Shrimp abundance and habitat relationships in tropical rain-forest streams, Sarawak, Borneo

Tomoya Iwata*[1], Mikio Inoue[†], Shigeru Nakano*, Hitoshi Miyasaka*, Atsushi Doi* and
Alan P. Covich[‡]

*Center for Ecological Research, Kyoto University, Hirano-cho, Kamitanakami, Otsu, Shiga 520–2113, Japan
†Department of Biology and Earth Sciences, Faculty of Science, Ehime University, Matsuyama 790–8577, Japan
‡Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins 80523, USA
(*Accepted 23 July 2002*)

Abstract: Microhabitat use and habitat–abundance relationships of four freshwater shrimps, *Atyopsis moluccensis*, *Macrobrachium pilimanus*, *Macrobrachium trompii* and *Macrobrachium neglectum*, were surveyed in tropical streams running through primary and secondary forests in Borneo, East Malaysia. Underwater observations revealed that *A. moluccensis* preferred relatively high water velocity and a boulder substrate. *Macrobrachium pilimanus* also preferred high water velocity and a cobble substrate, whereas *M. trompii* occupied stream margins with slow current and fine substrates (from POM (particulate organic matter) to pebbles). In contrast, *M. neglectum* was distributed relatively evenly through the stream channel. The abundance of *A. moluccensis*, *M. pilimanus* and *M. trompii* in the stream reaches was best explained by the abundance of boulders, cobbles and POM, respectively, suggesting that the amount of preferred microhabitat is an important factor affecting shrimp abundances in the tropical rain-forest streams. The primary-forest reaches were dominated by coarse substrates, such as cobbles and boulders, while a great proportion of the streambeds in the secondary-forest reaches were covered with sand. Owing probably to such habitat differences, the abundance of both *A. moluccensis* and *M. pilimanus*, which preferred coarse substrates, was less in the secondary- than in the primary-forest reaches. These suggested that loss of preferred habitat, namely decreased coarse substrate availability, by sedimentation resulting from riparian deforestation had altered the shrimp assemblage structures.

Key Words: Borneo, freshwater shrimps, habitat–abundance relationship, microhabitat use, riparian deforestation, tropical stream

INTRODUCTION

Freshwater shrimps are major faunal components in many tropical headwater streams (Covich 1988, Dudgeon 1999, Hunte 1978). They play important roles in tropical stream food webs through the consumption of a variety of foods, including detrital, algal and animal resources (Covich *et al*. 1999, Dudgeon 1999). Their foraging activities can alter the distribution and abundance of benthic organisms of lower trophic levels, such as algae and aquatic insects, by top-down processes (Crowl & Covich 1994, Pringle 1996, Pringle *et al*. 1993). Detritivorous shrimps also contribute greatly to leaf litter breakdown and transport in tropical streams (Crowl *et al*. 2001, March *et al*. 2001). Fine particles and nutrients converted from leaf litter by shrimps can become readily available to other macroconsumers, primary producers and bacteria, and thus affect food-web structures by bottom-up processes (Covich *et al*. 1999). Therefore, shrimps can be key organisms in tropical stream communities (Covich *et al*. 1999), and knowledge of their distribution and habitat use is essential for an understanding of the ecology of tropical streams.

Stream organisms generally exhibit preferences for specific microhabitats and the abundance of preferred habitat often limits species abundance. Numerous studies have shown significant correlations between certain physical attributes of stream habitat and the local abundance of fishes (Inoue *et al*. 1997, Urabe & Nakano 1999), aquatic insects (Huryn & Wallace 1987, Rabeni & Minshall 1977) and crustaceans (Covich *et al*. 1996, Pyron *et al*. 1999). Therefore, habitat modification resulting from human activities (e.g. riparian deforestation) strongly influences the distribution and abundance of stream organisms (Gurtz & Wallace 1984, Inoue *et al*. 1997, Jones *et al*. 1999). However, studies on shrimp habitats, such as assessment of habitat use and habitat–abundance relationships, have rarely been conducted in tropical streams, where anthropogenic habitat modification has increasingly threatened many stream organisms (Dudgeon 1999, 2000). In addition, although much attention has been

