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Colonization Patterns of Aquatic Instects on Artificial Substrates: Effects of Substrate Sizes

【Research report】

底質大小對水棲昆蟲拓殖之影響【研究報告】

Sen-Her Shieh* and Ping-Shih Yang
謝森和*、楊平世

*通訊作者E-mail : colonization, aquatic insects, artificial substrates, substrate size, streams.

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Abstract

Experiments on the colonization of artificial substrates by aquatic insects were conducted to test the effects of two different sizes of substrate (cobbles=64-128mm and gravel =16-32mm) in the upper Chingmei Stream, Taiwan. The artificial substrates were colonized by aquatic insects for periods of 3, 6, 12, 21, 30, and 42 d from 14 March to 25 April 1991. The substratum types influenced only the total number of individuals colonizing baskets. In general, aquatic insect taxa on the gravel substrate had greater daily colonization rates than did those on the cobble substraate. The gravel substrate provided more surface area for aquatic insects and supported more individuals. Baetis spp. and chironomid larvae were most abundant; they accounted for over 84% of the individuals from days 6 to 42 on both gravel and cobble. The chironomid larvae comprised 36-65% of the fauna on the gravel substrate and 35-79% of the fauna on the cobble substrate. The results of association analysis on the abundance of taxa pairs within the same functional feeding group showed that there were more taxa paris with significant associations on the cobble than on the gravel, indicating that biological interatctions might be important in determining the development of community on the cobble substrate. Disturbance caused by floods, occurring just after day 12. influenced the colonization patterns, especially on the gravel substrate. It reset the artificial substrates back to earlier conditions. However, the results from longormal distribution indicated that aquatic insect communities on the gravel substrate showed a higher degree of equilibrium than did those on the gravel substrate showed a higher degree of equilibrium than did those on the cobble substrate. The degree of equilibrium and the intensity of biological interactions appeared to be reflected in the stability of substrate which is related to the size of the substrate.

摘要

本研究之目的是探討兩種不同大小的人工底質(鵝卵石=64-128 mm、碎石=16-32 mm)，對水棲昆蟲拓殖的影響。試驗地點是位於景美溪的上游，從1991年3月14日到1991年4月25日，人工底質分別被水棲昆蟲拓殖3、6、12、21、30、及42天。試驗結果顯示人工底質的大小，只影響水棲昆蟲拓殖的總個體數，但並不影響種類數及歧異度，碎石的底質提供較多的表面積，作為水棲昆蟲的棲地，因此有較多的個體數。Baetis spp.和Chironomidae是最早的拓殖者，及個體數最多的種類，不論是在碎石或鵝卵石的底質，從拓殖的第6天到第42天，它們的個體數超過總個體數的84%。在此試驗期間，Chironomidae在碎石及鵝卵石的底質，分別佔整個水棲昆蟲相的36-66%及35-79% 。依據功能攝食群內的種類相關分析推測，生物的交互作用對水棲昆蟲群落的發展，在鵝卵石比在碎石更為重要。然而，由洪水所造成的干擾，也影響水棲昆蟲的拓殖型式，特別是對碎石的底質影響尤大，洪水使得人工底質上的水棲昆蟲群落結構，重新回復到早期的拓殖情形。另外，由指數常態分布模式，判別群落在拓殖過程中的平衡程度，結果顯示在碎石的底質比在鵝卵石的底質，更符合此模式，亦即水棲昆蟲在較不穩定的環境比在較穩定的環境，更易達到平衡狀態。

Key words: colonization, aquatic insects, artificial substrates, substrate size, streams.

關鍵詞: 拓殖、水棲昆蟲、人工底質、底質大小、河流

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Colonization Patterns of Aquatic Insects on Artificial Substrates: Effects of Substrate Sizes

Sen-Her Shieh* and Ping-Shih Yang Department of Entomology, National Taiwan University, Taipei 106, Taiwan, R.O.C.

ABSTRACT

Experiments on the colonization of artificial substrates by aquatic insects were conducted to test the effects of two different sizes of substrate (cobbles = 64-128 mm and gravel = 16-32 mm) in the upper Chingmei Stream, Taiwan. The artificial substrates were colonized by aquatic insects for periods of 3, 6, 12, 21, 30, and 42 d from 14 March to 25 April 1991. The substratum types influenced only the total number of individuals colonizing baskets. In general, aquatic insect taxa on the gravel substrate had greater daily colonization rates than did those on the cobble substrate. The gravel substrate provided more surface area for aquatic insects and supported more individuals. *Baetis* spp. and chironomid larvae were most abundant; they accounted for over 84% of the individuals from days 6 to 42 on both gravel and cobble. The chironomid larvae comprised 36-65% of the fauna on the gravel substrate and 35-79% of the fauna on the cobble substrate. The results of association analysis on the abundance of taxa pairs within the same functional feeding group showed that there were more taxa pairs with significant associations on the cobble than on the gravel, indicating that biological interactions might be important in determining the development of community on the cobble substrate. Disturbance caused by floods, occurring just after day 12, influenced the colonization patterns, especially on the gravel substrate. It reset the artificial substrates back to earlier conditions. However, the results from lognormal distribution indicated that aquatic insect communities on the gravel substrate showed a higher degree of equilibrium than did those on the cobble substrate. The degree of equilibrium and the intensity of biological interactions appeared to be reflected in the stability of substrate which is related to the size of the substrate.

Key words: colonization, aquatic insects, artificial substrates, substrate size, streams.

Introduction

Substrate has been considered to be one of the most important factors affecting stream aquatic insect assemblages (Minshall, 1984; Ward, 1992). The factors of substrates that influence aquatic insect colonizers are changes in the surface

*Correspondence/reprint request address

characteristics of substrates and the size of substrate particles (Mackay, 1992). The size of substrate particle affects the colonization of aquatic insects in two ways: stability of the substrate and accumulation and size of detritus particles (Mackay, 1992). The stability of the substrate is defined as the degree of resistance to movement and is generally proportional to the size of the particle (Minshall, 1984). Large pebbles and cobbles tend to be more stable than small pebbles and gravel. McAuliffe (1983) indicated that small stones would have a higher probability of being overturned by flood waters. However, small pebbles and gravel tend to trap more fine particulate organic matter than do coarser substrates (Rabeni and Minshall, 1977; Wise and Molles, 1979; Parker, 1989). These characteristics of substrate particle size, therefore, play important roles in determining the distribution and abundance of stream macroinvertebrates (Minshall, 1984) and in mediating their responses to disturbance (Gurtz and Wallace, 1984).

Stream ecosystems in Taiwan are frequently disturbed by different flood events, such as typhoons and heavy rains. Typhoons and heavy rains often give rise to unpredictable flooding on different scales. The floods affect aquatic insect abundance and community composition both by causing bed-load movement and by increasing the amount of suspended sediment that settles in the substrate trays. Increased current velocity and bed-load movement cause catastrophic drift of aquatic insects, physical damage to some individuals, and reduction in the food supply available by abrading algal populations from the substrate (Sagar, 1986). This study dealt with the colonization of substrata by aquatic insects in the upper Chingmei Stream in subtropical northern Taiwan. It was undertaken with a view to comparing the patterns of colonization of two different sizes of substrate: cobbles (higher stability of substrate) and gravel (lower stability of substrate), examining the relationship between dominance and community structure of aquatic insects during the process of colonization, and assessing the effects of floods on colonization patterns and community structure of aquatic insects in the two different sizes of substrate, if any floods occurred during the experimental period.

Materials and Methods

Study area

The experiments were conducted in the upper reaches of the Chingmei Stream (lat. 25°01′N, log. 121°41′E) flowing through Shihting Township, Taipei County, about 25 km east of Taipei City in northern Taiwan. The strata in the area are of Miocene and Pliocene age, and the soil group is yellow earth (Hsieh, 1964). The annual average precipitation is about 4000 mm. The study reach of the stream has a riparian zone with evergreen hardwood vegetation: *Boehmeria densiflora* (Urticaceae), *Piper kadsura* (Piperaceae), *Acacia confusa* (Leguminosae), *Ficus erecta* (Moraceae), and *Diospyros morrisiana* (Ebenaceae); and herbs: *Alpinia speciosa* (Zingiberaceae), *Miscanthus floridulus* (Gramineae), and *Eclipta prostrata* (Compositae). The headwaters of the streams are in agricultural areas with tea plantations of *Thea sinensis* (L) Sims. The fish were dominated by an omnivorous goby (*Rhinogobius brunneus* (Temminck et Schlegel)) and the herbivorous *Crossostoma lacustre* (Steindachner). Filamentous algae (*Cladophora* sp., *Spirogyra* sp., and *Oscillatoria* sp.) commonly covered the upper surface of cobbles and small stones throughout the entire year.

