Colonization Patterns of Aquatic Insects after Typhoons

颱風後水棲昆蟲之拓殖模式

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Abstract

To understand the colonization patterns of aquatic insects by the impacts of typhoon, an intensive investigation was carried out after typhoon hits from April 2007 to March 2008. The study found that the structure pattern of the aquatic insects community shifted back toward that of pre-typhoon period. The pre-typhoon dominant taxa *Baetis* spp. and *Ecdyonurus* spp. were replaced by *Pseudocloeon* spp. and *Rhithrogena* spp. after environmental impacts by a typhoon. *Baetis* spp. and chironomids distributed in slow running water, while *Hydroptila* sp. scattered amongst filamentous algae at the bank. Among the functional feeding groups, a higher ratio of predators was found in the early stage of colonization after typhoon disturbance. The proportion of predators decreased gradually with an increased abundance of scrapers, followed by an increase in relative abundance of collector-gatherers, which subsequently caused a decrease in scraper ratio. Population density of collector-filterers was also found to be lower than that in the pre-flood period while the ratio of piercers increased.

摘　要

本研究藉由颱風侵襲後進行較密集之調查，以了解颱風影響後水棲昆蟲之拓殖情形。調查結果顯示水棲昆蟲群聚於颱風影響後有趨向於颱風前之結構型式發展；優勢分類群於颱風引起之環境衝擊後，由 *Baetis* spp.及 *Ecdyonurus* spp.轉變爲 *Pseudocloeon* spp.及 *Rhithrogena* spp.。岸邊之調查顯示 *Baetis* spp.及搖蚊科 (Chironomidae) 偏好分布於流速較緩之河岸，*Hydroptila* sp.於河岸隨絲狀藻呈零散分布。依功能性攝食群探討，颱風影響後，水棲昆蟲拓殖初期捕食者比例較高，之後捕食者比例逐漸下降，刮食者比例上升；而刮食者相對密度升高後，集食性採食者相對密度也逐漸升高，故之後刮食者相對密度呈下降趨勢；濾食性採食者族群密度顯示較以往低；刺吸者比例較以往高。

keywords：aquatic insects, flood, disturbance, colonization, recovery

關鍵詞：水棲昆蟲、洪泛、干擾作用、拓殖、恢復

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Introduction

Taiwan is frequently hit by typhoons in the summer and autumn. Continuous and intensive rainfall causes an increase in discharge, and community structure of aquatic insects is vigorously altered (Huang 2005; Yang and Wong 2005). Contemporary climate change scenarios predict an increase in extreme weather events, which include changing precipitation patterns resulting in severe floods and droughts (IPCC 2007). Flooding is the most important natural disturbance in stream environments (Sagar 1986; Giller *et al.* 1991). Taxa abundance and population density of macroinvertebrates are reduced by increased discharge (Sagar 1986; Scrimgeour and Winterbourn 1989; Fritz and Dodds 2004). Despite the subsequent occurrence of small floods following the large flood, community structure of benthic macroinvertebrates recovers rapidly (Scrimgeour *et al.* 1988). Time required for recovery following a large flood varies, depending on factors including stream type, magnitude of disturbance and other factors under investigation, ranging from a few months to a year or more (Fisher *et al.* 1982). Rapid recolonization by macroinvertebrates after flooding is attributed by the utilization of refugia and interstitial habitats (Angradi 1997), drift from undamaged areas (Williams and Hynes 1976; Scrimgeour *et al.* 1988), and oviposition by aerial adults (Gray and Fisher 1981). Nearby areas of the flood-affected areas, such as tributaries, calmer areas and deep substrates play an important part in maintaining the resilience of aquatic ecosystems (Minshall and Petersen 1985). The relative abundance of invertebrates in nearby areas is higher since these areas might be less affected by floods. Scrimgeour *et al.* (1988) discovered that deep pools formed during flooding provided shelters for invertebrates, which act as important sources of colonists when the pool reconnects with the main channel.

The aim of the present study is to describe the aquatic insects' response to flooding caused by heavy rainfall, discriminate the characteristic and dominant species, and discuss their assemblages under different hydraulic conditions.

Materials and Methods

(1) Study Area

The study was carried out in Shakadang Stream, the first tributary of Liwu Stream basin, located in Taroko National Park in eastern Taiwan. Shakadang Stream flows 17.2km and drains 60.11km^2 directly eastward into the Pacific Ocean. The gorges of Shakadang Stream are mostly steep wall crags and the riparian vegetation is rich, comprising subtropical rainforest formation, with Ficus plants (Moraceae), large-leaved machilus (*Machilus kusanoi* (Lauraceae)) and red bark slugwood (*Beilschmiedia erythrophloia*) as dominant species.

Two sites were selected for sampling and designed to stable hydrological gradients across the Shakadang Stream, as aquatic insects there are susceptible to extreme hydraulic impacts. The sites were located about 1km (Site 1) and 1.6km (Site 2) upstream of the Shakadang Bridge respectively (Fig. 1).