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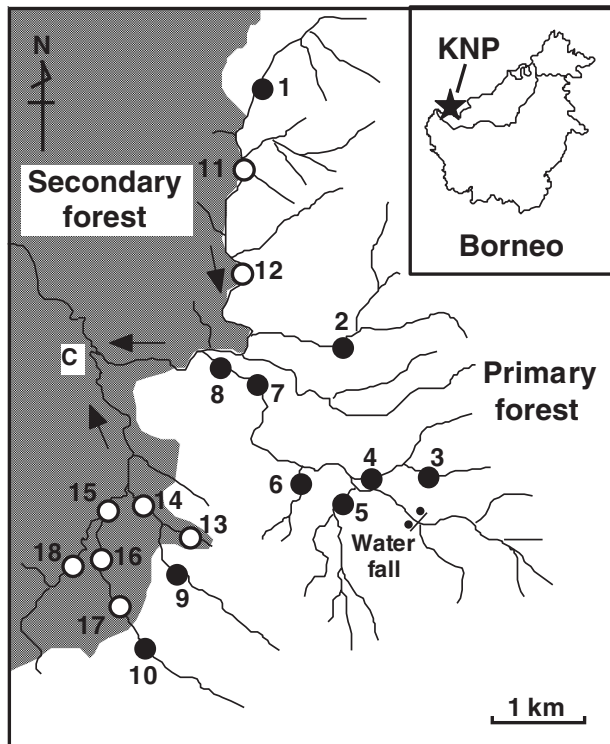[1] Corresponding author: Email: iwata@ecology.kyoto-u.ac.jp

Figure 1. Map of the Rayu River system with locations of the study reaches in the Kubah National Park (KNP), Sarawak, East Malaysia. Solid and open circles indicate primary- and secondary-forest reaches, respectively. Figures assigned for study reaches correspond to those listed in Table 1. Underwater observations were performed in the study reach No. 8. The confluence of tributaries used to determine upstream distance of each study reach is indicated by C (see text). Arrows indicate flow direction.

directed to the roles of shrimps in organizing tropical stream communities (Crowl *et al*. 2001, March *et al*. 2001, Pringle 1996, Pringle *et al*. 1993), such studies have been conducted mostly in Neotropical streams. Information from tropical Asia is relatively scarce (Dudgeon 1999, 2000; Jackson & Sweeney 1995).

Here we describe microhabitat use and habitat–abundance relationships for four freshwater shrimps in tropical rain-forest streams in Borneo, East Malaysia. In addition, we examined the effects of past riparian deforestation on stream habitat and shrimp abundance by comparing streams running through primary and secondary forests.

STUDY SITE

A field survey was conducted during August to September 1998 in headwater streams of the Rayu River, discharging into the South China Sea from the north-western coast of Borneo, Sarawak, East Malaysia (Figure 1). The upper-middle part of the watershed is located within the Kubah National Park (hereafter KNP; 1°37′N, 110°09′E). The

watershed is predominantly underlain by sandstone, supplemented by mudstone and tuff (S. Yamada, *pers. comm.*). The region receives an annual precipitation of 6000–7000 mm, with December–February generally having greater rainfall than March–November.

The watershed in KNP originally comprised three forest types, tropical lowland evergreen rain forest, lower montane rain forest and heath forest. However, in the middle part of the watershed, intensive slash-and-burn agriculture started in 1978, the forest being cleared for the development of farm sites. These farm sites were abandoned after cultivation for several years (generally 2 or 3 y), and adjacent forests were subsequently cleared for the creation of new sites. Such slash-and-burn agricultural practices continued until the establishment of KNP in 1989, the area thereafter being protected from any forest clearance. At the time of our survey in 1998, the forest had redeveloped on the previously deforested areas as a result of succession processes (Figure 1). We established 18 study reaches (25–100 m length, including one to three 'pool and riffle' sets) on tributaries running through the primary (10 reaches) and secondary forests (eight reaches) in KNP (Figure 1 and Table 1). Although stream size was similar between the primary- (mean wetted width, 5.1 ± 1.8 SD m; mean depth, 27.1 ± 13.4 cm) and secondary-forest reaches (4.4 ± 1.4 m; 30.5 ± 8.9 cm), the secondary-forest reaches were generally located in lower elevations (26 ± 5 m) and had lower channel gradients ($0.9 \pm 0.8\%$) than the primary-forest reaches (elevation, 56 ± 36 m; gradient, 3.1 ± 2.7 %). The mean basal area of the riparian stands in the primary- and secondary-forest reaches was 46.6 ± 9.3 cm^2 m^{-2} (mean $\pm$ SD, range = 34.7–67.4, n = 10) and 20.7 ± 9.5 cm^2 m^{-2} (6.3–37.3, n = 8), respectively (T. Iwata, unpubl. data).

