AN ABSTRACT OF THE THESIS OF

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Title: Colonization Patterns of Stream Benthos on Artificial Substrates in Taiwan

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N. H. Anderson

Experiments on the colonization of artificial substrates by stream benthos were conducted in upper Chingmei Stream, Taiwan. The artificial substrates were colonized by stream benthos for periods of 3, 6 12, 21, 30 and 42 days.The two experiments were designed for different purposes. Experiment I from December 15, 1990 to January 29, 1991 investigated the colonization patterns of stream benthos at two sites: a polluted site caused by coal mining activities (Site 1) and a recovery site further downstream of the polluted site (Site 2). Experiment II from March 14, 1991 to April 28, 1991 tested the effect of two different sizes of substrate (cobble and gravel) on the colonization patterns of stream benthos at Site 2.

In Experiment I, the total number of individuals and taxa were significantly affected by exposure period of experimental substrates and sites which indicate the occurrence of succession and the detrimental effect of coal mining activities on the benthic community. At Site 1, only *Caenis sp., Euphaea sp.* and Chironomidae occurred on all sampling dates and were abundant. The other taxa may just continue to drift away from the site. The chironomid larvae were most abundant. They accounted for over 90% of the colonizing

individuals from day 12 to day 42. At Site 2, *Baetis sp.A* and Chironomidae were most abundant. They accounted for over 80% during the experiment, except on day 21. The relative abundance shifted from *Baetis sp.A* to Chironomidae with an increase in colonization time. Association analysis was performed on the abundance of taxa pairs within the same functional feeding group at Site 2. The results suggest that filter-feeders and predators have concordant colonization patterns. The relationship between taxa and abundance at the two sites also was tested by lognormal distribution to determine the degree of equilibrium of the community.

In Experiment II, the substratum types influenced only the total number of individuals colonizing baskets. The gravel substrate provides more surface area for stream benthos and supports more individuals. *Baetis sp.A* and chironomid larvae were abundant; they accounted for over 84% of the individuals from day 6 to 42 on both gravel and cobble. The chironomid larvae comprised 36% 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 cobble than on gravel. The negatively significant associations also occurred more on the cobble substrate. This indicates that biological interactions may be important in determining the development of community on the cobble substrate. Disturbance caused by floods influenced the colonization patterns, especially on the gravel substrate. It reset the artificial substrates back to earlier conditions. This study only suggests that competition may occur in the subtropical Taiwanese stream and further experimentation is needed to demonstrate whether competition occurs.

Colonization Patterns of Stream Benthos on Artificial Substrates in Taiwan

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INTRODUCTION

Sheldon (1984) defined colonization as the sequence of events through which individuals, or groups of individuals, become established in habitats where they were absent. He viewed the world of stream insects as an everchanging mosaic of environments in which elements arise, vanish, and reappear with different periodicities and predictabilities. The description shows the importance of colonization for stream benthos.

The factors influencing colonization and subsequent change of macroinvertebrate populations in streams may be allogenic (external, abiotic), or autogenic (internal, biotic). The allogenic factors may be the characteristics of substrate, seasonal changes and unpredictable disturbance. The autogenic factors may be interactive, where the present community influences establishment of future communities, or noninteractive, such as species life histories (Fisher 1983; Sheldon 1984). Current ecological thought holds that interactive biotic factors must operate under equilibrium conditions (May 1973). In general, allogenic and autogenic causes are interactive. For example, seasonal change may alter the intensity of interspecific competition and the quantity and quality of resources available are mediated through the abiotic environment.

The principal colonization pathways of stream benthos are aerial movements, downstream drift, and upstream and vertical movement from deep substrates (Williams and Hynes 1976). In permanent streams, downstream drift is most important (Townsend and Hildrew 1976; Williams and Hynes 1976). This indicates the importance of drift in immigration and emigration of lotic benthic invertebrates and in the effects of drift on benthic community structure.

In stream ecosystems, the change in community composition after disturbance at a site, or the seasonal change in the life cycles of stream invertebrates may be called succession. The ecosystems may be disturbed by factors such as floods, drought, forest cutting, dredging, application of toxic chemicals, and so on. Seasonal succession in life cycle provides reproductive isolation and allows nymphal growth period to be staggered and thereby lessen competition for food and space (Kerst and Anderson 1970).

Fisher (1983) explored two aspects of succession in streams: site-specific temporal and longitudinal succession. The temporal succession is the change in communities with time following disturbance. He suggested that the site-specific temporal succession should not occur since the system of stream ecosystem is heterogeneous in New England. Peckarsky's (1986) study, however, documented the existence of temporal succession of invertebrates in a temperate woodland stream. The longitudinal succession has been loosely defined as the sequence of communities in streams from headwaters to larger rivers. Hynes (1970) indicated that running water display longitudinal biotic zonation. Vannote et al. (1980) used the River Continuum Concept to explain the longitudinal distribution of stream benthos.

Minshall and Petersen (1985) proposed that the community structure on individual rocks or substratum patches in a stream changes with time in a manner analogous to the colonization of oceanic islands (MacArthur and Wilson 1963, 1967; Sheldon 1977; Shaw and Minshall 1980; Minshall et al. 1983; Minshall et al. 1985; Lake and Doeg 1985). Their study documented that the development of species composition on individual rocks or habitat patches in stream conforms to the MacArthur-Wilson equilibrium model for colonization of oceanic islands. They suggested that the drift of stream benthos can be viewed as the major means of immigration to and emigration from the rock "islands" for many species. Thus, the role of drift is of great importance in determining species richness on these habitats.

Wilson (1969) described two basic forms of the MacArthur-Wilson equilibrium model: (1) a noninteractive equilibrium associated with colonization of newly opened habitats and most likely the result of density-independent factors; and (2) an interactive equilibrium usually occurring at a later stage in the community development process and attributable to density-dependent factors. The two equilibria are visualized as following each other in time from a noninteractive state to an interactive state. On the other hand, Minshall and Petersen (1985) suggested that stream macroinvertebrate communities on rock islands are the result of an interplay between stochastic and deterministic forces acting on the component population. The community structure in a noninteractive equilibrium state is primarily dependent on stochastic forces and in an interactive equilibrium state is dependent on deterministic forces.

Substrate may affect the distribution and abundance of stream macroinvertebrate (Minshall 1984), and may mediate their response to disturbance (Gurtz and Wallace

1984). The effect of physical disturbance on substrate stability also influences the amount of detritus trapped between the particles and it generally will be proportional to the size of the particle (Minshall 1984).

In Taiwan the water pollution problem has reached crisis proportion because of rapid economic development. Most rivers have been polluted on the different scales by the industrial and domestic sewage. It is becoming increasingly important to identify and understand the impact of pollutants on aquatic insects. However, most aquatic insects in Taiwan have not been named and their biology have not been studied.

In terms of the geographical position of Taiwan, it lies off the east coast of Asia, about 160 km of the China coast, and athwart the Tropic of Cancer. The island is surrounded by warm ocean currents and enjoys an oceanic and subtropical monsoon climate. The climate is subtropical in the north and tropical in the south. The size of the island is about 400 km long and 140 km broad, with an area 3600 km^2. Rugged mountains cover more than two-thirds of the island. Sixty peaks tower above 3000 m. The highest point on the island is about 4000 m. The high altitude of the island's mountains provide climatic zones from tropical to alpine. Therefore, the insect fauna in the island is abundant and diverse. For the habitats of stream insects, most rivers in Taiwan originate from peaks of more than 2000 m in elevation and flow toward the east or the west. Since the distance between the high mountain peaks and the coastal margins in less than 100 km, the general characteristics of the rivers in Taiwan are naturally short and steep. The characteristics of rivers and the features of climate in

Taiwan make the aquatic insects worthy to be studied.

This study deals with the colonization of substrata by macroinvertebrates in the upper Chingmei Stream in subtropical northern Taiwan. It was undertaken with a view to (1) examining the colonization of new substrate patches and the subsequent patterns of species dominance and functional feeding groups at two sites: a site impacted by coal mining activities (polluted site), and a site further downstream where the impacts of the mine have been diluted by water from another tributary (recovery site); (2) comparing the patterns of colonization of two different sizes of substrate; and (3) examining the relationship between dominance and community structure during the process of colonization.

STUDY SITE

The experiments were conducted in upper Chingmei Stream (lat. 25°, 01'N, log. 121°, 41' E) flowing through Shihtin Shoung, Taipei County, and 25 km east of Taipei City in northern Taiwan (Fig. 1). The area is of Miocene and Pliocene age, and soil group is yellow earth (Hsieh 1964). The annual average precipitation is about 4000 mm. Most of the rain falls in winter (the average rainfall in January is about 400 -500 mm) but it is spread over the entire period so it does not result in flooding. Although the total rainfall is less in summer (the average in July is about 200 - 300 mm), the typhoons that occur often give rise to unpredictable flooding on different scales.

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). These provide allochthonous material which is trapped in the streambed and so provides a potential source of food for the benthic fauna during the whole year. The headwaters of the streams are in agricultural areas with tea plantations (*Thea sinensis* (L) Sims). A road was built along the stream and was finished in October, 1990. The stream therefore receives surface runoff from farmland and rural dirt roads.

Two study sites were selected for the experiments (Fig. 1). Site 1 is on a third-order stream at an altitude of 200 m. Site 2 is on a fourth-order stream at an altitude of

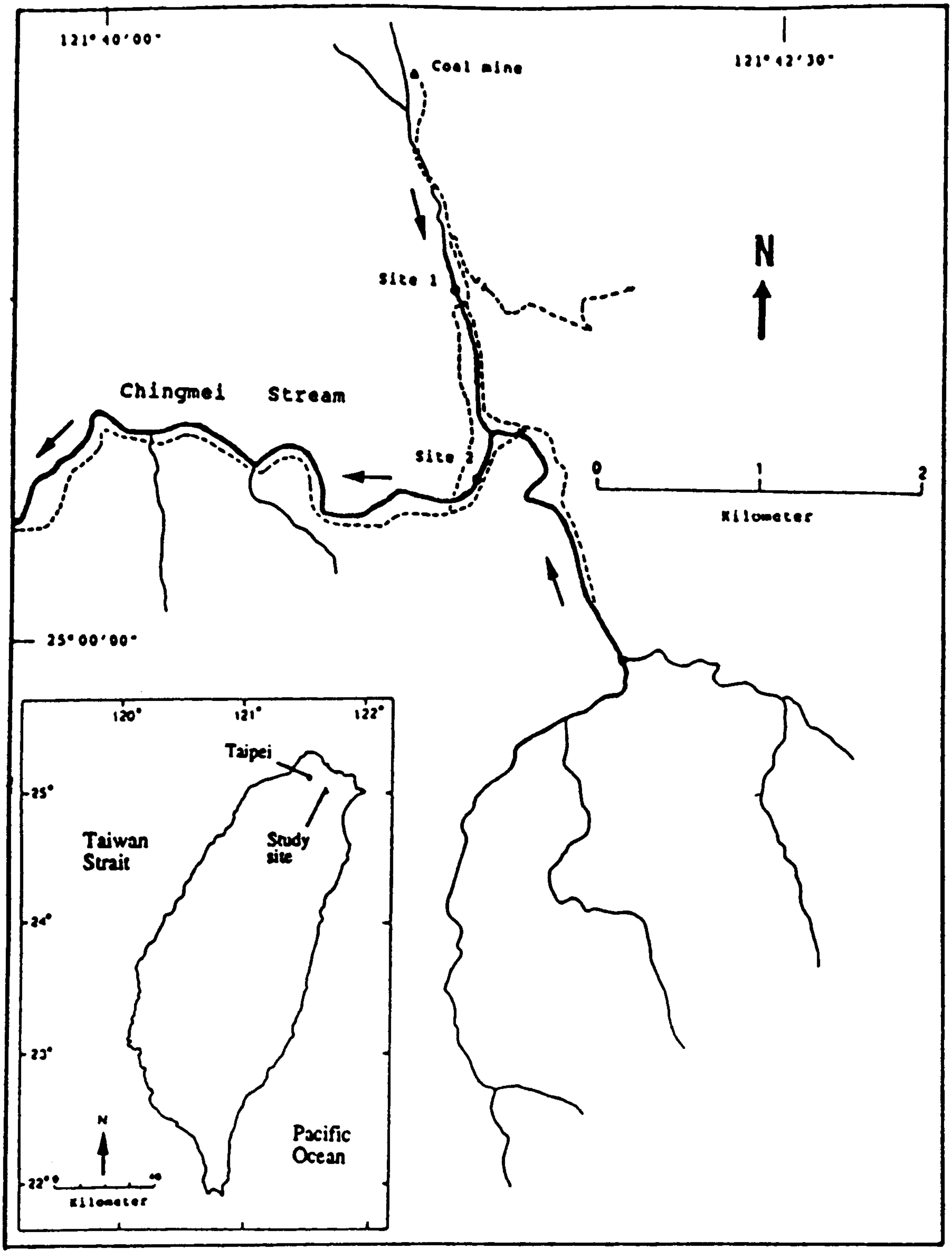

Fig. 1. Location of the study sites on the Chingmei Stream. Insert map shows location of study area in Taiwan. The dashed lines shown above indicate roads.

150 m, and about 2 km downstream of site 1. The two sites are riffles with heterogenous substrate and open canopy. Upstream of Site 1 there is a coal mine about 2 km away. The coal has been dug here since 1970. Stream water is used to clean coal; this causes highly turbid conditions at least once per day. Therefore, the stream section of Site 1 is disturbed frequently by physical and chemical factors from the mine. Site 2 is located downstream of Site 1 and it receives additional runoff from major tributaries. The influence of physical and chemical disturbance at Site 1 on the stream section of Site 2 is decreased by this dilution.

In the two study areas, the fish were dominated by omnivorous goby (*Rhinogobius brunneus* (Temminck et Schlegel)) and herbivorous *Crossostoma lacustre* (Steindachner). In addition, filamentous algae (*Cladophora sp.*, *Spirogyra sp.* and *Oscillatoria sp.*) commonly covered the upper surface of cobbles and small stones in the whole year.

MATERIALS AND METHODS

Sampling Methods

In this study, two field experiments were carried out. In Experiment I, from December 15, 1990 to January 29, 1991, the community structure and colonization patterns of stream macroinvertebrate were compared between Site 1 and Site 2. A mixture of particle sizes was used as artificial substrate. Plastic baskets (mesh = 4 mm, dimension 25x20x6 cm) were filled with 20 pieces of gravel (16 - 32 mm), 9 pebbles (32 - 64 mm) and 6 cobbles (64 - 128 mm). In Experiment II, from March 14, 1991 to April 28, 1991, the community structure and colonization patterns of stream macroinvertebrates on gravel and on cobble substrate were compared at Site 2. Plastic baskets were filled with one of the two substratum types: cobble or gravel.

The cobble and pebble were collected from the dry streambed and the gravel was collected from a quarry. Each stone was washed in stream water. In Experiment II the number of particles per sediment basket was determined by count for cobble. For gravel the mass per particle and the total mass per basket were weighed, and the total number of particles calculated (Table 1 column 1). Total rock surface area per basket was determined by wrapping rocks in aluminum foil and then weighing (Table 1 column 2). To measure the interstitial volume per basket, a plastic pan was packed with substrate, water was added until it was full, then the water was decanted and measured (Table 1 column 3).

Table 1. Physical properties of substrates used in the colonization experiments in Chingmei Stream, Taiwan.

	Mean number of particles per basket	Mean surface area per basket	Mean interstitial volume per basket
Gravel	343.7 (n = 27)	6133.50 cm^2 (n = 50)	1071 ml (n = 27)
Cobble	8.0 (n = 27)	1747.36 cm^2 (n = 50)	1132 ml (n = 27)

Sampling Procedure

In Experiment I, all baskets at both study sites were placed randomly in the stream bottom on December 15, 1990. 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 days. Each treatment had four replicates, so at least 8 baskets were sampled on each sampling date. The total 24 baskets for each study site were arranged randomly into 4(columns) x 6(rows). The space between columns and between rows was at least 1.5 m.

In Experiment II, the sampling procedure was similar to Experiment I. However, the baskets for periods of 3, 6, 12 days were replaced in the stream for the periods of 42, 30 and 21 days, respectively. Twenty four baskets, plus an additional six baskets as a safety factor, were arranged randomly into 6 (columns) x 5 (rows).

At the end of the colonization period a basket was lifted off the streambed and transferred into a basket with 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 animals and other macroinvertebrates. The other sediment in the basket was placed in labeled individual plastic bags.

A Surber sampler (50 x 50 cm^2 and mesh = 0.25 mm) was used to collect benthos samples for comparison with the artificial substrates. In Experiment I the samples were collected on days 12 and 42. In Experiment II they were collected on day 42. Each sample had three replicates.

To compare the differences in the physical and chemical characteristics between Site 1 and Site 2 and to monitor whether floods occurred 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.

In the laboratory, the sediment was transferred to a white plastic pan and the macroinvertebrates picked. All animals were preserved in 70% ethyl alcohol. Then the animals were keyed to genus whenever possible by Kawai (1985), Merritt and Cummins (1984) or Wiggins (1977). All Chironomidae found were only counted. The data obtained included numbers of insects, number of taxa, and a diversity index for every substratum basket. Diversity indices were depressed because of the groupings listed above. To measure the amounts of organic matter trapped by baskets, the sediment was oven-dried at 60 °C for at least 24 hours and weighed. It was then combusted at 500°C for 2 hours, cooled and reweighed to determine organic content.

The specimens in the experiments were deposited in the collection of Department of Plant Pathology and Entomology, National Taiwan University and Department of Entomology, Oregon State University for further identification.