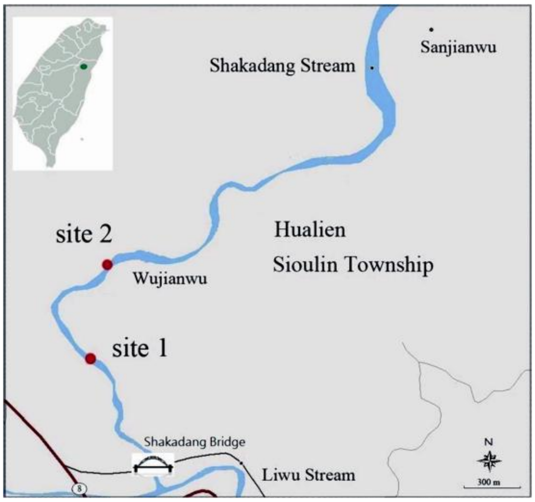

Fig. 1. The locations of the sampling sites (Site1-2) along the Shakadang Stream.

(2) Collection of environmental variables

Environmental variables were sampled in each site, totaling three samples for each variable. Current velocity and depth were measured with a Global Flow Probe FP101 for each sample. Conductivity, dissolved oxygen, pH, temperature, and turbidity were measured with portable sensors in each sampling occasion. We used a modified Went-worth scale to record the dominant grain size class in the quadrat (Surber sampler 50cm x 50cm), ranging from gravel to boulder (gravel 0-2cm, pebble 2-5cm, small cobble 5-10cm, medium cobble 10-20cm, large cobble 20-30cm, boulder >30cm).

(3) Collection of aquatic insects

Samples were collected at both banks and the middle of the stream at monthly intervals from April 2007 to March 2008 using a Surber net sampler (50cm x 50cm, mesh size 0.7mm).

Besides the above sampling design, we also took three replicate samplings at each site (along the left stream bank and 1m from the shore) between 12th August, 2007 and 24th November, 2007 to compare the distribution and abundance of aquatic insects before and after typhoon hits. After typhoon Pabuk hit on 9th August, 2007 and typhoon Sepat from 18th to 19th August, 2007, samplings were carried out at three-day intervals using the same method as that for the monthly samplings. Specimens were also sampled from 9th to 15th and 15th to 29th September, 2007 at six-day and 14-day intervals respectively. Samples were collected at seven day intervals after typhoon Krosa stuck on 6th October, 2007 and lasted for 49 days.

Each sample was preserved in 80% ethanol, labeled, and returned to the laboratory for examination. At the laboratory, organisms were sorted, identified to the lowest possible taxonomic level, counted, and kept in 75% ethanol.

(4) Statistical Analysis / Data Analysis

The number of organisms in each taxon in each sampling (both bank and middle stream, or three replicates sampling at left stream bank) was pooled for data analysis. Data transformation was performed prior to analysis: abundance of aquatic insects was log(x+1)-transformed, environmental variables were log(x)-transformed, while arcsine square root transformation (arcsin ($p^{1/2}$)) was applied to percentage data (Zar 1996). Pearson's correlation coefficient was used to determine whether the various environmental parameters were correlated with the abundance of aquatic insect taxa. Temporal and spatial changes of aquatic insect community structure were analyzed by non-metric multi-dimensional scaling (MDS) using the PRIMER v.5 software package (Clark and Warwick 1994; Clarke and Gorley 2001).

Results

1. Environmental features

The annual rainfall during the study period was 3,050mm with a peak occurring in August (963.5mm). Water temperature ranged from 17.5℃ (February) to 26.5℃ (July). Minimal water depth was 3.3cm (September) and maximum 105cm (August). Water velocity varied between 0.59m/s (September) and 4.18m/s (August). Minimum discharge was 0.53m^3/s (July) and maximum 41.39m^3/s (August) (Table 1). Substratum was dominated by medium cobble (31%) and small cobble (26.89%) (Table 2).

Table 1. Range, mean, and standard deviation of main environmental variables of sampling sites

	Minimum-maximum (mean±SD) Site 1 Site 2		
Variables	Before typhoon	After typhoon (1-49-days)	After typhoon (49-days-later)
	Apr.- Jul.	Aug.- Nov.	Dec.- Mar.
Water temperature (℃)	20.20-25.30 (23.00±2.00)	19.13-23.20 (20.89±1.19)	17.90-19.30 (18.80±0.59)
	21.4-26.50 (24.43±1.98)	18.47-23.80 (20.39±1.32)	17.50-19.00 (18.08±0.58)
Depth (cm)	25.17-12.69 (7.33±41.67)	3.33-78.00 (20.94±19.66)	9.33-19.67 (13.33±3.88)
	6.33-20.67 (11.75±5.96)	9.00-105.00 (41.50±33.60)	6.33-10.67 (8.92±1.66)
Current velocity (m/s)	1.29-2.43 (1.77±0.44)	0.79-4.18 (1.93±0.96)	1.18-2.260 (1.70±0.38)
	0.69-1.52 (1.26±0.34)	0.59-4.06 (1.91±1.00)	1.00-1.48 (1.20±0.20)
Discharge (m^3/s)	1.10-14.07 (6.17±4.82)	0.75-22.69 (5.49±6.49)	1.33-3.96 (2.82±1.01)
	0.53-4.05 (1.99±1.34)	1.36-41.39 (15.47±11.80)	1.42-3.53 (2.46±0.76)

Table 2. Substrate composition of sampling sites in Shakadang Stream

%	Gravel 0-2cm	Pebble 2-5cm	Small cobble 5-10cm	Medium cobble 10-20cm	Large cobble 20-30cm	Boulder >30cm
Site 1	7.43	16.48	23.26	31.67	10.87	10.29
Site 2	6.21	14.77	30.68	30.30	15.23	2.80
Site 1 and 2	6.84	15.64	26.89	31.00	13.00	6.63

2. Aquatic insect community structure

Community structure of aquatic insects underwent huge changes after a typhoon attack. Samples from site 1 and 2 collected after typhoons Pabuk, Sepat and Krosa deviated from the samples prior to the typhoon attacks. With time, samples tended to resume a similar species composition with those before typhoon (Fig. 2, 3).