The river system was inhabited by six species of large shrimp (> 50 mm in maximum total length); one species of Atyidae, *Atyopsis moluccensis* (De Haan, 1849), and five species of Palaemonidae, *Macrobrachium pilimanus* (De Man, 1879), *Macrobrachium trompii* (De Man, 1898), *Macrobrachium neglectum* (De Man, 1905), *Macrobrachium lanchesteri* (De Man, 1911) and *Macrobrachium rosenbergii* (De Man, 1879). Among these, *A. moluccensis*, *M. pilimanus*, *M. trompii* and *M. neglectum* were the most abundant shrimps and examined in this study. According to direct underwater observations and gut content analyses (T. Iwata, unpubl. data), *A. moluccensis* was regarded as a detritivore, which feeds mainly on drifting detrital particles by filtering from the water column with the cheliped setae. The other three *Macrobrachium* species exhibited omnivorous feeding habits, feeding on aquatic insects, small shrimps, algae and detrital particles, by picking up from substrates with pinchers. However, prey use considerably differed individually even within a single *Macrobrachium* species; some individuals were

Table 1. General description of the study reaches of the Rayu River system in the Kubah National Park (KNP).

Study reach	Riparian forest	Elevation (m)	Upstream distance (km)	Gradient (%)	Mean wetted width (m)	Mean depth (cm)
1	Primary	50	4.7	0.7	5.8	34
2	Primary	30	3.0	1.2	4.8	29
3	Primary	140	4.4	3.8	3.4	9
4	Primary	80	3.5	7.3	5.5	27
5	Primary	80	3.7	7.7	3.8	31
6	Primary	40	3.0	0.7	4.5	16
7	Primary	20	1.6	0.9	7.8	49
8	Primary	20	1.3	0.9	8.5	46
9	Primary	50	2.6	4.0	4.2	16
10	Primary	50	3.0	3.7	2.9	15
11	Secondary	30	4.1	0.7	5.3	33
12	Secondary	20	2.9	1.0	4.8	34
13	Secondary	30	2.1	2.6	2.1	21
14	Secondary	20	1.6	0.3	3.7	38
15	Secondary	20	1.5	0.3	7.1	46
16	Secondary	30	2.0	1.4	3.7	23
17	Secondary	30	2.6	0.2	3.9	20
18	Secondary	30	2.1	0.2	4.7	29

Note: Upstream distance indicates the distance between each study reach and the lowermost confluence in the study area (see text).

highly predaceous while others were herbivore or detritivore. The river system was also inhabited by three species of small shrimp (< 35 mm in maximum total length), *Caridina nilotica peninsularis* Kemp, 1918, *Caridina weberi sumatrensis* De Man, 1892 and unidentified *Caridina* sp., two species of crab, *Isolapotamon consobrinum* (De Man, 1899) and *Parathelphusa oxygona* Nobili, 1901, and 27 species of freshwater fish (see Doi *et al.* 2001).

METHODS

Microhabitat use by shrimps

Microhabitat use by shrimps was surveyed by direct observations from 23 August to 1 September 1998 in a primary-forest reach (hereafter observation reach; 57 m length, 8.7 m mean wetted width and 495.9 m² area; Figure 1), where the four large shrimps, *A. moluccensis*, *M. pilimanus*, *M. trompii* and *M. neglectum*, occurred. The reach is located at 20 m elevation and comprised two pools, one glide and one riffle (see Bisson *et al.* 1982 for classification), including multiple types of microhabitats. Observations were implemented during nighttime (20h00–01h00) because shrimps were generally invisible during the daytime and it was difficult to ensure sufficient sample size for the analyses of daytime microhabitat use. Underwater observations were made using a hand-held flashlight, which did not appear to frighten shrimp provided that the observer moved very slowly and stayed > ≈1 m away from the focal individual. The observers lay motionless at the downstream end of the observation reach for at least 10 min before beginning observations, and then moved upstream systematically in a zigzag fashion to randomize any bias associated with nearshore or midstream observations. When a shrimp (≥ 20 mm in total length) was encountered, its position was marked with a coloured sinker. We did not record the position of shrimp whose behaviour had already been disturbed when detected. Such observations were conducted seven times in the observation reach on different days, giving an approximately 20 person-h observation during the study period. A total of 94 locations for *A. moluccensis*, 51 for *M. pilimanus*, 78 for *M. trompii* and 124 for *M. neglectum* were recorded.

