

Colonization Patterns of Aquatic Insects on Artificial Substrates in a Taiwan Stream

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ABSTRACT

Experiments on colonization patterns of artificial substrates by aquatic insects were conducted in the upper Chingmei Stream, Taiwan. Artificial substrates were colonized by aquatic insects for periods of 3, 6, 12, 21, 30, and 42 days from 15 Dec. 1990 to 26 Jan. 1991 at 2 sites: a polluted site caused by coal mining activities (Site 1) and a recovery site further downstream of the polluted site (Site 2). Total numbers of individuals and taxa were significantly affected by exposure period of experimental substrates and sites, indicating the occurrence of succession and the detrimental effect of coal mining activities on aquatic insect communities. At Site 1, only *Caenis* sp., *Euphaea* sp., and Chironomidae occurred on all sampling dates and were abundant. The other taxa may have just continued 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* spp. and Chironomidae were most abundant. They accounted for over 80% of individuals during the experiment, except on day 21. The relative abundance shifted from *Baetis* spp. to Chironomidae with an increase in colonization time. A large number of positive correlation was found within the functional groups of filter-feeders and predators at Site 2. Taxa within the two groups tended to overlap in their distribution among baskets. The lognormal distribution was a better fit at Site 1 than at Site 2, suggesting that it is easier for a community to attain a state of equilibrium in a stressed environment than in a less-polluted environment. Mechanisms determining the colonization patterns of aquatic insects were reflected by the susceptibility of organisms to mining activities at Site 1, and the influence of biological interactions and disturbance caused by high discharges at Site 2 during the experimental period.

Key words: colonization, aquatic insects, artificial substrates, stream, Taiwan.

Introduction

Colonization is defined as the sequence of events through which individuals, or groups of individuals become es-

tablished in habitats where they were absent (Sheldon 1984). The factors influencing colonization and subsequent change of insect populations in streams may be allogenic (external, abiotic) or auto-

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genic (internal, biotic) (Peckarsky 1986). The allogenic factors may include characteristics of the substrate, seasonal changes, and unpredictable disturbances. Autogenic factors may be interactive, where the present community influences establishment of future communities, or noninteractive, such as with species life histories (Fisher, 1983; Sheldon, 1984). The principal colonization pathways of aquatic insects are aerial movements, downstream drift, and upstream and vertical movement from deep substrates (Williams and Hynes, 1976). Townsend and Hildrew (1976) and Williams and Hynes (1976) suggested that downstream drift is most important in permanent streams.

Stream ecosystems in Taiwan are frequently disturbed by flood events, contamination by toxic chemicals, industrial and domestic sewage, and so on. It becomes increasingly important to understand the colonization mechanisms of aquatic insects. Mackay (1992) suggested that studies on recovery following disturbance in stream ecosystems should show the colonization mechanisms responsible for restoring a community to its predisturbance state. This study deals with the colonization of substrata by aquatic insects in the upper Chingmei Stream, a subtropical stream in northern Taiwan. The objectives of the study were to examine the colonization mechanisms of aquatic insects on new substrate patches, to describe the subsequent patterns of species dominance and functional feeding groups, and to compare colonization patterns of aquatic insects 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).

Materials and Methods

A. Study area

The experiments were conducted in

the upper Chingmei Stream (lat. 25° 01' N, log. 121° 41' E) flowing through Shihing, Taipei Co., and 25 km east of Taipei City in northern Taiwan. The area is of Miocene and Pliocene age, and the soil group is yellow earth (Hsieh 1964). The annual average precipitation is about 4000 mm. The study reach of the stream has a riparian zone with evergreen hardwood vegetation consisting of *Boehmeria densiflora* (Urticaceae), *Piper kadsura* (Piperaceae), *Acacia confusa* (Leguminosae), *Ficus erecta* (Moraceae) and *Diospyros morrisiana* (Ebenaceae), and herbs including *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 entire year. The headwaters of the streams are in agricultural areas with tea plantations (*Thea sinensis* (L.) Sims).

Two study sites were selected for the experiments. Site 1 is on a 3rd-order stream at an elevation of 200 m. Site 2 is on a 4th-order stream at an elevation of 150 m. The 2 sites were located at riffle sections with heterogeneous substrate and open canopy. Upstream of Site 1 is a coal mine about 2 km away. Stream water was used to clean coal. Site 2 is located about 2 km downstream of Site 1 and receives additional runoff from major tributaries. The influences of mining activities at Site 1 on the stream section of Site 2 were decreased by this dilution.

B. Benthic sampling

In this study, community structure and colonization patterns of aquatic insects were compared between Site 1 and Site 2 from 15 Dec. 1990 to 26 Jan. 1991. A mixture of particle sizes was used as artificial substrate. Plastic baskets (mesh = 4 mm, dimension 25 × 20 × 6 cm³) were filled with 20 pieces of gravel (16-32 mm), 9 pebbles (32-64 mm), and 6 cobbles (64-128

mm). Cobbles and pebbles were collected from the dry stream bed, and the gravel was collected from a quarry. Each stone was washed in stream water.

All baskets at both study sites were placed in the stream bottom at least 1 m away from banks on 15 Dec. 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 4 replicates, so at least 8 baskets were sampled on each sampling date. The total 24 baskets for each study site were arranged randomly into a 4 (columns) × 6 (rows) matrix. The space between columns and between rows was at least 1.5 m. At the end of the colonization period, a basket was lifted off the streambed and transferred into a basket of the same size but without mesh. The stones in the basket were washed carefully with stream water which was sieved (mesh = 0.25 mm) to collect sessile and other insects. The other sediment in the basket was placed in labeled individual plastic bags. Moreover, a Surber sampler (50 × 50 cm² and mesh = 0.25 mm) was used to collect benthic samples for comparison with artificial substrates. Samples were collected on days 12 and 42.

To compare differences in physical and chemical characteristics between Site 1 and Site 2, 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 aquatic insects were sorted. All animals were preserved in .75% ethyl alcohol. Then the animals were identified to genus whenever possible based on Kawai (1985), Merritt and Cummins (1984), or Wiggins (1977). Ephemeroptera were

identified using Kang (1993) and Kang and Yang (1994a and 1994b). All Chironomidae found were only counted. All Hydropsychidae individuals were not further identified, because a lot of first instar larvae were collected during the sampling period. In addition, taxa were classified into functional feeding groups based on Merritt and Cummins (1984). Since most taxa within grazers are also collector-gatherers, they were grouped as grazers/collectors. Chironomidae taxa were classified as both filter-feeders and grazers/collectors because Tanytarsini are filter-feeders and Chironomini are collector-gatherers.

C. Data analysis

The design was a 2-way factorial analysis of variance with site (2 levels: Site 1 and Site 2) and time (6 sample dates) as factors (2 × 6 design with 12 treatment combinations). There were 4 replicates of each combination. The following parameters were analyzed in the designs described above: total number of individuals, total number of taxa, Shannon-Weaver diversity, and evenness for every substratum basket. Numerical data were log-transformed to stabilize variance. Spearman rank correlation coefficients were used to examine potential biological interactions between taxa within a functional group. The signed-rank test (Devore and Peck, 1986) was conducted to compare differences in physical and chemical characteristics between Site 1 and Site 2. The lognormal distribution (Ludwig and Reynolds, 1988) was used to examine the degree of equilibrium of aquatic insect communities on colonization baskets, indicated by the coefficient of determination of the least-squares fit (r). The equilibrium state was viewed as a continuum between $r^2 = 1$ for equilibrium and $r^2 = 0$ for maximum non-equilibrium.

Results

A. Physical and chemical factors

Values for physical and chemical characteristics at the 2 study sites during the field experiment (from 15 Dec. 1990 to 26 Jan. 1991) are given in Table 1. Using signed-rank test to compare differences in physical and chemical characteristics between Site 1 and Site 2 showed that water depth, current velocity, discharge, and pH values were significantly higher at Site 2 than at Site 1 ($p < 0.05$). pH values of the 2 sites showed that the streams are slightly alkaline. Conductivity values at Site 1 were significantly higher than those at Site 2 ($p < 0.05$). This is probably due to mining activities which released water high in inorganic ions.

B. Aquatic insect fauna

During the experiment, 26 taxa were collected at Site 1 (Table 2) and 44 taxa were collected at Site 2 (Table 3) in the colonization baskets. Of the 20 taxa found only at Site 2 were 4 Ephemeroptera, 2 Odonata, 5 Trichoptera, 4 Diptera, and 5 Coleoptera. At Site 1, there were 3 taxa of Odonata and *Parachauliodes* sp. (Megaloptera) that were not recorded from Site 2.