Sampling methods

From 14 March to 25 April 1991, the community structure and colonization patterns of aquatic insects on the gravel and cobble substrate were compared. Plastic baskets (mesh = 4 mm, dimension = 25×20×6 cm) were filled with one of the two substratum types: cobbles (64-128 mm) or gravel (16-32 mm). Cobbles were collected from the dry streambed, and gravel was collected from a quarry. Each stone was washed in stream water. All baskets were placed randomly in the stream bottom on 14 March 1991. These baskets were flush with the surface of the substrate and left in the stream for periods of 3, 6, 12, 21, 30, and 42 d. Each treatment had four replicates, so at least 8 baskets were sampled on each sampling date. Forty-eight baskets were arranged randomly into an 8 (columns)×6 (rows) matrix. The space between columns and between rows was at least 1 m. During the experiment period, disturbance due to floods, occurring between day 12 and day 21, was observed.

At the end of the colonization period, a basket was lifted off the streambed and transferred into a basket of the same size but without mesh. The rocks in the basket were washed carefully with stream water which was sieved (mesh = 0.25 mm) to collect sessile and other insects. The other sediment in the basket was placed in labeled individual plastic bags.

During the experiment, water temperature, water depth, stream width, current velocity (Hydro-bio Kiel digital flow meter), discharge, pH (WTW pH 90/set pH meter), conductivity (WTW LF90 conductivity meter), and dissolved oxygen (Jenway 9070 oxygen meter) were measured at a fixed transect of the stream on each sampling day. To measure the amounts of organic matter trapped by baskets, the sediment was oven-dried at 60°C for at least 24 h and weighed. It was then combusted at 500°C for 2 h, cooled, and reweighed to determine organic content.

In the laboratory, the sediment was transferred to a white plastic pan and the aquatic insects picked. All animals were preserved in 70% ethyl alcohol. Then the animals were keyed to genus whenever possible according to Kawai (1985), Merritt and Cummins (1984), or Wiggins (1977). Ephemeroptera were identified using Kang (1993) and Kang and Yang (1994a, b). All Chironomidae found were counted. Hydropsychidae were not identified further, because many first instar larvae were collected during the sampling period. In addition, taxa were classified into functional feeding groups based on Merritt and Cummins (1984). Since most taxa within grazers also were collector-gatherers, they were grouped as grazers/collector-gatherers. Members of the Chironomidae were classified as filter-feeders and grazers/collectors because Tanytarsini are filter-feeders and Chironomini are collector-gatherers.

Data analysis

The design was a two-way factorial analysis of variance with substrate (two levels: cobble and gravel) and time (six sample dates) as factors (2×6 design with 12 treatment combinations). There were four replicates of each combination. The total number of individuals, total number of taxa, Shannon-Weaver diversity, and evenness for every substratum basket were analyzed in the designs described above (see Ludwing and Reynolds [1988] for calculation of Shannon-Weaver diversity and evenness). Numerical data were log-transformed to stabilize variance. Simple regression ($Y = a + bX$, where Y = number of individuals of a given taxon and X = number of day for colonization) was used to determine daily colonization rates (b) of the 18 most dominant taxa on the two different substrates. Spearman rank correlation coefficients were used to examine potential biological interactions between taxa. The lognormal distribution (Ludwig and Reynolds, 1988) was used to examine the degree of equilibrium of aquatic insect communities in the colonization baskets. The equilibrium state was viewed as a continuum between $r^2 = 1$

for equilibrium and $r^2=0$ for maximum nonequilibrium.

Results

Physicochemical factors and organic matter

Values for physical and chemical characteristics during the experiment (from 14 March to 25 April 1991) are given in Table 1. During the experiment, water temperature and conductivity had a tendency to increase. The pH values showed the stream water to be slightly alkaline. Heavy rains occurring just after day 12 resulted in floods (pers. observ.), yet the discharge on day 21 did not reflect the situation. The amount of organic matter collected by trays did not increase until day 12 (Fig. 1). There was more organic matter in the cobble substrate than in the gravel substrate. This may partly be due to the greater amount of periphyton growing on the cobble substrate.

Aquatic insect fauna

During this experiment, a total of 51 taxa were collected from the experimental substrates (Appendices 1 and 2). There were 45 taxa collected in the cobble baskets and 43 taxa collected in the gravel baskets. Trichoptera were the most diver-

Table 1. Physical and chemical characteristics on each sampling day in the Chingmei Stream, Taiwan

	Sampling day					
	3	6	12	21	30	42
Temperature (℃)	16.2	20.9	21.5	23.8	20.8	24.0
Stream width (m)	9.2	8.6	10.2	8.4	8.5	8.3
Depth (cm)	20.7	22.3	24.8	18.4	19.1	13.8
Velocity (m/s)	0.51	0.69	0.42	0.35	0.23	0.19
Discharge (m^3/s)	0.97	1.32	1.06	0.54	0.37	0.22
pH	7.92	8.10	7.58	8.07	7.79	8.34
Conductivity (μs/cm)	172	180	125	224	217	324
Dissolved oxygen (ppm)	10.1	10.3	9.1	9.4	9.8	10.7

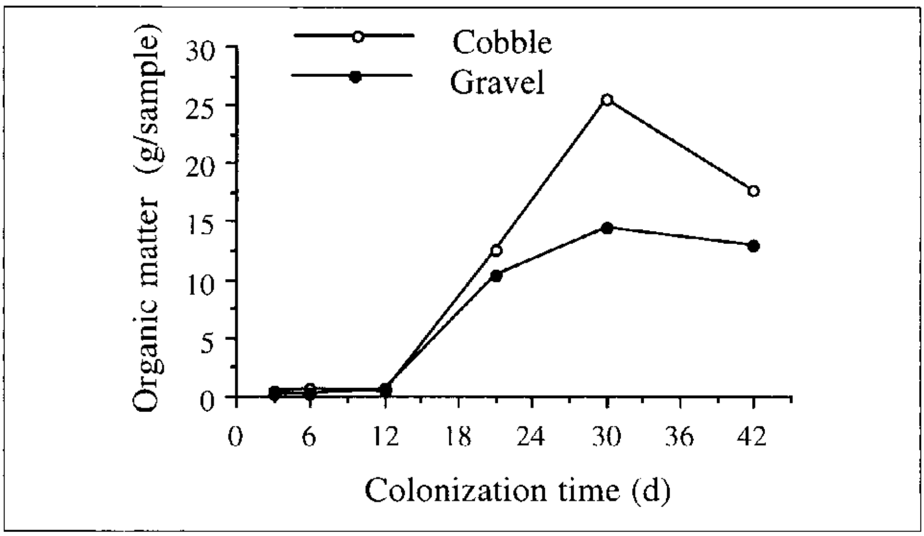

Fig. 1. Amounts of orgnic matter collected by colonizing baskets filled with cobbles and gravel on each sampling day in the Chingmei Stream, Taiwan.

se, with 13 taxa; while Ephemeroptera and Diptera each had 12 taxa. Numbers of taxa for the other orders were: 7 (Coleoptera), 4 (Plecoptera), 3 (Odonata), 1 (Lepidoptera), and 1 (Hemiptera).

The most abundant Ephemeroptera for the cobble substrate was *Baetis* spp. with the greatest abundance (9465 m^{-2}) occurring on day 6 (Appendix 1). The more abundant Trichoptera were Hydropsychidae (1255 m^{-2}) and Stenopsychidae (910 m^{-2}); the largest numbers of these occurred on day 42. The most abundant Diptera was Chironomidae, and the greatest abundance (53560 m^{-2}) occurred on day 42. Comparing *Baetis* spp. and Chironomidae, the latter were always more abundant than were *Baetis* spp. during the entire study.

The most abundant Ephemeroptera for the gravel substrate was *Baetis* spp. which reached a density of 17,220 m^{-2}on day 42 (Appendix 2). The most abundant caddisflies were Hydropsychidae (3,860 m^{-2}) and Stenopsychidae (1,800 m^{-2}) which also peaked on day 42. The largest number of Chironomidae (50,730 m^{-2}) also occurred on day 42. Comparing *Baetis* spp. and Chironomidae, there was a shift from *Baetis* spp. to Chironomidae being the most abundant taxon after day 3. Moreover, comparing the cobble and gravel substrate, the most abundant taxa in different orders had higher abundances on the gravel substrate than on the cobble substrate, except the Chironomidae.