Statistical Design and Data Analysis

The design was a two-way factorial analysis of variance with site (two levels: Site 1 and Site 2) or substrate (two levels: cobble and gravel) and time (six sample dates) as factors (2 x 6 design with 12 treatment combinations). There were four replicates of each combination. The following parameters were analyzed in the designs described above: total number of individuals, total number of taxa, Shannon-Wiener's H', and evenness for every substratum basket. Numerical data were log-transformed to stabilize variance. To examine potential biological interactions, Spearman rank correlation coefficients were used to compare between-species pairs per basket. This analysis is more sensitive than presence/absence indices (Pielou 1977), since relationships are expressed as a gradient of abundances.

RESULTS

Experiment I

Physical and Chemical Factors

Values for physical and chemical characteristics at the two study sites during the field experiment (from December 15, 1990 to January 29, 1991) are given in Table 2. Using signed-rank test (Devore and Peck 1986) to compare the differences in the physical and chemical characteristics between Site 1 and Site 2, showed that the water depth, current velocity, discharge and pH values were significantly higher at Site 2 than at Site 1 ($P < 0.05$). The pH values of the two sites showed the streams are slightly alkaline. The conductivity values at Site 1 were significantly higher than that at Site 2 ($P < 0.05$). This is due to the mining activities which released water that was high in inorganic ions. The mean weight of organic matter for the two study sites is shown Fig. 2 and standard errors are given in Appendix 1. The organic matter did not significantly increase until day 30 at the two study sites. The amount at Site 1 was significantly higher than that at Site 2 during the experiment ($P < 0.05$).

Stream Benthos Fauna

During the experiment, 28 taxa were collected at Site 1 (Table 3) and 46 taxa were collected at Site 2 (Table 4) in the colonization baskets. Of the 20 taxa found only at Site 2, there were 4 Ephemeroptera, 2 Odonata, 5 Trichoptera, 4 Diptera, and 5 Coleoptera. At Site 1, there were 3 taxa of Odonata and *Parachauliodes sp.*

Table 2. Physical and chemical characteristics of Site 1 and Site 2 on each sampling day in Experiment I, Chingmei Stream, Taiwan.

		Sampling date					
		3	6	12	21	30	42
Temperature (°C)	Site 1	17.5	17.2	17.0	16.0	17.1	17.8
	Site 2	16.3	17.0	15.5	16.8	17.2	18.0
Stream width (m)	Site 1	6.9	7.1	6.0	6.8	6.9	7.0
	Site 2	6.8	7.0	6.6	6.7	7.0	7.0
Depth (cm)	Site 1	16.2	14.7	14.8	21.2	20.0	19.2
	Site 2	21.5	20.6	18.3	22.0	22.5	23.7
Velocity (m/sec)	Site 1	0.11	0.15	0.05	0.16	0.21	0.24
	Site 2	0.45	0.64	0.15	0.51	0.47	0.45
Discharge (m^3/sec)	Site 1	0.123	0.157	0.044	0.231	0.290	0.323
	Site 2	0.658	0.923	0.181	0.752	0.740	0.747
pH	Site 1	8.03	8.02	8.09	8.01	7.95	7.64
	Site 2	8.41	8.31	8.35	8.28	8.20	8.12
Conductivity (μs/cm)	Site 1	345	331	318	239	255	280
	Site 2	159	176	197	260	185	177

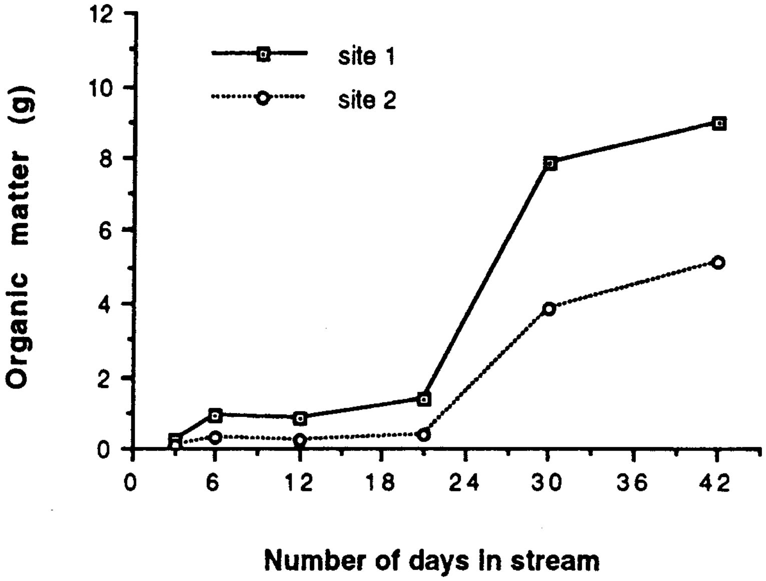

Fig. 2. Amounts of organic matter collected by artificial substrate trays on each sampling day in Experiment I, Chingmei Stream, Taiwan.

Table 3. Density (per m²) of benthic macroinvertebrate fauna colonizing baskets of mixed substrates on each sampling day at Site 1 in Experiment I, Chingmei Stream, Taiwan. "Total" column is the sum of numbers collected from Day 3 to 42.

	Day 3	*Day 6*	*Day 12*	*Day 21*	*Day 30*	*Day 42*	*Total*
Ephemeroptera							
Baetiella bispinosa	5	0	0	0	0	0	5
Baetiella sp.B	130	55	20	0	0	0	205
Baetis sp.A	65	55	115	40	0	0	275
Baetis sp.B	5	0	10	0	0	0	15
Caenis sp.	25	45	30	110	10	30	250
Cincticostella sp.	0	0	0	0	10	0	10
Dipteromimus sp.	0	0	5	40	0	0	45
Ecdyonurus sp.	5	15	10	0	0	0	30
Ephemera sp.	0	0	0	5	0	5	10
Paraleptophlebia sp.	0	0	0	0	0	5	5
Plecoptera							
Amphinemura sp.	20	10	20	10	0	0	60
Neoperla sp.	0	0	0	5	5	5	15
Odonata							
Euphaea sp.	25	50	80	70	45	55	325
Sieboldius sp.	0	0	0	0	0	5	5
Stylogomphus sp.	0	0	0	0	5	20	25
Stylurus sp.	0	0	0	0	0	5	5
Megaloptera							
Parachauliodes sp.	0	0	0	5	0	10	15
Trichoptera							
Hydropsychidae	10	10	20	5	5	5	55
Melanotrichia sp.	0	5	0	0	0	0	5
Stenopsyche sp.	25	5	0	5	10	0	45
Diptera							
Antocha sp.	0	0	0	10	10	5	25
Atherix sp.	0	5	0	5	10	5	25
Ceratopogonidae	0	0	0	5	20	25	50
Chironomidae	395	1105	2970	4385	2265	2745	13865
Hemerodromia sp.	0	0	5	15	45	40	105
Coleoptera							
Grouvellinus sp.	0	0	0	0	10	5	15
Hydrophilidae	0	5	0	0	0	0	5
Zaitzevia sp.	0	0	0	0	5	0	5
Total	710	1365	3285	4715	2455	2970	15500
Total without Chironomidae	315	260	315	330	190	225	1635

Table 4. Density (per m^2) of benthic macroinvertebrate fauna colonizing baskets of mixed substrates on each sampling day at Site 2 in Experiment I, Chingmei Stream, Taiwan. "Total" column is the sum of numbers collected from Day 3 to 42.

	Day3	*Day6*	*Day12*	*Day21*	*Day30*	*Day42*	*Total*
Ephemeroptera							
Baetiella bispinosa	20	0	0	1325	260	425	2030
Baetiella sp.B	1110	755	425	3560	350	255	6455
Baetis sp.A	5240	5365	9400	17275	6600	8020	51900
Baetis sp.B	30	65	75	755	910	1195	3030
Caenis sp.	20	30	45	110	385	360	950
Choroterpes sp.	0	0	0	0	0	5	5
Cincticostella sp.	0	0	10	0	0	10	20
Dipteromimus sp.	60	5	30	75	0	0	170
Ecdyonurus sp.	15	20	65	100	205	185	590
Epeorus sp.	0	5	0	20	50	20	95
Ephemera sp.	0	0	0	0	5	10	15
Paraleptophlebia sp.	0	0	0	0	20	10	30
Serratella sp.	0	0	0	0	50	10	60
Torleya sp.	0	0	0	0	0	5	5
Plecoptera							
Amphinemura sp.	5	0	25	215	55	75	375
Neoperla sp.	0	0	0	10	40	30	80
Odonata							
Euphaea sp.	5	0	10	5	20	10	50
Lestidae	0	0	0	5	0	0	5
Onychogomphus sp.	0	0	0	0	0	5	5
Trichoptera							
Chimarra sp.	0	5	0	115	75	165	360
Hydropsychidae	135	200	615	2420	960	1290	5620
Hydroptila sp.	0	0	5	0	0	0	5
Melanotrichia sp.	0	0	0	0	0	15	15
Oecetis sp.	0	0	5	0	0	0	5
Rhyacophila sp.A	0	0	5	15	20	60	100
Stactobia sp.	0	0	0	5	0	0	5
Stenopsyche sp.	20	60	55	95	125	120	475

Table 4. Continued.

	Day 3	Day 6	Day 12	Day 21	Day 30	Day 42	Total
Diptera							
Antocha sp.	0	0	25	70	240	360	695
Atherix sp.	0	0	0	0	5	0	5
Bibiocephala sp.	0	0	0	0	0	5	5
Ceratopogonidae	0	0	0	0	20	0	20
Chironomidae	2335	2800	11180	15330	14170	15135	60950
Hemerodromia sp.	0	5	15	35	15	30	100
Prosimulium sp.	325	225	445	2490	340	440	4265
Simulium sp.	10	15	0	210	70	75	380
Wiedemannia sp.	0	0	0	35	15	15	65
Coleoptera							
Grouvellinus sp.	0	5	0	10	5	35	55
Hydrophilidae	0	0	0	0	0	5	5
Limnichidae	0	0	0	0	5	0	5
Mataeopsephus sp.	0	0	0	0	0	5	5
Orectochilus sp.	0	0	0	0	5	5	10
Psephenoides sp.	0	0	0	0	0	5	5
Ptiliidae	0	0	0	5	0	0	5
Zaitzevia sp.	0	0	0	0	5	10	15
Lepidoptera							
Eoophyla sp.	0	0	0	0	10	5	15
Hemiptera							
Micronecta sp.	0	0	0	0	5	0	5
Total	9330	9560	22435	44290	25040	28410	139065
Total without Chironomidae	6995	6760	11255	28960	10870	13275	78115

(Megaloptera) that were not recorded from Site 2. In benthos samples, which were collected on day 12 and day 42, 33 taxa were collected at Site 1 and 32 taxa were collected at Site 2 (Table 5). There was no difference in the number of taxa in orders between the two sites except in the orders Ephemeroptera and Odonata. Seven mayfly taxa were collected at Site 1 and 11 at Site 2. Four damselfly taxa were collected at Site 1 and two at Site 2.

At Site 1 the Chironomidae was the most numerous taxon in the colonization baskets. From day 12 to 42 they accounted for over 90% of the colonizing individuals. In contrast at Site 2 they comprised 35 - 57% of the fauna during the same interval. In benthos samples at Site 1 on day 12 and day 42, chironomid larvae were 61% and 74% of the total fauna, and at Site 2 they are 42% and 45% of the total fauna.

In the colonization baskets, the most abundant Ephemeroptera were *Baetiella sp.B*, *Baetis sp.A* and *Caenis sp.* at Site 1 (Table 3). For the three taxa the largest number of individuals of each occurred on a different sampling day. *Baetiella sp.B* (130 / m^2) occurred on day 3, *Baetis sp.A* (115 / m^2) occurred on day 12, and *Caenis sp.* (110 / m^2) occurred on day 21. Of the three taxa, only *Caenis sp.* occurred on each sampling day. The dominant Odonata was *Euphaea sp.* damselflies. They were consistently more abundant at Site 1 than at Site 2. In the benthos samples, the damselflies were also more abundant at Site 1 than at Site 2. In addition, *Caenis sp.* at Site 1 accounted for about 10% of the colonizing individuals without Chironomidae on days 12 and 42 in the colonizing baskets. In contrast with the benthos samples, they only comprised 2% of the same fauna on days 12 and none was collected on day 42.

Table 5. Density (per m²) of total benthic macroinvertebrate fauna collected by Surber sampler at Site 1 and Site 2 on day 12 and day 42.

	Site 1		Site 2	
	Day 12	Day 42	Day 12	Day 42
Ephemeroptera				
Baetiella bispinosa	1	0	4	97
Baetiella sp.B	80	0	216	104
Baetis sp.A	23	11	1296	805
Baetis sp.B	0	0	32	113
Caenis sp.	5	0	11	64
Cincticostella sp.	5	1	0	0
Dipteromimus sp.	0	0	1	0
Ecdyonurus sp.	0	1	15	25
Epeorus sp.	0	0	0	3
Ephemera sp.	4	5	0	23
Paraleptophlebia sp.	0	0	0	3
Serratella sp.	0	0	1	3
Plecoptera				
Amphinemura sp.	9	0	1	8
Neoperla sp.	7	0	4	16
Taeniopterygidae	0	1	0	0
Odonata				
Calopterygidae	8	3	0	0
Euphaea sp.	25	32	7	5
Onychogomphus sp.	19	13	5	1
Stylogomphus sp.	1	4	0	0
Megaloptera				
Parachauliodes sp.	1	0	0	0
Protohermes sp.	4	1	0	1
Trichoptera				
Chimarra sp.	1	0	21	81
Goera sp.	0	0	1	0
Helichopsyche sp.	0	1	0	0
Hydropsychidae	13	0	43	140
Rhyacophila sp.A	0	3	4	11
Rhyacophila sp.B	3	3	0	0
Stenopsyche sp.	0	0	19	15

Table 5. Continued.

	Site 1		*Site 2*	
	Day 12	*Day 42*	*Day 12*	*Day 42*
Diptera				
Antocha sp.	*3*	*8*	*12*	*75*
Atherix sp.	*5*	*1*	*0*	*0*
Ceratopogonidae	*16*	*37*	*12*	*7*
Chironomidae	*404*	*473*	*1227*	*1359*
Eriocera sp.	*0*	*4*	*1*	*4*
Hemerodromia sp.	*0*	*1*	*1*	*0*
Prosimulium sp.	*0*	*0*	*3*	*13*
Wiedemannia sp.	*3*	*0*	*3*	*7*
Coleoptera				
Grouvellinus sp.	*4*	*5*	*1*	*11*
Hydrophilidae	*1*	*0*	*1*	*0*
Mataeopsephus sp.	*0*	*1*	*0*	*0*
Psephenoides sp.	*0*	*0*	*0*	*3*
Zaitzevia sp.	*17*	*29*	*3*	*13*
Lepidoptera				
Eoophyla sp.	*1*	*1*	*0*	*0*
Total	*665*	*643*	*2945*	*3009*
Total without Chironomidae	*261*	*169*	*1719*	*1651*

Euphaea sp. accounted for 1% and 3% of the individuals (excluding Chironomidae) on day 12 and day 42 in the colonization baskets. In the benthos samples, they accounted for 10% and 19% of the same fauna on day 12 and day 42.

At Site 2, the most abundant Ephemeroptera was *Baetis sp.A* (Table 4). Its greatest abundance (17275 / m^2), which was about 160 times more than that at Site 1, occurred on day 21. The most abundant Trichoptera was Hydropsychidae and its largest abundance (2420 / m^2) also occurred on day 21. The most abundant Diptera was Chironomidae and its largest abundance (15330 / m^2) also occurred on day 21. Comparing the abundance of *Baetis sp.A* and Chironomidae, *Baetis sp.A* was more abundant on days 3, 6 and 21, and Chironomidae was more abundant on days 12, 30 and 42. This indicates that the relative abundance shifted from *Baetis sp.A* to Chironomidae with the increase of colonization time.

A similar condition did not occur at Site 1. The chironomid larvae were always most abundant at Site 1. Furthermore, the two taxa accounted for 81 - 91% of the colonizing individuals during the experiment except on day 21 (74%) at Site 2. The relative abundance of *Baetis sp.A* decreased from 56% on day 3 to 26% on day 30 and increased to 28% on day 42. The chironomid larvae had the opposite tendency to that of *Baetis sp.A*. Their relative abundance increased from 25% on day 3 to 57% on day 30 and decreased to 53% on day 42. In the benthos samples the two taxa comprised 86% and 72% of the fauna on day 12 and day 42, respectively. *Baetis sp.A* accounted for 44% and 27% and the chironomid larvae accounted for 42% and 45% on the same sampling dates.

At Site 2, *Baetiella sp.B* accounted for 2% and 1% of colonizing individuals on day 12 and 42 day in the colonization baskets. In the benthos samples, they comprised 7% and 4% of the fauna on days 12 and 42. Hydropsychidae accounted for 3% and 5% of colonization individuals on the same sampling dates in the colonization baskets. In the benthos samples, they comprised 2% and 5% of the fauna on day 12 and day 42. *Prosimulium sp.* accounted for 2% of the colonizing individuals on both day 12 and day 42 in the colonization baskets. In the benthos samples, they comprised below 1 % of the fauna on both day 12 and day 42.