Four microhabitat variables, water depth and velocity, substrate type and distance to the nearest bank, were measured at each marked point on the days following the underwater observations. The water velocity was measured 1 cm above the bottom at each marked point using a portable current meter (Model CR-7WP, Cosumo-Riken Inc., Kashihara, Japan). The dominant substrate type in a 25 × 25-cm quadrat around each marked point was classified as particulate organic matter (POM), sand (dominant particle size < 2 mm), gravel (2–16 mm), pebble (17–64 mm), cobble (65–256 mm), boulder (> 256 mm) or bedrock. The distance from each marked point to the nearest bank was measured and divided by the wetted width for conversion into a percentage value (hereafter bank distance; range = 0–50%).

On 1 September, 29 equally spaced transects (2-m intervals) with equally spaced measurement points (1-m intervals) were established in the observation reach (237 points in total) to quantify microhabitat availability. The nearest measurement point to the right-hand bank of each transect was spaced 20 cm from the shoreline to include edge habitats. At each measurement point, water depth and velocity, substrate type and distance to the nearest

bank were measured in the same manner as used for the shrimp positions.

Microhabitat preference of each shrimp species was examined using the formula of Jacobs (1974), calculated as:

$$D_{sa} = (r_{sa} - p_{sa}) / (r_{sa} + p_{sa} - 2\ r_{sa}p_{sa})$$

where D_{sa} is the preference value for range a of variable s, r_{sa} is the proportion of shrimps using range a of variable s, and p_{sa} is the proportion of measurement points within range a of variable s in the available microhabitat. Preferences for microhabitat variables range from −1 (never used) to +1 (only one range used), 0 indicating that a given habitat is used in proportion to its availability.

Shrimp abundance and habitat characteristics

The abundance of the four species, *A. moluccensis*, *M. pilimanus*, *M. trompii* and *M. neglectum*, was surveyed in the 18 study reaches by electrofishing during daytime hours (09h00–16h00) from 13 August to 9 September 1998. Each end of the study reach was blocked with a 5-mm mesh seine and three removal passes made using an electrofishing unit (300–500 v, AC 90 HZ; Smith-Root Model 15, Vancouver, WA, USA). We maintained the duration of electroshocking of ≈10 s per unit area (m^2) while collecting organisms, with more than 30 min elapsing between successive passes. Shrimps collected from each pass were immediately preserved in 10% buffered formalin solution. In the laboratory, specimens were identified to species and the total length from tip of rostrum to posterior margin of telson was subsequently measured to the nearest 1 mm. The abundance of each species was expressed as the total number of individuals (collected from the three passes) per unit area (m^2). To alleviate any size-dependent bias in capture probability, shrimps < 20 mm in total length were excluded from the analyses.

Reach habitat variables were measured in each study reach from 19 August to 23 September. The gradient of each study reach was measured with a level and levelling rod. Transects were set at 8-m intervals in larger streams (⩾ 5.5 m mean wetted width) and at 3-m intervals in smaller streams (< 5.5 m), and the wetted width at each transect was measured to obtain the mean wetted width of each study reach. Water depth was measured at five equally spaced points along each transect to obtain the mean depth of each study reach (range = 35–135 points). The dominant substrate type in a 25 × 25-cm quadrat around each depth-measurement point was classified in the same manner as used for the microhabitat-use survey. The relative frequency of each substrate type in each study reach was then calculated. In addition, the elevation of each study reach and the distance between each study reach and the lowermost confluence in the study area (see Figure 1; hereafter upstream distance) were measured

with a map wheel and 1/50 000 topographical map so as to express the elevational and longitudinal position of each study reach in the watershed.

Statistical analyses

To identify physical habitat factors influential in determining shrimp abundance, the relationships between shrimp abundance and habitat characteristics were examined using stepwise multiple regression analysis. The abundance of each species was used as a dependent variable, and elevation (m), upstream distance (km), gradient (%), mean wetted width (m), mean depth (cm), and relative frequencies of POM (%), sand (%), gravel (%), pebble (%), cobble (%), boulder (%) and bedrock (%) as independent variables.

To examine the effects of riparian deforestation on shrimp abundance, the abundance of each shrimp species was compared between the primary- and secondary-forest reaches, using a t-test. The percentages of POM, sand, gravel, pebble, cobble, boulder and bedrock were compared between the primary- and secondary-forest reaches to examine deforestation effects on substrate characteristics, using one-way analysis of covariance (ANCOVA) or t-tests. One-way ANCOVA was used to consider effects of channel gradient, which is one of the most important geomorphic factors determining the substrate composition (Church 2002). Because the secondary-forest reaches had lower gradient than did primary-forest reaches (see Table 1), the difference in gradient can confound deforestation effects on substrates when comparing the two riparian forest types. The effect of gradient on the percentage of each substrate type was first examined by Pearson's correlation analysis. When a significant correlation was found, the percentage of the substrate type was compared between the two riparian forest types using one-way ANCOVA, with gradient as a covariate. When not significant in Pearson's correlation, the variable was compared using a t-test.