For the gravel substrate, *Baetis* spp. and chironomid larvae accounted for 84-95% of the colonizing individuals from days 3 to 42. The chironomid larvae comprised 36-65% of the fauna during the same interval. For the cobble substrate, the two taxa accounted for over 85% of individuals from days 6 to 42. They only comprised 49% of the same fauna on day 3. *Prosimulium* spp. accounted for the other 44% of the fauna on day 3. Chironomid larvae accounted for 35-79% of the fauna from days 3 to 42.

The number of taxa in each order changed with time of colonization on the two substrates (Fig. 2). For Ephemeroptera, the number of taxa remained almost constant on both the cobble and gravel substrates during the experiment, except day 3 on the cobble substrate and day 21 on the gravel substrate. For Trichoptera, the number of taxa increased on both cobble and gravel substrates during the experiment except day 30 on the gravel substrate. For Diptera, the number of taxa increased before day 21, decreased on day 21 and then increased on both cobble and gravel substrates. Coleoptera usually occurred in the later period of colonization.

The decrease in the total number of taxa on day 21 for both the cobble and gravel substrates was probably due to floods which occurred just after day 12 (Fig. 2). The colonization was reset to earlier conditions because of the major disturbance by floods. For the gravel substrate, day 21 is more similar to 3 d than to 21 d of colonization. In comparing the number of taxa in each order between days 12 and 21, those of Ephemeroptera, Plecoptera, and Diptera decreased, while the number of taxa of Trichoptera and Odonata increased for both cobble and gravel substrates. The number of Coleoptera taxa increased on the cobble substrate but decreased on the gravel substrate. The results indicate that some Ephemeroptera, Plecoptera, and Diptera were easily dislodged by the floods. The Odonata and Trichoptera appeared to be less affected by the floods.

The abundance of some taxa was also highly affected by floods which occurred just after day 12. The floods resulted in significant decreases in *Baetis* spp., *Caenis* sp., *Afronurus hyalinus, Paraleptophlebia* sp., and Chironomidae on the gravel substrate (Appendix 2), and *Baetiella bispinosa, Baetis* spp., and *Caenis* sp. on the cobble substrate (Appendix 1). This indicates that some taxa were more

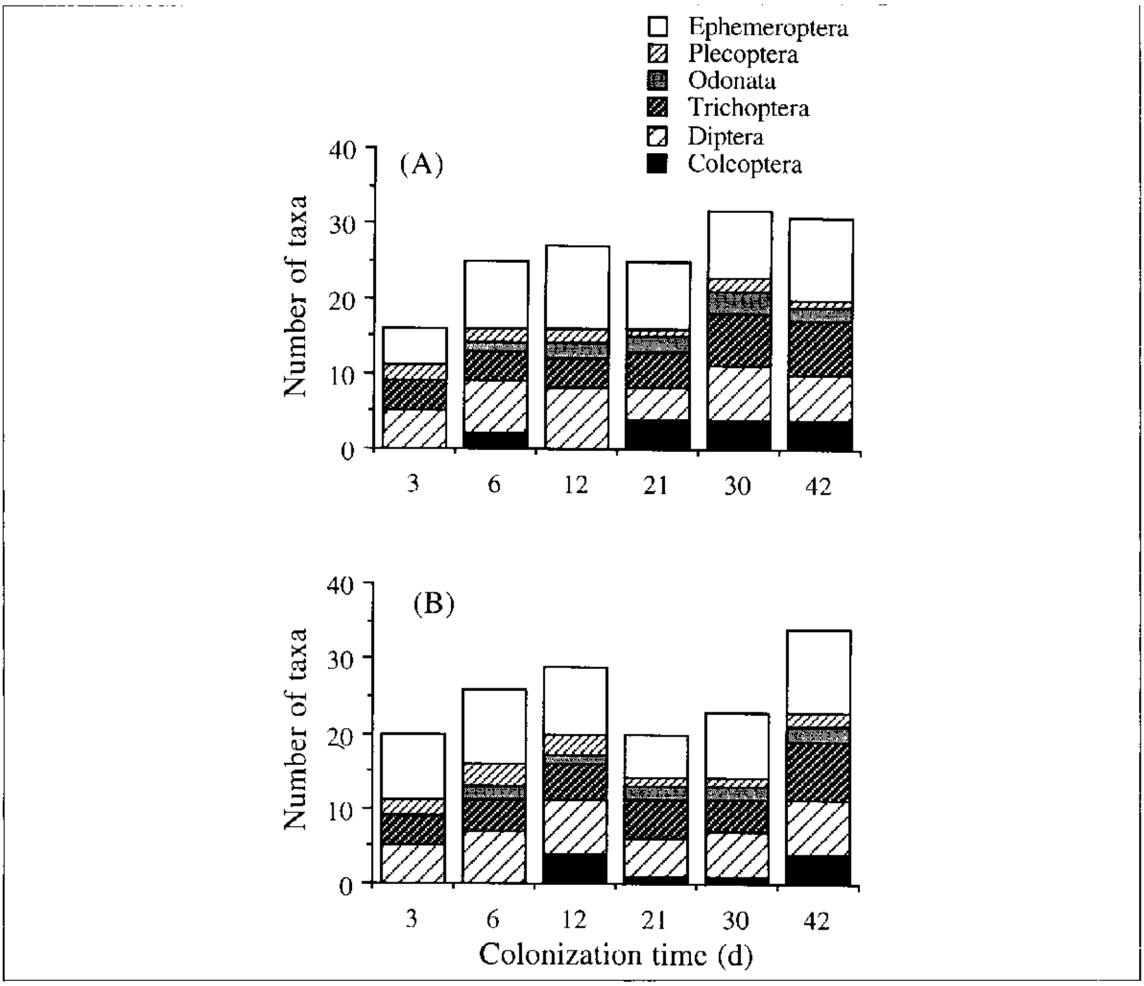

Fig. 2. Number of taxa in each order colonizing baskets filled with cobbles (A) and gravel (B) on each sampling day in the Chingmei Stream, Taiwan.

easily affected by floods on the gravel substrate than on the cobble substrate. Some taxa showed significant increases in numbers of individuals on day 21, such as *Serratella* sp., *Neoperla* sp., Hydropsychidae, *Stenopsyche* sp., and *Antocha* sp. in baskets filled with cobbles, and *Neoperla* sp., *Stenopsyche* sp., *Antocha* sp., and *Zaitzevia* sp. in baskets filled with gravel. This suggests that some taxa were less impacted by floods and continued colonizing the artificial substrate.

Colonization patterns of aquatic insect communities

The mean number of individuals per basket was significantly affected by the duration of baskets in the stream ($p < 0.0001$) and by substrate ($p = 0.048$) (Table 2), and there was no significant effect of interaction between duration of exposure and substrate on mean number of individuals per basket. In addition, mean number of taxa was highly affected by the duration of exposure of baskets to colonization ($p < 0.0001$) but was not affected by the substrate, or the interaction between the duration of exposure and the substrate. Likewise, mean diversity was affected by the duration of exposure ($p = 0.002$), but was not affected by the substrate and the interaction between the duration of exposure and the substrate (Table 2). Mean evenness differed in the duration of exposure of baskets in the stream ($p < 0.0001$), but not in the substrate. The effect of interaction between duration of exposure and substrate on mean evenness was significant ($p = 0.044$). According to the results, it is suggested that the four community indices were highly affected by the length of time the baskets remained in the stream with lesser effects of substrate and the interaction between the duration of exposure and substrate.

The mean number of taxa per basket for the cobble substrate increased before day 30 and then decreased (Fig. 3A). For the gravel substrate, it increased by arithmetical progression between days 3 and 12 and between days 21 and 42. It decreased somewhat between days 12 and 21. Furthermore, the colonization patterns of mean total number of individuals per basket were similar to each other between the two kinds of substrate (Fig. 3B). Numbers appeared to level off between days 3 and 21, but they increased by arithmetical progression after day 21. There were about three times more on day 42 than on day 21. The patterns of diversity during the process of colonization for the cobble and gravel substrates were similar to each other on each sampling day except day 42 (Fig. 3C). They decreased between days 3 and 6 and then appeared to level off between days 6 and 30. For the cobble substrate they decreased, but for the gravel substrate they increased between days 30 and 42.

