ABSTRACT OF THE THESIS OF Leigh Ellis-Neill for the Master of Science in Biology presented 28 July 1987.

Title: Distribution and Production Dynamics of Benthic Invertebrates in a Tropical Stream on Guam

Approved: Lynn Raulerson

Lynn Raulerson, Chairman, Thesis Committee

The factors influencing the distribution of benthic invertebrates in the Pigua River, Guam (Mariana Islands) were investigated. Current velocity, substrate particle size, seasonality and amount of leaf litter were found to be important parameters in the distribution of stream invertebrates. The secondary production of the dominant atyid shrimps was used as a indicator of the relationship between the shrimps and their habitat. Secondary production rates varied significantly between sampling sites. This variance was correlated with differences in secondary production in pool and riffle sites. No correlation was found between secondary production and substrate particle size.

DISTRIBUTIONAL AND PRODUCTION DYNAMICS OF BENTHIC INVERTEBRATES IN A TROPICAL STREAM ON GUAM

BY

Leigh Ellis-Neill

A thesis submitted in partial fullfillment of the requirements for the degree of

MASTER OF SCIENCE

in

BIOLOGY

UNIVERSITY OF GUAM

JULY 1987

TO THE OFFICE OF THE GRADUATE SCHOOL AND RESEARCH

The members of the Committee approve the thesis of Leigh Ellis-Neill presented 28 July 1987.

Lynn Raulerson
Lynn Raulerson, Chairman

Richard H. Randall
Richard H. Randall, Member

James A. Marsh, Jr.
James A. Marsh, Jr., Member

Oscar Levand
Oscar Levand, Member

ACCEPTED:

James A. Marsh, Jr.
Dean, Graduate School and Research

Date

ACKNOWLEDGEMENTS

I would like to take this opportunity to thank those people whose help and support made this research possible. Dr. Patty Jo Hoff and Mr. Clayton Carlson provided invaluable rainfall data throughout this study. I also had much support and advice while working with the taxanomic difficulties of the invertebrates. In particular, Dr. Lu Eldredge provided many references on the crustaceans; Dr. Donald Nafus and Dr. Ilse Schreiner gave advice and support while working with the aquatic insects. Dr. G. F. Edmonds from the University of Utah identified the Ephemeroptera and Dr. M. J. Westfall, Jr. from the University of Florida confirmed the identifications of the Odonata. The Water and Energy Research Institute at the University of Guam provided transportation into the field and many graduate students voluteered their time to hike up muddy streams and collect samples. And finially, Bruce Neill assisted in all phases of this research; his unselfish support was instrumental in the completion of this study.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Stream ecologists have long been concerned with the distribution and abundance of invertebrates. A knowledge of distributional patterns is essential to the understanding of community structure and regulation. In temperate streams, many factors influence the distribution of lotic invertebrates, including current velocity (Scott, 1958; Edington, 1968; Hynes, 1970), substrate characteristics (Cummins and Lauff, 1969; Minshall and Minshall, 1977; Reice, 1977; Hart, 1981) and the sources and forms of organic inputs (Ross, 1963; Petersen and Cummins, 1974; Reice, 1980). Temperate communities of stream invertebrates are thought to be organized so that optimal resource utilization is accomplished through species replacement on both longitudinal and temporal scales (Vannote et al., 1980; Winterbourn et al., 1981; Statzner and Hilger, 1985).

Although fewer studies have been carried out in the tropics, some information on the distribution of invertebrates in both continental and insular streams is available. In continental streams, the presence or absence of prawns in Malayan streams was correlated with the ability to tolerate salinity (Johnson, 1967). Substrate characteristics were important factors governing distribution within a given Malayan stream

(Bishop, 1973), and leaf litter was a major determinant in the abundance of stream invertebrates in the Amazon (Walker and Ferreira, 1985). In insular tropical streams, Hunte (1978) found that an ability to tolerate salinity influenced community composition in Jamaican streams. Harrison and Rawkin (1975) reported invertebrate densities to be highest in litter debris, and at sites of agricultural eutrophication in the Virgin Islands. To date, the distributional ecology of the stream invertebrates in the Indo-Pacific remains undescribed.