In addition to Baetis sp.A and Chironomidae at Site 2, most taxa had the largest number of individuals on day 21 in the colonization baskets; these included *Baetiella sp.B*, Hydropsychidae, *Prosimulium sp.*, and *B. bispinosa.* Some taxa had the largest number of individuals on day 30, such as *Caenis sp.*, *Ecdyonurus sp.* and *Stenopsyche sp.* and others on day 42, such as *Baetis sp.B* and *Antocha sp.*

Mayflies were the major colonists at the beginning of the colonization process at Site 1 (Fig. 3A). Then they were replaced by Odonata and Diptera. Chironomidae accounted for 56% of the fauna on day 3, but over 80% thereafter. The taxa of Trichoptera roughly decreased with the colonization time. In the benthos samples, the number of mayfly taxa decreased from 6 on day 12 to 4 on day 42. In the colonization basket, they also decreased from 6 on day 12 to 3 on day 42. Number of Diptera taxa increased from 5 on day 12 to 6 on day 42 in the colonization baskets. They increased from 2 on day 12 to 5 on day 42 in the benthos samples. The other orders did not differ in the number of taxa between the two sampling dates in the benthos samples.

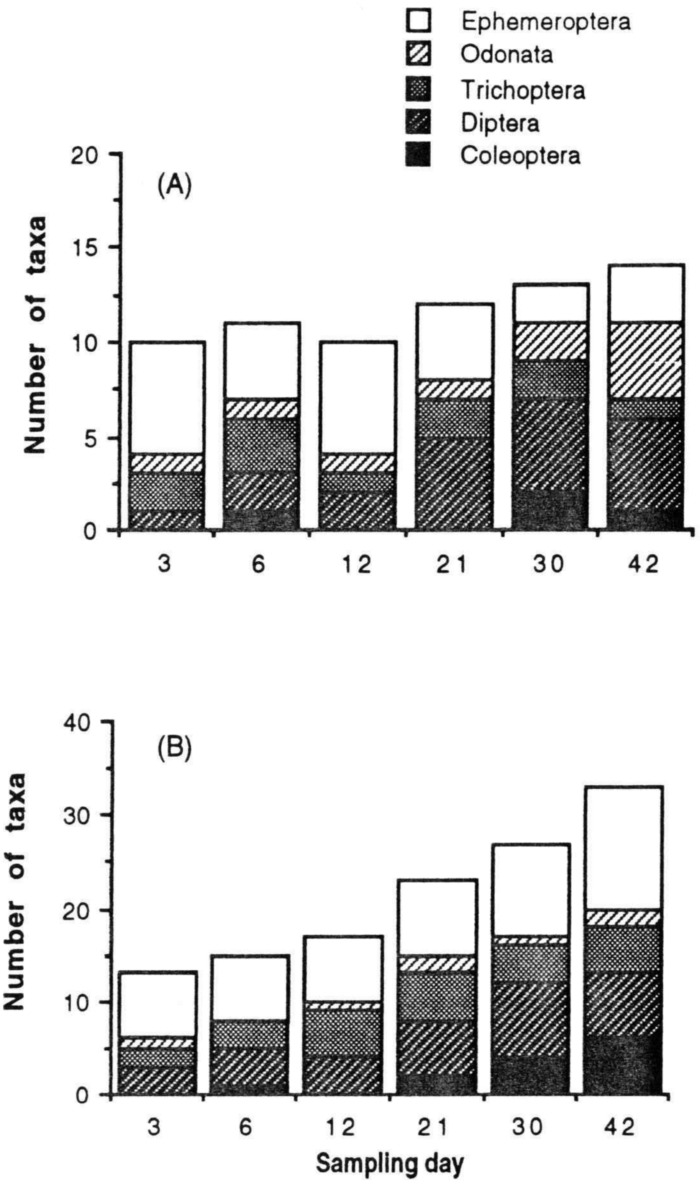

Fig. 3. Number of taxa in each order colonizing artificial substrate trays at Site1 (A) and Site 2 (B) on each sampling day in Experiment I, Chingmei Stream, Taiwan. All Chironomidae are included as one taxon.

At Site 2, the Ephemeroptera were also the major colonists at the early stage of the colonization period (Fig. 3B). However, they were not replaced by other taxa and by day 42 there were 13 taxa of mayflies compared with 7 on day 3. The number of taxa of Trichoptera appeared to level off after day 12. The number of Diptera taxa also increased with the colonization time. It was worth noting that the Coleoptera occurred later than other orders at both sites and only increased after day 21 at Site 2. In the benthos samples, the mayfly taxa increased from 7 on day 12 to 10 on day 42. They also increased from 7 on day 12 to 13 on day 42 in the colonization baskets. The number of taxa in the other orders did not significantly change between day 12 and day 42 in the benthos samples.

Colonization Patterns of the Benthic Community

To compare the community structure and colonization patterns of stream macroinvertebrates between Site 1 and Site 2, the heterogeneous stones were used as artificial substrates. Three of the four community structure indices (number of individuals, number of taxa, diversity, and evenness) were significantly affected by the amount of time that baskets were exposed in the stream (Table 6); the diversity index was not significant (P = 0.13). The four community structure indices were also significantly affected by sites. The interaction between the exposure period in the stream and sites also significantly influenced all community structure indices except the number of individuals (P = 0.56).

The colonization patterns of number of taxa are quite different between the two

Table 6. Results of two-way ANOVA for total number of individuals, total number of species, species diversity, and evenness versus duration of exposure of substrate to colonization and sites in Experiment I, Chingmei Stream, Taiwan (* = significant, ns = not significant).

	F	P	Significance
Individuals:	F = 69.98	P < 0.0001	
No. of days	20.70	< 0.0001	*
Sites	316.38	< 0.0001	*
Interaction	0.79	0.532	ns
Species:	F = 24.92	P < 0.0001	
No. of days	8.82	< 0.0001	*
Sites	105.40	< 0.0001	*
Interaction	6.34	0.0003	*
Diversity:	F = 12.20	P < 0.0001	
No. of days	1.83	0.1320	ns
Sites	64.04	< 0.0001	*
Interaction	5.12	0.0012	*
Evenness:	F = 14.21	P < 0.0001	
No. of days	11.36	< 0.0001	*
Sites	28.48	< 0.0001	*
Interaction	6.98	< 0.0001	*

sites (Fig. 4A; see Appendix 1 for standard errors). The mean number of taxa at Site 1 did not increase with the exposure period of baskets in the stream but at site 2 this did increase with a longer exposure period. At Site 2 it kept increasing during the 42 days of colonization. The greatest increase in species accumulation was from day 6 to day 30.

The two study sites had similar colonization patterns of total number of individuals but density was much higher at Site 2 (Fig. 4B; see Appendix 1 for standard errors). The mean number of individuals at the two sites was highest on day 21 and then decreased. This was associated with flood events which occurred just after day 21. Therefore, the current velocity and discharge did not significantly increase on day 30. However, the number of individuals was very different between the two sites. The mean of number of individual per m^2 on all sampling days is 2580 at Site 1 and 23160 at Site 2, or about 10 times greater at Site 2.

The patterns of diversity (Fig. 4C; see Appendix 1 for standard errors) also are quite different at the two study sites. The diversity at Site 1 decreased before day 12 and then remained almost constant. At Site 2 the diversity increased significantly only between day 12 and day 21. In the other periods there was no significant increase or decrease in diversity at Site 2.

Colonization Patterns of Individual Taxa

The colonization patterns of individual taxon at Site 2 were tested statistically, using Spearman rank correlation coefficients, for significant associations between

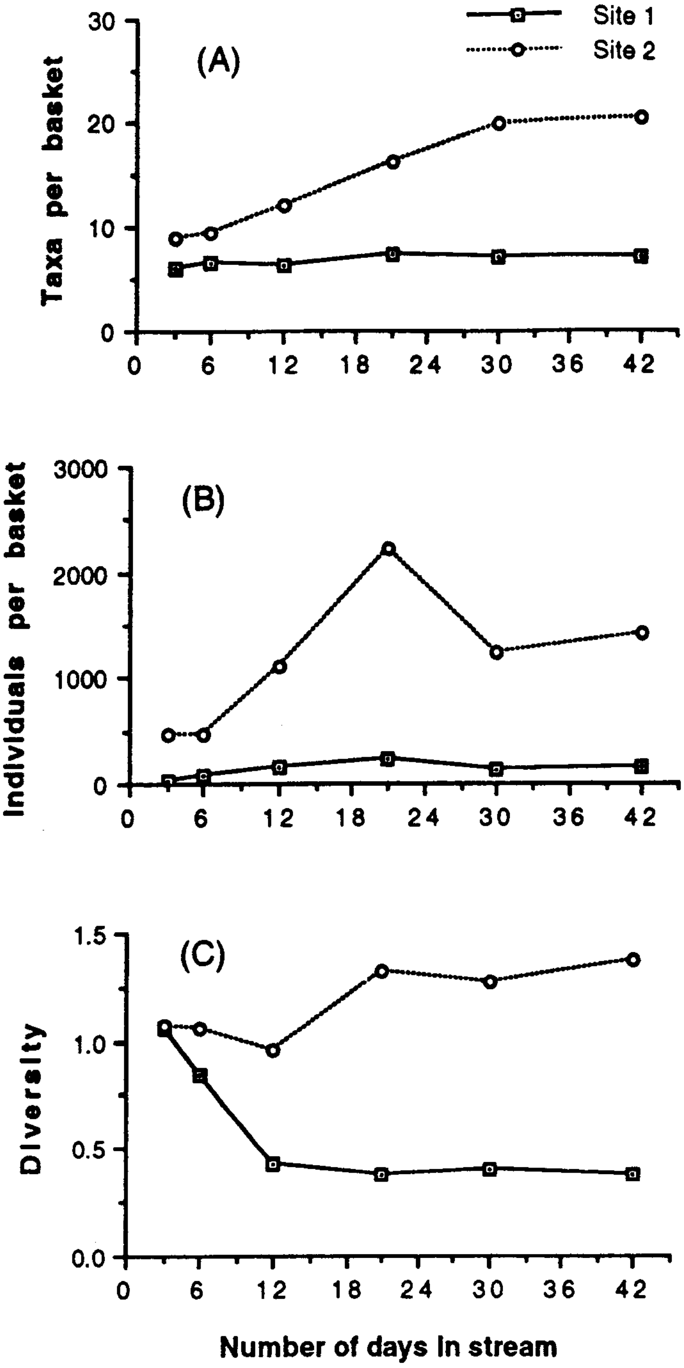

Fig.4. Mean number of taxa (A), number of individuals (B), and species diversity (Shannon-Wiener H') (C) colonizing baskets left in the stream for 3 - 42 days in Experiment I, Chingmei Stream, Taiwan.

population density and days of colonization. The 19 taxa which were most abundant were chosen. Most taxa (14/19) showed a significant increase in number per basket with increasing days in stream (Table 7). Three of 19 (*Baetiella sp.B*, *Prosimulium sp.* and *Dipteromimus sp.*) showed decreasing patterns of colonization with time but without statistical significance. *Baetis sp.A* and *Simulium sp.* had no consistent pattern between colonization and time of exposure. Peak abundance was on day 21.

To examine the colonization patterns of functional feeding groups, taxa were classified into groups based on Merritt and Cummins (1984). Ten of 19 taxa were classified as grazers (including scrapers and collector-gatherers), six as filter-feeders and four as predators. Chironomidae were classified as both grazers and filter-feeders because Tanytarsini are filter-feeders and Chironomini are grazers. The colonization patterns of functional feeding groups showed that both grazer and filter-feeders are the major groups at the two study sites (Fig. 5). The mean relative abundance of grazers at Site 1 decreased with the exposure period of baskets but after day 12 the relative abundance remained almost constant. The filter-feeder group had the opposite colonization pattern to that of grazers, and their relative abundances were almost equal. The mean relative abundances of the two groups at Site 2 had the same tendency as they did at Site 1. Grazers were about twice as abundant as the filter-feeder group at Site 2.

In the early stage of colonization, grazers were the major group of taxa at both sites (Fig. 6). The number of taxa of grazers decreased at Site 1 but increased at Site 2 during the colonization period. The number of filter-feeder taxa did not significantly

Table 7. Summary of results of Spearman rank correlation on numbers of individuals per basket versus days in stream for 19 abundant taxa at Site 2 in Experiment I, Chingmei Stream, Taiwan.

Functional feeding groups	Increase in number with days in stream	Decrease in number with days in stream	No consistent pattern with days in stream
Grazer	*Baetis sp.B*	*Dipteromimus sp.*	*Baetis sp.A*
	B. bispinosa	*Baetiella sp.B*	
	Ecdyonurus sp.		
	Caenis sp.		
	Amphinemura sp.		
	Chironomidae		
	Antocha sp.		
Filter-feeder	*Stenopsyche sp.*	*Prosimulium sp.*	*Simulium sp.*
	Chimarra sp.		
	Hydropsychidae		
	Chironomidae		
Predator	*Neoperla sp.*		
	Rhyacophila sp.		
	Hemerodromia sp.		
	Wiedemannia sp.		

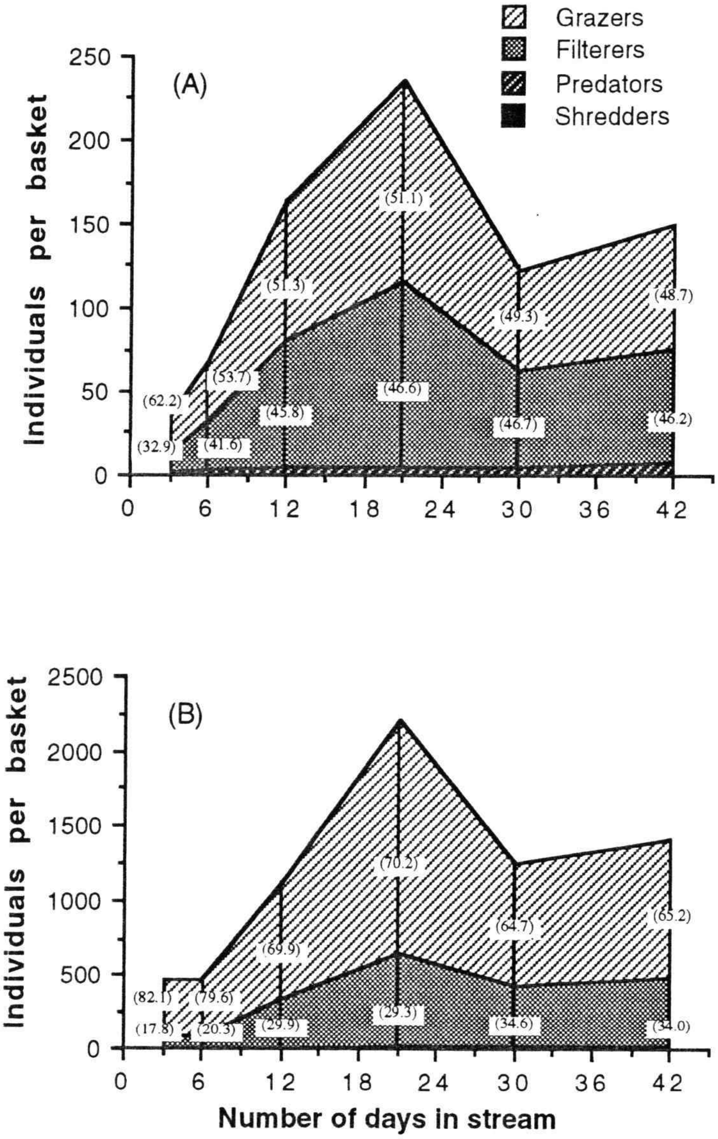

Fig. 5. Mean number of individuals of functional feeding groups on each sampling day at Site1(A) and Site 2 (B). Numbers in parentheses indicate the percentage of each groups.

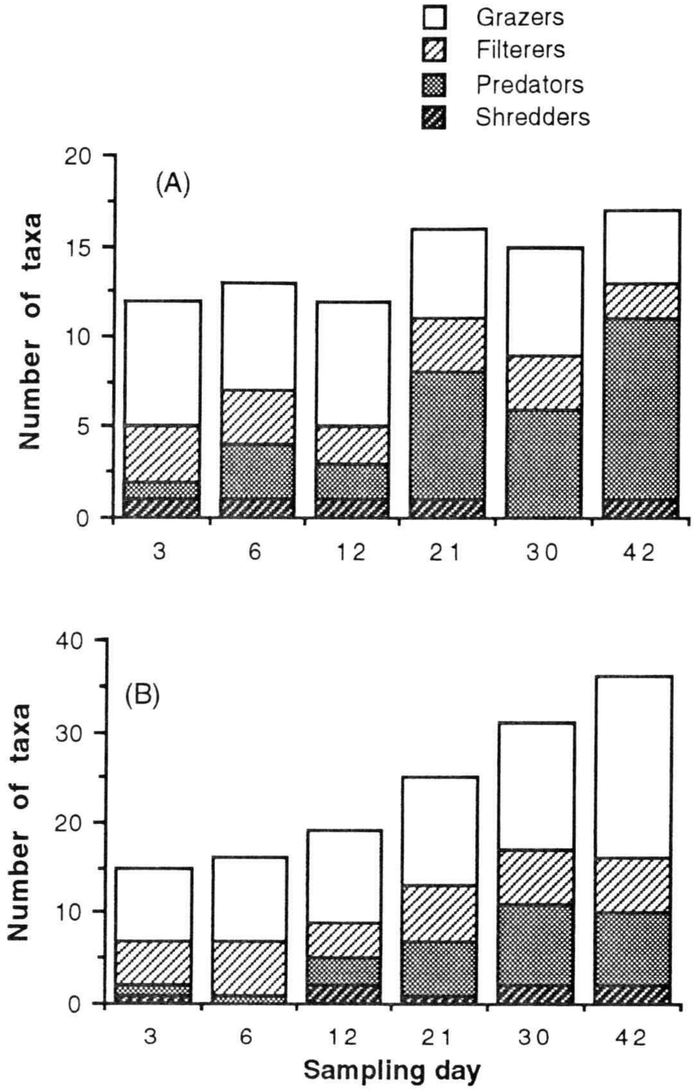

Fig. 6. Number of taxa in each functional feeding group at Site 1 (A) and Site 2 (B) on each sampling day in Experiment I, Chingmei Stream, Taiwan.

change at either Site 1 or Site 2. The number of taxa of predators increased during the colonization process, especially at Site 1 where they became a major group in the number of taxa.