Structure of aquatic insect community among the two sampling sites was compared between the pre-typhoon and post-typhoon periods (Fig. 2, 3). Six samplings were conducted at site 1 after typhoon Sepat struck in mid August 2007. The community structure was found to be different between 12 days (31st August, 2007) to 49 days (29th September, 2007) after typhoon Sepat. Subsequent change in community structure has been recorded after another typhoon Krosa came in early October 2007, though the change was of a smaller scale. The variation of dynamic changes in aquatic insect community recorded between December 2007 and March 2008 was found to be gentler. The result indicated that the community structure became more stable and less stochastic over time as the impact of typhoon attack subsided gradually (Fig. 2).

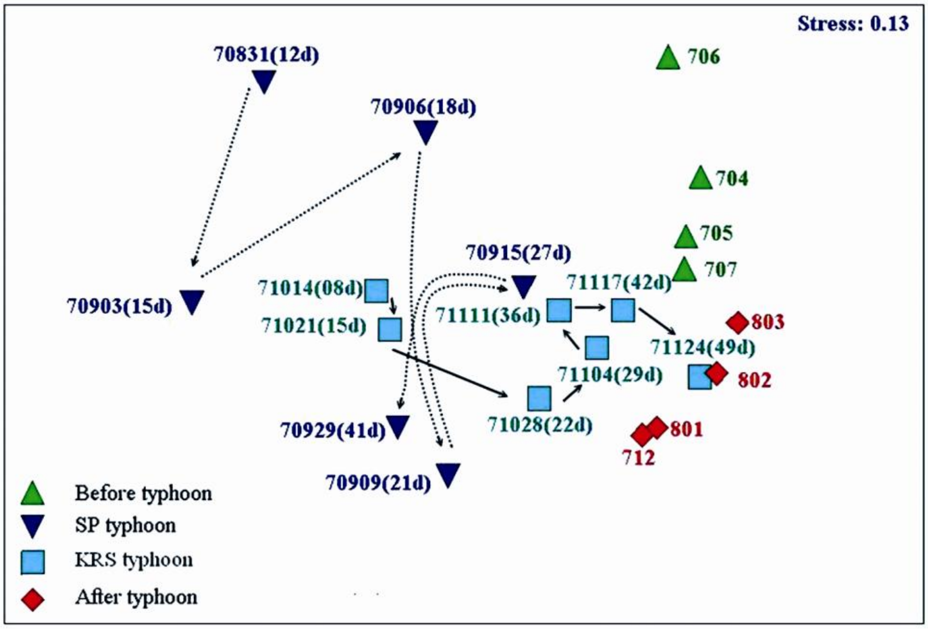

Fig. 2. MDS plots of community structure of aquatic insects at site 1 in the Shakadang Stream from April 2007 to March 2008. Samples were labeled with numbers. The first digit indicates the year, the second and third digits indicate the month, the fourth and fifth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 70831 (12d) indicates 31st August, 2007 and 12 days after typhoon. The number 803 indicates March 2008. SP typhoon: Sepat typhoon. KRS typhoon: Krosa typhoon.

A change in aquatic insect community structure at site 2 was recorded before and after typhoon attack (Fig. 3). The community structure was relatively stable and demonstrated little variation in the pre-typhoon period. A slight change in community structure has been noted after attack by typhoon Pabuk in early August 2007. The attack of typhoon Sepat 15 days later resulted in a different change in community structure. The change in aquatic insect community structure reached maximum at 41 days after the attack. The change in community structure recorded eight days after attack by typhoon Krosa (early October 2007) was of small scale. Like site 1, community structure observed during subsequent weekly samplings (14th October, 2007- 24th November, 2007) shifted toward the pre-typhoon structure pattern (Fig. 3).