In benthic samples, which were collected on days 12 and 42, there were 32 taxa collected at Site 1 and 30 taxa at Site 2 (Table 4).

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

In the colonization baskets, the most abundant Ephemeroptera taxa were *Baetiella bispinosa*, *Baetis* spp., and *Caenis* sp. at Site 1 (Table 2). For the 3 taxa, the largest number of individuals of each occurred on a different sampling day. *B. bispinosa* ($135/m^2$) occurred on day 3, *Baetis* spp. ($125/m^2$) on day 12, and *Caenis* sp. ($110/m^2$) on day 21. Of the 3 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 (Tables 2 and 3). In benthic samples, damselflies were also more abund-

Table 1. Physical and chemical characteristics of Site 1 and Site 2 on each sampling day in the 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

Table 2. Density (per m²) of aquatic insect fauna colonizing baskets of mixed substrates on each sampling day at site 1 in the Chingmei Stream, Taiwan. "Total" column is the sum of numbers collected from Day 3 to Day 42.

Taxa	FFG*	Day 3	Day 6	Day 12	Day 21	Day 30	Day 42	Total
Ephemeroptera								
<i>Afronurus hyalinus</i>	G/C	5	15	10	0	0	0	30
<i>Ameletus motivagus</i>	G/C	0	0	5	40	0	0	45
<i>Baetiella bispinosa</i>	G/C	135	55	20	0	0	0	210
<i>Baetis</i> spp.	G/C	70	55	125	40	0	30	320
<i>Caenis</i> sp.	G/C	25	45	30	110	10	0	220
<i>Cincticostella</i> sp.	G/C	0	0	0	0	10	0	10
<i>Ephmera</i> sp.	G/C	0	0	0	5	0	5	10
<i>Paraleptophlebia</i> sp.	G/C	0	0	0	0	0	5	5
Plecoptera								
<i>Amphinemura</i> sp.	S	20	10	20	10	0	0	60
<i>Neoperla</i> sp.	P	0	0	0	5	5	5	15
Odonata								
<i>Euphaea</i> sp.	P	25	50	80	70	45	55	325
<i>Sieboldius</i> sp.	P	0	0	0	0	0	5	5
<i>Stylogomphus</i> sp.	P	0	0	0	0	5	20	25
<i>Stylurus</i> sp.	P	0	0	0	0	0	5	5
Megaloptera								
<i>Parachauliodes</i> sp.	P	0	0	0	5	0	10	15
Trichoptera								
Hydropsychidae	F	10	10	20	5	5	5	55
<i>Melanotrichia</i> sp.	G/C	0	5	0	0	0	0	5
<i>Stenopsyche</i> sp.	F	25	5	0	5	10	0	45
Diptera								
<i>Antocha</i> sp.	G/C	0	0	0	10	10	5	25
<i>Atherix</i> sp.	P	0	5	0	5	10	5	25
Ceratopogonidae	P	0	0	0	5	20	25	50
Chironomidae	G/C,F	395	1105	2970	4385	2265	2745	13865
<i>Hemerodromia</i> sp.	P	0	0	5	15	45	40	105
Coleoptera								
<i>Growellinus</i> sp.	G/C	0	0	0	0	10	5	15
Hydrophilidae	P	0	5	0	0	0	0	5
<i>Zaitzevia</i> sp.	G/C	0	0	0	0	5	0	5
Total		705	1350	3270	4675	2455	2970	15425

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

ant at Site 1 than at Site 2 (Table 4).

At Site 2, the most abundant Ephemeroptera taxa were *Baetis* spp. (Table 3). Their greatest abundance (18,030/m²), about 160 times greater than that at Site 1, occurred on day 21. The most abundant Trichoptera was Hydropsychidae and its largest abundance (2,420/m²) also occu-

red on day 21. The most abundant Diptera was the Chironomidae, and its largest abundance (15,330/m²) also occurred on day 21. Comparing the abundance of *Baetis* spp. and Chironomidae, *Baetis* spp. were more abundant on days 3, 6, and 21, and Chironomidae was more abundant on days 12, 30, and 42. This indicates that re-

Table 3. Density (per m²) of aquatic insect fauna colonizing baskets of mixed substrates on each sampling day at Site 2 in the Chingmei Stream, Taiwan. "Total" column is the sum of numbers collected from Day 3 to Day 42.

Taxa	FFG*	Day 3	Day 6	Day 12	Day 21	Day 30	Day 42	Total
Ephemeroptera								
<i>Afronurus hyalinus</i>	G/C	15	20	65	100	205	185	590
<i>Ameletus motivagus</i>	G/C	60	5	30	75	0	0	170
<i>Baetiella bispinosa</i>	G/C	1130	755	425	4885	610	680	8485
<i>Baetis</i> spp.	G/C	5270	5430	9475	18030	7510	9215	54930
<i>Caenis</i> sp.	G/C	20	30	45	110	385	360	950
<i>Choroterpes</i> sp.	G/C	0	0	0	0	0	5	5
<i>Cincticostella</i> sp.	G/C	0	0	10	0	0	10	20
<i>Epeorus</i> sp.	G/C	0	5	0	20	50	20	95
<i>Ephemera</i> sp.	G/C	0	0	0	0	5	10	15
<i>Paraleptophlebia</i> sp.	G/C	0	0	0	0	20	10	30
<i>Serratella</i> sp.	G/C	0	0	0	0	50	10	60
<i>Torleya</i> sp.	G/C	0	0	0	0	0	5	5
Plecoptera								
<i>Amphinemura</i> sp.	S	5	0	25	215	55	75	375
<i>Neoperla</i> sp.	P	0	0	0	10	40	30	80
Odonata								
<i>Euphaea</i> sp.	P	5	0	10	5	20	10	50
Lestidae	P	0	0	0	5	0	0	5
<i>Onychogomphus</i> sp.	P	0	0	0	0	0	5	5
Hemiptera								
<i>Micronecta</i> sp.	P	0	0	0	0	5	0	5
Lepidoptera								
<i>Eoophyla</i> sp.	G/C	0	0	0	0	10	5	15
Trichoptera								
<i>Chirrarra</i> sp.	F	0	5	0	115	75	165	360
Hydropsychidae	F	135	200	615	2420	960	1290	5620
<i>Hydroptila</i> sp.	G/C	0	0	5	0	0	0	5
<i>Melanotrichia</i> sp.	G/C	0	0	0	0	0	15	15
<i>Oecetis</i> sp.	P	0	0	5	0	0	0	5
<i>Rhyacophila</i> sp.A	P	0	0	5	15	20	60	100
<i>Stactobia</i> sp.	G/C	0	0	0	5	0	0	5
<i>Stenopsyche</i> sp.	F	20	60	55	95	125	120	475
Diptera								
<i>Antocha</i> sp.	G/C	0	0	25	70	240	360	695
<i>Atherix</i> sp.	P	0	0	0	0	5	0	5
<i>Bibiocephala</i> sp.	G/C	0	0	0	0	0	5	5
Ceratopogonidae	P	0	0	0	0	20	0	20
Chironomidae	G/C,F	2335	2800	11180	15330	14170	15135	60950
<i>Hemerodromia</i> sp.	P	0	5	15	35	15	30	100
<i>Prosimulium</i> spp.	F	325	225	445	2490	340	440	4265
<i>Simulium</i> spp.	F	10	15	0	210	70	75	380
<i>Wiedemannia</i> sp.	P	0	0	0	35	15	15	65
Coleoptera								
<i>Grouvellinus</i> sp.	G/C	0	5	0	10	5	35	55
Hydrophilidae	P	0	0	0	0	0	5	5
Limnidae	G/C	0	0	0	0	5	0	5
<i>Mataeopsephus</i> sp.	G/C	0	0	0	0	0	5	5
<i>Orectochilus</i> sp.	P	0	0	0	0	5	5	10
<i>Psephenoides</i> sp.	G/C	0	0	0	0	0	5	5
Ptilliidae	P	0	0	0	5	0	0	5
<i>Zaitzevia</i> sp.	G/C	0	0	0	0	5	10	15
Total		9255	9535	22340	44115	24835	28225	138305

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

Table 4. Density (per m²) of total aquatic insect fauna collected by Surber sampler at Site 1 and Site 2 on Day 12 and Day 42 in the Chingmei Stream, Taiwan.