To examine the potential influence of biological interactions the Spearman rank correlation coefficient was used to determine whether significant positive or negative associations occurred between taxa sharing common resources. The 19 most abundant taxa were chosen. The results were summarized in Table 8. For grazers, 20 of 45 taxon pairs has significantly positive associations and 4 of 45 taxon pairs had significantly negative associations. A large number of positive associations occurred among filter-feeders (80% of which were positively associated) and predators (83% of which were positively associated). These data indicate that filter-feeders and predators tend to overlap within their functional groups in their distribution among baskets. The 20 of 45 comparisons among grazer species that showed significant positive associations, suggests a moderate overlap in resource utilization among taxa within this functional group.

Equilibrium of the Benthic Community

The benthic invertebrate artificial substrate data can also be expressed as a pattern of colonization (immigration) and extinction (emigration) of species. The colonization rates of taxa per day were calculated as the number of new taxa occurring on each sampling day divided by the time period. The extinction rates were calculated as the number of eliminated taxa on each sampling day over time. An equilibrium in species

Table 8. Summary of species associations among members of the same functional feeding groups at Site 2 in Experiment I, Chingmei Stream, Taiwan. Significant correlation coefficients are given and noted with asterisks (N = 24; ns = not significant).

Grazer	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Baetis sp.A (1)	--	0.53*	ns	0.54*	ns	ns	ns	0.75*	ns	0.48*
Baetis sp.B (2)		--	0.54*	ns	-0.41*	0.59*	0.50*	0.73*	0.77*	0.70*
B. bispinosa (3)			--	ns	ns	ns	ns	0.55*	ns	0.58*
Baetiella sp.B (4)				--	ns	ns	-0.61*	0.48*	ns	ns
Dipteromimus sp. (5)					--	ns	ns	-0.44*	-0.42*	ns
Ecdyonurus sp. (6)						--	0.82	ns	0.82*	0.75*
Caenis sp. (7)							--	ns	0.82*	0.64*
Amphinemura sp. (8)								--	0.41*	0.44*
Antocha sp. (9)									--	0.80*
Chironomidae (10)										--

Filter-feeder	(1)	(2)	(3)	(4)	(5)	(6)
Stenopsyche sp. (1)	--	0.56*	0.75*	0.41*	ns	0.42*
Chimarra sp. (2)		--	0.73*	0.54*	0.52*	0.71*
Hydropsychidae (3)			--	0.45*	0.55*	0.53*
Chironomidae (4)				--	ns	ns
Prosimulium sp. (5)					--	0.64*
Simulium sp. (6)						--

Predator	(1)	(2)	(3)	(4)
Neoperla sp. (1)	--	0.55*	ns	0.81*
Rhyacophila sp.A (2)		--	0.53*	0.51*
Hemerodromia sp. (3)			--	0.58*
Wiedemannia sp. (4)				--

number marking the end of substantial colonization is considered to occur when the colonization rate is equal to the extinction rate (MacArthur & Wilson 1963, 1967; Dickson & Cairns 1972; Stauffer et al. 1976; Williams & Hynes 1977). Using such a criterion as an indication, an equilibrium number of species was approached at Site 1 but not at Site 2 (Fig. 7). The results indicated that the equilibrium of species number at Site 1 occurred about on day 10 after the beginning of colonization but at Site 2 it required more than 42 days to get the equilibrium.This is due to the colonization rates which were always greater than the extinction rates at Site 2 during the period of experiment. Moreover, Simberloff & Wilson (1969) and Brown & Kodric-Brown (1977) suggested that extinction rates at equilibrium are equivalent to turnover rates. Turnover rate for Site 1, therefore, was roughly 0.67 taxa/d at 10 days.

Minshall et al. (1985) suggested that a high degree of conformity with the lognormal distribution, indicated by the coefficient of determination of the least-squares fit, shows a community in a high degree of equilibrium. They viewed the equilibrium state as a continuum between $r^2 = 1$ for equilibrium and $r^2 = 0$ for maximum nonequilibrium. For each sampling day, the coefficients of determination at Site 1 were greater than those at Site 2 from day 12 to day 42 (Fig. 8 and 9). This indicated that during the colonization period the relative equilibrium of the community at Site 1 was greater than that at Site 2. For the two study sites, the coefficients of determination increased roughly but irregularly with the time of colonization, so they did not show any patterns. Furthermore, it was found that the distance between colonization and extinction rates (Fig. 7) was associated with the coefficient of

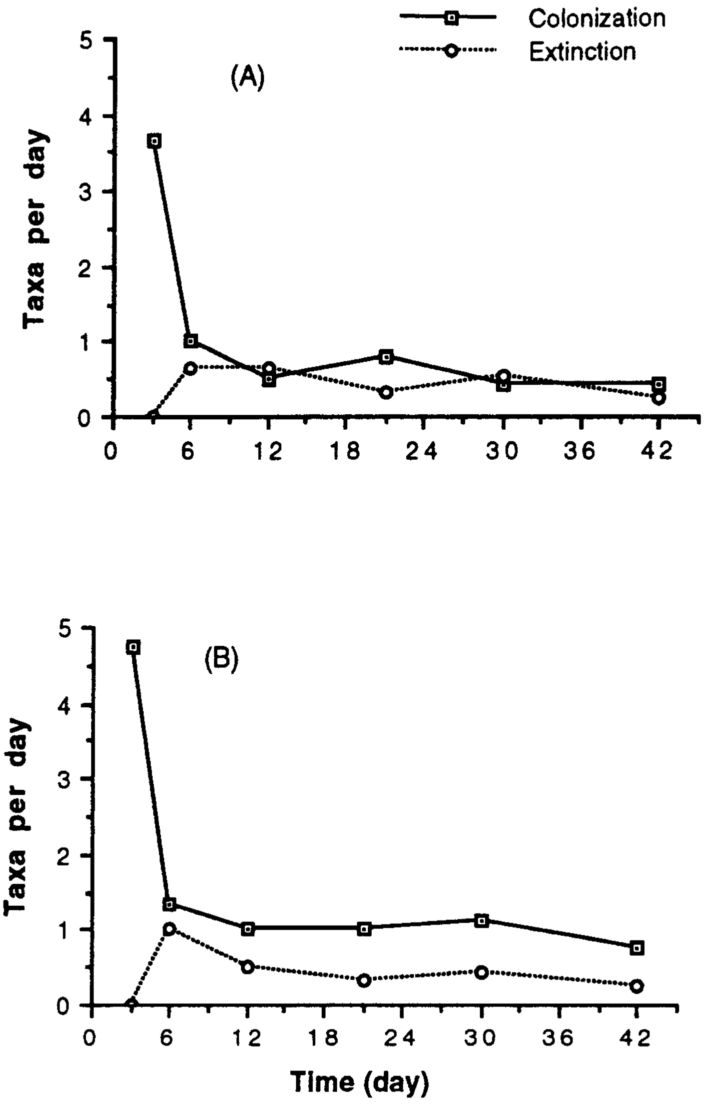

Fig. 7. Colonization and extinction rates of benthic macroinvertebrates at Site 1 (A) and Site 2 (B) in Experiment I, Chingmei Stream, Taiwan.

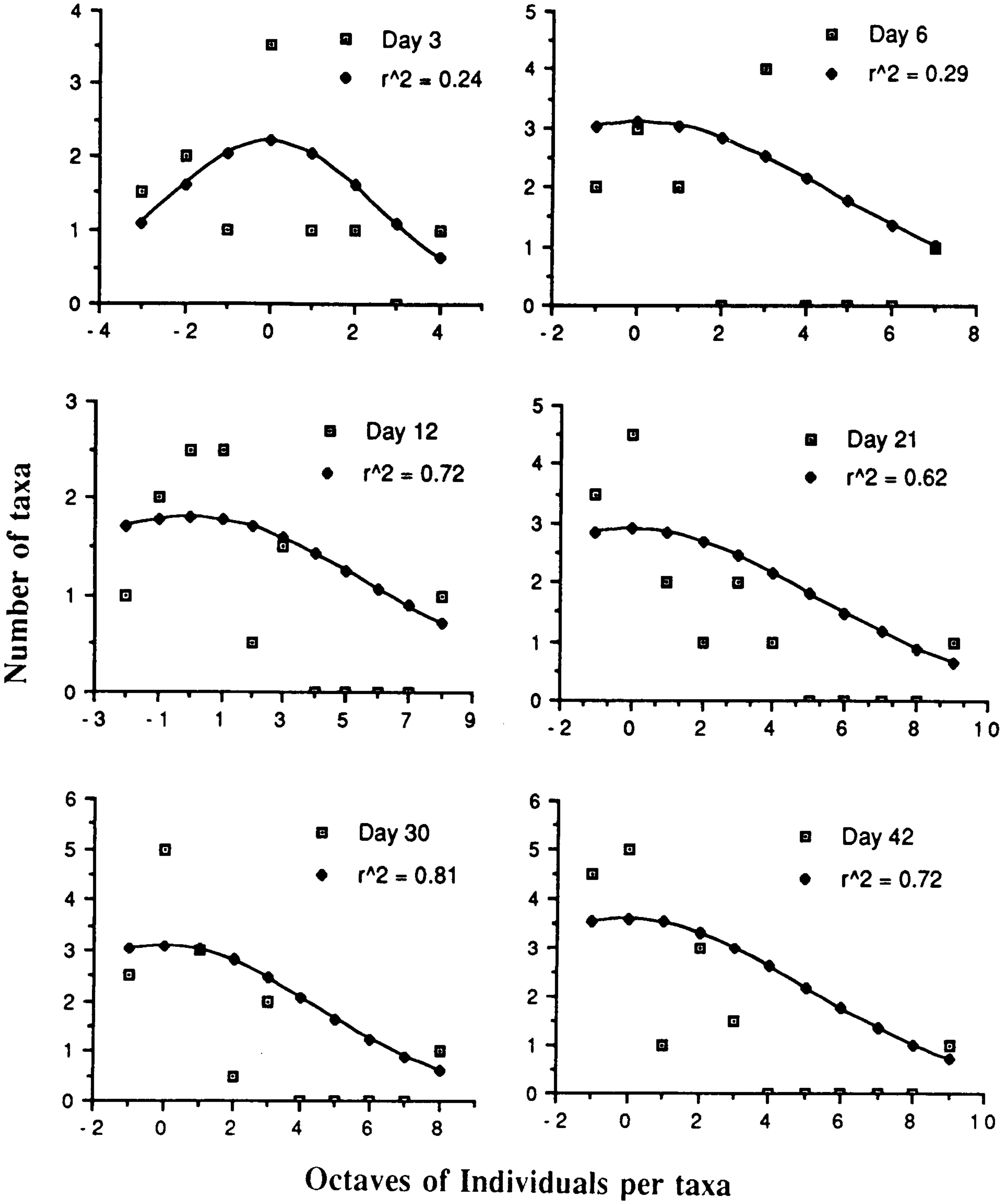

Fig. 8. Fit of taxa abundance curves to a lognormal model on each sampling day at Site 1 in Experiment I, Chingmei Stream, Taiwan.

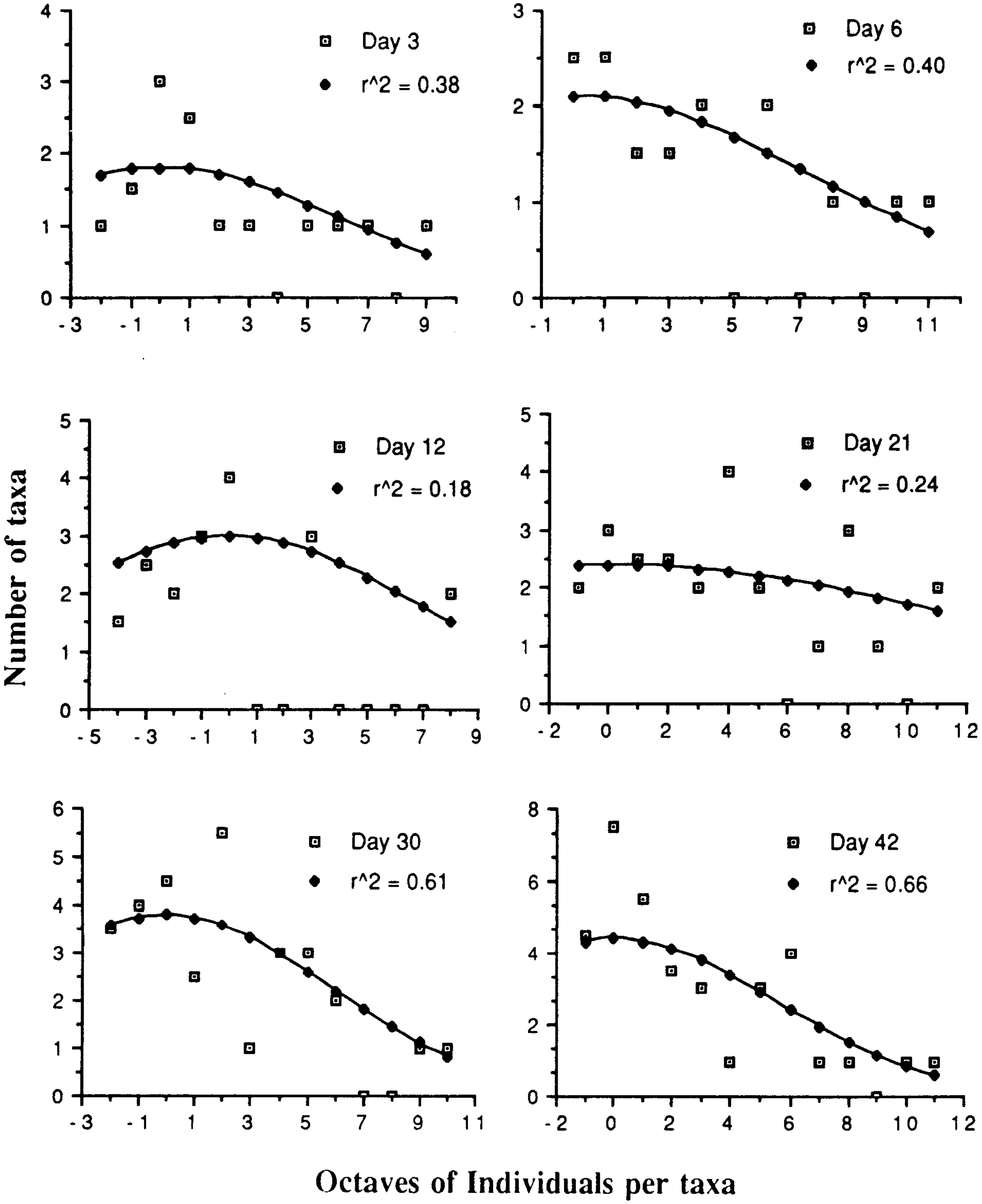

Fig. 9. Fit of taxa abundance curves to a lognormal model on each sampling day at Site 2 in Experiment I, Chingmei Stream, Taiwan.

determination as compared with Fig. 8 and 9. The smaller the distance between colonization and extinction rates the larger the coefficient of determination so the community was in a higher degree of equilibrium.

Experiment II

Physical and Chemical Factors

Values for physical and chemical characteristics at Site 2 during the experiment (from March 14, 1991 to April 28, 1991) are given in Table 9. During the experiment water temperature and conductivity had a tendency to increase. The pH values showed the stream water was slightly alkaline. Heavy rains between day 6 and day 21 resulted in floods. The substrate trays filled with gravel were washed away and only six trays remained after day 21. Thus, there were only two replicates on each sampling date after day 21.

The amount of organic matter collected by trays did not increase until day 12 (Fig. 10; see Appendix 2 for standard errors). There was more organic matter in the cobble substrate than in the gravel substrate. This may be partly due to the greater amount of periphyton growing on the cobble substrate.

Stream Benthos Fauna

During this experiment 53 taxa were collected from the experimental substrates

Table 9. Physical and chemical characteristics of Site 2 on each sampling day in Experiment II, Chingmei Stream, Taiwan.

	Sampling date					
	3	6	12	21	30	42
Temperature (°C)	16.2	20.9	20.5	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

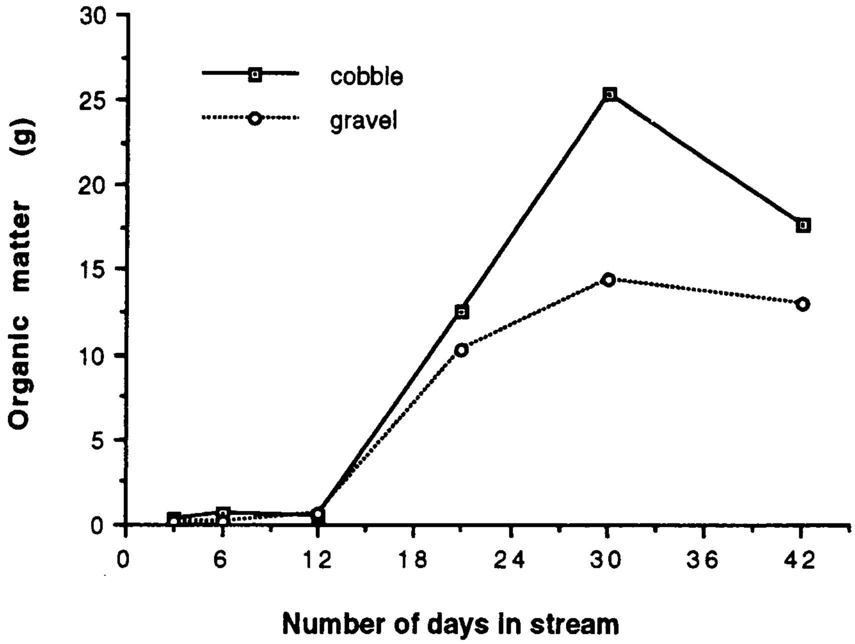

Fig. 10. Amounts of organic matter collected by artificial substrate trays on each sampling day in Experiment II, Chingmei Stream, Taiwan.