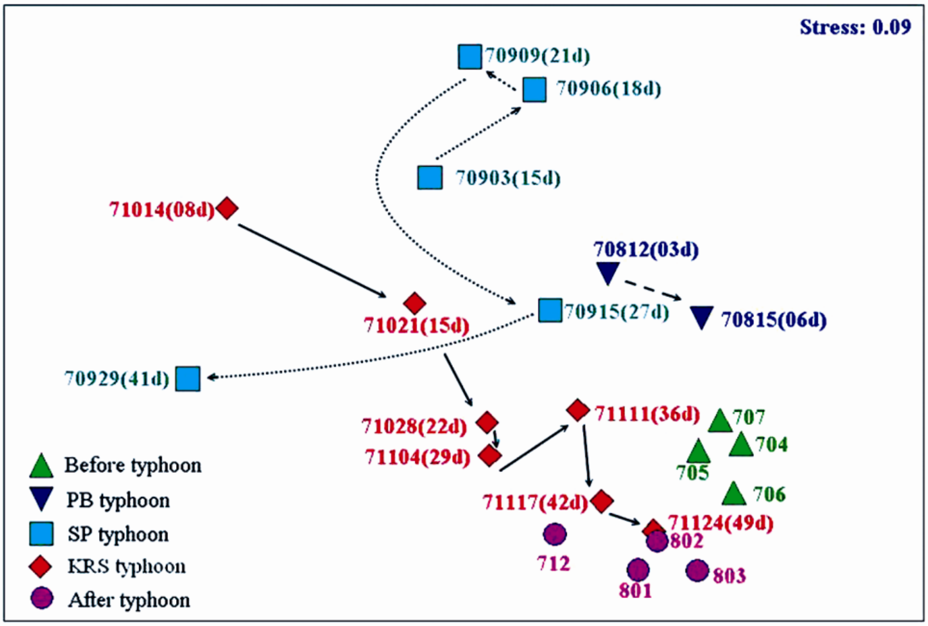

Fig. 3. MDS plots of community structure of aquatic insects at site 2 in the Shakadang Stream from April 2007 to March 2008. Samples were labeled with numbers. The first digit indicates the year, the second and third digits indicate the month, the fourth and fifth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 70831 (12d) indicates 31st August, 2007 and 12 days after typhoon. The number 803 indicates March 2008. PB typhoon: Pabuk typhoon. SP typhoon: Sepat typhoon. KRS typhoon: Krosa typhoon.

The relationship between physio-chemical environmental variables and the abundance of the dominant aquatic insects are demonstrated in Table 3. Conductivity, pH, current velocity, water depth, water temperature, and turbidity were highly correlated to *Baetis* spp.; *Pseudocloeon* spp., *Epeorus erratus*, and *Rhithrogena* spp appeared to have a significant positive correlation with dissolved oxygen (DO) and pH, but negative correlation with water temperature and turbidity. *Hydroptila* sp. showed significant negative correlation with current velocity and water depth. Except for the larvae of caddisfly, *Hydroptila* sp. appeared to have a significant positive correlation with pebbles. The five remaining mayflies were negatively correlated with the small substrate particles, such as gravels and pebbles (Table 3).

Table 3. The correlation coefficients and p values of *Baetis* spp., *Pseudocloeon* spp., *Ecdyonurus* spp., *Epeorus erratus*, *Rhithrogena* spp., *Hydroptila* sp., and environmental variables in the Shakadang Stream

Environment variables	*Baetis* spp.	*Pseudocloeon* spp.	*Ecdyonurus* spp.	*Epeorus erratus*	*Rhithrogena* spp.	*Hydroptila* sp.
Conductivity	0.19***	0.06	0.25***	0.01	0.06	0.10
DO	-0.11*	0.29***	-0.33***	0.23***	0.30***	-0.01
pH	0.21***	0.24***	-0.06	0.20***	0.23***	0.04
Current velocity	-0.25***	-0.05	-0.19**	0.01	-0.04	-0.11*
Water depth	-0.25***	-0.26***	0.07	-0.17**	-0.21***	-0.11*
Water temperature	-0.18**	-0.39***	0.15**	-0.35***	-0.46***	-0.07
Gravel	-0.12*	-0.20***	-0.16**	-0.16**	-0.15**	-0.03
Pebble	-0.01	-0.09	-0.14**	-0.12*	-0.01	0.11*
Small cobble	0.08	0.01	-0.01	-0.03	0.03	0.08
Medium cobble	0.05	0.10	0.11*	0.08	0.09	-0.02
Large cobble	-0.03	0.03	0.04	0.03	0.00	-0.10
Boulder	-0.05	0.02	0.04	0.09	-0.05	-0.06
Turbidity	-0.31***	-0.31***	-0.19**	-0.20**	-0.27***	-0.08

*：$p < 0.05$； **：$p < 0.01$；***：$p < 0.001$

3. Dominant taxa

Analysis of the pooled samples collected by the banks and the middle stream found *Baetis* spp. and *Ecdyonurus* spp. to be the dominant taxa prior to typhoon (Fig. 4, 5). *Pseudocloeon* spp. was the most abundant numerically and increased most rapidly after typhoon damage, thus it became the dominant species (Fig. 4, 5). *Ecdyonurus* spp. was one of the dominant species before typhoon and its population drastically decreased after typhoon while the abundance of *Rhithrogena* spp., also a Heptageniidae member, increased (Fig. 4, 5). The relative abundance of *Epeorus erratus* was also higher than that in the pre-typhoon period (Fig. 4, 5).

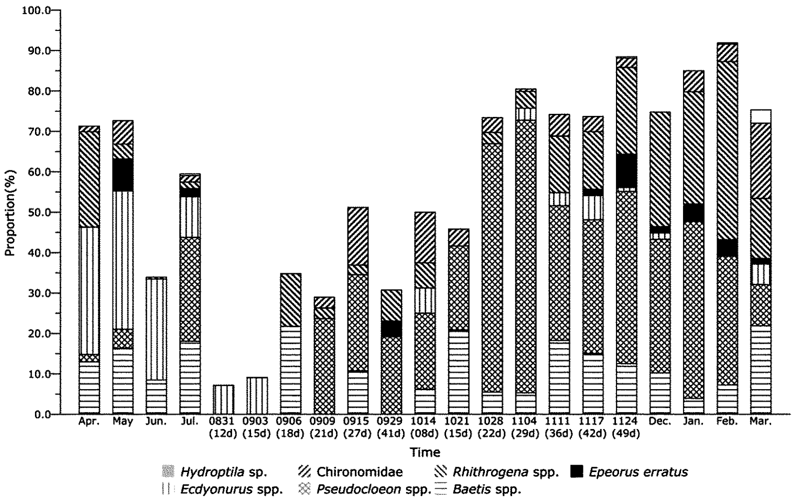

Fig. 4. Proportion of the dominant taxa abundance at site 1 in the Shakadang Stream from April 2007 to March 2008. Samples were labeled with numbers. The first and second digits indicate the month, the third and fourth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 0831 (12d) indicates 31st August and 12 days after typhoon.