Colonization patterns of individual taxon

The colonization patterns of individual taxa on the cobble substrate and on the gravel substrate were compared using Spearman rank correlation coefficients for significant association between population density per basket and days of colonization. The 18 taxa which were most abundant were chosen. For the cobble substrate, 13 of 18 taxa showed a significant increase in number per basket with increasing days in the stream; four taxa decreased, and one taxa had no consistent pattern (Table 3). For the gravel substrate, nine of 18 showed significant increases in number per basket with increasing days in stream, five taxa decreased, and four taxa showed no consistent pattern (Table 3). In comparing the two types of substrates, there were three taxa (*Baetis* spp., *Caenis* sp., and Hydropsychidae) that increased in number with the length of exposure period on the cobble substrate but showed no consistent pattern on the gravel substrate. Two taxa (*Rhyacophila* sp.A and *Paraleptophlebia*

Table 2. Results of two-way ANOVA For log (density), total number of aquatic insect taxa, Shannon-Weaver diversity, and evenness versus duration of exposure of substrate to colonization and substrate in the Chingmei Stream, Taiwan (n.s. = not significant, $p < 0.05^{*}$, $p < 0.01^{**}$, $p < 0.001^{***}$)

	Source of variation		
	No. of days (n = 6)	Substrate (n = 2)	Interaction (n = 6×2)
Log (density)	10.34^{***}	4.25^{*}	1.14n.s.
No. of taxa	8.51^{***}	3.71n.s.	0.86n.s.
Diversity	4.89^{**}	0.71n.s.	1.20n.s.
Evenness	22.85^{***}	0.50n.s.	2.63^{*}

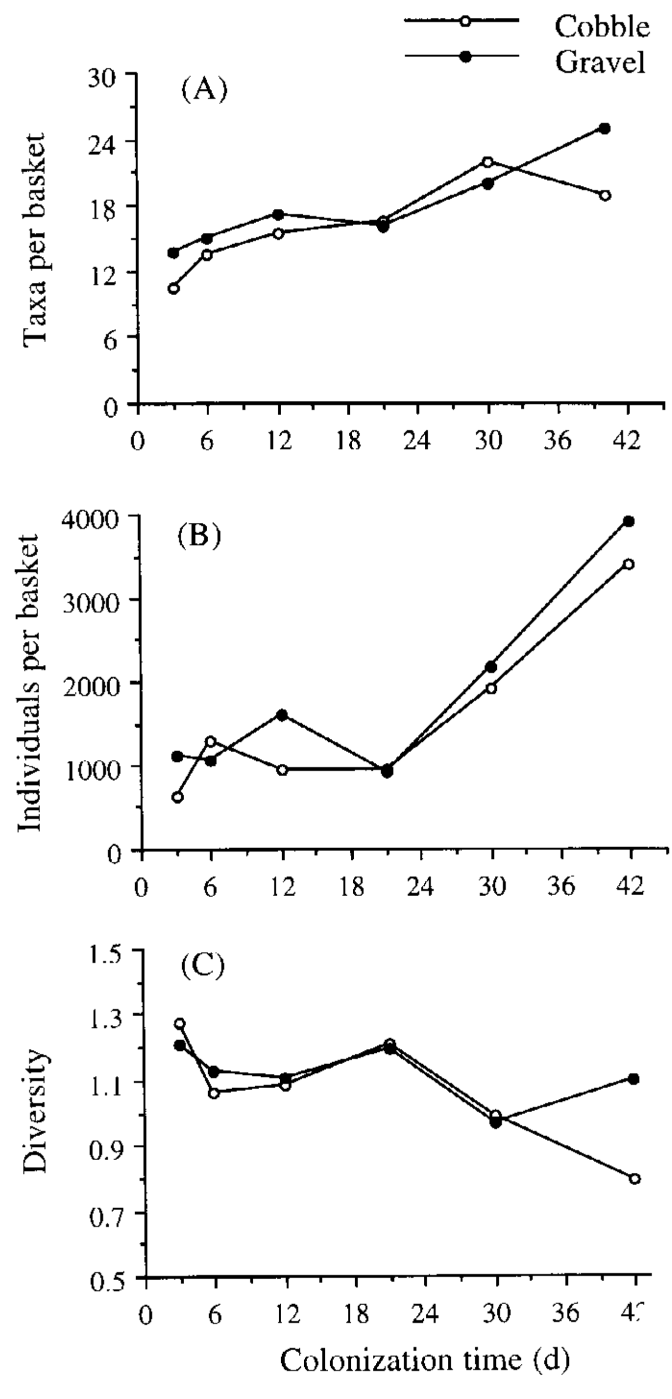

Fig. 3. Mean number of taxa (A), number of individuals (B), and species diversity (C) of colonizing baskets filled with cobbles and gravel left in the stream for 3-42 days in the Chingmei Stream, Taiwan.

Table 3. Summary of results of Spearman rank correlation on numbers of individuals per basket filled with cobbles and gravel versus days in stream for 18 abundant taxa in the Chingmei Stream, Taiwan

Functional feeding group	Increase in number with days in stream	Decrease in number with days in stream	No consistent pattern with days in stream
Cobbles			
Grazers/collectors	*Afronurus hyalinus* *Caenis* sp. *Serratella* sp. *Paraleptophlebia* sp. Chironomidae *Antocha* sp.	*Baetiella bispinosa*	*Baetis* spp.
Filter-feeders	*Stenopsyche* sp. Hydropsychidae Chironomidae	*Prosimulium* spp. *Simulium* spp.	
Predators	*Euphaea* sp. *Neoperla* sp. *Rhyacophila* sp. A *Hemerodromia* sp. Ceratopogonidae		
Shredders		*Protonemura* sp.	
Gravel			
Grazers/collectors	*Afronurus hyalinus* *Serratella* sp. Chironomidae *Antocha* sp.	*Paraleptophlebia* sp.	*Baetis* spp. *Baetiella bispinosa* *Caenis* sp.
Filter-feeders	*Stenopsyche* sp. Chironomidae	*Prosimulium* spp. *Simulium* spp.	Hydropsychidae
Predators	*Euphaea* sp. *Neoperla* sp. *Hemerodromia* sp. Ceratopogonidae	*Rhyacophila* sp. A	
Shredders		*Protonemura* sp.	

sp.) with a pattern of increase on the cobble substrate showed a decrease on the gravel substrate. *B. bispinosa* with a decreasing pattern on the cobble substrate showed no consistent pattern on the gravel substrate.

The daily rates of colonization for a given taxon on both cobble substrate and gravel substrate were compared using least-squares regression (Table 4). Thirteen of 18 taxa on the cobble substrate and 12 of 18 taxa on the gravel substrate showed a slope of the regression line with statistical significance ($p < 0.05$). In these taxa with significant slopes, ten occurred on both cobble and gravel substrates at the same time. Seven of the ten taxa on the gravel substrate had greater daily colonization rates than those on the cobble substrate. Using signed-rank test (Devore and Peck, 1986) to compare the daily colonization rates of the nine taxa (with Chironomidae excluded), showed that there was a significant difference in the daily colonization rates between the gravel and cobble substrates ($p < 0.05$).

The Spearman rank correlation coefficient was used to examine the potential influence of biological interaction between species sharing common re-

Table 4. Values for the constants a and b obtained from the regression model ($y=a+bx$) with numbers of day in stream as the independent variable(x) and numbers of individuals per basket filled with cobbles or gravel as the dependent variable(y). r^2 = coefficient of detrmination, n = 24, p = significance level of the model (*p < 0.05; **p < 0.01; ***p < 0.001; ns = not significant)

Taxa	Cobbles				Gravel			
	a	b	r^2	p	a	b	r^2	p
Ephemeroptera								
Afronurus hyalinus	0.53ns	0.29***	0.67	***	1.67ns	0.30***	0.52	***
Baetiella bispionsa	9.35***	-0.24*	0.22	*	9.74ns	-0.23ns	0.02	ns
Baetis spp.	226.46**	4.78ns	0.10	ns	373.67***	8.09*	0.19	*
Caenis sp.	11.49ns	0.51ns	0.14	ns	34.66*	0.03ns	0.01	ns
Paraleptophlebia sp.	0.08ns	0.04ns	0.08	ns	0.52ns	0.05ns	0.17	ns
Serratella sp.	-1.02ns	0.30**	0.39	**	0.43ns	0.17***	0.78	***
Plecoptera								
Neoperla sp.	-0.43ns	0.12***	0.54	***	-0.99ns	0.29***	0.79	***
Protonemura sp.	0.78**	-0.02*	0.18	*	1.06ns	-0.03ns	0.02	ns
Odonata								
Euphaea sp.	-0.11ns	0.05**	0.30	**	-0.15ns	0.05*	0.26	*
Trichoptera								
Hydropsychidae	-7.97ns	1.20*	0.17	*	-22.23ns	3.34*	0.29	*
Rhyacophila sp. A	-1.20ns	0.17**	0.34	**	-1.89ns	0.42*	0.27	*
Stenopsyche sp.	-3.05ns	1.05***	0.49	***	2.02ns	1.61***	0.52	***
Diptera								
Antocha sp.	-1.65ns	2.15***	0.79	***	-17.10*	2.66***	0.77	***
Ceratopogonidae	0.48ns	0.08*	0.26	*	-0.72ns	0.12***	0.54	***
Chironomidae	-44.88ns	55.06***	0.71	***	241.06ns	45.87***	0.75	***
Hemerodromia sp.	0.39ns	0.03ns	0.06	ns	0.12ns	0.05***	0.35	**
Prosimulium spp.	156.72**	-4.97*	0.22	*	53.85**	-1.75ns	0.17	ns
Simulium spp.	11.22*	-0.35ns	0.16	ns	1.89*	-0.06ns	0.12	ns

sources. For the cobble substrate, 13 of 21 taxon pairs in the group of grazers/collectors were significantly positively associated, and four of 21 taxon pairs were significantly negatively associated (Table 5). In the filter-feeders, four of ten taxon pairs were significantly positively associated and three of ten taxon pairs were significantly negatively associated. Among predator taxon pairs, six of ten were significantly positively associated, and in none was there a significant negative association. These data indicate that the order of the degree of biological interactions among functional feeding groups was grazers/collectors, filter-feeders, and predators.