Taxa	FFG*	Site 1		Site 2	
		Day 12	Day 42	Day 12	Day 42
Ephemeroptera					
<i>Afronurus hyalinus</i>	G/C	0	1	15	25
<i>Ameletus motivagus</i>	G/C	0	0	1	0
<i>Baetiella bispinosa</i>	G/C	81	0	220	201
<i>Baetis</i> spp.	G/C	23	11	1328	918
<i>Caenis</i> sp.	G/C	5	0	11	64
<i>Cincticostella</i> sp.	G/C	5	1	0	0
<i>Epeorus</i> sp.	G/C	0	0	0	3
<i>Ephemer</i> sp.	G/C	4	5	0	23
<i>Paraleptophlebia</i> sp.	G/C	0	0	0	3
<i>Serratella</i> sp.	G/C	0	0	1	3
Plecoptera					
<i>Amphinemura</i> sp.	S	9	0	1	8
<i>Neoperla</i> sp.	P	7	0	4	16
Taeniopterygidae	P	0	1	0	0
Odonata					
Calopterygidae	P	8	3	0	0
<i>Euphaea</i> sp.	P	25	32	7	5
<i>Onychogomphus</i> sp.	P	19	13	5	1
<i>Stylogomphus</i> sp.	P	1	4	0	0
Megaloptera					
<i>Parachauliodes</i> sp.	P	1	0	0	0
<i>Protohermes</i> sp.	P	4	1	0	1
Lepidoptera					
<i>Eoophyla</i> sp.	G/C	1	1	0	0
Trichoptera					
<i>Chirmarra</i> sp.	F	1	0	21	81
<i>Goera</i> sp.	G/C	0	0	1	0
<i>Helicopsyche</i> sp.	G/C	0	1	0	0
Hydropsychidae	F	13	0	43	140
<i>Rhyacophila</i> sp.A	P	0	3	4	11
<i>Rhyacophila</i> sp.B	P	3	3	0	0
<i>Stenopsyche</i> sp.	F	0	0	19	15
Diptera					
<i>Antocha</i> sp.	G/C	3	8	12	75
<i>Atherix</i> sp.	P	5	1	0	0
Ceratopogonidae	P	16	37	12	7
Chironomidae	G/C,F	404	473	1227	1359
<i>Eriocera</i> sp.	P	0	4	1	4
<i>Hemerodromia</i> sp.	P	0	1	1	0
<i>Prosimulium</i> spp.	F	0	0	3	13
<i>Wiedemannia</i> sp.	P	3	0	3	7
Coleoptera					
<i>Grouvellinus</i> sp.	G/C	4	5	1	11
Hydrophilidae	P	1	0	1	0
<i>Mataeopsephus</i> sp.	G/C	0	1	0	0
<i>Psephenoides</i> sp.	G/C	0	0	0	3
<i>Zaitzevia</i> sp.	G/C	17	29	3	13
Total		663	638	2929	2985

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

relative abundance shifted from *Baetis* spp. to Chironomidae with an increase of colonization time. A similar condition, however, did not occur at Site 1. The chironomid larvae were always most abundant at Site 1. Furthermore, the 2 taxa accounted for 81-91% of colonizing individuals during the experiment except on day 21 (74%) at Site 2. The relative abundance of *Baetis* spp. decreased from 57% on day 3 to 30% on day 30, they increased to 33% on day 42. The chironomid larvae had the opposite tendency to that of *Baetis* spp. Their relative abundance increased from 25% on day 3 to 57% on day 30, then decreased to 53% on day 42. In benthic samples, the 2 taxa comprised 86% and 72% of the fauna on days 12 and 42, respectively, at Site 1. *Baetis* spp. accounted for 45% and 31% and chironomid larvae accounted for 42% and 45% on the same sampling dates at Site 2.

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

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

tween the 2 sampling dates in benthic samples.

At Site 2, the Ephemeroptera were also the major colonists at the early stage of the colonization period (Fig. 1B). However, they were not replaced by other taxa and by day 42 there were 11 taxa of mayflies compared with 5 on day 3 (Table 3). The number of Trichopteran taxa appeared to level off after day 12. The number of Dipteran taxa also increased with colonization time. It is worth noting that the Coleoptera occurred later than other orders at both sites and only increased after day 21 at Site 2. In benthic samples, mayfly taxa increased from 6 on day 12 to 8 on day 42. They also increased from 7 on day 12 to 13 on day 42 in the colonization baskets.

C. Colonization patterns of aquatic insect communities

Three of the 4 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 ($p < 0.001$) (Table 5), but the diversity index was not significant ($p = 0.13$). The 4 community structure indices were also significantly affected by site ($p < 0.001$). The interaction between exposure period in the stream and sites also significantly influenced all community structure indices ($p < 0.001$), except number of individuals ($p = 0.56$).

Colonization patterns of number of taxa are quite different between the 2 sites (Fig. 2A). The mean number of taxa at Site 1 did not increase with exposure period of baskets in the stream, but at Site 2 this did increase with a longer exposure period. At Site 2, it continually increased during the 42 days of colonization. The greatest increase in species accumulation was from days 6 to 30. In addition, the 2 study sites had similar colonization patterns of total numbers of individuals, but density was much higher at

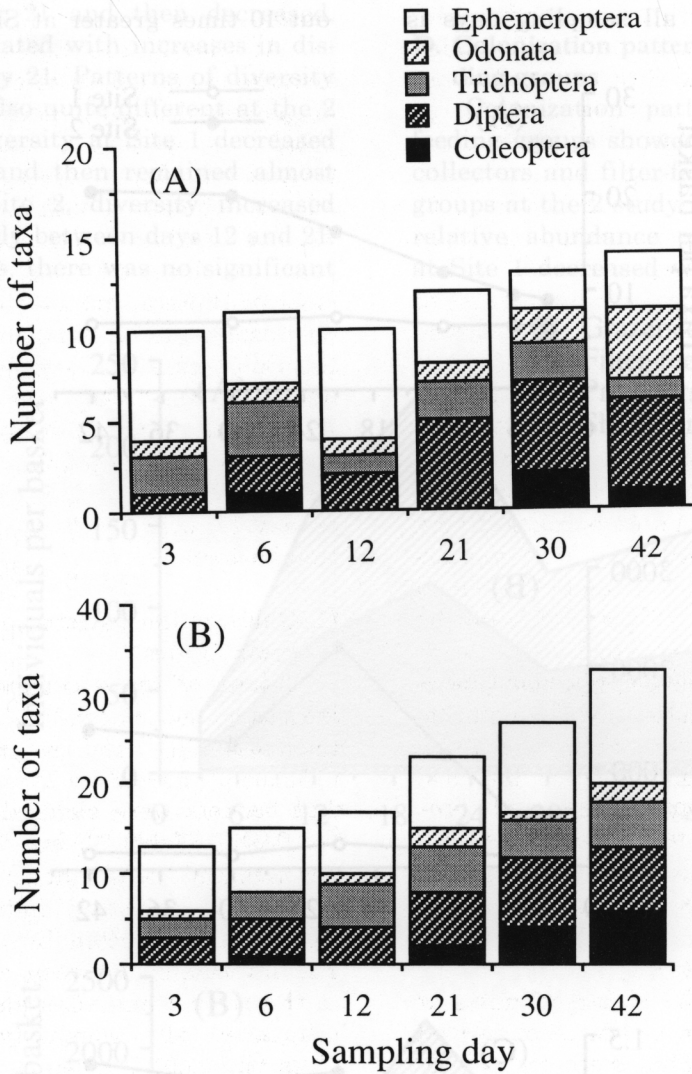


Fig. 1. Number of taxa in each order colonizing artificial substrate trays at Site 1 (A) and Site 2 (B) on each sampling day in the Chingmei Stream, Taiwan.

Table 5. Results of two-way ANOVA for log (density), total number of aquatic insect taxa, Shannon-Weaver diversity, and evenness versus duration of exposure of substrate to colonization and sites in the Chingmei Stream, Taiwan (n.s.=not significant, $p < 0.05^*$, $p < 0.01^{**}$, $p < 0.001^{***}$).