The invertebrate communities of insular tropical streams are interesting groups for study because they differ in many aspects from communities in temperate streams. One difference is that freshwater caridean shrimps of the family Atyidae are often the dominant invertebrates in insular tropical systems throughout the world (Hunte, 1978; Bright, 1982; Chase, 1983). Another difference is that shredder guilds are reduced or absent in many tropical streams. In small temperate streams, shredder guilds play an important role in detrital processing (Cummins et al., 1973; Anderson and Sedell, 1979). The absence of such groups in tropical streams would result in different structure and functioning within tropical stream communities.

Seasonality in tropical streams is exemplified by seasonal flooding and drying of the stream channels (Zaret and Rand, 1971; Bishop, 1973; Felgenhauer and Abele, 1983). Changes in invertebrate abundances concomitant with seasonal variation in precipitation have been noted (Bishop, 1973; Walker and Ferreira, 1985; Wolda and Flowers, 1985), as has seasonal synchronization of reproduction patterns (Abele and Blum, 1977; Walker and Ferriera, 1985). Community response to environmental variation would be predicted to differ between temperate and tropical streams subjected to different seasonally associated changes in the physical environment.

The quantification of the relationship between stream organisms and their environment has been generally achieved through correlative analyses or by experimental manipulations. Recent work has indicated that secondary production estimates also provide a means of understanding the relationship between consumers and their environments (Benke et al., 1984). Other investigations have demonstrated the need to incorporate an array of habitats to access accurately the overall production of invertebrate populations (Resh, 1977; Benke et al., 1984). Accurate estimates of secondary productivity also require that aspects of species-specific habitat segregation and patchiness be examined. Studies of secondary production of North American benthos are numerous (reviewed by Waters, 1977), but few estimates of invertebrate secondary production in tropical aquatic systems have been made (Rzoska, 1967; Bishop, 1973). Two studies include one lentic habitat (Hart, 1981) and one insular lotic habitat (Bright, 1982); neither examined the influence of site characteristics on secondary production.

Many gaps thus exist in our understanding of invertebrate communities in insular tropical systems. Inference from temperate counterparts will be inaccurate given the environmental and biological differences which exist between the two geographic regions. This thesis was designed to describe the relationships between lotic invertebrates and their environment in an insular tropical stream. Invertebrate responses to seasonality, water quality, current velocity, substrate characteristics and leaf litter were examined. Secondary production and temporal biomass trends of the dominant atyid shrimps (*Atyoida pilipes* Newport, *Caridina nilotica* H. Milne Edwards and *Caridina typus* P. Roux) as influenced by habitat type and substrate size were also assessed.

STUDY SITE

The study site was the Pigua River, a second-order stream on the southwestern tip of Guam, Mariana Islands, (Figure 1). Guam is located at 13° 16' 27"N and has a tropical climate with seasons differentiated by rainfall. Although there is significant variability, the dry season typically extends from December through May, while the wet season occurs from June through November.

The Pigua watershed has an area of 99 ha and an average stream slope of 11.9% (Best and Davidson, 1981). The water is characterized by high total hardness (108.7-180.0 mg/l) and an overall pH range of 6.91-8.33 (Zolan and Ellis-Neill, 1986). Temperatures range from 24.9°C to 28.0°C. Diel temperature variation is greater than annual temperature variation (Zolan and Ellis-Neill, 1986). The underlying substrate is volcanic in origin and the stream traverses three distinct geologic formations (Reagan and Meijer, 1984) and ultimately drains into Bile Bay. Correspondingly, substantial changes in substrate, canopy types and sources of organic inputs occur within short linear distances along the stream.

Four sampling stations were selected on the basis of substrate, canopy, organic inputs and degree of shading (Figure 2). The four stations represent the major habitat types encountered in the river. At each station, sampling was conducted at two sites, one pool and one riffle (Table