On the other hand, for the gravel substrate, ten of 21 taxon pairs were significantly positively associated, and one of 21 taxon pairs were significantly negatively associated in the group of grazers/collectors (Table 5). In filter-feeders and predators, two of ten taxon pairs were significantly positively associated, and none of them was negatively associated. These data indicate that the order of the degree of biological interactions among functional feeding groups was grazers/collectors, filter-feeders, and predators. In addition, the results also indicate that the intensity of biological interaction on the cobble substrate was greater than that on the gravel substrate.

Table 5. Summary of species associations among members of the same functional feeding groups in baskets filled with cobbles or gravel in the Chingmei Stream, Taiwan. Significant correlations are given and noted with asterisks (n = 24; n.s. = not significant)

Cobbles

Grazers/collectors	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Afronurus hyalinus (1)	–	n.s.	0.72*	0.58*	0.71*	0.67*	0.71*
Baetis spp. (2)		–	n.s.	0.47*	n.s.	0.75*	0.45*
Beaetiella bispinosa (3)			–	-0.46*	-0.66*	n.s.	-0.45*
Caenis sp. (4)				–	0.71*	0.64*	0.48*
Serratella sp. (5)					–	0.54*	0.70*
Chironomidae (6)						–	0.67*
Antocha sp. (7)							–

Filter-feeders	(1)	(2)	(3)	(4)	(5)
Stenopsyche sp. (1)	–	0.45*	0.67*	-0.78*	-0.62*
Hydropsychidae (2)		–	0.67*	n.s.	n.s.
Chironomidae (3)			–	0.56*	n.s.
Prosimulium spp. (4)				–	0.78*
Simulium spp. (5)					

Predators	(1)	(2)	(3)	(4)	(5)
Euphaea sp. (1)		0.64*	n.s	0.48*	0.34*
Neoperla sp. (2)		–	0.60*	0.47*	n.s.
Rhyacophila sp. A (3)				n.s.	n.s.
Prosimulium sp. (4)				–	0.45*
Ceratopogonidae (5)					–

Gravel

Grazers/collectors	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Afronurus hyalinus (1)	–	n.s.	n.s.	0.51*	0.81*	0.83*	0.83*
Baetis spp. (2)			0.50*	n.s.	n.s.	0.52*	n.s.
Baetiella bispinosa (3)			–	-0.53*	n.s.	n.s.	n.s.
Caenis sp. (4)					n.s.	0.50*	n.s.
Serratella sp. (5)					–	0.72*	0.85*
Chironomidae							0.75*
Antocha sp. (7)							–

Filter-feeders	(1)	(2)	(3)	(4)	(5)
Stenopsyche sp. (1)	–	0.51*	n.s.	n.s.	n.s.
Hydropsychidae (2)			n.s.	n.s.	n.s.
Chironomidae (3)			–	n.s.	n.s.
Prosimulium spp. (4)				–	0.78*
Simulium spp. (5)					–

Predators	(1)	(2)	(3)	(4)	(5)
Euphaea sp. (1)	–	0.57*	n.s.	n.s.	n.s.
Neoperla sp. (2)		–	n.s.	n.s.	0.66*
Rhyacophila sp. A (3)			–	n.s.	n.s.
Hemerodromia sp. (4)				–	n.s.
Ceratopogonidae (5)					

Equilibrium of aquatic insect communities

Colonization rates and extinction rates, expressed as number of taxa per day, were in agreement with the MacArthur-Wilson equilibrium model (1963 and 1967) (Fig. 4). The colonization rates for the cobble and gravel substrate did not level off until around day 12. The extinction rate for gravel substrate declined with time except between days 3 and 6 and between days 12 and 21 (Fig. 4B). The extinction rates for cobble substrate did not decline until day 12 and increased between days 30 and 42 (Fig. 4A). Equilibrium is the point where the curves for colonization and extinction cross. On the gravel substrate, it occurred around day 15 and on the cobble substrate it occurred around day 19. Furthermore, extinction rates are equivalent to turnover rates at equilibrium. The turnover rate for the gravel substrate was 0.93 taxa/day at 15 d, and for cobble substrate was 1.16 taxa/day at 19 d.

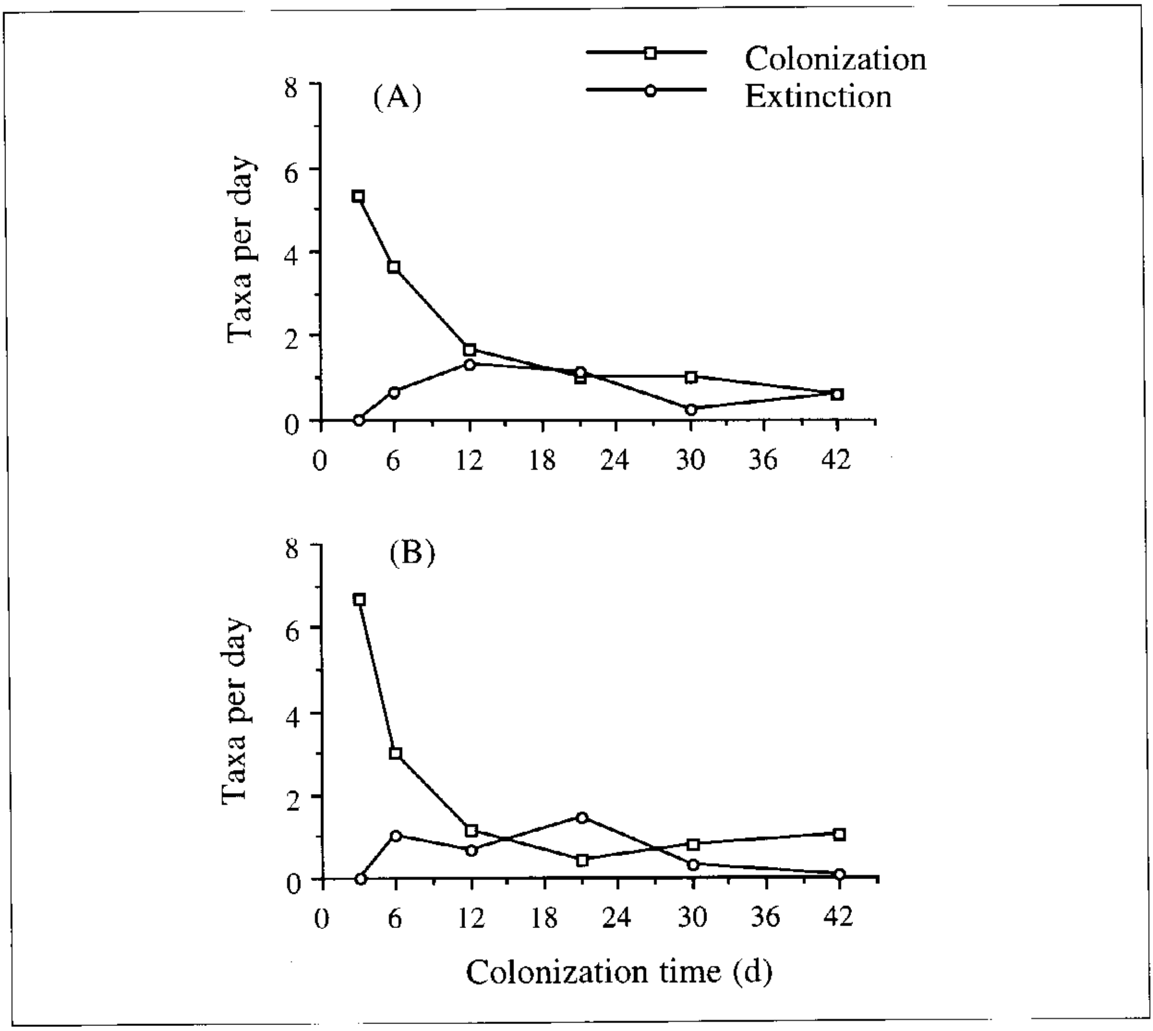

Fig. 4. Colonization and extinction rates of aquatic insects colonizing baskets filled with cobbles (A) and gravel (B) in the Chingmei Stream, Taiwan.