	Source of variation		
	No. of days	Sites	Interaction
Log (density)	20.70 ^{***}	316.38 ^{***}	0.79n.s.
No. of taxa	8.82 ^{***}	105.40 ^{***}	6.34 ^{***}
Diversity	1.83n.s.	64.04 ^{***}	5.12 ^{**}
Evenness	11.36 ^{***}	28.48 ^{***}	6.98 ^{***}

Site 2 (Fig. 2B). The mean number of individual per m^2 on all sampling days is

2,580 at Site 1 and 23,160 at Site 2, or about 10 times greater at Site 2. The mean

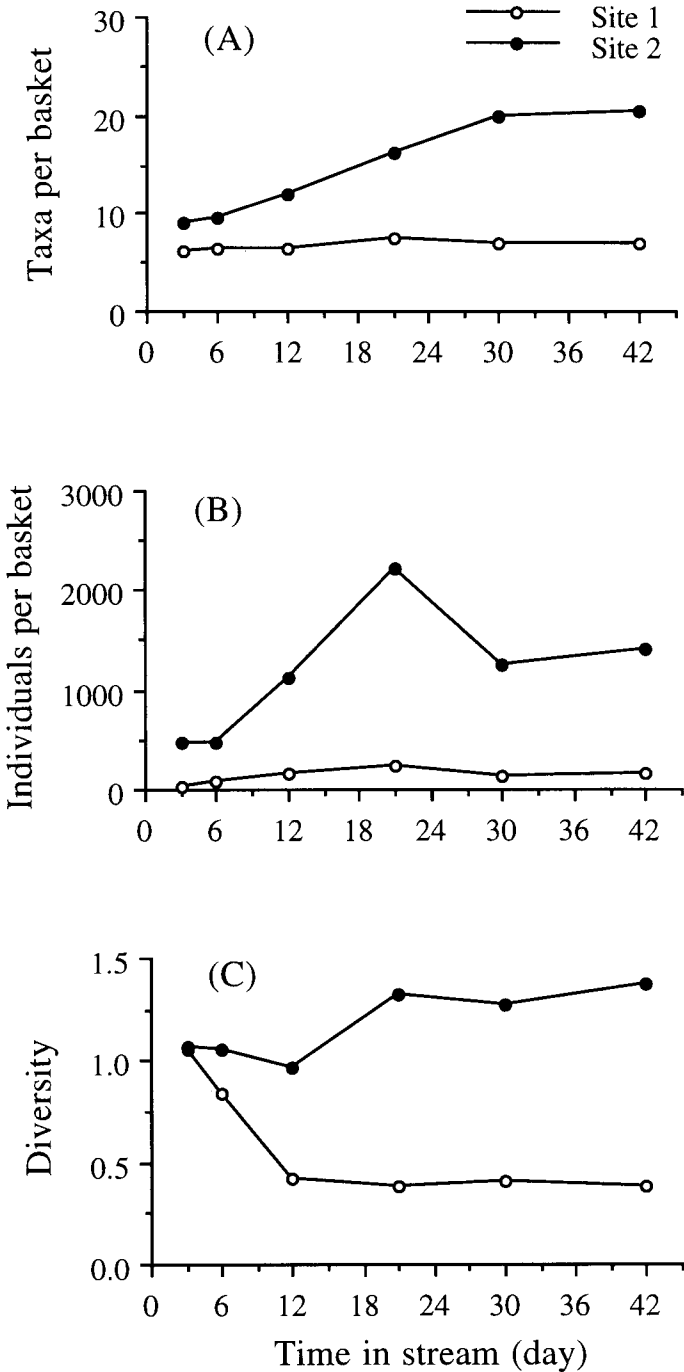


Fig. 2. Mean number of taxa (A), number of individuals (B), and Shannon-Weaver diversity (C) for colonizing baskets left in the stream for 3-42 days at Site 1 and Site 2 in the Chingmei Stream, Taiwan.

number of individuals at the 2 sites was highest on day 21 and then decreased. This was associated with increases in discharge after day 21. Patterns of diversity (Fig. 2C) are also quite different at the 2 study sites. Diversity at Site 1 decreased before day 12 and then remained almost constant. At Site 2, diversity increased significantly only between days 12 and 21. In other periods, there was no significant

increase or decrease in diversity at Site 2.

D. Colonization patterns of functional feeding groups

Colonization patterns of functional feeding groups showed that both grazers/collectors and filter-feeders are the major groups at the 2 study sites (Fig. 3). Mean relative abundance of grazers/collectors at Site 1 decreased with exposure period

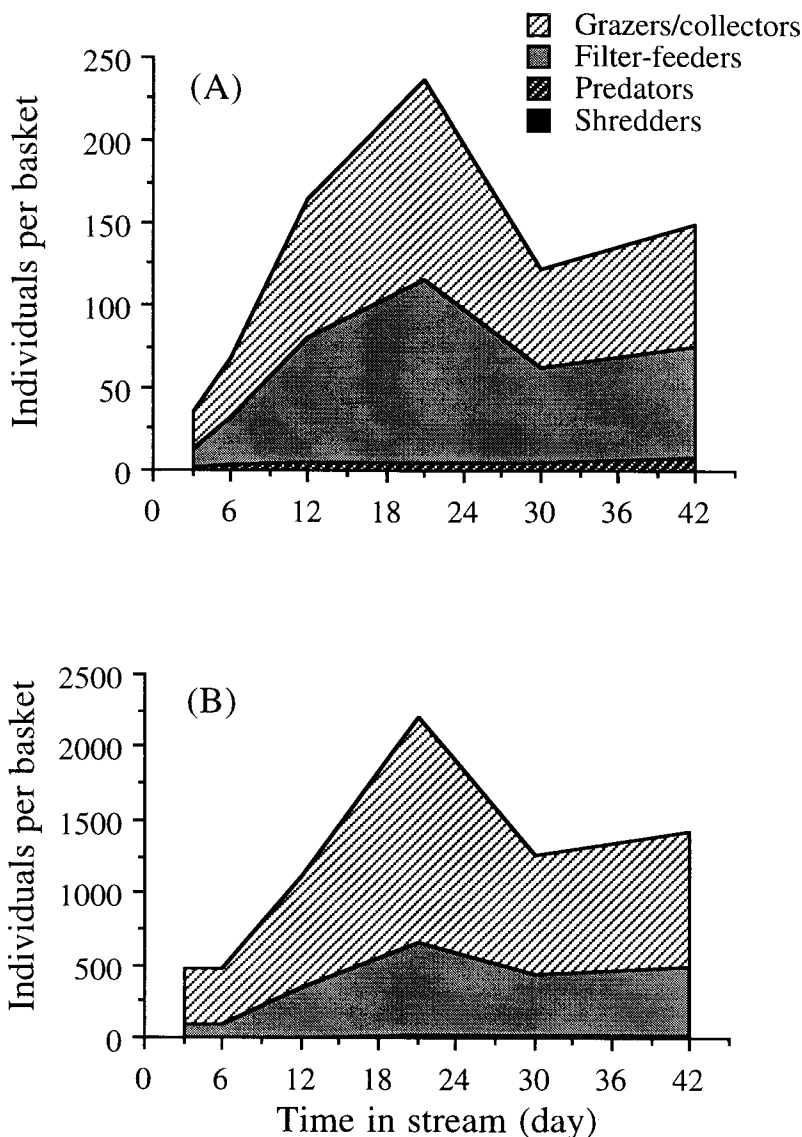


Fig. 3. Mean number of individuals of functional feeding groups colonizing baskets left in the stream for 3-42 days at Site 1 (A) and Site 2 (B) in the Chingmei Stream, Taiwan.

of baskets, but relative abundance remained almost constant after day 12. The filter-feeder group had the opposite colonization pattern to that of grazers/collectors, and their relative abundances were almost equal. Mean relative abundance of the 2 groups at Site 2 had the same tendency as they did at Site 1. Grazers/collectors were about twice as abundant as the filter-feeder group at Site 2.

In the early stage of colonization, grazers/collectors were the major group of taxa at both sites (Fig. 4). The number of taxa of grazers/collectors decreased at Site 1, but increased at Site 2 during the colonization period. The number of filter-feeder taxa did not significantly change at either Site 1 or Site 2. The number of taxa of predators increased during the colonization process, especially at Site 1