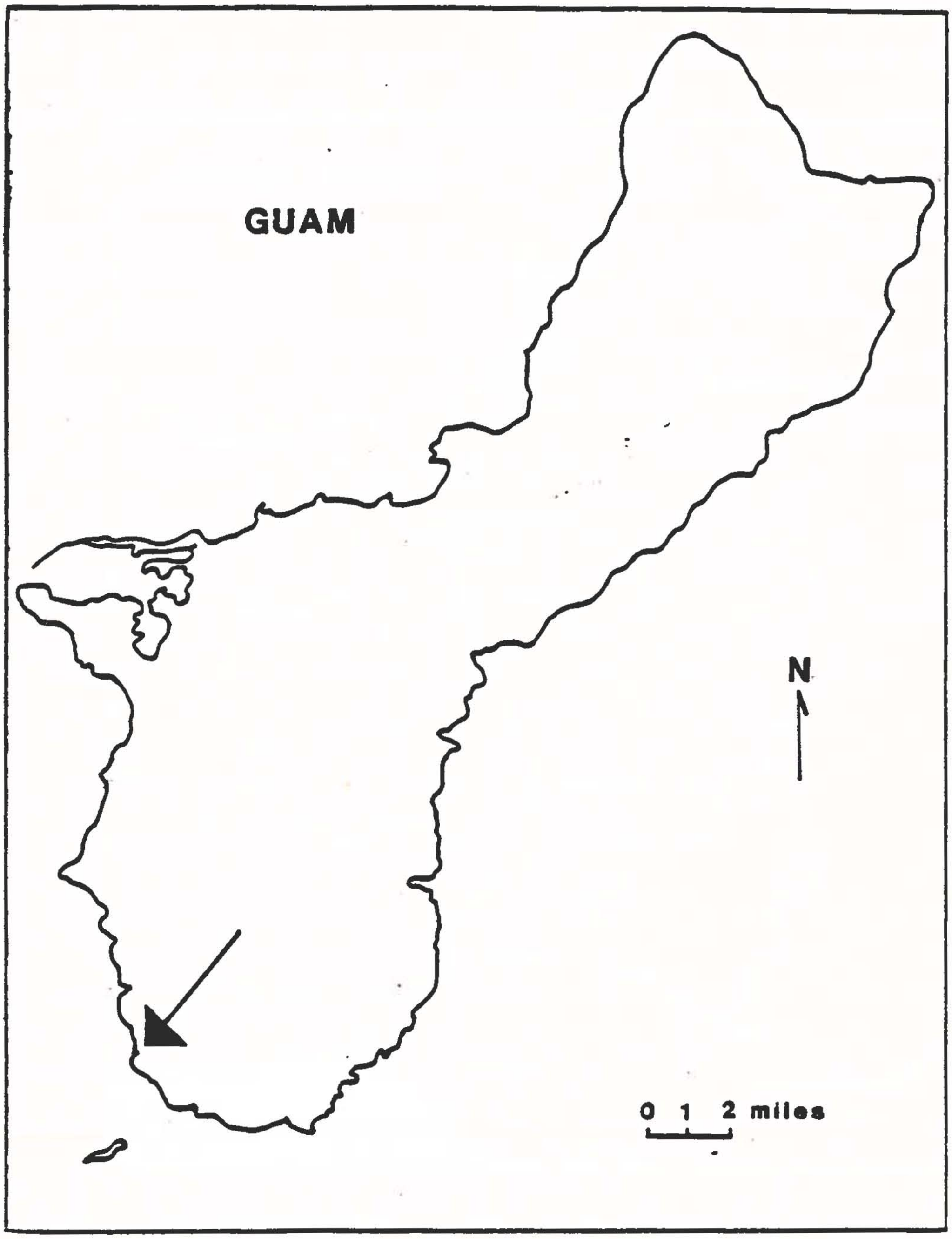

Figure 1. Map of Guam showing the location of the Pigua River.