(Tables 10 and 11). There were 47 taxa collected in the cobble baskets and 45 taxa collected in the gravel baskets. Trichoptera were the most diverse, with 13 taxa; Ephemeroptera and Diptera each had 12 taxa. The number of taxa for the other orders was: Coleoptera (7), Plecoptera (4), Odonata (3), Lepidoptera (1) and Hemiptera (1).

The most abundant Ephemeroptera for the cobble substrate was *Baetis sp.A* with the largest abundance (9310 / m^2) occurring on day 9 (Table 10). 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 largest abundance (53560 / m^2) occurred on day 42. Comparing *Baetis sp.A* and Chironomidae, the latter were always more abundant than were *Baetis sp.A* during the entire study.

The most abundant Ephemeroptera for the gravel substrate was *Baetis sp.A* which reached a density of 17060 / m^2 on day 42 (Table 11). The most abundant caddisflies were Hydropsychidae (3680 / m^2) and Stenopsychidae (1800 / m^2) which also peaked on day 42. The largest number of Chironomidae (50370 / m^2) also occurred on day 42. Comparing *Baetis sp.A* and Chironomidae, there was a shift from *Baetis sp.A* to Chironomidae being the most abundant taxon after day 3. Moreover, comparing the cobble and gravel substrate these most abundant taxa in different orders had higher abundance on the gravel substrate than on the cobble substrate, except Chironomidae.

For the gravel substrate, the *Baetis sp.A* and chironomid larvae accounted 84 - 95% of the colonizing individuals from day 3 to 42. The chironomid larvae comprised 36 - 65% of the fauna during the same interval. For the cobble substrate, the two taxa

Table 10. Density (per m^2) of benthic macroinvertebrate fauna colonizing baskets filled with cobble substrate on each sampling day in Experiment II, Chingmei Stream, Taiwan. "Total" column is the sum of numbers collected from Day 3 to 42.

	Day 3	*Day 6*	*Day 12*	*Day 21*	*Day 30*	*Day 42*	*Total*
Ephemeroptera							
Baetiella bispinosa	*80*	*30*	*5*	*5*	*0*	*35*	*155*
Baetiella sp.B	*190*	*235*	*75*	*25*	*5*	*50*	*580*
Baetis sp.A	*1750*	*9310*	*5845*	*4885*	*7205*	*9075*	*38070*
Baetis sp.B	*10*	*155*	*165*	*35*	*80*	*65*	*510*
Caenis sp.	*0*	*285*	*645*	*410*	*720*	*475*	*2535*
Cincticostella sp.	*0*	*0*	*5*	*0*	*0*	*0*	*5*
Dipteromimus sp.	*0*	*5*	*0*	*0*	*20*	*50*	*75*
Ecdyonurus sp.	*0*	*35*	*110*	*145*	*200*	*225*	*715*
Epeorus sp.	*5*	*10*	*10*	*0*	*0*	*5*	*30*
Ephemera sp.	*0*	*0*	*5*	*20*	*30*	*5*	*60*
Paraleptophlebia sp.	*0*	*0*	*10*	*10*	*80*	*5*	*105*
Serratella sp.	*0*	*5*	*45*	*105*	*210*	*205*	*570*
Plecoptera							
Amphinemura sp.	*5*	*10*	*0*	*0*	*5*	*0*	*20*
Neoperla sp.	*0*	*0*	*5*	*75*	*65*	*85*	*230*
Protonemura sp.	*25*	*5*	*10*	*0*	*0*	*0*	*40*
Odonata							
Euphaea sp.	*0*	*5*	*0*	*25*	*45*	*30*	*105*
Onychogomphus sp.	*0*	*0*	*5*	*5*	*5*	*5*	*20*
Sieboldius sp.	*0*	*0*	*5*	*0*	*5*	*0*	*10*
Trichoptera							
Chimarra sp.	*0*	*0*	*5*	*0*	*10*	*25*	*40*
Goera sp.	*0*	*0*	*0*	*10*	*20*	*20*	*50*
Hydropsychidae	*85*	*130*	*60*	*120*	*140*	*1255*	*1790*
Hydroptila sp.	*5*	*0*	*0*	*0*	*0*	*0*	*5*
Melanotrichia sp.	*0*	*0*	*0*	*10*	*10*	*10*	*30*
Orthotrichia sp.	*0*	*0*	*5*	*0*	*0*	*0*	*5*
Plectrocnemia sp.	*0*	*0*	*0*	*0*	*0*	*10*	*10*
Rhyacophila sp.A	*0*	*10*	*0*	*60*	*25*	*160*	*255*
Rhyacophila sp.B	*0*	*0*	*0*	*0*	*5*	*0*	*5*
Stactobia sp.	*5*	*25*	*0*	*0*	*0*	*0*	*30*
Stenopsyche sp.	*60*	*105*	*130*	*340*	*480*	*910*	*2025*

Table 10. Continued.

	Day 3	Day 6	Day 12	Day 21	Day 30	Day 42	Total
Diptera							
Antocha sp.	45	160	300	1225	1450	1520	4700
Atherix sp.	0	0	5	15	20	0	40
Ceratopogonidae	0	5	10	0	60	60	135
Chironomidae	4245	12865	11085	11035	27355	53560	120145
Dolichopodidae	5	0	0	0	0	0	5
Eriocera sp.	0	0	0	0	20	0	20
Hemerodromia sp.	0	5	10	45	40	10	110
Prosimulium sp.	5390	1905	175	0	0	5	7475
Psychoda sp.	0	5	0	0	0	0	5
Simulium sp.	400	115	20	0	5	0	540
Wiedemannia sp.	0	0	5	0	0	5	10
Coleoptera							
Grouvellinus sp.	0	5	0	10	0	5	20
Hydrophilidae	0	40	0	5	5	5	55
Mataeopsephus sp.	0	0	0	0	5	0	5
Stenelmis sp.	0	0	0	5	10	5	20
Zaitzevia sp.	0	0	0	5	10	5	20
Lepidoptera							
Eoophyla sp.	0	0	0	10	5	40	55
Hemiptera							
Micronecta sp.	0	0	0	0	0	20	20
Total	12305	25465	18755	18640	38350	67945	181460
Total without Chironomidae	8060	12600	7670	7605	10995	14385	61315

Table 11. Density (per m^2) of benthic macroinvertebrate fauna colonizing baskets filled with gravel substrate on each sampling day in Experiment II, Chingmei Stream, Taiwan. "Total" column is the sum of numbers collected from Day 3 to 42.

	Day 3	*Day 6*	*Day 12*	*Day 21*	*Day 30*	*Day 42*	*Total*
Ephemeroptera							
Baetiella bispinosa	70	10	5	0	0	180	265
Baetiella sp.B	380	75	30	0	20	130	635
Baetis sp.A	10735	7300	8630	7180	11540	17060	62445
Baetis sp.B	360	665	920	60	110	160	2275
Caenis sp.	75	680	1675	260	750	450	3890
Dipteromimus sp.	0	5	0	0	10	30	45
Ecdyonurus sp.	35	50	195	100	190	300	870
Epeorus sp.	15	0	0	0	0	60	75
Ephemera sp.	0	15	10	0	40	30	95
Paraleptophlebia sp.	5	10	45	10	60	40	170
Serratella sp.	5	5	40	50	80	140	320
Plecoptera							
Amphinemura sp.	0	5	5	0	0	10	20
Neoperla sp.	0	20	45	130	90	260	545
Paragnetina sp.	5	0	0	0	0	0	5
Protonemura sp.	35	5	10	0	0	0	50
Odonata							
Euphaea sp.	0	5	10	20	10	50	95
Onychogomphus sp.	0	0	0	10	20	10	40
Sieboldius sp.	0	5	0	0	0	0	5
Trichoptera							
Chimarra sp.	0	0	5	10	0	10	25
Goera sp.	0	0	0	20	20	20	60
Hydropsychidae	220	145	120	110	70	3860	4525
Melanotrichia sp.	0	0	0	0	0	10	10
Oecetis sp.	0	5	5	0	0	0	10
Rhyacophila sp.A	45	35	20	50	70	470	690
Rhyacophila sp.B	0	0	0	0	0	30	30
Stactobia sp.	10	0	0	0	0	0	10
Stenopsyche sp.	295	330	265	450	690	1800	3830
Tinodes sp.	0	0	0	0	0	10	10

Table 11. Continued.

	Day 3	Day 6	Day 12	Day 21	Day 30	Day 42	Total
Diptera							
Antocha sp.	20	70	90	500	890	2350	3920
Atherix sp.	0	0	5	0	20	0	25
Ceratopogonidae	0	5	0	40	40	100	185
Chironomidae	8190	11350	19760	9040	28870	50730	127940
Empididae sp.A	0	0	5	0	0	0	5
Eriocera sp.	0	0	0	30	0	10	40
Hemerodromia sp.	5	10	15	10	50	40	130
Prosimulium sp.	1890	325	235	0	10	50	2510
Psychoda sp.	0	5	0	0	0	0	5
Simulium sp.	60	20	5	0	0	0	85
Wiedemannia sp.	0	0	0	0	0	10	10
Coleoptera							
Grouvellinus sp.	0	0	15	0	0	20	35
Hydrophilidae	0	0	0	0	10	10	20
Psephenoides sp.	0	0	5	0	0	10	15
Staphylinidae	0	0	5	0	0	0	5
Zaitzevia sp.	0	0	5	90	0	10	105
Lepidoptera							
Eoophyla sp.	0	0	0	0	10	10	20
Total	22455	21155	32180	18170	43670	78470	216100
Total without Chironomidae	14265	9805	12420	9130	14800	27740	88160

accounted for over 85% of the individuals from day 6 to 42. They only comprised 49% of the same fauna on day 3. *Prosimulium sp.* accounted for the other 44% of the fauna on day 3. The chironomid larvae accounted for 35 - 79% of the fauna from day 3 to 42. In the benthos samples, the *Baetis sp.A* and chironomid larvae were 75% of the total fauna on day 42 (Table 12). Each of them accounted for 36% of the fauna. In contrast with Experiment I at Site 2, the two taxa accounted for 81 - 91% of the individuals except on day 21 (74%). The chironomid larvae were 25 - 57% from day 3 to 30 and were 53% on day 42. In the benthos samples of Experiment I at Site 2, the two taxa also were 72% of the total fauna and the chironomid larvae accounted for 45% of the fauna on day 42.

The number of taxa in each order changed with the time of colonization on the two substrates (Fig. 11). For Ephemeroptera the number of taxa remained almost constant on both the cobble and gravel substrate during the experiment, except day 3 on the cobble substrate and day 21 on the gravel substrate. For Trichoptera the number of taxa increased in both the 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 the cobble and gravel substrates. Coleoptera usually occurred in the later period of colonization.

The decrease in the total number taxa on day 21 for both the cobble and gravel substrate was due to the floods which occurred between day 12 and day 21 and washed away some baskets filled with gravel (Fig. 11). The colonization was reset to earlier conditions because of the major disturbance by floods. For the gravel substrate,

Table 12. Density (per m^2) of total benthic macroinvertebrate fauna collected by Surber sampler on day 42 in Experiment II, Chingmei Stream, Taiwan.

	Day 42		Day 42
Ephemeroptera		Diptera	
Baetiella bispinosa	125	Antocha sp.	40
Baetiella sp.B	144	Ceratopogonidae	5
Baetis sp.A	1013	Chironomidae	1000
Baetis sp.B	5	Eriocera sp.	3
Caenis sp.	8	Hemerodromia sp.	3
Ecdyonurus sp.	3	Prosimulium sp.	27
Epeorus sp.	5	Wiedemannia sp.	3
Serratella sp.	3	Coleoptera	
Plecoptera		Grouvellinus sp.	48
Neoperla sp.	16	Psephenoides sp.	3
Odonata			
Euphaea sp.	19		
Trichoptera		Total	2805
Chimarra sp.	3		
Hydropsychidae	179		
Rhyacophila sp.A	16	Total without Chironomidae	1805
Stenopsyche sp.	136		

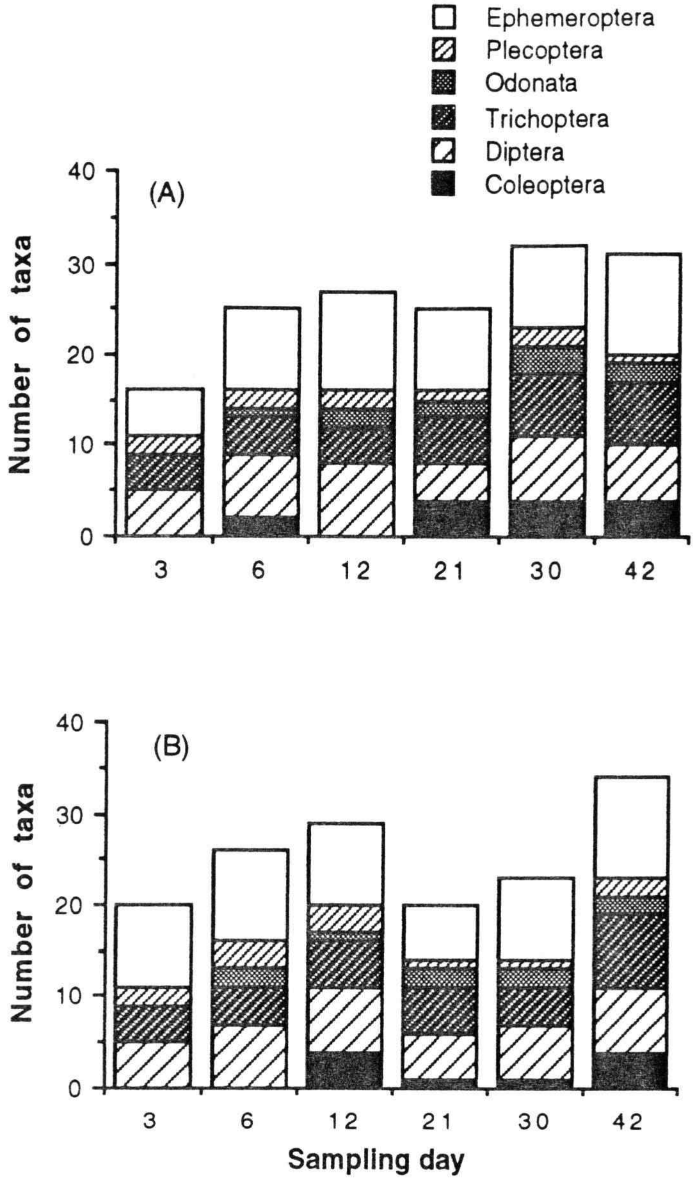

Fig. 11. Number of taxa in each order colonizing baskets filled with cobbles (A) and gravel (B) on each sampling day in Experiment II, Chingmei Stream, Taiwan. All Chironomidae are included as one taxon.

day 21 is more similar to 3 days than to 3 weeks of colonization. In comparing the number of taxa in each order between day 12 and day 21, those of Ephemeroptera, Plecoptera and Diptera decreased, while the number of taxa of Trichoptera and Odonata increased for both the cobble and gravel substrate. The number of Coleoptera taxa increased on the cobble substrate but decreased on the gravel substrate. The results indicated 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 between day 12 and day 21. The floods resulted in significant decreases in *Baetis sp.A*, *Baetis sp.B*, *Caenis sp.*, *Ecdyonurus sp.*, *Paraleptophlebia sp.* and Chironomidae on the gravel substrate (Table 11), and *Baetiella sp.B*, *Baetis sp.A*, *Baetis sp.B* and *Caenis sp.* on the cobble substrate (Table 10). It indicated that some taxa were more easily affected by floods on the gravel substrate than on the cobble substrate.

Colonization Patterns of the Benthic Community

The study was conducted at Site 2 to examine the community structure and colonization patterns of stream macroinvertebrates with two sizes of substrate (gravel: 16 - 32 mm and cobble: 64 - 128 mm). The results indicated that 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 13), and there was a significant effect of interaction between duration of exposure and substrate on mean

Table 13. Results of two-way ANOVA for total number of individuals, total number of species, species diversity, and evenness versus duration of exposure of substrate to colonization and substrate (* = significant, ns = not significant).

	F	P	Significance
Individuals:	F = 8.902	P < 0.0001	
No. of days	10.339	< 0.0001	*
Substrate	4.251	0.0480	*
Interaction	1.142	0.3603	ns
Species:	F = 7.278	P = 0.0001	
No. of days	8.512	< 0.0001	*
Substrate	3.708	0.0673	ns
Interaction	0.863	0.5171	ns
Diversity:	F = 4.339	P = 0.0029	
No. of days	4.894	0.0022	*
Substrate	0.707	0.4160	ns
Interaction	1.200	0.3331	ns
Evenness:	F = 19.078	P < 0.0001	
No. of days	22.853	< 0.0001	*
Substrate	0.503	0.4911	ns
Interaction	2.632	0.0435	*

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 13). 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 effect 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. 12A; see Appendix 2 for standard errors). For the gravel substrate they increased by arithmetical progression between day 3 and 12 and between day 21 and 42. They decreased somewhat between day 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. 12B; see Appendix 2 for standard errors). Numbers appeared to level off between day 3 and day 21, but they increased by arithmetical progression after day 21. There were about three times more on day 42 than on day 21.