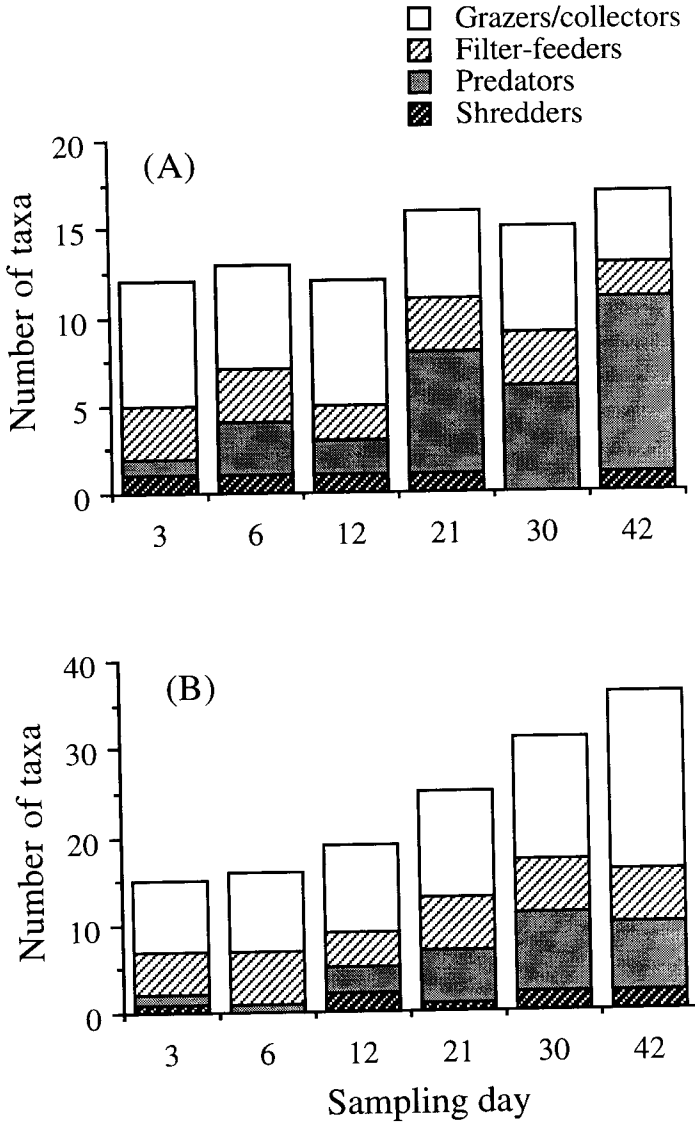


Fig. 4. Number of taxa in each functional feeding group on each sampling day at Site 1 (A) and Site 2 (B) in the Chingmei Stream, Taiwan.

where they became a major group in the number of taxa.

Colonization patterns of individual taxa at Site 2 were tested statistically, using Spearman rank correlation coefficients, for significant associations between population density and days of colonization. The 18 taxa which were most abundant were chosen. Most taxa (13/18) showed a significant increase in numbers per basket with increasing time in the stream (Table 6). Three of 18 (*B. bipinosa*, *Prosimulium* spp., and *Ameletus motivagus*) showed decreasing patterns of colonization with time but without statistical significance. *Baetis* spp. and *Simulium* spp. had no consistent pattern between colonization and time of exposure.

Results of the Spearman rank correlation coefficient between taxa within a functional feeding groups are summarized in Table 7. For grazers/collectors, 13 of 28 taxon pairs had significant positive associations, and 2 of 28 taxon pairs had significant negative associations. This suggests a moderate overlap in resource utilization among taxa within this functional group. 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.

E. Equilibrium of aquatic insect communities

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

equilibrium in species number marking the end of substantial colonization is considered to occur when the colonization rate is equal to the extinction rate (MacArthur and Wilson, 1963, 1967; Dickson and Cairns, 1972; Stauffer *et al.*, 1976; Williams and 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. 5). The results indicate 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 reach the equilibrium. This is due to colonization rates always being greater than extinction rates at Site 2 during the experimental period. Moreover, Simberloff and Wilson (1969) and Brown and Kodric-Brown (1977) suggested that extinction rates at equilibrium are equivalent to turnover rates. The turnover rate for Site 1, therefore, was roughly 0.67 taxa per day at day 10.

Results of fit of aquatic insect data to the lognormal distribution on each sampling date at Sites 1 and 2 are given in Figs. 6 and 7. For each sampling day, coefficients of determination at Site 1 were greater than those at Site 2 from days 12 to 42. 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 2 study sites, coefficients of determination increased roughly but irregularly with time of colonization. Furthermore, it was found that the distance between colonization and extinction rates (Fig. 5) was associated with the coefficient of determination as compared in Figs. 6 and 7. 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.

Table 6. Summary of results of Spearman rank correlation on numbers of individuals per basket versus days in stream for 18 abundant taxa at Site 2 in the Chingmei Stream, Taiwan.

Functional feeding group	Increase in number with days in stream	Decrease in number with days in stream	No consistent pattern with days in stream
Grazers/collectors	<i>Afronurus hyalinus</i> <i>Caenis</i> sp. <i>Amphinemura</i> sp. Chironomidae <i>Antocha</i> sp.	<i>Ameletus motivagus</i> <i>Baetiella bispinosa</i>	<i>Baetis</i> spp.
Filter-feeders	<i>Stenopsyche</i> sp. <i>Chimarra</i> sp. Hydropsychidae Chironomidae	<i>Prosimulium</i> spp.	<i>Simulium</i> spp.
Predators	<i>Neoperla</i> sp. <i>Rhyacophila</i> sp. <i>Hemerodromia</i> sp. <i>Wiedemannia</i> sp.		

Table 7. Summary of species associations among members of the same functional feeding group at Site 2 in the Chingmei Stream. Significant correlations are given and noted with asterisks (n=24; ns=not significant).

Grazers/collectors	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
<i>Afronurus hyalinus</i> (1)	-	ns	ns	0.54*	0.82*	ns	0.82*	0.75*
<i>Baetis</i> spp. (2)		-	0.54*	ns	ns	0.75*	ns	0.48*
<i>Baetiella bispinosa</i> (3)			-	ns	-0.61*	0.48*	ns	ns
<i>Ameletus motivagus</i> (4)				-	ns	-0.44*	-0.42*	ns
<i>Caenis</i> sp. (5)					-	ns	0.82*	0.64*
<i>Amphinemura</i> sp. (6)						-	0.41*	0.44*
<i>Antocha</i> sp. (7)							-	0.80*
Chironomidae (8)								-
Filter-feeders	(1)	(2)	(3)	(4)	(5)	(6)		
<i>Stenopsyche</i> sp. (1)	-	0.56*	0.75*	0.41*	ns	0.42*		
<i>Chimarra</i> sp. (2)		-	0.73*	0.54*	0.52*	0.71*		
Hydropsychidae (3)			-	0.45*	0.55*	0.53*		
Chironomidae (4)				-	ns	ns		
<i>Prosimulium</i> spp. (5)					-	0.64*		
<i>Simulium</i> spp. (6)						-		
Predators	(1)	(2)	(3)	(4)				
<i>Neoperla</i> sp. (1)	-	0.55*	ns	0.81*				
<i>Rhyacophila</i> sp. (2)		-	0.53*	0.51*				
<i>Hemerodromia</i> sp. (3)			-	0.58*				
<i>Wiedemannia</i> sp. (4)				-				

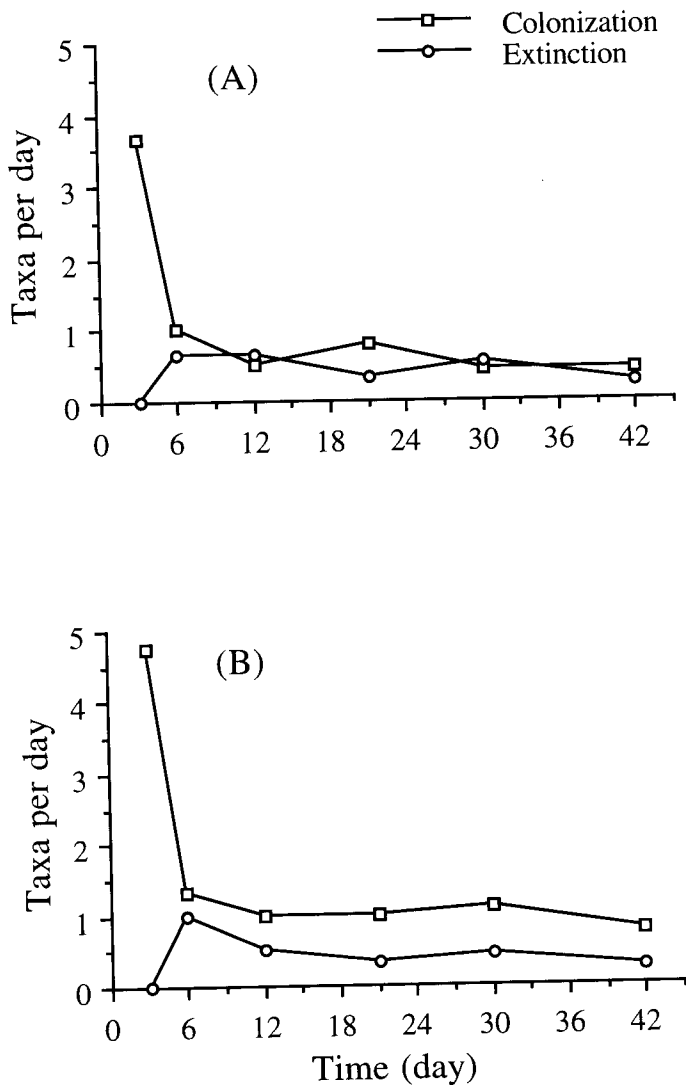


Fig. 5. Colonization and extinction rates of aquatic insects colonizing baskets left in the stream for 3-42 days at Site 1 (A) and Site 2 (B) in the Chingmei Stream, Taiwan.