A high degree of fit to the lognormal model indicates a community in a high degree of equilibrium (Minshall *et al.*, 1985). The coefficient of determination of the least-squares fit was used to examine the degree of equilibrium in a community. For the cobble substrate, the coefficient of determination increased with time until day 30, and it declined on day 42 (Fig. 5). For the gravel substrate, the coefficient of determination increased with time except for the period between days 12 and 21 when the floods occurred (Fig. 6). Comparing the two kinds of substrate, the coefficients of determination for the gravel substrate were greater than those for the cobble substrate between 3 and 12 d and on day 42. This suggests that the time to reach community equilibrium for the gravel substrate was less than that for the cobble substrate.

Discussion

Colonization patterns of aquatic insect communities

In this study, artificial substrates were used to determine the effects of substrate size on colonization patterns of aquatic insect communities in the upper Chingmei Stream. Species colonization was rapid, with representatives of most species arriving within 3 d of the start of the experiment, except for Odonata and Coleoptera (Fig. 2). *Baetis* spp., Chironomidae, and *Prosimulium* spp. which dominated on day 3 had rapid colonization on both cobble and gravel substrates (Appendices 1 and 2). Rapid colonization of disturbed or new substrata by *Baetis* spp., and Chironomidae has also been noted by Ulfstrand *et al.* (1974), Gore (1979), Khalaf and Tachet (1980), Ciborowski and Clifford (1984), Robinson and Minshall (1986), and Boulton *et al.* (1988). These being early colonizers is consistent with their ability to exploit earliest food materials on bare substrates (Mackay, 1992).

Variation in the response of taxa to disturbance caused by floods, which occurred just after day 12 and resulted in rock overturning, was expected and found. The overturning of rocks dislodged some individuals, such as *Baetis* spp., *Caenis* sp., *A. hyalinus, Paraleptophlebia* sp., and Chironomidae on the gravel substrate (Appendix 2), and *B. bispinosa, Baetis* spp., and *Caenis* sp. on the cobble substrate (Appendix 1). However, some taxa seemed to be little affected by floods and continued colonizing the artificial substrates. These taxa were *Serratella* sp., *Neoperla* sp., Hydropsychidae, *Stenopsyche* sp., and *Antocha* sp. on the cobble substrate, and *Neoperla* sp., *Stenopsyche* sp., *Antocha* sp., and *Zaitzevia* sp. on the gravel substrate. Differences in morphology lead to differential ability to hold onto shifting substrate or to resist being crushed. For example, hydropsychid caddisflies are semi-sessile. They are able to build a retreat to resist being dislodged (Wiggins, 1977). Furthermore, the number of taxa in each order was reduced by the floods, except Trichoptera, which increased from 4 to 5 on the cobble substrate (Fig. 2).

Substratum type had a significant influence on the total number of colonizing individuals (Table 2). Gravel substrate had more individuals than did cobble substrate (Fig. 3B). The results are consistent with those of Minshall and Minshall (1977) and Wise and Molles (1979) who found significantly higher total numbers on smaller substrate. Minshall and Minshall (1977) suggested that more individuals colonize smaller substrate because more surface area is available. Rabeni and Minshall (1977) suggested that small particle size tends to accumulate large amounts of small detrital particles and that benthic insects concentrate where the food is most abundant. In this study, the cobble substrate had more organic matter than did gravel substrate (Fig. 1). This does not mean that the suggestion of

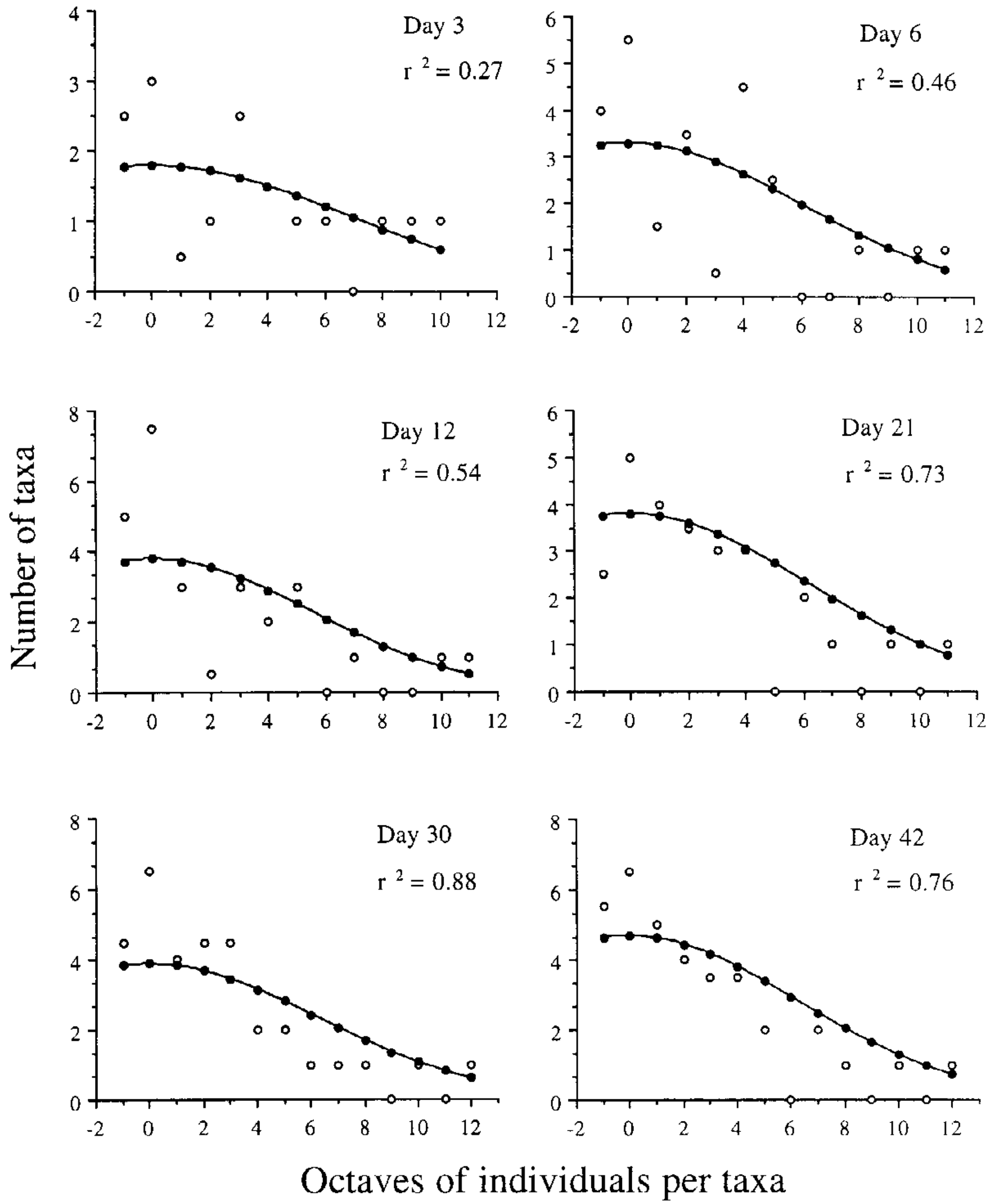

Fig. 5. Fit of taxa-abundance curves to a lognormal model for baskets filled with cobbles on each sampling day in the Chingmei Stream, Taiwan.