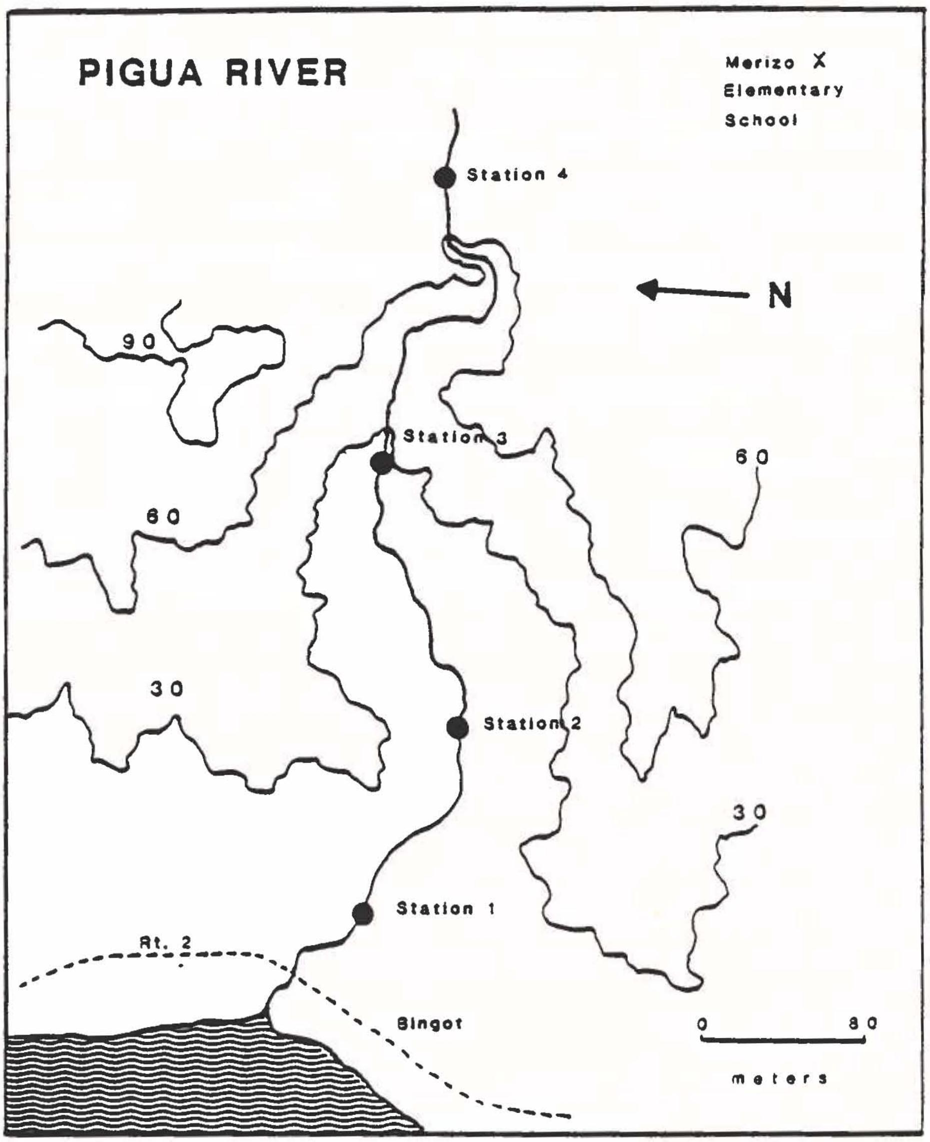

Figure 2. Topographic map of the Pigua River showing the locations of the sampling stations.

1); pools were designated as depositional areas and riffles as erosional areas. This sampling regime permitted comparisons of pools and riffles with similar canopy and often similar substrate types. There were other prevalent differences in the sampling sites. Site 6 was distinct in that the substrate was covered with a mat of fine roots. Sites 7 and 8 were located in a savanna dominated by *Miscanthus floridulus*. These unshaded sites (7 & 8) supported dense algal growth composed of filamentous greens and blue-greens. The algae appeared to be ungrazed and sloughed off continuously throughout the duration of this study, thereby entering the detrital pool of the Pigua River.

Table 1. Summary of sampling site characteristics in the Pigua River. Elevation is given in meters above sea level. Sediment size is based on the phi-scale (Hynes, 1970).

St.	Site	Elevation	Canopy	Pool/Riffle	Sediment Size
1	1	1.5	*Bambusa vulgaris*	pool	0 to 1
	2	1.5	*Bambusa vulgaris*	riffle	-1
2	3	6.6	*Hibiscus tiliaceus*	pool	2 to 3
	4	6.6	*Hibiscus tiliaceus*	riffle	-1
3	5	26.4	*Hibiscus tiliaceus*	pool	-5
	6	26.4	*Hibiscus tiliaceus*	riffle	-6 to -7
4	7	64.5	*Miscanthus floridulus*	pool	-8
	8	64.5	*Miscanthus floridulus*	riffle	-8