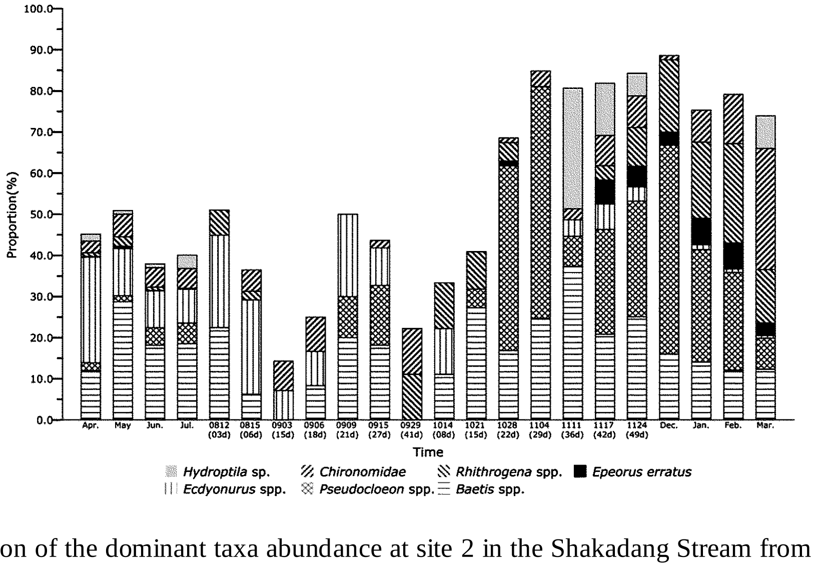

Fig. 5. Proportion of the dominant taxa abundance at site 2 in the Shakadang Stream from April 2007 to March 2008. Samples were labeled with numbers. The first and second digits indicate the month, the third and fourth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 0812 (03d) indicates 12th August and three days after typhoon.

After the typhoon Krosa struck, three replicate samples collected along the left stream bank at site 2 were pooled and analyzed. The most abundantly found species was *Baetis* spp. and not *Pseudocloeon* spp. (Figure 6).

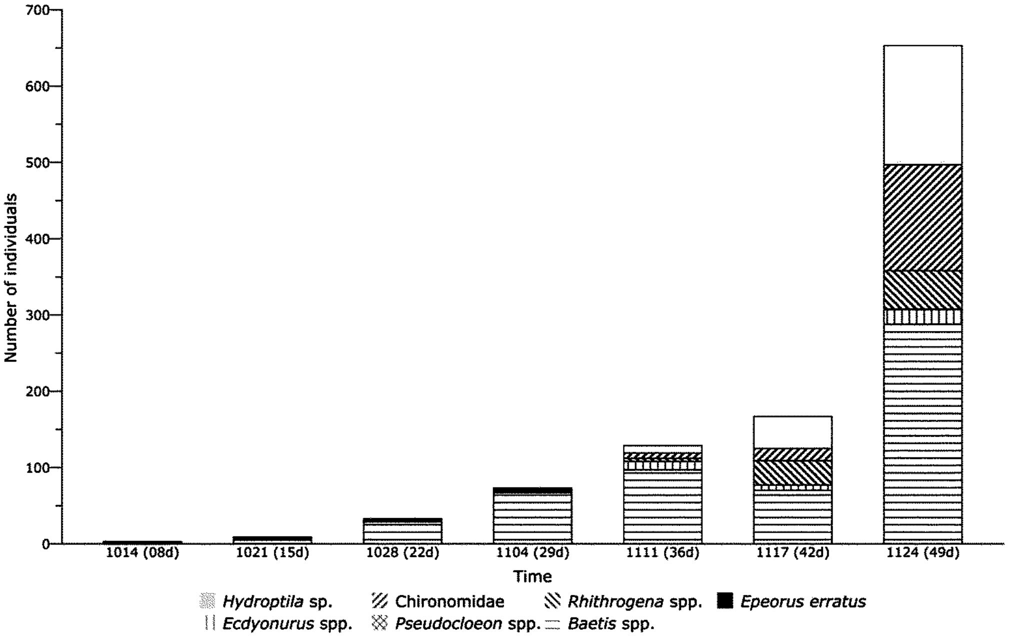

Fig. 6. Abundance of the dominant taxa along the left stream bank of site 2 in the Shakadang Stream from 14th October, 2007 to 24th November, 2008. Samples were labeled with numbers. The first and second digits indicate the month, the third and fourth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 1014 (08d) indicates 14th October and eight days after typhoon.