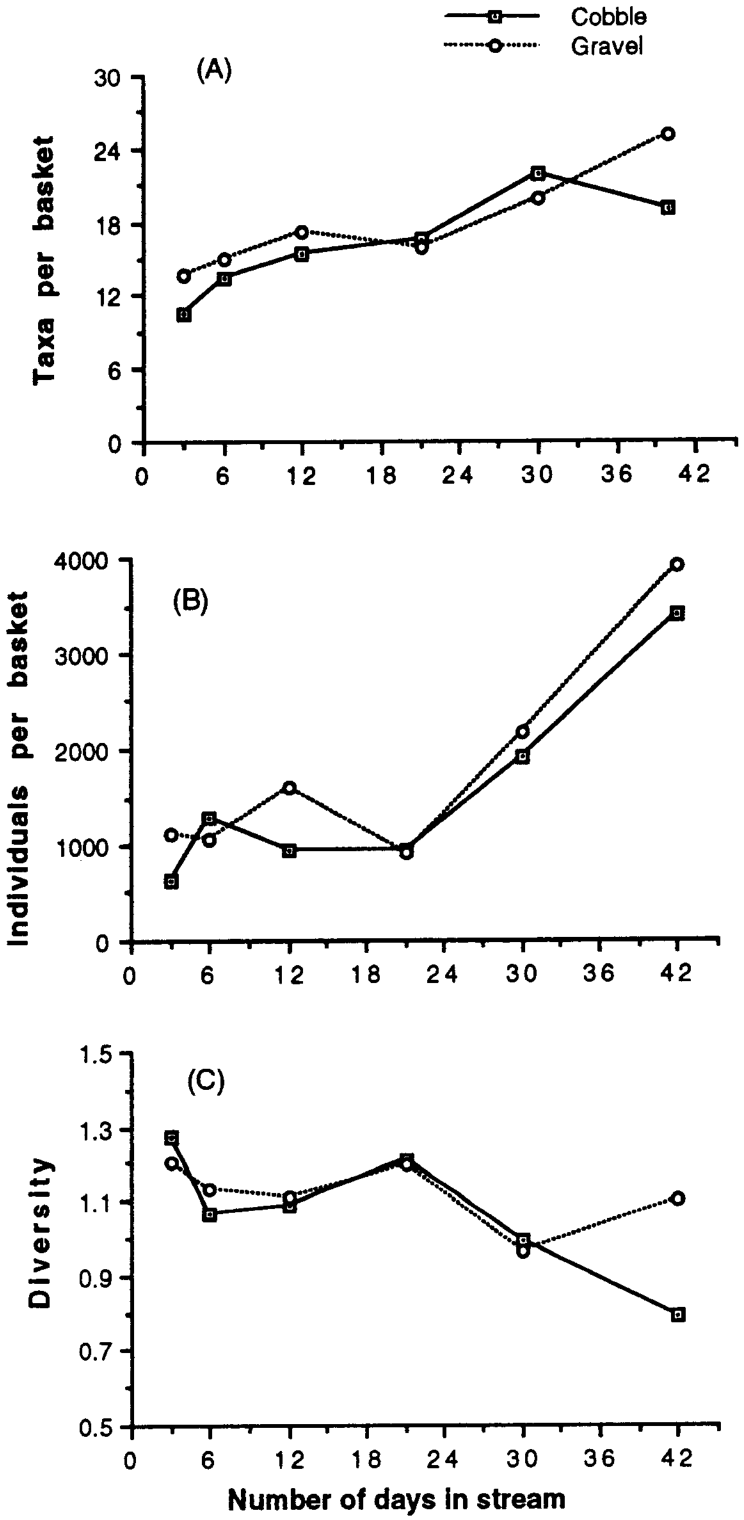

Fig. 12. Mean number of taxa (A), number of individuals (B), and species diversity (Shannon-Wiener H') (C) colonizing baskets left in the stream for 3 -42 days in Experiment II, Chingmei Stream, Taiwan.

The patterns of diversity during the process of colonization for the cobble and gravel substrate were similar to each other on each sampling day except day 42 (Fig. 12C; see Appendix 2 for standard errors). They decreased between day 3 and 6 and then appeared to level off between day 6 and day 30. For the cobble substrate they decreased but for the gravel substrate they increased between day 30 and 42.

Colonization Patterns of Individual Taxa

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 twenty taxa which were most abundant were chosen. For cobble substrate, 14 of 20 taxa showed a significant increase in number per basket with increasing days in stream; 4 taxa decreased and 2 taxa had no consistent pattern (Table 14). For gravel substrate, 9 of 20 showed significant increases in number per basket with increasing days in stream, 6 taxa decreased and 5 taxa showed no consistent pattern (Table 15). In comparing the two types of substrates, there were 3 taxa (*Baetis sp.A, Caenis sp.A* and Hydropsychidae) that increased in number with the length of exposure period on the cobble substrate but showed no consistent patterns on the gravel substrate. Two taxa (*Rhyacophila sp.A* and *Paraleptophlebia sp.*) with a pattern of increase on the cobble substrate showed a decrease on the gravel substrate. *Baetiella sp.B* with a decreasing pattern on the cobble substrate showed no consistent patterns on the gravel substrate. *Baetis sp.B* with no consistent pattern on the cobble substrate showed a

Table 14. Summary of results of Spearman rank correlation on numbers of individuals per basket filled with cobbles versus days in stream for 20 abundant taxa in Experiment II, Chingmei Stream, Taiwan.

Functional feeding groups	Increase in number with days in stream	Decrease in number with days in stream	No consistent pattern with days in stream
Grazer	*Baetis sp.B* *Ecdyonurus sp.* *Caenis sp.* *Serratella sp.* *Chironomidae* *Antocha sp.*	*Baetiella sp.B*	*Baetis sp.B* *B. bispinosa*
Filter-feeder	*Stenopsyche sp.* *Hydropsychidae* *Chironomidae*	*Prosimulium sp.* *Simulium sp.*	
Predator	*Euphaea sp.* *Neoperla sp.* *Rhyacophila sp.* *Hemerodromia sp.* *Ceratopogonidae*		
Shredder	*Paraleptophlebia sp.*	*Protonemura sp.*	

Table 15. Summary of results of Spearman rank correlation on numbers of individuals per basket filled with gravel versus days in stream for 20 abundant taxa in Experiment II, Chingmei Stream, Taiwan.

Functional feeding groups	Increase in number with days in stream	Decrease in number with days in stream	No consistent pattern with days in stream
Grazer	*Ecdyonurus sp.* *Serratella sp.* *Chironomidae* *Antocha sp.*	*Baetis sp.B*	*Baetis sp.A* *B. bispinosa* *Baetiella sp.B* *Caenis sp.*
Filter-feeder	*Stenopsyche sp.* *Chironomidae*	*Prosimulium sp.* *Simulium sp.*	*Hydropsychidae*
Predator	*Euphaea sp.* *Neoperla sp.* *Hemerodromia sp.* *Ceratopogonidae*	*Rhyacophila sp.*	
Shredder		*Paraleptophlebia sp.* *Protonemura sp.*	

decreasing pattern on the gravel substrate.

The daily rates of colonization for a given taxon on both the cobble substrate and gravel substrate were compared using least-squares regression (Tables 16 and 17). Thirteen of 20 taxa on the cobble substrate and 12 of 20 taxa on the gravel substrate showed a slope of the regression line with statistical significance ($P < 0.05$). In these taxa with significant slopes, 10 occurred on both the cobble and gravel substrate at the same time. Seven of the ten on the gravel substrate had greater daily colonization rates than that on the cobble substrate. Using signed-rank test (Devore and Peck 1986) to compare the daily colonization rates of the 9 taxa (Chironomidae was 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 resources. For the cobble substrate, 17 of 36 taxon pairs in the grazer group were significantly positively associated and 7 of 36 taxon pairs were significantly negatively associated (Table 18). In the filter-feeders, 4 of 10 taxon pairs were significantly positively associated and 3 of 10 taxon pairs were significantly negatively associated. Among predator taxon pairs, 6 of 10 were significantly positively associated and in none was there a significantly negative association. These data indicated that the order of the degree of biological interactions among functional feeding groups was filter-feeders, grazers, and predators.

On the other hand, for the gravel substrate, in the grazer group 11 of 36 taxon pairs

Table 16. Summary of results of simple regression on numbers of individuals per basket filled with cobbles versus days in stream for 20 abundant taxa (N = 24; * = significant; ns = not significant).

Species	*Regression functions on cobble substrate*	*P*	*Significance*
Ephemeroptera			
Baetiella bispinosa	Y=2.0412-0.0395X	0.2980	ns
Baetiella sp.B	Y=9.3517-0.2378X	0.0125	*
Baetis sp.A	Y=226.457+4.7800X	0.1189	ns
Baetis sp.B	Y=4.9954+0.0392X	0.6586	ns
Caenis sp.	Y=11.486+0.5073X	0.0685	ns
Ecdyonurus sp.	Y=0.5346+0.2855X	< 0.0001	*
Paraleptophlebia sp.	Y=0.0791+0.0419X	0.1933	ns
Serratella sp.	Y=-1.0233+0.3039X	0.0012	*
Plecoptera			
Neoperla sp.	Y=-0.4289+0.1234X	< 0.0001	*
Protonemura sp.	Y=0.7839-0.0237X	0.0331	*
Odonata			
Euphaea sp.	Y=-0.1104+0.0519X	0.0057	*
Trichoptera			
Hydropsychidae	Y=-7.9701+1.2046X	0.0434	*
Rhyacophila sp.A	Y=-1.1975+0.1749X	0.0027	*
Stenopsyche sp.	Y=-3.0472+1.0485X	0.0001	*
Diptera			
Antocha sp.	Y=-1.6462+2.1481X	< 0.0001	*
Ceratopogonidae	Y=-0.4794+0.0844X	0.0084	*
Chironomidae	Y=-44.8823+55.0574	< 0.0001	*
Hemerodromia sp.	Y=0.3903+0.0277X	0.2492	ns
Prosimulium sp.	Y=156.715-4.9696X	0.0210	*
Simulium sp.	Y=11.2207-0.3537X	0.0553	ns

Table 17. Summary of results of simple regression on numbers of individuals per basket filled with gravels versus days in stream for 20 abundant taxa (N = 18; * = significant; ns = not significant).

Species	*Regression functions on gravel substrate*	*P*	*Significance*
Ephemeroptera			
Baetiella bispinosa	*Y=0.4167+0.1019X*	*0.2256*	*ns*
Baetiella sp.B	*Y=9.7407-0.2346X*	*0.2319*	*ns*
Baetis sp.A	*Y=373.667+8.0926X*	*0.0404*	*
Baetis sp.B	*Y=33.6296-0.679X*	*0.0993*	*ns*
Caenis sp.	*Y=34.6636+0.0298X*	*0.9635*	*ns*
Ecdyonurus sp.	*Y=1.6605+0.3004X*	*< 0.0001*	*
Paraleptophlebia sp.	*Y=0.5216+0.0504X*	*0.0892*	*ns*
Serratella sp.	*Y=-0.4290+0.1656X*	*< 0.0001*	*
Plecoptera			
Neoperla sp.	*Y=-0.9938+0.2922X*	*< 0.0001*	*
Protonemura sp.	*Y=1.0648-0.0340X*	*0.2909*	*ns*
Odonata			
Euphaea sp.	*Y=-0.1451+0.0504X*	*0.0045*	*
Trichoptera			
Hydropsychidae	*Y=-22.2284+3.3375X*	*0.0217*	*
Rhyacophila sp.A	*Y=-1.8920+0.4187X*	*0.0271*	*
Stenopsyche sp.	*Y=2.0247+1.6132X*	*0.0008*	*
Diptera			
Antocha sp.	*Y=-17.0988+2.6584X*	*< 0.0001*	*
Ceratopogonidae	*Y=-0.7191+0.1183X*	*0.0005*	*
Chironomidae	*Y=241.0560+45.8704*	*< 0.0001*	*
Hemerodromia sp.	*Y=0.1173+0.0514X*	*0.0056*	*
Prosimulium sp.	*Y=53.8519-1.7531X*	*0.0781*	*ns*
Simulium sp.	*Y=1.8858-0.0628X*	*0.1619*	*ns*

Table 18. Summary of species associations among members of the same functional feeding groups in baskets filled with cobbles in Experiment II, Chingmei Stream, Taiwan. Significant correlation coefficients are given and noted with asterisks (N = 24; ns = not significant).

Grazer	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Baetis sp.A (1)	--	0.70*	ns	ns	ns	0.47*	ns	0.75*	0.45*
Baetis sp.B (2)		--	ns	ns	ns	0.51*	ns	0.45*	ns
B. bispinosa (3)			--	0.59*	-0.43*	-0.62*	-0.64*	ns	ns
Baetiella sp.B (4)				--	-0.72*	-0.46*	-0.66*	ns	-0.45*
Ecdyonurus sp. (5)					--	0.58*	0.71*	0.67*	0.71*
Caenis sp. (6)						--	0.71*	0.64*	0.48*
Serratella sp. (7)							--	0.54*	0.70*
Chironomidae (8)								--	0.67*
Antocha sp. (9)									--

Filter-feeder	(1)	(2)	(3)	(4)	(5)
Stenopsyche sp. (1)	--	0.45*	0.67*	-0.78*	-0.62*
Hydropsychidae (2)		--	0.67*	ns	ns
Chironomidae (3)			--	-0.56*	ns
Prosimulium sp. (4)				--	0.78*
Simulium sp. (5)					--

Predator	(1)	(2)	(3)	(4)	(5)
Euphaea sp. (1)	--	0.64*	ns	0.48*	0.34*
Neoperla sp. (2)		--	0.60*	0.47*	ns
Rhyacophila sp.A (3)			--	ns	ns
Hemerodromia sp. (4)				--	0.45*
Ceratopogonidae (5)					--

were significantly positive associated, and 2 of 36 taxon pairs were significantly negative associated (Table 19). In filter-feeders and predators, 2 of 10 taxon pairs were significantly positive associated and none of them was negatively associated. These data indicated that the order of the degree of biological interactions among functional feeding groups were grazers, filter-feeders, and predators. In addition, the results also indicated that the intensity of biological interaction on the cobble substrate was greater than on the gravel substrate.

The colonization patterns of functional feeding groups showed that grazer and filter-feeder groups are the major groups on the two kinds of substrate (Fig. 13). On each sampling date the two groups comprised over 98% of total abundance on both cobble and gravel substrate. The relative abundance of grazers per basket on cobble substrate increased between 3 and 6 days and then appeared to level off at 65% until day 30. It decreased between 30 and 42 days. The relative abundance of filter-feeders had the opposite tendency to that of the grazer group. It decreased between days 3 and 6 and appeared to level off in relative abundance (34%) until 30 days. It increased between 30 and 42 days. For the gravel substrate, the relative abundance of grazer and filter-feeder groups seemed to remain constant (69% and 30% respectively) between 3 and 21 days, and it decreased for grazers and for filter-feeders it increased until day 42.

For the cobble substrate the number of grazer taxa remained almost constant after day 3 (Fig. 14A). The number of taxa of filter-feeders kept constant during the experiment except day 21. The number of taxa in the predator increased with time of

Table 19. Summary of species associations among members of the same functional feeding groups in baskets filled with gravel in Experiment II, Chingmei Stream, Taiwan. Significant correlation coefficients are given and noted with asterisks (N = 18; ns = not significant).

Grazer	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Baetis sp.A (1)	--	ns	ns	0.50*	ns	ns	ns	0.52*	ns
Baetis sp.B (2)		--	ns	ns	ns	ns	ns	ns	ns
B. bispinosa (3)			--	0.80*	ns	-0.66*	ns	ns	ns
Baetiella sp.B (4)				--	ns	-0.53*	ns	ns	ns
Ecdyonurus sp. (5)					--	0.51*	0.81*	0.83*	0.83*
Caenis sp. (6)						--	ns	0.50*	ns
Serratella sp. (7)							--	0.72*	0.85*
Chironomidae (8)								--	0.75*
Antocha sp. (9)									--

Filter-feeder	(1)	(2)	(3)	(4)	(5)
Stenopsyche sp. (1)	--	0.51*	ns	ns	ns
Hydropsychidae (2)		--	ns	ns	ns
Chironomidae (3)			--	ns	ns
Prosimulium sp. (4)				--	0.78*
Simulium sp. (5)					--

Predator	(1)	(2)	(3)	(4)	(5)
Euphaea sp. (1)	--	0.57*	ns	ns	ns
Neoperla sp. (2)		--	ns	ns	0.66*
Rhyacophila sp.A (3)			--	ns	ns
Hemerodromia sp. (4)				--	ns
Ceratopogonidae (5)					--

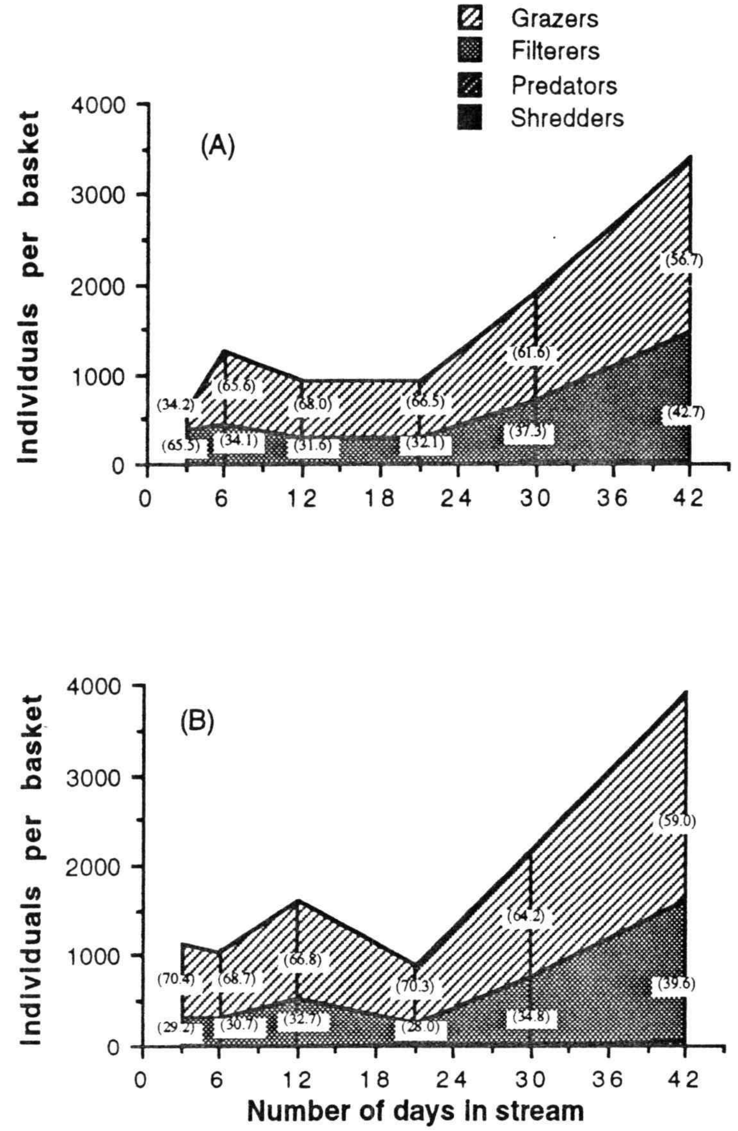

Fig. 13. Mean number of individuals of functional feeding groups colonizing baskets filled with cobbles (A) and gravel (B) on each sampling day. Numbers in parentheses indicate the percentage of each group.