In the statistical analyses, all variables were transformed as $\log_{10}(x)$ or $\log_{10}(x + 1)$ for exact values or as arcsine ($p^{0.5}$) for percentage values so as to standardize variances and improve normality (Zar 1999). The alpha value was set, a priori, at 0.05. All of the analyses were performed using Stat-View Version 5.0 (SAS Institute, Inc., Cary, USA).

RESULTS

Microhabitat use by shrimps

In the observation reach, three of the four shrimp species, *A. moluccensis*, *M. pilimanus* and *M. trompii*, exhibited strong preferences for specific microhabitats (Figure 2). The preference value (D) indicated that *A. moluccensis*
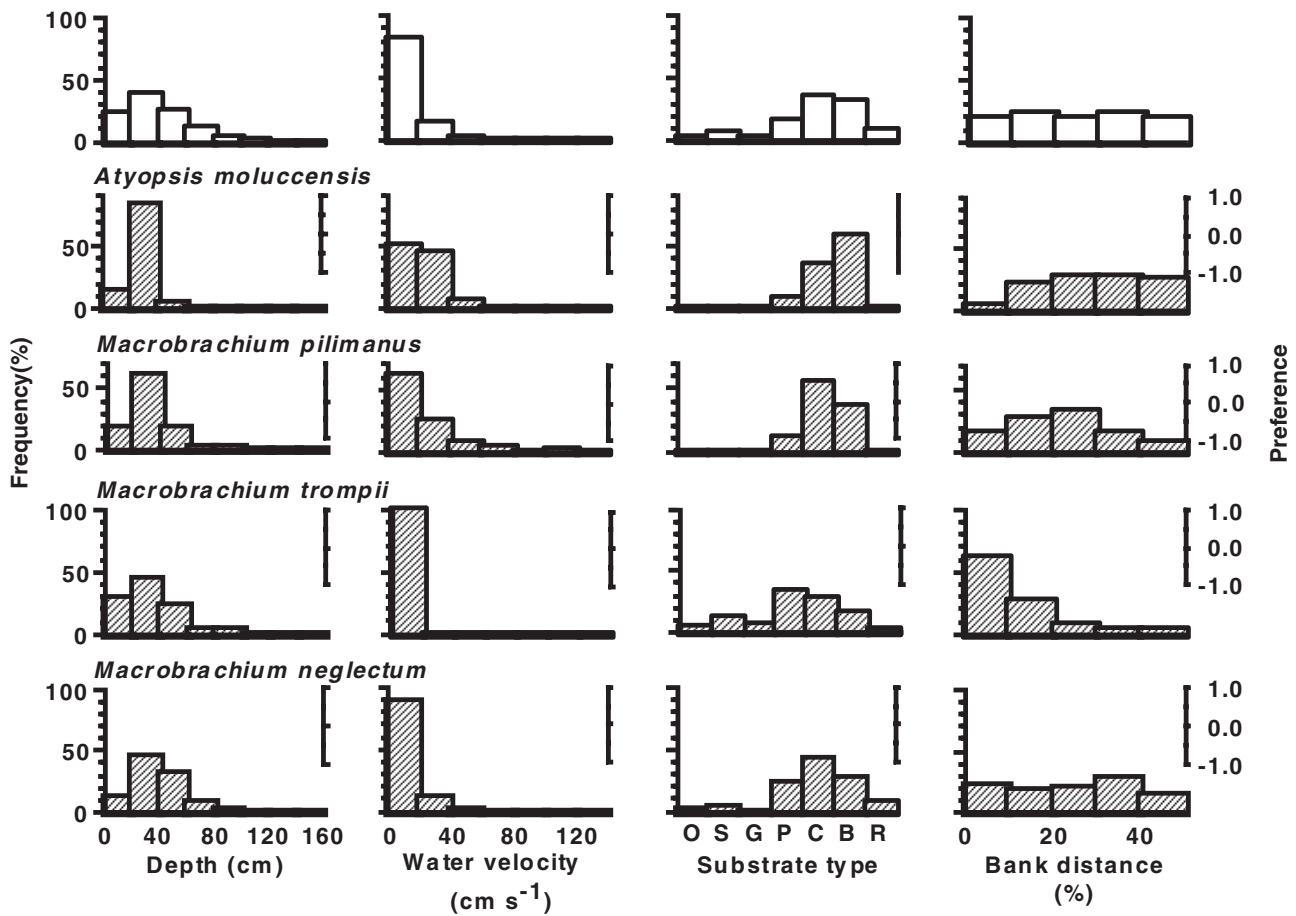
Figure 2. Microhabitat available, shrimp microhabitat use and habitat preference in the observation reach. Substrate type classification: O = particulate organic matter; S = sand; G = gravel; P = pebble; C = cobble; B = boulder, R = bedrock. Preference revealed by Jacobs index (D) was represented by solid ($\geqslant 0.3$) or open (< 0.3) circles (value not calculated when availability was zero).