4. Colonization of aquatic insects at the bank

In site 2, the number of *Hydroptila* sp. prior to typhoon damage was small, with a highest record of 15 specimens. A total of 35 *Hydroptila* sp. specimens were collected at both banks and the middle stream, while 156 specimens were collected in three replicate samplings at the left stream bank in 49 days after typhoon Krosa (Fig. 6). In the same period, a total of 49 chironomids were collected at both banks and the middle stream, while three replicate samplings at the left stream bank collected 139 specimens (Fig. 6).

In site 1, heavy rainfall brought by the typhoons Pabuk, Sepat, and Krosa raised the stream water level and flooded the land which was originally undrained. The water rose until the water-level reached 9m far from the original shore. A total of 16 insect specimens belonging to 11 taxa, including Baetidae, Heptageniidae, Perlidae, Hydropsychidae and Chironomidae, were collected by the bank. The water level subsided 15 days after typhoon, and the left stream bank was three meters away from the original bank where 24 insect specimens belonging to 10 taxa were collected, with the addition of Tipulidae besides the above-mentioned taxa. The left stream bank was 1.5 meters away from the original bank 22 days after typhoon and 104 insect specimens belonging to 13 taxa were collected, with Simuliidae and Euphaeidae newly added to the samples. Water level dropped, from a position 0.4m from the original edge to a stable position 29-49 days after typhoon. Taxa richness of aquatic insects increased from 17 to 25, and the number of specimens collected increased from 196 to 303. New taxa collected were Caenidae, Leptophlebiidae, Elmidae, Psephenidae, Blepharoceridae, *Protohermes grandis*, Hydroptilidae, Leptoceridae, Philopotamidae, Rhyacophilidae, and *Gumaga* sp. Numeric abundance of *Pseudocloeon* spp., *Epeorus erratus*, and *Rhithrogena* spp. increased the most.

Discussion

There are many more factors determining population dynamic and different population size over various growth periods. Ecological theory predicts that the K-selected species will dominate stable or predictable conditions, whereas r-selected species will increasingly dominate as the level of disturbance increases (Warwick 1986; Warwick *et al.* 1987). The r-selected species are frequently fast-growing, small body size, and have opportunistic strategy (high fecundity) (Reznick *et al.* 2002). Species of this type go through irregular and unstable boom-and-bust cycles in population size, and usually have a high level of mortality among the young. This means that beside biological characteristics, environmental influence is also a factor that determines population size. If the life history has been well-studied in all aquatic insect species, the mechanism and relationship within the population dynamic can perhaps be fully understood. If not, information about the basic biology of aquatic insects would be useful. Therefore, this study is an attempt to understand and explain the population fluctuation of aquatic insect under extreme environmental change that is all dependent on the basic biology of aquatic insects.

1. Dominant Taxa

(1) *Baetis* spp. and *Pseudocloeon* spp.

As reported in previous studies, the colonizing ability of *Baetis* spp. is strong (Ciborowski and Clifford 1984; Mackay 1992; Zuellig *et al.* 2002), thus it is the dominant taxon in the community structure of aquatic insects after flooding (Molles 1985; Vieira *et al.* 2004; Rader *et al.* 2008). The present study found that the number of *Baetis* spp. individuals showed significant negative correlation with current velocity (r = -0.25, $p < 0.001$) (Table 3). The number of *Pseudocloeon* spp. did not show significant correlation with current velocity (Table 3). Movement of *Baetis* spp. is mainly accomplished by swimming while *Pseudocloeon* spp. moves by crawling (Merritt and Cummins 1996) and thus can withstand a higher maximum current velocity than *Baetis* spp. High current flow also hindered sedimentation of organic matters, which brought down food supply and renders environment unfavorable for collector-gatherers like *Baetis* spp. Current velocity increased after typhoon, which was more prominent in the middle of the stream, and *Baetis* spp. preferred areas near the banks where the current was slower.

Twenty-two to 49 days after typhoon, the current velocity was between 0.92- 1.96 m/s and 0.17- 0.93 m/s along the right bank and left bank respectively. Since *Baetis* spp. was the dominant species before the typhoon and the maximum current velocity that it can tolerate is lower than that of *Pseudocloeon* spp. *Baetis* spp. dominated in the samples collected in the left bank, with a highest record of 117 specimens collected 49 days after typhoon while only 12 specimens of *Pseudocloeon* spp. were collected. *Pseudocloeon* spp. dominated the right bank 49 days after typhoon, with a total of 174 *Pseudocloeon* spp. specimens collected, while only 48 *Baetis* spp. were harvested. Since the flow of the right bank was faster and attached algae were available in the substrate for scrapers, more *Pseudocloeon* spp. specimens were collected from the right bank. When the samples were pooled for counting, *Pseudocloeon* spp. dominated site 2 while *Baetis* spp. was dominant in sites from the left stream bank.

Investigations from the left stream bank of site 1 showed that the increase in abundance of *Pseudocloeon* spp. was higher than that of *Baetis* spp., and this finding was different from the results of site 2. The left stream bank in site 2 was a gradually sloping bank, and the current velocity was slower after the water receded where it was suitable for *Baetis* spp. inhabitation. Because the left stream bank in site 1 was a steeply sloping bank, even though the waters began to recede, the stream water still flowed faster. As higher velocity in general was not considered a favorable environment for *Baetis* spp., *Pseudocloeon* spp. out-numbered *Baetis* spp. at site1.

In general, the ability of aquatic insect to cling to the substratum decides its survival chance after typhoon (Townsend *et al.* 1997). The insect would be drifted to the downstream or die if failed to cling to the substratum or refugia. Since *Pseudocloeon* spp. is a better clinger than *Baetis* spp., it dominated in areas having fast current after typhoon.