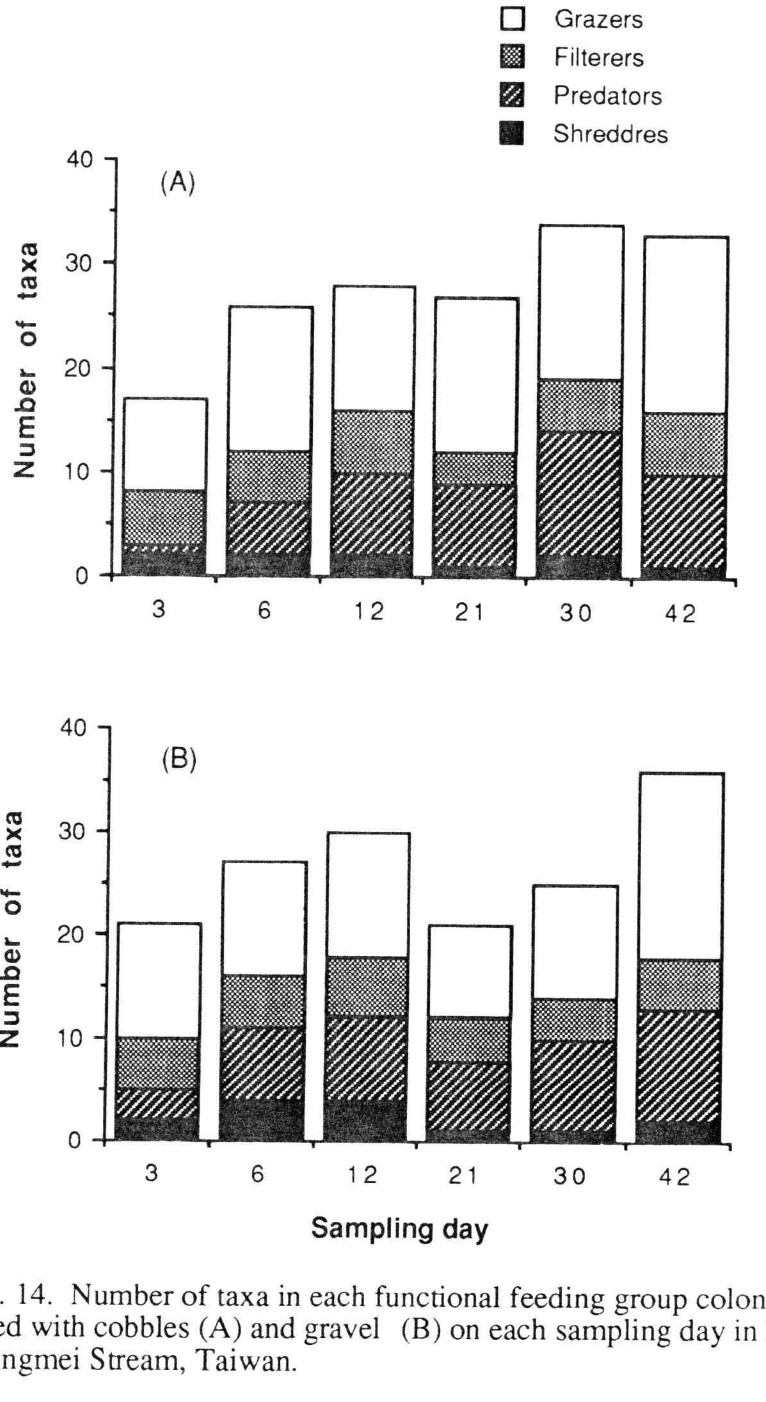

Fig. 14. Number of taxa in each functional feeding group colonizing baskets filled with cobbles (A) and gravel (B) on each sampling day in Experiment II, Chingmei Stream, Taiwan.

colonization. For the gravel substrate, the number of taxa in the grazer and filter feeder groups remained constant before day 12, decreased on day 21 and then increased (Fig. 14B). The number of predator taxa increased during the colonization process.

Equilibrium of the Benthic Community

Colonization rates and extinction rates, expressed as number of taxa per day, were in agreement with the MacArthur-Wilson equilibrium model (Fig. 15). 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 3 and 6 days and between 12 and 21 days. The extinction rates for cobble substrate did not decline until day 12 and increased between 30 and 42 days.

Equilibrium is the point where the curves for colonization and extinction cross. On gravel substrate it occurred around day 15 and on cobble substrate in occurred around day 19. As compared in Fig. 20, the number of taxa present on cobble and gravel substrate did not fully stabilize even though equilibrium appeared to have been attained on the day when the curves for colonization and extinction rates cross. Furthermore, extinction rates at equilibrium are equivalent to turnover rates. The turnover rate for gravel substrate was 0.93 taxa/day at 15 days and for cobble substrate was 1.16 taxa/day at 19 days.

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

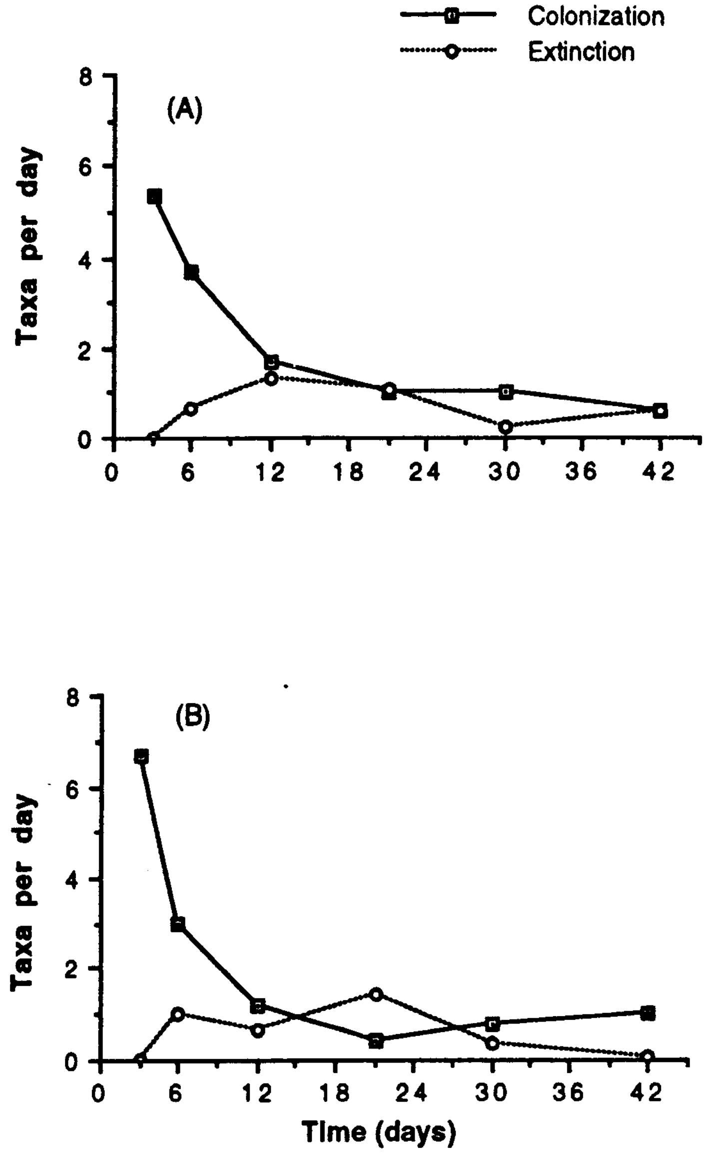

Fig. 15. Colonization and extinction rates of benthic macroinvertebrates colonizing baskets filled with cobbles (A) and gravel (B) in Experiment II, Chingmei Stream, Taiwan.

cobble substrate the coefficient of determination increased with time until day 30 and it declined on day 42 (Fig. 16). For the gravel substrate the coefficient of determination increased with time except the period between 12 and 21 day when the floods occurred (Fig. 17). Comparing the two kinds of substrate, the coefficient of determination for the gravel substrate was greater than that for the cobble substrate between 3 and 12 days and on day 42. This suggests that the time to reach community equilibrium for the gravel substrate is less than that for the cobble substrate.

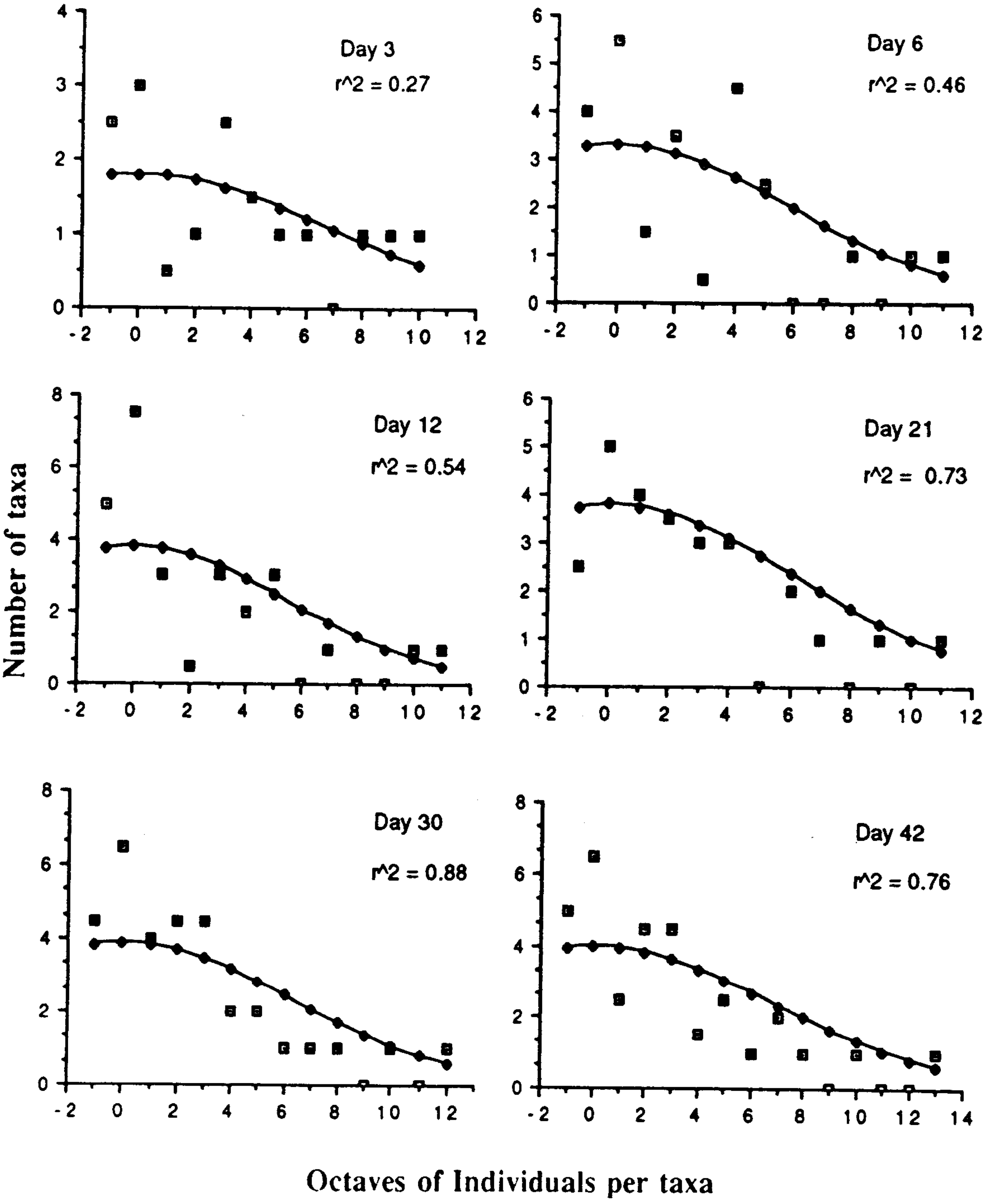

Fig. 16. Fit of taxa abundance curves to a lognormal model for baskets filled with cobbles on each sampling day in Experiment II, Chingmei Stream, Taiwan.

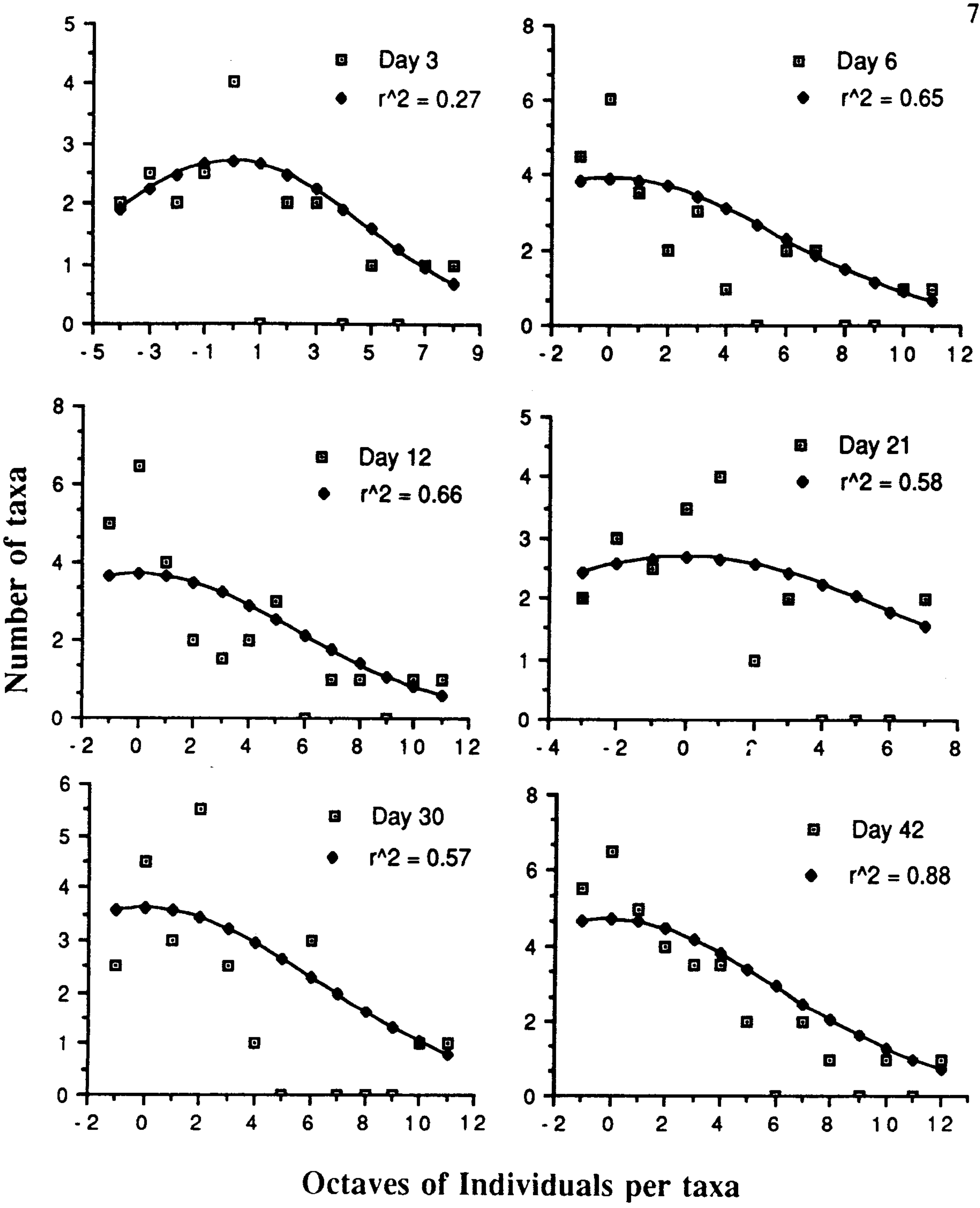

Fig. 17. Fit of taxa abundance curves to a lognormal model for baskets filled with gravel on each sampling day in Experiment II, Chingmei Stream, Taiwan.