selected 20–40 cm depth, relatively high water velocity (20–60 cm s^{-1}) and a boulder substrate, at the same time avoiding stream margins (i.e. 0–10% bank distance). *Macrobrachium pilimanus* preferred 20–40 cm depth, relatively high water velocity (20–80 cm s^{-1}) and a cobble substrate. *Macrobrachium trompii* selectively utilized microhabitats with slow water velocity (0–20 cm s^{-1}), finer substrates (from POM to pebble) and stream margin (0–10% bank distance). *Macrobrachium neglectum* did not exhibit a distinct preference for any microhabitat variables.

Shrimp abundance and habitat characteristics

The abundance of each shrimp species was associated with reach habitat variables, with species-specific patterns being evident (Table 2 and Figure 3). Stepwise multiple regression indicated that the abundance of *A. moluccensis* was best explained by a combination of per cent boulder and upstream distance, with the positive effect of the former being greater. The abundances of *M. pilimanus*

and *M. trompii* were best modelled by per cent cobble and per cent POM, respectively, both effects being positive. The abundance of *M. neglectum* was best modelled by upstream distance and per cent cobble, the relative importance of the former being greater.

The t-tests revealed significant differences in abundance of *A. moluccensis* and *M. pilimanus*, but not of *M. trompii* and *M. neglectum*, between the primary- and secondary-forest reaches (Table 3). The abundances of *A. moluccensis* and *M. pilimanus* were both significantly lower in the secondary- than in the primary-forest reaches.

The substrate composition significantly differed between the two riparian forest types (Table 4). Pearson's correlation analyses revealed that gradient was significantly correlated with per cent sand (r = −0.63, P = 0.005) and per cent boulder (r = 0.68, P = 0.001) but not with the percentages of the other substrate types (r = −0.26–0.28, P = 0.261–0.474, n = 18 for all). Therefore, differences in per cent sand and per cent boulder between the two riparian forest types were examined by one-way ANCOVA, and the other substrate types by t-tests. One-

Table 2. Results of stepwise multiple regression analysis using shrimp abundance (number of individuals per m^2) as a dependent variable and reach habitat variables as independent variables for the study reaches (n = 18).

| Species	Independent variable	Regression coefficient	Standard regression coefficient	Model		
				R^2	F	P
Atyopsis moluccensis	Boulder	0.004	0.774	0.54	8.87	0.003
	Upstream distance	−0.358	−0.411			
	Constant	0.215				
Macrobrachium pilimanus	Cobble	0.003	0.603	0.36	9.16	0.008
	Constant	0.030				
Macrobrachium trompii	POM	0.006	0.654	0.43	12.0	0.003
	Constant	0.006				
Macrobrachium neglectum	Upstream distance	−0.338	−0.677	0.53	8.54	0.003
	Cobble	0.002	0.400			
	Constant	0.222				
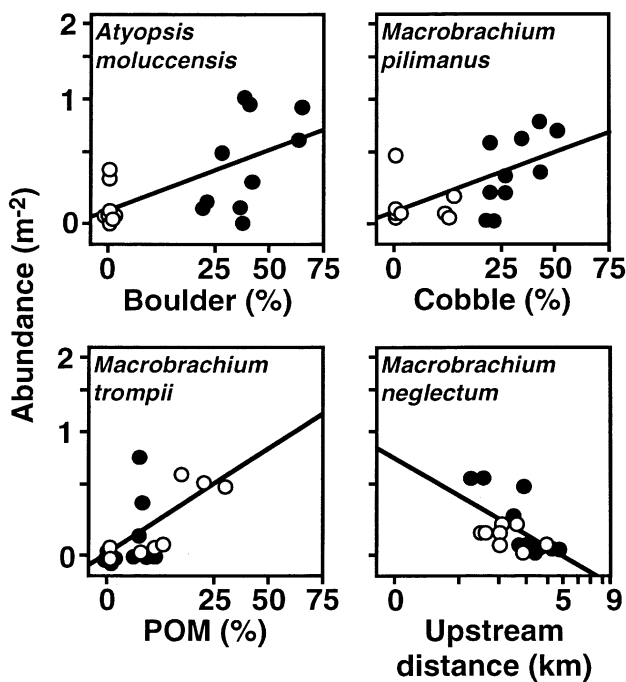
Figure 3. Relationships between shrimp abundance and reach habitat variables included in stepwise multiple regression model as the best predictor (see Table 2). Solid and open circles indicate primary- and secondary-forest reaches, respectively. Axes for shrimp abundance and upstream distance are logarithmic scale and those for substrates are arcsine scaled.