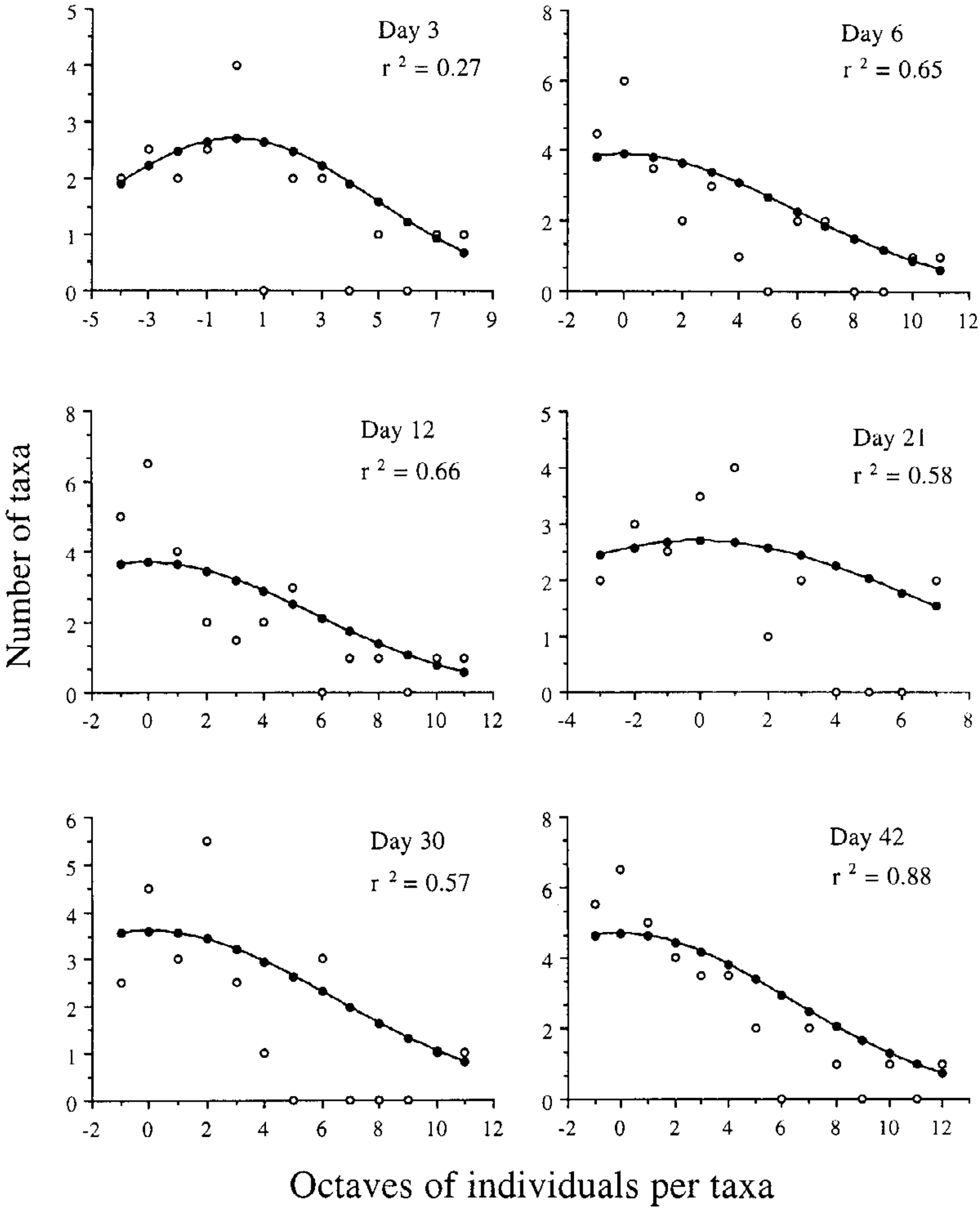

Fig. 6. Fit of taxa-abundance curves to a lognormal model for baskets filled with gravel on each sampling day in the Chingmei Stream, Taiwan.

Rabeni and Minshall cannot explain the results, since the amounts of detritus and primary production were not measured separately. According to field observations, more filamentous algae grew on the cobble substrate, while the organic matter in the gravel could have been detritus.

Equilibrium of aquatic insect communities

The total abundance and number of taxa colonizing either the cobble or gravel substrates did not approach an asymptote during the experimental period (Fig. 3). Therefore, an equilibrium, using these as criteria, was not attained. This was due to the flooding events which occurred after day 12 which disturbed the substrates and reset the biota back to earlier conditions. Wise and Molles (1979) conducted a 19-d colonization experiment comparing substrate size. The number of individuals and species appeared to stabilize on day 9 for both small substrate (10-25 mm) and large substrate (>75 mm). An equilibrium number of species can be established for both gravel and cobble substrates (Fig. 4), when the MacArthur-Wilson equilibrium model is used as the criterion. The equilibrium number of species for both gravel and cobble substrates occurred between days 12 and 21 when floods occurred. For the gravel substrate, the equilibrium may be due to the increasing extinction rate on day 21 which was caused by floods. For the cobble substrate, however, the extinction rate did not increase on day 21. This may be because the cobble substrate was more stable and was not overturned by high current velocity.

The turnover rate of species refers to the rate at which one species is lost and a replacement gained (Smith, 1990). The cobble substrate had higher turnover rates than did the gravel substrate. Moreover, the turnover rates were intermediate in the study site as compared with other places. The turnover rate for the gravel substrate was 0.93 taxa/d at 15 d and was 1.16 taxa/d for the cobble substrate at 19 d. The turnover rate was about 0.02 taxa/d at 625 d for a site where the breaking of a dam had destroyed the fauna (Minshall *et al.*, 1983), about 0.10 taxa/d at 109 d for a newly formed stream channel (Williams and Hynes, 1977), about 1.00 taxa/d at 8 d for river stones (Lake and Doeg, 1985), and about 1.35 taxa/d at 42 d for floating artificial substrates (Dickson and Cairns, 1972). The different results are probably due to the degree of disturbance before recolonization began and the size of the area to be colonized.

In this study, the state of equilibrium was affected by the particle sizes of the substrate, flooding events, and biological interactions (Figs. 5 and 6). The lognormal distribution was a better fit for the gravel substrate than for the cobble substrate. The results were in accordance with a previous study which found that aquatic insect communities in more variable environments had a higher degree of equilibrium than those in more stable environments (Shieh and Yang, 1999). The floods occurring just after day 12 led to the movement or overturning of gravel substrate and obviously decreased the degree of equilibrium of aquatic insect communities on the gravel substrate. The displacement of some taxa from the cobble substrate may have given rise to the decrease in the diversity index and the degree of equilibrium on day 42 (Figs. 3C and 5). This may be due to biological interactions, such as competition, with the increased abundance of superior competitors resulting in a decrease of inferiors. The disturbance caused by floods may inhibit the occurrence of competition on the gravel substrate and thus give rise to an increase in diversity (Fig. 3C). The results can be explained by the intermediate disturbance hypothesis (Connell, 1978) which is based on a presumption of a competitive hierarchy in a community. Under equilibrium conditions this hierarchy results in simplification of the community by the competitive exclusion of poorer competitors. However, analyses of associations are not a definitive indication of competitive interactions. Direct experimental evidence is needed to test whether competition does occur in subtropical Taiwanese streams. These streams are subject to frequent and unpredictable flooding disturbances which are likely to interrupt biotic interactions such as competition.

Biological interactions of aquatic insect communities

The association analysis in the same functional feeding group suggests that potential biological interactions occurred in the gravel and cobble substrate. The number of significant associations is a measure of the intensity of biological interactions. Thus, the communities on the cobble substrate possessed stronger potential biological interaction than did those on the gravel substrate. The cobble substrate in the condition of disturbance caused by floods provided aquatic insects with a more stable substratum type which resulted in more intensive biological interactions. Inversely, the gravel substrate was less stable during the floods which reduced the intensity of biological interactions. Moreover, positive associations between taxon pairs in the same functional feeding group may arise from a common response to environment gradients or the same response to the availability of resources. Negative associations between taxon pairs usually mean competition between the two taxa (Schluter, 1984). In Peckarsky's (1986) and Reice's (1981; 1983) studies, they did not find negative associations between potential competitor species and interpreted the results as lack of evidence for competition. Minshall and Minshall (1977) suggested that competition often plays a minor role in structuring communities of the stream benthos. In this study, negative associations were found in groups of grazers/collectors and filter-feeders on the cobble substrate.

The colonization patterns of individual species are consistent with the hypothesis that biological interactions may influence alterations in species dominance in the benthic community (Sheldon, 1984). In the colonization process, opportunistic species may be replaced by superior competitors that are slower colonizers. Hemphill and Cooper (1983) suggested that the succession from opportunistic species to superior species is common in streams. In this study, *B. bispinosa* was replaced by *A. hyalinus, Serratella* sp., and *Antocha* sp.; and simuliids were displaced by stenopsychids and hydropsychids on the cobble substrate (Table 5). Similar displacements among species were also observed by other investigators (Ulfstrand *et al.*, 1974; Allan, 1975; Fisher *et al.*, 1982; Hemphill and Cooper, 1983; McAuliffe, 1983, 1984; Malmqvist and Otto, 1987;).