MATERIALS AND METHODS

Benthic samples were collected monthly at the four stations between July 1984 and June 1985. At each station, replicate samples were obtained from a pool and a riffle site by placing a quadrat (.01m^2) upstream and adjacent to a benthic net (263 µm mesh). In deep pools, the net was pulled rapidly through the sediments to a depth of 5 cm over a known distance. The substrate was perturbed by hand to a depth of 5 cm and invertebrates and loose substrate were collected. Visual observations indicated little net avoidance with either sampling procedure. In areas of soft substrate, a depth of 5 cm was sampled but at stations in which bedrock was encountered less than 5 cm beneath the substrate surface, the entire substrate profile was disturbed. Additionally, to evaluate the importance of leaf litter, adjacent samples were obtained at Station 1; one sample included submerged leaf litter and the other was without debris. Samples were preserved in the field in 10% formalin and later transferred to 75% ethanol.

After benthic samples were collected, current velocity, pH, dissolved oxygen concentrations and temperature were measured. Current velocity was measured in triplicate with a Pygmy Gurley current meter as close to the substrate as possible in order to get a better indication of the velocity near the benthos. Most current velocity measurements were obtained 3 to 5 cm above the substrate. Dissolved oxygen and temperature were measured with a YSI Model 51B dissolved oxygen and temperature meter. A Corning model 610A pH meter was used to measure the pH of the water. Rainfall was collected and recorded to the nearest 0.1 cm daily near the mouth of the Pigua.

Sediment samples were collected at each sampling site (top 10 cm), dried, sieved by particle size, and weighed. In areas where cobbles or boulders were present, in-field estimates of particle size were made. Particle size was determined four times throughout this investigation according to the classification of Cummins (1962) as modified by Hynes (1970). The particle size range which represented greater than 70 percent of the sediment composition was recorded.

Invertebrates were separated from the benthic samples by using a dissecting microscope; atyid carapace length was measured to the nearest 0.1 mm with a stage micrometer. Specimens were identified on the descriptions by Chase (1983) and Holthius (1965). Odonate larvae were identified according to Lieftnick (1962). Mayflies were identified to the generic level by G. F. Edmunds (pers. comm.). Atyids were grouped into designated size classes for production estimates. Size classes (SC) based on carapace length (in mm) were as follows: SC1) 0.9 - 1.1, SC2) 1.2 - 1.6, SC3) 1.7 - 2.1, SC4) 2.2 - 2.6, SC5) 2.7 - 3.1, SC6) 3.2 - 3.6, SC7) 3.7 - 4.2, SC8) 4.3 - 5.0. Course particulate organic matter (CPOM) was also separated from the benthic sample, dried to a constant weight and weighed.

A product-moment correlation analysis was utilized to evaluate the relationship between current velocity, sediment size, temperature, oxygen concentrations, pH, leaf debris and invertebrate densities in pool and riffle sites. Taxa which were rare or present for only a short period were not included in this analysis. The samples collected at station 1 with and without leaf litter were compared statistically with a paired-comparisons t-test for the most common taxa.

In order to evaluate the effect that leaf type has on invertebrate colonization and abundance, mesh litter bags containing two leaf types and shredded plastic from thick garbage bags were placed in the Pigua River at three sites. The litter bags were constructed of nylon meshing (40 mm^2 mesh size) and were 14 x 19 cm. Senescent leaves of <u>Bambusa vulgaris</u> and <u>Hibiscus tiliaceus</u> were collected prior to abscission. The leaves and plastic were washed with deionized water, dried to a constant weight, preweighed (7.5 g dry weight) and placed into the litter bags. Bags filled with one of the three litter types were attached to substrate in pools between stations 1 and 3. After 8 weeks the bags were removed from the stream by placing an enamel pan under the litter bag and lifting the pan out of the water. As the water depth was always less than 8 cm, there was little chance of losing invertebrates as the pan was lifted out. Invertebrates were picked out of the sample in the field and preserved in 70% ethanol. A 3-way ANOVA (Sokal and Rohlf, 1981) was used to examine the differences in colonization between substrate types.

Dry weights of atyid shrimp were measured for standing stock biomass estimates and production determinations. Three replicate samples for each 0.1mm increment in carapace length were dried and weighed for each species. Specimens were dried at 65°C for 24 hours or until a constant weight was obtained. Size/weight curves were calculated with three different algorithms (linear, logarithmic and exponential). Residual sums of squares were compared to determine the best fit.