way ANCOVA revealed significant effects of forest type on both per cent sand and per cent boulder (Table 4), with no significant interaction effects being evident (forest by gradient; $F_{1,14} = 0.28$–2.76, $P = 0.119$–0.604). The results indicated that per cent sand was higher but per cent boulder was lower in the secondary- than in the primary-forest reaches even when controlling the effect of gradient. In addition, the t-tests revealed that per cent POM was significantly higher in the secondary- than in the primary-forest reaches, while per cent cobble was significantly higher in the primary-forest reaches (Table 4).

DISCUSSION

In the study stream, differences in microhabitat use were observed among the four shrimp species. Of the four shrimps observed here, *A. moluccensis*, *M. pilimanus* and *M. trompii* exhibited strong preferences for particular microhabitats. Both *A. moluccensis* and *M. pilimanus* preferred relatively fast currents and coarse substrates, while *M. trompii* utilized stream margins with slow current and fine substrates. In contrast, *M. neglectum* exhibited no distinct preference for any microhabitat variable. Habitat use by stream decapods, such as shrimps and crayfishes, is generally affected by predation (Crowl & Covich 1994), food availability (Covich *et al.* 1991), interference competition (Rabeni 1985) and/or physiological stress (de Silva & de Silva 1988). Owing to the lack of information

Table 3. Comparisons of shrimp abundance (number of individuals per m^2) between study reaches in primary (n = 10) and secondary forests (n = 8) by t-test.

Species	Primary forest	Secondary forest	t_{16}	P
Atyopsis moluccensis	0.45 ± 0.39	0.11 ± 0.13	−2.36	0.031
Macrobrachium pilimanus	0.38 ± 0.27	0.13 ± 0.15	−2.31	0.034
Macrobrachium trompii	0.12 ± 0.24	0.22 ± 0.26	0.94	0.362
Macrobrachium neglectum	0.21 ± 0.23	0.13 ± 0.06	−0.79	0.441

Note: Mean ± SD is shown.

Table 4. Comparisons of the percentages of substrate types between study reaches in primary (n = 10) and secondary forests (n = 8) by t-test (t) or one-way ANCOVA (F) with gradient as a covariate.

Variable	Primary forest	Secondary forest	t_{16}	$F_{1,15}$	P
POM (%)	1.5 ± 1.5	9.3 ± 10.4	2.21		0.042
Sand (%)	2.5 ± 2.0	58.2 ± 19.1		64.6	< 0.001
Gravel (%)	5.0 ± 6.0	9.7 ± 9.0	1.12		0.279
Pebble (%)	19.8 ± 7.2	16.6 ± 17.5	−1.02		0.322
Cobble (%)	30.1 ± 11.5	2.6 ± 3.6	−7.74		< 0.001
Boulder (%)	39.1 ± 15.5	0.0 ± 0.0		115.6	< 0.001
Bedrock (%)	1.9 ± 5.0	3.7 ± 5.6	0.82		0.423

Note: Mean ± SD is shown.

on the ecology of shrimps examined, this study cannot clarify factors underlying species-specific microhabitat use by the three *Macrobrachium* species. However, the habitat selection by *A. moluccensis*, which filters drifting detrital particles while clinging to a substrate, appears to be affected by factors related to food supply and physiological stress. In general, suspension feeders dwelling in headwater streams prefer high water velocity, because food intake rate is proportional to current velocity (Georgian & Thorp 1992, Loudon & Alstad 1990, Smith-Cuffney & Wallace 1987). However, their metabolic costs of holding positions increase with current velocity (see Allan 1995, Fausch 1984, Hill & Grossman 1993). Therefore, for *A. moluccensis*, coarse substrates with relatively fast currents may be a better habitat in terms of potential energy profit, because the wakes behind coarse substrate materials can provide velocity refuge (see Poff & Ward 1990) while the adjacent fast water provides high drift availability.