In conclusion, substratum type had a significant influence on the total number of colonizing individuals, but did not have a significant influence on the number of taxa, diversity, or evenness. The gravel substrate provided more surface area for aquatic insects and supported more individuals of some taxa which characteristically have high colonization rates. Disturbance caused by floods led to movement or overturning of cobble and gravel substrate which dislodged some individuals of certain taxa. The floods obviously decreased the degree of equilibrium of the aquatic insect communities and the intensity of potential biological interactions on the gravel substrate. This was probably due to the gravel substrate having a higher probability of being overturned by floods. The results of log-normal analysis conformed to the concept that aquatic insect communities in more variable environments have a higher degree of equilibrium than those in more stable environments. However, direct experimental evidence is needed to test whether competition does occur in Taiwanese streams.

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Appendix 1. Density (per m²) of aquatic insect fauna colonizing baskets filled with cobble substrate on each sampling day in the Chingmei Steam, Taiwan. The "Total" column is the sum of numbers collected from days 3 to 42

Taxa	FFG*	Day 3	Day 6	Day 12	Day 21	Day 30	Day 42	Total
Ephemeroptera								
Afronurus hyalinus	G/C	0	35	110	145	200	225	715
Ameletus motivagus	G/C	0	5	0	0	20	50	75
Baetiella bipinosa	G/C	270	265	80	30	5	85	735
Baetis spp.	G/C	1760	9465	6010	4920	7285	9140	38580
Caenis sp:	G/C	0	285	645	410	720	475	2535
Cincticostella sp.	G/C	0	0	5	0	0	0	5
Epeorus sp.	G/C	5	10	10	0	0	5	30
Ephemera sp.	G/C	0	0	5	20	30	5	60
Paraleptophlebia sp.	G/C	0	0	10	10	80	5	105
Serratella sp.	G/C	0	5	45	105	210	205	570
Plecoptera								
Amphinemura sp.	S	5	10	0	0	5	0	20
Neoperla sp.	P	0	0	5	75	65	85	230
Paragnetina sp.	P	0	0	0	0	0	0	0
Protonemura sp.	S	25	5	10	0	0	0	40
Odonata								
Euphaea sp.	P	0	5	0	25	45	30	105
Onychogomphus sp.	P	0	0	5	5	5	5	20
Sieboldius sp.	P	0	0	5	0	5	0	10
Trichoptera								
Chimarra sp.	F	0	0	5	0	10	25	40
Goera sp.	G/C	0	0	0	10	20	20	50
Hydropsychidae	F	85	130	60	120	140	1255	1790
Hydroptila sp.	G/C	5	0	0	0	0	0	5
Melanotrichia sp.	G/C	0	0	0	10	10	10	30
Oecetis sp.	P	0	0	0	0	0	0	0
Orthotrchia sp.	G/C	0	0	5	0	0	0	5
Plectrocnemia sp.	G/C	0	0	0	0	0	10	10
Rhyacophila sp.A	P	0	10	0	60	25	160	255
Rhyacophila sp.B	P	0	0	0	0	5	0	5
Stactobia sp.	G/C	5	25	0	0	0	0	30
Stenopsyche sp.	F	60	105	130	340	480	910	2025
Tinodes sp.	G/C	0	0	0	0	0	0	0
Diptera								
Antocha sp.	G/C	45	160	300	1225	1450	1520	4700
Atherix sp.	P	0	0	5	15	20	0	40
Ceratopogonidae	P	0	5	10	0	60	60	135
Chironomidae	G/C,F	4245	12865	11085	11035	27355	53560	120145
Dolichopodidae	P	5	0	0	0	0	0	5
Eriocera sp.	P	0	0	0	0	20	0	20
Hemerodromia sp.	P	0	5	10	45	40	10	110
Prosimulium spp.	F	5390	1905	175	0	0	5	7475
Psychoda sp.	G/C	0	5	0	0	0	0	5
Simulium spp.	F	400	115	20	0	5	0	540
Wiedemannia sp.	P	0	0	5	0	0	5	10

Appedix 1. Continued

Taxa	FFG*	Day 3	Day 6	Day 12	Day 21	Day 30	Day 42	Total
Coleoptera								
Grouvellinus sp.	G/C	0	5	0	10	0	5	20
Hydrophilidae	P	0	40	0	5	5	5	55
Mataeopsphus sp.	G/C	0	0	0	0	5	0	5
Psephenoides sp.	G/C	0	0	0	0	0	0	0
Stenelmis sp.	G/C	0	0	0	5	10	5	20
Zaizevia sp.	G/C	0	0	0	5	10	5	20
Lepidoptera								
Eoophyla sp.	G/C	0	0	0	10	5	40	55
Hemiptera								
Micronecta sp.	P	0	0	0	0	0	20	20
Total		12305	25465	18755	18640	38350	67945	181460

*FFG = functional feeding groups; G/C = grazers/collectors; F = filter-feeders; P = predators; S = shredders.

Appendix 2. Density (per m^2) of aquatic insect fauna colonizing baskets filled with gravel substrate on each sampling day in the Chingmei Stream, Taiwan. The "Total" coulumn is the sum of numbers collected from days 3 to 42

Taxa	FFG*	Day 3	Day 6	Day 12	Day 21	Day 30	Day 42	Total
Ephemeroptera								
Afronurus hyalinus	G/C	35	50	195	100	190	300	870
Ameletus motivagus	G/C	0	5	0	0	10	30	45
Baetiella bipinosa	G/C	450	85	35	0	20	310	900
Baetis spp.	G/C	11095	7965	9550	7240	11650	17220	64720
Caenis sp.	G/C	75	680	1675	260	750	450	3890
Cincticostella sp.	G/C	0	0	0	0	0	0	0
Epeorus sp.	G/C	15	0	0	0	0	60	75
Ephemera sp.	G/C	0	15	10	0	40	30	95
Paraleptophlebia sp.	G/C	5	10	45	10	60	40	170
Serratella sp.	G/C	5	5	40	50	80	140	320
Plecoptera								
Amphinemura sp.	S	0	5	5	0	0	10	20
Neoperla sp.	P	0	20	45	130	90	260	545
Paragnetina sp.	P	5	0	0	0	0	0	5
Protonemura sp.	S	25	5	10	0	0	0	40
Odonata								
Euphaea sp.	P	0	5	10	20	10	50	95
Onychogomphus sp.	P	0	0	0	10	20	10	40
Sieboldius sp.	P	0	5	0	0	0	0	5
Trichoptera								
Chimarra sp.	F	0	0	5	10	0	10	25
Goera sp.	G/C	0	0	0	20	20	20	60
Hydropsychidae	F	220	145	120	110	70	3860	4525
Hydroptila sp.	G/C	0	0	0	0	0	0	0
Melanotrichia sp.	G/C	0	0	0	0	0	10	10
Oecetis sp.	P	0	5	5	0	0	0	10
Orthotrchia sp.	G/C	0	0	0	0	0	0	0
Plectrocnemia sp.	G/C	0	0	0	0	0	0	0
Rhyacophila sp.A	P	45	35	20	50	70	470	690
Rhyacophila sp.B	P	0	0	0	0	0	30	30
Stactobia sp.	G/C	10	0	0	0	0	0	10
Stenopsyche sp.	F	295	330	265	450	690	1800	3830
Tinodes sp.	G/C	0	0	0	0	0	10	10
Diptera								
Antocha sp.	G/C	20	70	90	500	890	2350	3920
Atherix sp.	P	0	0	5	0	20	0	25
Ceratopogonidae	P	0	5	0	40	40	100	185
Chironomidae	G/C,F	8190	11350	19760	9040	28870	50730	127940
Dolichopodidae	P	0	0	0	0	0	0	0
Eriocera sp.	P	0	0	0	30	0	10	40
Hemerodromia sp.	P	5	10	15	10	50	40	130
Prosimulium spp.	F	1890	325	235	0	10	50	2510
Psychoda sp.	G/C	0	5	0	0	0	0	5
Simulium spp.	F	60	20	5	0	0	0	85
Wiedemannia sp.	P	0	0	0	0	0	10	10

Appedix 2. Continued

Taxa	FFG*	Day 3	Day 6	Day 12	Day 21	Day 30	Day 42	Total
Coleoptera								
Grouvellinus sp.	G/C	0	0	15	0	0	20	35
Hydrophilidae	P	0	0	0	0	10	10	20
Mataeopsphus sp.	G/C	0	0	0	0	0	0	0
Psephenoides sp.	G/C	0	0	5	0	0	10	15
Stenelmis sp.	G/C	0	0	0	0	0	0	0
Zaizevia sp.	G/C	0	0	5	90	0	10	105
Lepidoptera								
Eoophyla sp.	G/C	0	0	0	0	10	10	20
Hemiptera								
Micronecta sp.	P	0	0	0	0	0	0	0
Total		22445	21155	32170	18170	43670	78470	216080

*FFG = functional feeding groups; G/C = grazers/collectors; F = filter-feeders; P = predators; S = shredders.