Discussion

High conductivity and turbidity may be associated with reduction in both abundance and number of taxa at Site 1 (Table 1). The high conductivity was due to water released from the coal mine which contained a high concentration of inorganic ions. Its effect on aquatic insects is still unknown. The high turbidity was

caused by the amount of suspended sand and coal particles in the water. These suspended and sedimentary materials 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 aquatic insects (Wiederholm, 1984; Waters, 1995). In addition, organisms can be affected directly by

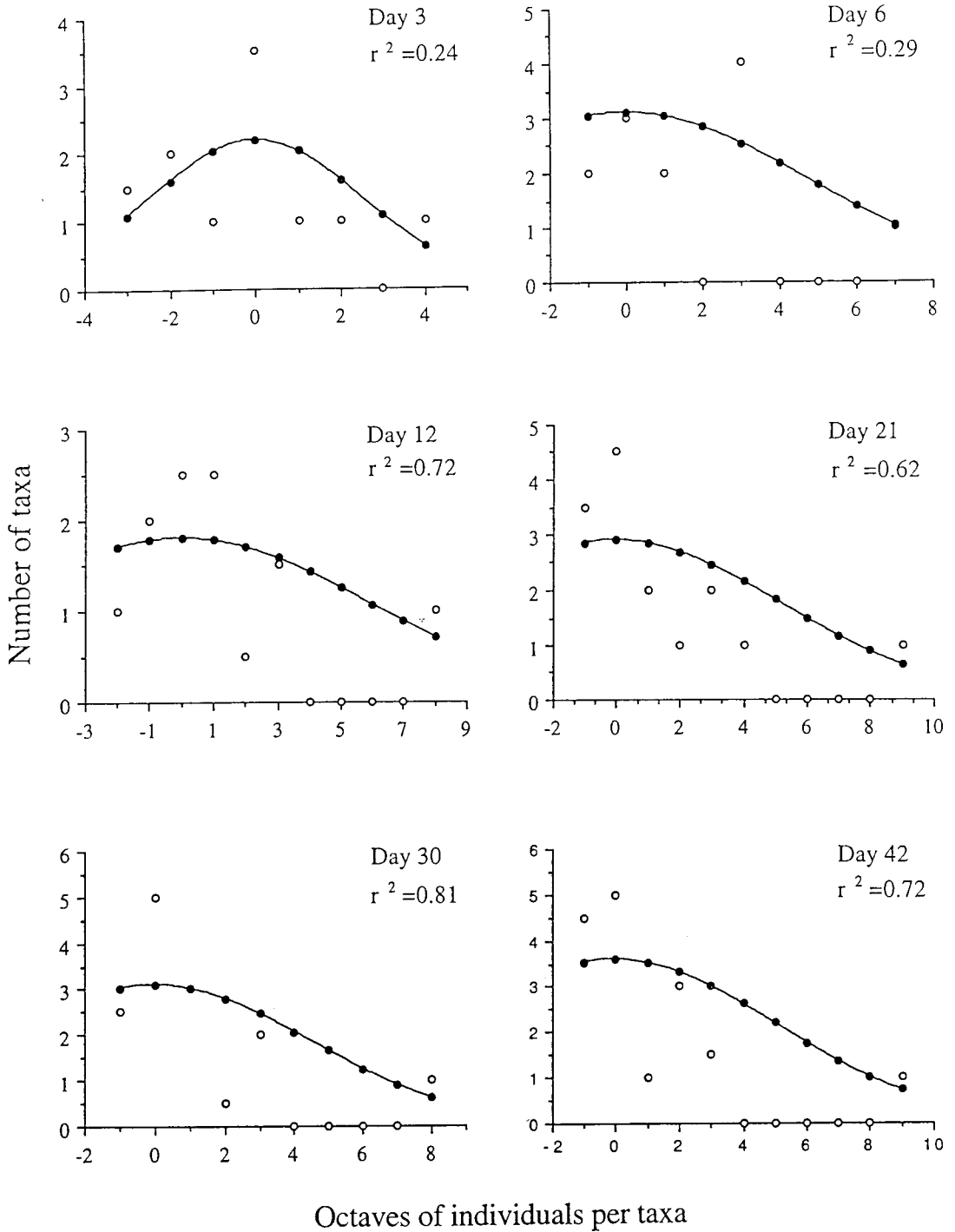


Fig. 6. Fit of taxa-abundance curves to a lognormal model on each sampling day at Site 1 in the Chingmei Stream, Taiwan.

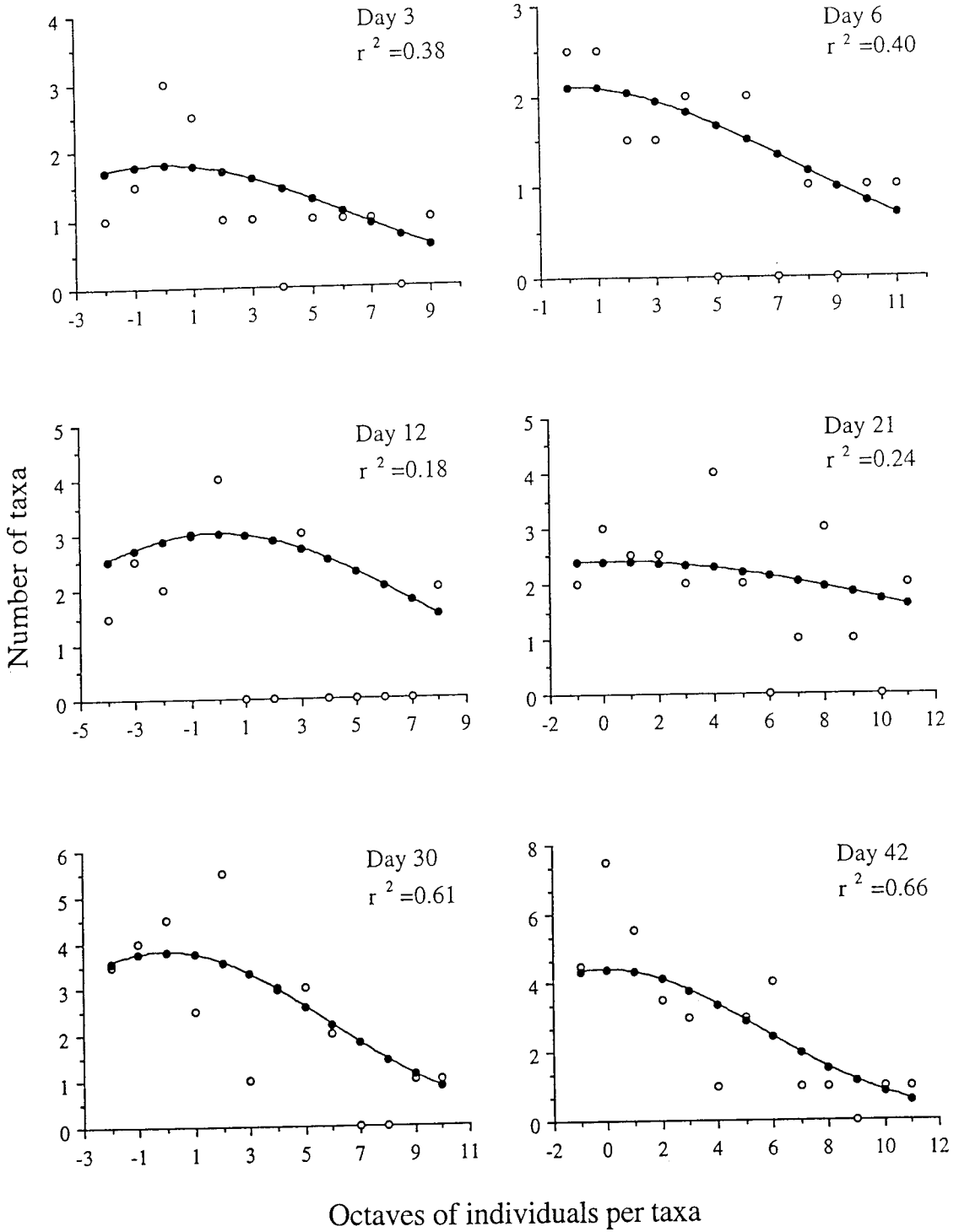


Fig. 7. Fit of taxa-abundance curves to a lognormal model on each sampling day at Site 2 in the Chingmei Stream, Taiwan.

high turbidity, such as when food collection or respiration is obstructed (Wiederholm, 1984).

