectly increasing food resources for *Baetis* and other epibenthic grazers. Such nutrient enhancement from insect larvae excretions has been recorded previously in streams. Pringle (cited in Pringle *et al.* 1988) found that chironomid tubes made of consolidated sand contained significantly greater amounts of nitrogen and phosphorus, and supported denser mats of diatoms, than nearby unconsolidated sand. Hershey *et al.* (1988) considered that fertilization of tube flora may be one reason why concentrations of chlorophyll-*a* were higher on larval chironomid tubes than on pupal tubes. In a process analogous to the fixation of nitrogen by soil bacteria, filterers such as *Cheumatopsyche* may play a more important role in the production of nutrient 'hotspots' than other functional feeding groups, because they capture and concentrate otherwise inaccessible nutrients contained in suspended particulate material. The generality of this process, however, is tempered by Winterbourn's (1990) finding that few diatoms occurred on the tubes of chironomids on nutrient-diffusing substrata in a New Zealand stream.

Another possible mechanism whereby *Cheumatopsyche* larvae may facilitate the presence of other taxa is the stabilization of surface sand particles through retreat construction. However, this mechanism is likely to be of limited importance in Branjee Creek where prolonged high winter and spring discharges destroy most of the low-flow patch types, including *Cheumatopsyche* patches (see O'Connor 1991; O'Connor and Lake 1993). In addition, only stationary sand appears to be colonized by epibenthic macroinvertebrates; hence epibenthic species appear to play no role in causing sand to settle.

Patch formation is a dynamic process in the summer-autumn low-flow period in Branjee Creek because of the slow lateral meandering of the thalweg. This results in the simultaneous erosion of *Cheumatopsyche* patches on the outer curves of meanders and deposition on the inner curves. If left unabated, this process may result in the gradual turnover of *Cheumatopsyche* patches. It is not known if entire patches are turned over and, if so, at what rate, but the results of the 48-h scour treatment in this study show that *Cheumatopsyche* larvae and other epibenthic species quickly recolonize recently deposited sand. Furthermore, the observation that stable sand patches always possessed an established epibenthic fauna indicates that faunal recolonization is faster than patch movement.

Patch formation may be a common process in soft-bottomed streams. For example, the substrate patch types described here resemble the algal patch types in an Arizonan desert stream, Sycamore Creek, described by Fisher *et al.* (1982). Although the method of description in that analysis of algal flora differs from the method in the present analysis of macroinvertebrate fauna, clearly some of the patch types were equivalent. Fisher *et al.*'s (1982) patch type 1, which consisted of bare sand without visible algae, was most common in mid-channel rapid water, and is represented in Branjee Creek by the thalweg. Patch types 4 and 5 of Fisher *et al.* (1982) were blue-green algae and *Cladophora*-blue-green algal mats, respectively. Blue-green algal mats in Branjee Creek were dominated by *Schizothrix*, whereas *Schizothrix* and *Anabaena* characterized Fisher *et al.*'s (1982) patch type 4.

Preliminary observations suggest that *Cheumatopsyche* patches occupy about 30% of the streambed during low flow. Given this widespread distribution, the interaction between *Cheumatopsyche* and *Baetis* may constitute a significant pathway of the stream's energy budget. Indeed, it may be more instructive to view such indirect effects in the wider context of food-web theory. For example, Power (1990b) gave a lotic example of an indirect interaction in a food-web context, in this instance a trophic cascade, showing that predation by California roach and juvenile steelhead trout on predatory insects and fish fry left herbivorous chironomid larvae free to crop algal turfs. Linking important mechanistic details of both direct (predation) and indirect (facilitation) effects in this fashion provides us with more dynamic descriptions of lotic community structure. The next step is to link these concepts with the environmental variability which is an inherent feature of lotic systems.

### Acknowledgments

I thank Dr P. S. Lake for his supervision of this research which formed part of a Ph.D. project undertaken at Monash University. I also thank Suzanne Moore, Sam Lake, Gerard Closs, Andrew Boulton and Richard Marchant for their constructive criticism of the manuscript, and Pat Malone for field assistance.

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Manuscript received 29 May 1992; revised and accepted 19 August 1992