DISCUSSION

Experiment I

The high conductivity, turbidity and amounts of organic matter (Table 2; Fig. 2) trapped by baskets may have resulted in reduction in both abundance and number of taxa at Site 1. The high conductivity was due to the water released from the coal mine which contained a high concentration of inorganic ions. Its effect on stream benthos is still unknown. The high turbidity was caused by the amount of suspended sand and coal particles in the water. These suspended and sedimented material can be deleterious to organisms because they reduce light penetration and consequently plant growth, smother hard surfaces, and fill interstices within the substrate which are used by some stream benthos (Wiederholm 1984). In addition, the organisms can be affected directly by the high turbidity, such as when food collection or respiration is obstructed. The accumulations of organic matter may result in low dissolved oxygen levels in local microhabitats (Anderson and Sedell 1979) and also fill the interstices that are used as living space by the biota.

The alteration of water quality caused by mining activities is detrimental to the community structure of stream benthos. In this study, the Ephemeroptera, Trichoptera, Coleoptera, and most Diptera were eliminated or greatly reduced in both abundance and number of taxa (Table 3 and Fig. 3). Similar results due to mine drainage were found by other investigators (Letterman and Mitsch 1978; Moon and Lucostic 1979;

Aanes 1980; Scullion and Edwards 1980). However, the Odonata and Megaloptera seem not to be affected by the alteration of water quality. Cherry et al. (1979) also found that Odonata and Chironomidae are less susceptible to the sediments of coal particles than are other types of insects.

There was a sequence of species colonization or replacement of species during the colonization process at both Site 1 and Site 2. However, the reasons for the sequence or the replacement are different. At Site 1 they are the tolerance or susceptibility of organisms to the pollutants such as high conductivity and turbidity. The Odonata and Chironomidae, which are more tolerant to the pollutants, gradually replace other taxa and become dominant (Fig. 3A). Those which are susceptible to the pollutants would be dislodged. There were only three taxa (*Caenis sp.*, *Euphaea sp.* and Chironomidae) which always occurred and were abundant during the experiment. Other taxa, which were sparse and of sporadic occurrence, may just continue to drift away from the site. Therefore, the extinction rates at Site 1 were similar to Site 2 while the number of taxa was very different between the two sites. At Site 2 the reasons for taxon replacement are the influence of biological interactions and disturbance caused by floods. The flood disturbance reset the substrates back to the earlier conditions.

The same reasons also led to the difference of composition in functional feeding groups on each sampling day. At Site 1 most predators were tolerant to the pollutants and increased in both abundance and number of taxa during the colonization period (Fig. 5A and 6A). Grazers were susceptible to the pollutants; thus the number of taxa decreased. Also, the abundance of predators may have reduced the number of grazers.

A special case was Chironomidae, some species of which can tolerate the conditions of oxygen deficiency (Frank 1980; Nagell and Landahl 1978) and sediment (Grimas and Wiederholm 1979) and caused the increase in abundance of grazers and filter-feeders.

Species richness at the two sites appeared to approach an asymptote by day 42 (Fig. 4A) but mean total abundance did not level off (Fig. 4B). This may be due to the floods which reset the substrates back to earlier conditions. However, the patterns of diversity (H') were different between Site 1 and Site 2 (Fig. 4C). The change in diversity at Site 1 was due to changes in abundance patterns rather than to changes in number of taxa. For Site 2 the change in diversity was due to the changes in the number of taxa. Lake and Doeg (1985), Gore (1979) and Ulfstrand et al. (1974) noted the correspondence between the increase in the number of species and the increase in diversity. This appears to be the case in the Site 2.

Various criteria have been used to determine when artificial substrates are fully colonized, or when the community in baskets is indistinguishable from that on the stream bottom. For example, Ulfstrand (1968) used the shape of curves of the densities of the members of various orders, while Dickson and Cairns (1972), Stauffer et al. (1976), Minshall et al. (1983) and Lake and Doeg (1985) used colonization rates and extinction rates of taxa. In this study in Taiwan, using the number of taxa as a criterion, colonization at Site 1 was complete by 10 days but still incomplete at Site 2 at the end of the experiment. Equilibrium at Site 2 was not attained in the experimental period of 42 days. There was continual invasion and settlement of new taxa over extended periods and a failure of the community to stabilize.

The time to reach an equilibrium number of taxa varies considerably from investigation to investigation. Ulfstrand (1968) reported that colonization of stones in trays reached equilibrium after only 6 - 8 days. Wise and Molles (1979) showed 9 days for artificial substrates in a stream. Lake and Doeg (1985) described 32 days for denuded stones in an undisturbed site. Townsend and Hildrew (1976) indicated 37.5 days for bottom trays. Dickson and Cairns (1972) suggested 42 days for floating artificial substrate. Williams and Hynes (1977) evaluated 109 days for a newly formed stream channel. Minshall et al. (1983) reported 439 days after catastrophic disturbance by the breaking of a dam. These broad differences were probably due to the size of the patch to be colonized, the distance between the patches to be colonized, the source of colonization and the time of year when experiments were conducted.

Three patterns of colonization were shown by the common taxa in this study at Site 2: (1) an increase in density with increased colonization time (e.g., *Baetis sp.B; Ecdyonurus sp.*); (2) a decrease in density after the first few sampling intervals (e.g. *Prosimulium sp.; Baetiella sp.B*); and (3) an increase followed by a decrease in density (e.g. *Baetis sp.A; Simulium sp.*) in the later period of exposure of baskets in the stream (Table 7). The first type suggested that the build-up in density is due to a steady increase in the suitability of the stone environment. The taxa that decreased after initial higher density can be regarded as the "pioneer" or "opportunistic" species that may be replaced by superior competitors that are slower colonizers. For example, baetid mayflies have been identified as early colonizers or opportunistic taxa in streams in

Colorado (Allan 1975), Arizona (Fisher et al. 1982), Montana (McAuliffe 1983), Idaho (Minshall et al. 1983), Alberta (Ciborowski and Clifford 1984) and North Carolina (Wallace and Gurtz 1986). As a whole, these patterns are consistent with the hypothesis that biological interactions may influence alterations in species dominance in the benthic community (Sheldon 1984).

In the theory of island colonization (MacArthur and Wilson 1963; 1967) the rate of establishment of new species is high in early colonization and decreases with time; extinction rate is expected to act conversely. Dickson and Cairns (1972) found a decreasing colonization rate and an increasing extinction rate for the macroinvertebrates colonizing small blocks of floating substrate anchored in a stream riffle. Minshall et al. (1983) also found such a case for macroinvertebrate recolonization in Idaho rivers. However, in this study and those of Minshall et al. (1985), Lake and Doeg (1985) and Williams and Hynes (1977), the colonization rate steadily decreased with time, while the extinction rate, after an initial rise, also decreased. Minshall et al. (1985) suggested that these high but gradually decreasing values are responsible in part for the curvilinear decline of the colonization rate and suggested a modification to the original logic of MacArthur and Wilson (1967). Lake and Doeg (1985) explained the reason that the extinction curves differ from the predicted forms was that in the colonization of vacant substrata in streams, drift is regarded as the principal means of transport. While many species arrive by means of the drift in the early stages of colonization many of these may rapidly leave the stones because the stones are relatively bereft of periphyton and of a normal surface organic layer and therefore do not provide a food source. The stones are somewhat inhospitable. When they develop periphyton and a surface organic layer they become attractive to more species. Walton (1978) has shown that some species of drifting macroinvertebrates show a degree of preference for natural stones over sterile stones. The increasing hospitability of the stones may explain the decline in the extinction rate with time. In my study, it was found that drift was the major means of transport since a lot of young and/or active larvae such as hydropsychids, stenopsychids and baetids were collected in the trays. Thus, Lake and Doeg's opinions are reasonable to explain the observations of this study.

A high degree of conformance with the lognormal model shows a community in a high degree of equilibrium (Minshall et al. 1985). In my study, the lognormal distribution was a better fit at Site 1 than at Site 2, and at the end of colonization period than in the first week. This suggests that it is easier for the community to attain a state of equilibrium in an environment polluted or stressed for a long time than in a unpolluted or less-polluted environment and that during the process of colonization the degree of equilibrium of a community increases with the exposure of experimental substrates to colonization.

The state of equilibrium is affected by environmental factors such as high discharge. At Site 2 the higher discharge occurred on day 6 and 21 (Table 2) and the coefficients of determination on the two sampling dates were lower than those on the other sampling dates. In addition, Site 1 is a more variable environment than Site 2 because of mining activities upstream of Site 1 which released water with high turbidity and conductivity at least once per day. The results are consistent with the suggestion that a relatively stable environment (Site 2) supports a complex but fragile community, while a relatively variable environment (Site 1) only allows the persistence of simpler, more robust communities (Begon et al. 1990).

The data from the experiment suggest the following conclusions. The mining activities have a deleterious impact on the community structures of stream benthos. The mechanisms which determine the colonization patterns are the susceptibility of organisms to the mining activities at Site 1, and the influence of biological interactions and disturbance caused by floods at Site 2. At Site 1 those which are less susceptible to the mining activities become more abundant during the later period of the colonization process. It is easier for the community to attain a state of equilibrium in an environment polluted or stressed (Site 1) than in an unpolluted or less-polluted environment (Site 2) because the community in the former is simpler and easier to reach equilibrium than that in a less polluted environment where the taxa continually invade over extended periods and fail to stabilize. However, although these data are suggestive, they are insufficient to draw rigorous conclusions. The experiment may not have had adequate samples, or a long enough colonization period and there are no benthos samples to support them.

Experiment II

Species colonization was rapid, with representatives of most species arriving within three days of the start of the experiment, except for Odonata and Coleoptera (Fig. 11). *Baetis sp.A*, Chironomidae and *Prosimulium sp.* which dominated on day 3 had rapid colonization on the both cobble and gravel substrate (Tables 10 and 11). Rapid colonization of disturbed or new substrata by related taxa have 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).

Variation in the response of taxa to disturbance caused by floods which occurred between day 12 and 21 and resulted in rock overturning was expected and was found. The overturning of rocks dislodges some individuals and may crush others. Differences in morphology lead to differential ability to hold on to the shifting substrate or to resist being crushed. 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. 11).

The substratum type had a significant influence on the total number of colonizing individuals (Table 13). Gravel substrate had more individuals than did cobble substrate (Fig. 12B). The results are consistent with those of Wise and Molles (1979) and Minshall and Minshall (1977) who employed similar experimental methods and observed 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) indicated another explanation for more individuals colonizing smaller substrate. They suggested that small particle size tends to accumulate large amounts of the 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. 10). This does not mean that the suggestion of Rabeni and Minshall can't 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.

The total abundance and number of taxa colonizing either the cobble or gravel substrate did not approach an asymptote during the experimental period. Therefore an equilibrium, using these as criteria, was not attained. This was due to the flooding events which occurred between day 12 and day 21 which disturbed the substrates and reset the biota back to earlier conditions. Wise and Molles (1979) conducted a 19-day colonization experiment of 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).

Stability of substrate is defined as the degree of resistance to movement and is generally proportional to the size of the particle (Minshall 1984). Reice (1985) suggested that the response of the fauna in a given patch depends on the sediment size of that patch. The total number of individuals and taxa fluctuated on the gravel substrate (Table 11 and Fig. 11B) since the gravel substrate is unstable during the floods. The floods affected invertebrate abundance and community composition both by causing bed-load movement and by increasing the amount of suspended sediment that settled in the substrate trays. Sagar (1986) found that increased current velocity and bed-load movement caused catastrophic drift of invertebrates, physical damage to some individuals, and reduction in the food supply available by abrading algal populations from the substrate. McAuliffe (1983) indicated that small stones are usually devoid of any moss cover, but moss cover increased as a function of stone size and that small stones would have a higher probability of being overturned by flood waters. The overturning of rocks may free space formerly occupied by other invertebrates.

While the colonization patterns of total number of individuals and taxa did not show a tendency to reach an asymptote, an equilibrium number of species is established for both gravel and cobble substrate (Fig. 15) when the MacArthur-Wilson equilibrium model is used as the criterion The equilibrium number of species for the both gravel and cobble substrate occurred between 12 and 21 day when floods occurred. For the gravel substrate the equilibrium may be due to increasing the extinction rate on day 21 which was caused by floods. For the cobble substrate, however, extinction rate did not increase on day 21. This may be because the cobble substrate is more stable and was not overturned by high velocity.

The turnover rate of species means 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 are intermediate in the study site as compared with other places. The turnover rate for the gravel substrate was 0.93 taxa/day at 15 days and for the cobble substrate was 1.16 taxa/day at 19 days. The turnover rate was about 0.02 taxa/day at 625 days for a site where the breaking of a dam had destroyed the fauna (Minshall et al. 1983), about 0.10 taxa/day at 109 days for a newly formed stream channel (Williams and Hynes 1977), about 1.00 taxa/day at 8 days for river stones (Lake and Doeg 1985), and about 1.35 taxa/day at 42 days 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 area to be colonized.

The association analysis in the same functional feeding group suggested 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 (Table 18 and 19). Positive associations between taxa 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 taxa pairs usually mean competition between the two taxa (Schluter 1984). In Peckarsky's (1986) and Reice's (1981; 1983) studies they did not find the negative associations between potential competitor species and interpreted the results as lack of evidence for competition. Minshall and Minshall (1977) suggested that competition often play a minor role in structuring communities of the stream benthos.

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 the 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 my study, *Baetiella spp.* were replaced by *Ecdyonurus sp., Serratella sp.,* and *Antocha sp.*, and simuliids were displaced by *Stenopsyche sp.* and chironomids on the cobble substrate (Table 18). Similar displacements among species were also observed by other investigators (Malmqvist and Otto 1987; McAuliffe 1983, 1984; Hemphill and Cooper 1983; Fisher et al. 1982; Allan 1975; Ulfstrand et al. 1974).

The displacement of same taxa from the cobble substrate may give rise to the decrease in the diversity index on day 42. This may be due to 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 the increase in diversity (Fig. 12C). 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, the 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.

The data from this experiment suggest the following conclusions. The gravel substrate provides more surface area available for invertebrates and supports more individuals of some taxa which characteristically have high colonization rates. The degree of equilibrium and intensity of biological interactions depends on the stability of substrate.

This is the first study on the colonization patterns of stream benthos in Taiwan. It provides another method of studying aquatic insects. Surber sample has been used in the routine survey in previous studies (Young et al. 1990). The artificial substrates used in the study are an effective method of collecting stream benthos. The stream ecosystems in Taiwan are frequently disturbed by flood events, application of toxin chemicals, and so on. It becomes increasingly important to understand the colonization mechanisms of stream benthos. On the other hand, the study suggests potential competitors that require future study, such as the interaction between stenopsychids and simuliids, to understand whether competition does occur. The data and specimens of the study are available for future study on aquatic insects of Taiwan.

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APPENDIX

Appendix 1. Organic matter, total number of taxa, total number of individuals, and diversity (Shannon-Wiener H') (mean ± 1 s.e. / basket; n = 4) at Site 1 and Site 2 in Experiment I, Chingmei Stream, Taiwan. (S1 = Site 1; S2 = Site 2)

		Sampling date					
		3	6	12	21	30	42
Organic matter (g) per basket	S1	0.25±0.13	0.92±0.40	0.83±0.19	1.39±0.23	7.83±1.81	8.97±2.05
	S2	0.06±0.02	0.31±0.12	0.23±0.10	0.39±0.15	3.84±1.20	5.15±1.18
No. of taxa per basket	S1	6.0±1.7	6.5±0.5	6.3±1.5	7.5±0.6	7.0±1.1	7.0±1.8
	S2	9.0±1.1	9.5±1.2	12.0±0.8	1.63±1.4	20.0±1.8	20.5±1.6
No. of individuals per basket	S1	36±15	68±20	164±21	236±37	123±23	149±16
	S2	467±126	478±146	1122±82	2215±432	1252±207	1421±107
Diversity	S1	1.06±0.25	0.84±0.13	0.42±0.10	0.38±0.05	0.41±0.05	0.38±0.09
	S2	1.07±0.10	1.06±0.07	0.96±0.11	1.32±0.20	1.28±0.11	1.37±0.10

Appendix 2. Organic matter, total number of taxa, total number of individuals, and diversity (Shannon-Wiener H') (mean ± 1 s.e. / basket; n = 4) for cobble and gravel substrates in Experiment II, Chingmei Stream, Taiwan. (C = cobble; G = gravel)

		Sampling date					
		3	6	12	21	30	42
Organic matter (g) per basket	C	0.35±0.13	0.66±0.36	0.54±0.28	12.51±2.07	25.39±5.91	17.72±3.25
	G	0.15±0.06	0.22±0.04	0.65±0.18	10.34±3.07	14.48±5.20	12.99±4.42
No. of taxa per basket	C	10.5±1.7	13.5±1.9	15.5±2.6	16.5±0.9	22.0±0	19.0±1.8
	G	13.8±0.9	15.0±2.0	17.3±1.3	16.0±2.0	20.0±0	25.0±2.0
No. of individuals per basket	C	615±238	1273±341	938±203	932±214	1918±158	3397±331
	G	1123±229	1058±205	1609±201	908±167	2184±162	3924±412
Diversity	C	1.28±0.06	1.06±0.09	1.08±0.07	1.21±0.02	0.99±0.06	0.79±0.13
	G	1.21±0.07	1.13±0.07	1.11±0.04	1.19±0.08	0.97±0.04	1.10±0.20