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 (Fig. 2). 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 to be unaffected by alteration of water quality. Cherry *et al.* (1979) also found that Odonata and Chironomidae are less susceptible to sediments of coal particles than are other types of insects.

Species richness at the 2 sites appeared to approach an asymptote by day 42 (Fig. 2A), but mean total abundance did not level off (Fig. 2B). This may be due to high discharge which reset the substrates back to earlier conditions. However, patterns of diversity were different between Sites 1 and 2 (Fig. 2C). 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 changes in the number of taxa. Lake and Doeg (1985), Gore (1979), and Ulfstrand *et al.* (1974) noted the correspondence between the increase in number of species and the increase in diversity. This appears to be the case at 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 density curves of 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, using co-

lonization rates and extinction rates of taxa as criteria, colonization at Site 1 was complete by 10 days but was 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 by aquatic insects in trays reached equilibrium after only 6-8 days. Wise and Molles (1979) showed 9 days for aquatic insects colonizing on gravel, cobble, and mixed substrates in a small New Mexico stream. Lake and Doeg (1985) described 32 days for colonization of aquatic insects on denuded stones in 2 upland southern Australian streams. Townsend and Hildrew (1976) indicated 37.5 days for stream benthos to colonize bottom trays filled gravel and stones. Dickson and Cairns (1972) suggested 42 days for floating artificial substrate. Williams and Hynes (1977) reported 109 days for benthic communities in a newly formed stream channel. Minshall *et al.* (1983) reported 439 days for aquatic insect colonization 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.

There was a sequence of species colonization or replacement of species during the colonization process at both Sites 1 and 2. However, reasons for the sequence or replacement were different. At Site 1, it was the tolerance or susceptibility of organisms to pollutants such as high conductivity and turbidity. The Odonata and Chironomidae, which were more tolerant to pollutants, gradually replaced other

taxa and became dominant (Fig. 1A). Those which were susceptible to the pollutants would be dislodged. Only 3 taxa (*Caenis* sp., *Euphaea* sp., and Chironomidae) always occurred and were abundant during the experiment. Other taxa, which were sparse and of sporadic occurrence, may have just continued to drift away from the site. Therefore, extinction rates at Site 1 were similar to those at Site 2 while the number of taxa was very different between the 2 sites.

Reasons for taxon replacement were the influence of biological interactions and disturbances caused by high discharges at Site 2. Disturbances due to high discharges reset the substrates back to earlier conditions. At this site, 3 colonization patterns (Table 6) were exhibited by the common taxa: (1) an increase in density with increased colonization time (e.g. *A. hyalinus* and *Caenis* sp.); (2) a decrease in density after the first few sampling intervals (e.g. *Prosimulium* spp. and *B. bispinosa*); and (3) an increase followed by a decrease in density (e.g. *Baetis* spp. and *Simulium* spp.) in the later period of exposure of baskets in the stream. The first type suggested that the build-up in density was due to a steady increase in the suitability of the stone environment. The taxa that decreased after the initial higher density could be regarded as "pioneer" or "opportunistic" species that might be replaced by superior competitors that were slower colonizers. For example, baetid mayflies have been identified as early colonizers or opportunistic taxa in streams in Montana (McAuliffe, 1983), Idaho (Minshall *et al.*, 1983), Alberta (Ciborowski and Clifford, 1984), and North Carolina (Wallace and Gurtz, 1986) and Simuliid blackflies as opportunistic taxa in a small California stream (Hemiphill and Cooper, 1983). These opportunists depended on disturbance (e.g., high discharge) to create required microhabitats and increased their abundance by day 21. As a whole,

these patterns agree with the hypothesis that biological interactions might influence alterations in species dominance in the benthic community (Sheldon, 1984).

The same reasons also led to differences of composition in functional feeding groups on each sampling day. At Site 1, most predators were tolerant of pollutants and increased in both abundance and number of taxa during the colonization period (Fig. 4A). Grazers/collectors were susceptible to pollutants, and, thus, the number of taxa decreased. Also, the abundance of predators might have reduced the number of grazers/collectors. A special case was Chironomidae, some species of which could tolerate the conditions of oxygen deficiency (Frank, 1980; Nagell and Landahl, 1978) and sediment (Grimas and Wiederholm, 1979) causing an increase in abundance of grazers/collectors and filter-feeders.

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 aquatic insects colonizing small blocks of floating substrate anchored in a stream riffle. Minshall *et al.* (1983) also found such a case for aquatic insect 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 that the reason extinction curves differ

from 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 drift in early stages of colonization, many of these may rapidly leave the stones. This is 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) documented that some species of drifting aquatic insects showed a degree of preference for natural stones over sterile stones. The increasing hospitality of stones may explain the decline in extinction rates with time. In the present study, we 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 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 this study, the lognormal distribution was a better fit at Site 1 than at Site 2 after day 12 (Figs. 6 and 7). This suggested that it should be easier for the community to attain a state of equilibrium in a polluted or stressed environment over a long time than in a unpolluted or less-polluted environment. In addition, Site 1 was a more variable environment than Site 2 because of mining activities upstream of Site 1. 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.* 1996).

The state of equilibrium was influenced by the exposure of experimental

substrates to colonization. The lognormal distribution was a better fit at the end of the colonization period than in the first week (Figs. 6 and 7). Therefore, the degree of equilibrium of a community increased with exposure of experimental substrates to colonization during the process of colonization. The state of equilibrium also was affected by environmental factors, such as high discharges. At Site 2, a large increase in discharge occurred on day 21 (Table 1), and the coefficient of determination on that sampling date was lower than those on other sampling dates with the exception of day 12 (Fig. 7). The results correspond with conclusions of Ciborowski and Clifford (1984) and Robinson *et al.* (1993) that the effects of discharge are of primary importance in determining the rate and pattern of benthic colonization. The effects of high discharge on the state of equilibrium of communities appear to be less at Site 1 than at Site 2. This is because the discharge at Site 1 was much lower than that at Site 2 (Table 1), and because the communities at Site 1 were simpler and more robust than those at Site 2.

Data from the experiment suggest the following conclusions. Mining activities have a deleterious impact on community structures of aquatic insects. Mechanisms which determined the colonization patterns are reflected by the susceptibility of organisms to mining activities at Site 1, and the influence of biological interactions and disturbance caused by high discharges at Site 2. At Site 1, those taxa less susceptible to mining activities become more abundant during the later period of the colonization process. It is easier for a 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 it is easier for it to reach equilibrium than that in a less polluted environment where taxa continually invade

over extended periods and fail to stabilize.

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References

- Aanes, K. J.** 1980. A preliminary report from a study on the environmental impact of pyrite mining and dressing in a mountain stream in Norway. pp. 419-442. *in*: J. F. Flannagan and K. E. Marshall, eds. *Advances in Ephemeroptera biology*. Proc. Third Internat. Conf. Ephemeroptera. Plenum Press, New York. 552 pp.
- Begon, M., J. L. Harper, and C. R. Townsend.** 1996. *Ecology: individuals, populations, and communities*. 3rd ed. Sinauer Associates Press, Sunderland, MA. 876 pp.
- Brown, J. H., and A. Kodrick-Brown.** 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58: 445-449.
- Cherry, D. S., S. R. Larrick, R. K. Guthrie, E. M. Davis, and F. F. Sherberger.** 1979. Recovery of invertebrate and vertebrate populations in a coal ash stressed drainage system. *J. Fish. Res. Bd. Canada* 36: 1089-1096.
- Ciborowski, J. J. H., and H. F. Clifford.** 1984. Short-term colonization patterns of lotic macroinvertebrates. *Can. J. Fish. Aquat. Sci.* 41: 1626-1633.
- Devore, J., and R. Peck.** 1986. *Statistics: the exploration and analysis of data*. West Press, St. Paul, MN. 699 pp.
- Dickson, K. L., and J. Cairns, Jr.** 1972. The relationship of freshwater macroinvertebrate communities collected by floating artificial substrates to the MacArthur-Wilson equilibrium model. *Am Midl. Nat.* 88: 68-75.
- Fisher, S. G.** 1983. Succession in streams. pp. 7-27. *in*: J. R. Barnes and G. W. Minshall, eds. *Stream ecology. Application and testing of general ecological theory*. Plenum Press, New York. 399 pp.
- Frank, C.** 1980. Lactate determinations in *Chironomus plumosus* L. larva after anaerobiosis. *Acta Univ. Carolinae - Biol.* 1978: 59-62.
- Gore, J. A.** 1979. Patterns of initial benthic recolonization of a reclaimed coal strip-mined river channel. *Can. J. Zool.* 57: 2429-2439.
- Grimas, U., and T. Wiederholm.** 1973. Biometry and biology of *Constempellina brevicosta* (Chironomidae) in a subarctic lake. *Holarctic Ecol.* 2: 119-124.
- Hemphill, N. and S. D. Cooper.** 1983. The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. *Oecologia* 58: 378-382.
- Hsieh, C.** 1964. *Taiwan - Ilha Formosa: a geography in perspective*. Waverly Press, Baltimore. 372 pp.
- Kang, S. C.** 1993. *Ephemeroptera of Taiwan (excluding Baetidae)*. Doctoral dissertation, National Chung Hsing University, Taichung, Taiwan.
- Kang, S. C. and C. T. Yang.** 1994a. Heptageniidae of Taiwan (Ephemeroptera). *J. Taiwan Mus.* 47: 5-36.
- Kang, S. C. and C. T. Yang.** 1994b. Three new species of the genus *Ameletus* from Taiwan (Ephemeroptera: Siphonuridae). *Chinese J. Entomol.* 14: 261-269.