Shrimp abundance and habitat relationships at reach scale were consistent with the pattern of species-specific microhabitat use. The regression model indicated that the abundance of *A. moluccensis* was best predicted by the abundance of boulders, which were selectively utilized by this species at the microhabitat scale. Similarly, the abundance of *M. pilimanus*, which exhibited a preference for cobbles, was related to cobble abundance. The abundance of *M. trompii* was related to the abundance of POM. At the microhabitat scale, this species selectively utilized stream margins with slow current and fine substrates. In particular, the highest value for habitat preference of *M. trompii* was detected for 0–20 cm s⁻¹ water velocity (D = 1.0, Figure 2), showing a strong dependence on habitat characterized by a slow current. Because POM tends to accumulate in such places (Kishi *et al.* 1999), the per cent POM included in the regression model may be indicative of the area of slow-current habitat in stream reaches. The results suggest that the amount of preferred habitat in a stream channel is an important factor affecting the local abundance of shrimp populations in this watershed.

In contrast with the above three shrimps, the abundance of *M. neglectum*, which exhibited no distinct preference for any microhabitat feature, was best explained by upstream distance, with stream reaches located in the lower part of the watershed having a greater abundance of this species. Most *Macrobrachium* species inhabiting tropical streams have amphidromous life cycles, migrating from estuaries to stream headwaters as they develop from post-larvae into reproductive adults (Covich *et al.* 1996, Dudgeon 1999, March *et al.* 1998). Since *M. neglectum* appeared to be a habitat generalist (Figure 2), the abundance of that species may be more strongly affected by the location of study reach (distance from estuary) than the structural characteristics of the reach, in association with amphidromy. Similar observations of the distribution and abundance being largely determined by longitudinal position in a watershed have often been reported for other *Macrobrachium* species (Covich *et al.* 1996, Dudgeon 1999).

Comparisons between primary- and secondary-forest reaches revealed distinct differences in substrate composition and shrimp abundance. Primary-forest reaches were dominated by coarse substrates, such as cobbles and boulders, while a great proportion of the streambeds in secondary-forest reaches was covered with sand (see Table 4). Although the secondary-forest reaches had lower gradients than did primary-forest reaches, the ANCOVA and t-tests indicated that the differences in substrate composition between the two riparian forest types did not result only from the difference in gradient. In fact, all of the tributaries running through the secondary forest had rocky substrate until the clearing of the riparian forests 9–20 y previously (M. S. Sabki, *pers. comm.*). Accordingly, it appears that riparian deforestation was responsible for increased fine sediment input, resulting in more sandy substrates in the secondary-forest reaches. Such heavy sedimentation in these secondary-forest reaches may have depressed the abundance of *A. moluccensis* and *M. pilimanus*, both of which exhibited a preference for coarse substrates, such as boulders and cobbles. Because the abundances of both species were positively related to boulder or cobble abundance, loss of their preferred habitat, namely decreased boulder and cobble availability, by sedimentation resulting from riparian deforestation is likely to have been a primary factor causing their lower abundance in the secondary-forest reaches.

The present study showed that the amount of preferred

microhabitat is an important factor affecting shrimp abundance in the tropical rain-forest streams. However, we did not evaluate the potentially important factors other than physical habitat features, such as biological interactions including predation (Crowl & Covich 1994) and competition (Rabeni 1985). Moreover, it should also be noted that our findings are based on a survey conducted within a short period, while shrimp distribution is known to vary temporally (Covich *et al*. 1996). Thus, for more proper understanding of shrimp abundance and habitat relationships, we emphasize a need for further studies assessing the temporal dynamics of shrimp distribution and its relationships with habitat characteristics and with biological interactions. However, our findings suggested that sedimentation resulting from riparian deforestation alters shrimp assemblage structures through habitat alteration. Numerous studies conducted in temperate regions have revealed that sedimentation accompanying riparian forest removal has lowered the abundance of many stream organisms (Gurtz & Wallace 1984, Jones *et al*. 1999). In tropical streams, where freshwater shrimps can affect community structure, energy flow and nutrient cycling (Covich *et al*. 1999, Crowl *et al*. 2001, Pringle 1996, Pringle *et al*. 1993), such detrimental effects of riparian deforestation on stream communities can be compounded by changes in the shrimp assemblage structure. The loss of preferred habitat by sedimentation resulting from riparian deforestation not only depresses shrimp abundances directly, but may also affect the remaining organisms via alteration of ecological processes driven by freshwater shrimps.

ACKNOWLEDGEMENTS

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