(2) *Ecdyonurus* spp., *Epeorus erratus*, and *Rhithrogena* spp.

Ecdyonurus spp. was the dominant species before typhoon. Since *Ecdyonurus* spp. showed significant negative correlation with current velocity (r= -0.19, $p < 0.01$) (Table 3), the increase in current velocity after typhoon decreased its abundance. Investigation by the bank also revealed that *Rhithrogena* spp. individuals out-numbered *Ecdyonurus* spp., and *Ecdyonurus* spp. did not establish along the bank with slow current. Vieira *et al.* (2004) pointed out that aquatic insects with weak adult dispersal ability and those with specialized feeding requirements, like heptageniid scrapers, could only establish stable population until attached algae re-established and floods magnitudes, substratum instability, suspended sediment loads were reduced.

The level of stream rose after typhoon, draining the land on the bank and scoured the attached algae on the substratum. The shades were dense along the bank, and the algae needed time to grow and provide food for scrapers after typhoon, so the population of *Ecdyonurus* spp., a heptageniid scraper collected in this study, decreased after typhoon. In contrast, generalists like *Epeorus erratus* and *Rhithrogena* spp. (both are collector-gatherers) displayed good population recovery ability (Townsend *et al.* 1997; Vieira *et al.* 2004).

2. Colonization of Aquatic Insects by the Bank

The genus *Hydroptila* mostly has univoltine cycle (one-year cycle) (Anderson 1967; Cloud and Stewart 1974).The number of *Hydroptila* sp. specimens collected at site 2 was abundant 49 days after typhoon Krosa hit (Figure 6). *Hydroptila* members are small in body size with a length of 5mm, use fine sand for case building (Kawai 1985; Wiggins 1996), and show a significant negative correlation with current velocity and water depth ($r = -0.11$, $p < 0.05$；$r = -0.11$, $p < 0.05$) (Table 3). Examination of *Hydroptila* sp. specimens show that the larval case reached around 5.5mm in length, so the larvae were assumed to be an older-instar and not the newly hatched individuals.

Hydroptila spp. was found distributed along the bank since current velocity and water depth in this area decreased rapidly after typhoon and the substratum contained fine sand. And the filamentous algae were found more abundant in slow flow and shallow water (Bohlen *et al.* 2003; Spencer 2003). *Hydroptila* sp. is a piercer and its distribution was found to be scattered with the presence of filamentous algae which it feeds on.

Fisher *et al.* (1982) conducted a study at Sycamore Stream in Arizona and the results showed that filamentous algae grew gradually 5 weeks after flood and the consumption ratio of filamentous algae by macroinvertebrate increased, which is similar with the results found in the present study.

Chironomids larvae were the most abundant organisms collected at site 2 along the left stream bank 49 days after typhoon attack. The life cycle of midges of the chironomids may be as short as a few weeks to one month (Kawai 1985), so it is likely that chironomids collected after flooding were not the same generation in the pre-flood period. Short life cycle, colonization through adult oviposition, and high reproductive rate are important factors in population recovery (Gray and Fisher 1981; Fisher *et al.* 1982; Kondo *et al.* 2001). The larvae of Chironomidae have the largest range of suitable conditions of any family of aquatic insects, a fact that enables them to be the first colonists of many new habitats (Daly *et al.* 1978). Since the chironomids are collector-gatherers and are free-living, they were more abundant in areas with a high sediment ratio of fine sand and low current velocity.

3. Functional Feeding Groups

The insects most abundantly found after typhoon attacks were taxa with strong crawling and moving ability (Baetidae, Heptageniidae, Perlidae and Hydropsychidae), or those preferring a benthic composition of fine sand (Gomphidae). Predators usually display a good ability for chasing their prey, clingers have a flattened body that avoids the main thrust of the current, and burrowers adapt well to the soft and small substrates (Wooton *et al.* 1996; Townsend *et al.* 1997; Matthaei *et al.* 1999; Maria *et al.* 2010). As perlids are clingers and gomphids are burrowers, they contribute a large proportion of individuals collected in the earliest recovery stage. Although predators out-numbered members from other functional feeding groups, only ten predator specimens were collected, not especially a large number.

According to a study conducted at Sycamore Creek in Arizona (Fisher *et al.* 1982), algae were scoured by flash flood but recovered quickly, reaching a biomass of $100g/m^2$ within two weeks. Current velocity decreased gradually after typhoon, attached algae on the substrate accrued, and *Pseudocloeon* spp. gradually colonized. The number of perlids and gomphids collected changed little, around 20, resulting in a gradual decline of predator ratio and an increase in scraper ratio. The collector-gatherers, *Epeorus erratus* and *Rhithrogena* spp., subsequently carried out colonization. Although the larvae of the mayfly family Baetidae, known to be common in fast-flowing habitat, the adaptive ability to higher current velocity may differ in different species (Matzinger and Bass 1995). During higher current velocity, *Pseudocloeon* spp was more abundant than *Baetis* spp., and the latter started to colonize when the current velocity declined. *Baetis* spp. is a collector-gatherer and its relative density increased with the scrapers, and the scraper increase was then slowed down by the increasing ratio of the collector-gatherers. The major collector-filterers collected was Hydropsychidae and its number increased slowly because filter-feeding was affected by the increase of suspending granules in the water after typhoon, and its population density were found to be lower than the pre-flood period. The population size of piercers was small and no samples were collected in the early post-flood period. Filamentous algae-consuming *Hydroptila* sp. collected at site 2 was more abundant 36-49 days after typhoon Krosa. The ratio of piercers was found to be higher comparing with the pre-flood period (Figure 7, 8).