- Kawai, T.** 1985. An illustrated book of aquatic insects of Japan. Dong-Hai Univ. Press, Tokyo. 409 pp.
- Lake, P. S., and T. J. Doeg.** 1985. Macroinvertebrate colonization of stones in two upland southern Australian streams. *Hydrobiologia* 126: 199-211.
- Letterman, R. D., and W. J. Mitsch.** 1978. Impact of mine drainage on a mountain stream in Pennsylvania. *Environ. Poll.* 17: 53-73.
- Ludwig, J. A. and J. F. Reynolds.** 1988. Statistical ecology: a primer on methods and computing. J. Wiley & Sons, New York. 337 pp.
- Mackay, R. J.** 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. *Can. J. Fish. Aquat. Sci.* 49: 617-628.
- MacArthur, R. J., and E. O. Wilson.** 1963. An equilibrium theory of insular zoogeography. *Evolution* 17: 373-387.
- MacArthur, R. J., and E. O. Wilson.** 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, N. J. 203 pp.
- McAuliffe, J. R.** 1983. Competition, colonization patterns, and disturbance in stream benthic communities. pp. 137-156. *in:* J. R. Barnes and G. W. Minshall eds. Stream ecology. Application and testing of general ecological theory. Plenum Press, New York. 399 pp.
- Merritt, R. W., and K. W. Cummins.** 1984. An introduction to the aquatic insects of North America. 2nd ed. Kendall/Hunt, Dubuque. IA. 722 pp.
- Minshall, G. W., and R. C. Petersen, Jr.** 1985. Towards a theory of macroinvertebrate community structure in stream ecosystems. *Arch. Hydrobiol.* 104: 49-76.
- Minshall, G. W., D. A. Andrews, and C. Y. Manuel-Faler.** 1983. Application of island biogeographic theory to streams: macroinvertebrate colonization of the Teton River, Idaho, pp.279-297. *in:* J. R. Barnes and G. W. Minshall eds. Stream ecology. Application and testing of general ecological theory. Plenum Press, New York. 399 pp.
- Minshall, G. W., R. C. Petersen, Jr., and C. F. Nimz.** 1985. Species richness and streams of different size from the same drainage basin. *Amer. Nat.* 125: 16-38.
- Moon, T. C., and C. M. Lucostic.** 1979. Effects of acid mine drainage on a southwestern Pennsylvania stream. *Water Air Soil Poll.* 11: 377-390.
- Nagell, B., and C.-C. Landahl.** 1978. Resistance to anoxia of *Chironomus plumosus* and *Chironomus anthracinus* (Diptera) larvae. *Holarctic Ecol.* 1: 333-336.
- Peckarsky, B. L.** 1986. Colonization of natural substrates by stream benthos. *Can. J. Fish. Aquat. Sci.* 43: 700-709.
- Robinson, C. T., G. W. Minshall, and L. V. Every.** 1993. Seasonal trends and colonization patterns of macroinvertebrate assemblages in two streams with contrasting flow regimes. *Great Basin Nat.* 53: 321-331.
- Scullion, J., and R. W. Edwards.** 1980. The effects of coal industry pollutants on the macroinvertebrate fauna of a small river in the South Wales coal field. *Freshwater Biol.* 10: 141-162.
- Sheldon, A. L.** 1984. Colonization dynamics of aquatic insects. pp.401-429. *in:* V. H. Resh and D. M. Rosenberg eds. Aquatic insect ecology. Praeger Scientific, New York. 625 pp.
- Simberloff, D. S., and E. O. Wilson.** 1969. Experimental zoogeography of islands: the colonization of empty islands. *Ecology* 50: 278-295.
- Stauffer, J. R., H. A. Beiles, T. W. Cox, K. L. Dickson and D. E. Simonet.** 1976. Colonization of macrobenthic communities on artificial substrates. *Rev. Biol.* 10: 49-61.
- Townsend, C. R., and A. G. Hildrew.** 1976. Field experiments on drifting, colonization, and continuous redistri-

- bution of stream benthos. *J. Anim. Ecol.* 45: 759-772.
- Ulfstrand, S.** 1968. Benthic animal communities in Lapland streams. A field study with particular reference to Ephemeroptera, Plecoptera, Trichoptera and Diptera Simuliidae. *Oikos*, Suppl. 10: 1-117.
- Ulfstrand, S., L. M. Nilsson, and A. Stevgar.** 1974. Composition and diversity of benthic species collectives colonizing implanted substrates in a south Swedish stream. *Entomol. Scand.* 5: 115-122.
- Wallace, J. B., and M. E. Gurtz.** 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. *Am. Midl. Nat.* 115: 25-41.
- Walton, O. E., Jr.** 1978. Substrate attachment by drifting aquatic insect larvae. *Ecology* 59: 1023-1030.
- Waters, T. F.** 1995. Sediment in streams: sources, biological effects, and control. American Fisheries Society Monograph 7. American Fisheries Society, Bethesda, MD.
- Wiederholm, T.** 1984. Responses of aquatic insects to environmental pollution. pp.508-557. *in:* V. H. Resh and D. M. Rosenberg eds. *Aquatic insect ecology*. Praeger Scientific, New York. 625 pp.
- Wiggins, G. B.** 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press, Toronto. 401 pp.
- Williams, D. D., and H. B. N. Hynes.** 1976. The recolonization mechanisms of stream benthos. *Oikos* 27: 265-272.
- Williams, D. D., and H. B. N. Hynes.** 1977. Benthic community development in a new stream. *Can. J. Zool.* 55: 1071-1076.
- Wise, D. H., and M. C. Molles, Jr.** 1979. Colonization of artificial substrates by stream insects: influence of substrate size and diversity. *Hydrobiologia* 65: 69-74.

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水棲昆蟲在人工底質的拓殖型式

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摘 要

本研究之目的是在不同的兩採樣站，比較水棲昆蟲在人工底質的拓殖情形。試驗地點是位於在景美溪的上游，第一站受到採礦活動的影響，而視為受污染站，第二站則位於第一站的下游，被視為微受污染站。從1990年12月15日到1991年1月26日，人工底質分別被水棲昆蟲拓殖3、6、12、21、30及42天。研究結果發現，水棲昆蟲的個體數及種類數顯著的會受到拓殖時間因素及採樣站的影響，此結果表示水棲昆蟲種類有消長的現象發生，及採礦活動對整個群落有不利的影響。在第一站，只有 *Caenis* sp.、*Euphaea* sp.、及 Chironomidae 出現在所有的採樣日，其他種類可能繼續漂移離開此站，Chironomidae 是此站最優勢的類群，從拓殖的第12天以後，其佔所有拓殖個體數的90%以上。在第二站，*Baetis* spp. 及 Chironomidae 是最優勢的類群，除了在拓殖的第21天以外，佔所有個體數的80%以上，而且相對的數量，隨著拓殖時間的增長，從 *Baetis* spp. 為最優勢，變為 Chironomidae 最優勢。另外，由指數常態分布模式，來判別群落在拓殖過程中的平衡程度，結果顯示在第一站比在第二站更符合此模式，亦即在一遭受污染的河域比在未受污染或微受污染的河域較易達到平衡狀態。

關鍵詞：拓殖、水棲昆蟲、人工底質、溪流、台灣。