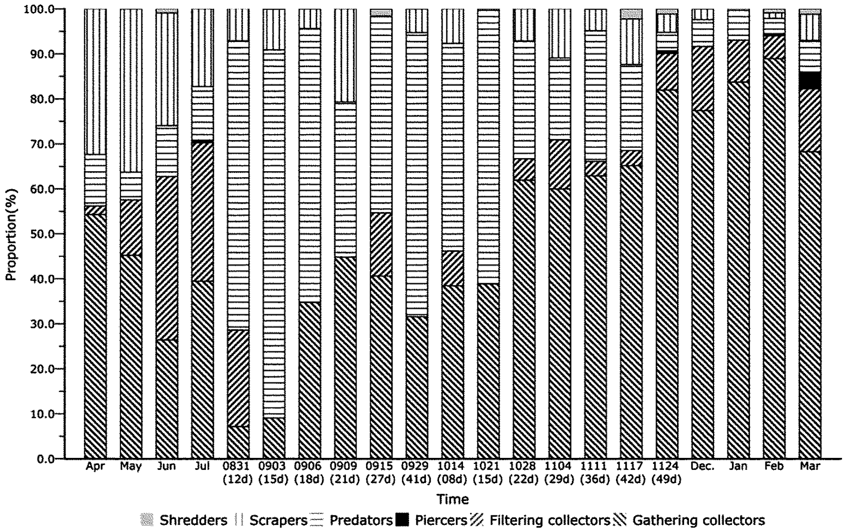

Fig. 7. Proportion of functional feeding groups abundance at site 1 in the Shakadang Stream from April 2007 to March 2008. Samples were labeled with numbers. The first and second digits indicate the month, the third and fourth digits indicate the day, and the first and second digits in the bracket indicate the days after typhoon. For example, 0831 (12d) indicates 31st August and 12 days after typhoon.

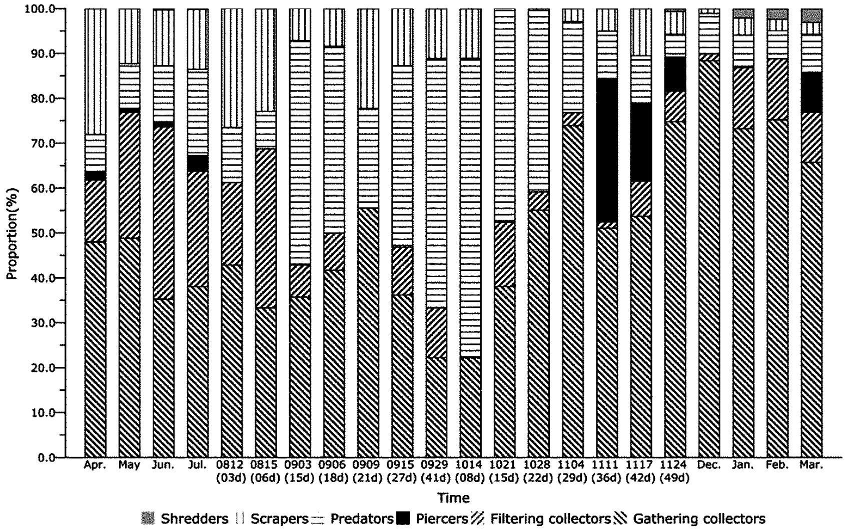

Fig. 8. Proportion of functional feeding groups abundance at site 2 in the Shakadang Stream from April 2007 to March 2008.

Conclusion

Aquatic insect community structure drastically changed and shifted toward the pre-typhoon structure pattern before typhoon hit. The dominant taxa *Baetis* spp. and *Ecdyonurus* spp. were replaced by *Pseudocloeon* spp., and *Rhithrogena* spp. *Pseudocloeon* spp. had better crawling ability, thus could endure a higher velocity than *Baetis* spp. During the higher current velocity, *Epeorus erratus* and *Rhithrogena* spp. was relatively more abundant than *Ecdyonurus* spp. Both *Epeorus erratus* and *Rhithrogena* spp. are collectors and thus had better population recovery potential. *Rhithrogena* spp. dominated over *Epeorus erratus* and it was found to out-number *Epeorus erratus*.

Investigation by the stream-bank showed that *Baetis* spp. and chironomids preferred areas with slower running velocity. *Hydroptila* sp. at the bank showed a scattered distribution associated with filamentous algae. Perlids (Perlidae) and gomphids (Gomphidae) were most abundant during the early stage of colonization after typhoon attack, resulting in a high relative abundance of predators. *Pseudocloeon* spp. started to colonize when attached algae became more abundant and resulted in a decrease in ratio of predators and increase in relative abundance of scrapers, which was followed by gradual colonization of *Rhithrogena* spp., *Epeorus erratus*, and *Baetis* spp. Subsequently, collector-gatherers became more abundant and scrapers less so. Population density of collector-filterers was also found to be lower than in the pre-flood period while the ratio of piercers increased.

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