Secondary production was estimated by the size-frequency method (Hynes and Coleman, 1968; Hamilton, 1969; Waters and Hokenstrom, 1980) as modified by Benke (1979). According to this method production was calculated by the formula

$$P = N \quad [(D_{a-1} - D_a)(W_a \cdot W_{a-1})^{0.5}]$$

where P is production, N is the number of size classes, D_a is the annual mean density of a size class, W_a is the mean weight of individuals in size class a. Annual production was then calculated for each species by the formula

$$P = P(365/CPI)$$

where the CPI (cohort production interval) is the number of days required for maturity to the largest size class. This method was chosen because it does not require the recognition of cohorts. The asynchronous reproductive cycles typical of many tropical crustaceans preclude the utilization of other methods for secondary production estimates (Waters, 1979). Atyid secondary production was estimated for the entire stream as well as for the eight sites separately. Confidence intervals for production estimates were calculated according to the equations of Krueger and Martin (1980). Cohort production intervals (CPI) were roughly determined by plotting densities of each size class through time for each species. The number of days to mature from a particular size class to another was determined by calculating the days between successive peaks in densities. Because the onset of this investigation followed a period of drought and low densities, it was possible to follow the initial increase in individuals through time to a particular size for each species.

Differences in site production which could be attributed to current velocity and substrate particle size were examined. Sites were categorized as pool or riffle and production differences were tested with paired-comparison t-tests for each species. Production variance correlated with substrate particle size was tested with a Spearman rank correlation analysis.

RESULTS

Physical and Chemical Water Characteristics

Oxygen concentrations, temperature and pH varied between stations and temporally during this study (Table 2). Dissolved oxygen concentrations ranged between 4.6 and 10.1 mg/l ($\bar{X}$=7.44, S^2=1.32); the greatest between-station differences occurred during the dry season. Persistently high oxygen concentrations at station 4 are probably attributable to the dense biomass of filamentous green and blue-green algae. Temperatures ranged from 24.9°C to 30.5°C (Table 2). Diel temperature differences were typically equal to, or greater than, the annual range. The upper stations (3 and 4) in or just below unshaded portions of the stream consistently had the warmest temperatures. The streamwater pH varied between 7.01 and 8.38 (Table 2). The diel pH range was similar to the annual range reported in this study (Figure 3).

No significant correlations were found between the densities of invertebrates and oxygen concentrations, temperature or pH. Oxygen concentrations as low as 4.6 mg/l occurred in deep pools during the dry season, but no changes in community composition coincided with the low oxygen concentrations.

Table 2. Temperature, pH and dissolved oxygen measurements at sampling stations. Dissolved oxygen is given in mg/l.

Dissolved Oxygen

Station	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June
1	7.4	7.8	7.6	6.8	7.6	7.7	6.2	6.4	4.9	5.0	4.6	6.3
2	7.0	7.9	7.8	6.4	7.6	7.2	5.9	6.3	4.8	5.2	5.6	6.8
3	7.5	8.2	8.0	7.1	7.8	8.0	7.1	7.4	7.0	8.5	8.0	8.2
4	8.6	8.9	8.7	8.2	8.2	8.7	8.4	9.1	9.3	9.6	10.1	9.8

Temperature

Station	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June
1	27.0	26.2	26.8	25.1	25.4	25.5	25.4	26.0	25.0	25.9	25.5	25.2
2	27.0	26.2	26.9	26.0	25.4	25.5	25.0	26.0	24.9	26.9	25.2	25.3
3	30.5	26.0	27.0	27.0	25.7	27.2	27.0	28.0	25.8	27.5	26.0	25.8
4	28.5	25.8	28.0	26.0	25.6	26.2	25.1	27.0	26.5	29.0	28.0	26.0

pH

Station	July	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June
1	7.45	7.20	7.51	7.01	7.41	7.41	7.03	7.33	7.31	7.54	7.01	7.01
2	7.59	7.30	7.55	7.20	7.52	7.57	7.12	7.46	7.29	7.50	7.13	7.05
3	8.20	7.08	7.95	7.45	7.80	8.11	8.09	8.30	8.00	8.21	7.91	8.04
4	8.00	7.06	7.98	7.35	7.78	7.89	8.03	8.10	8.38	8.20	7.96	8.06

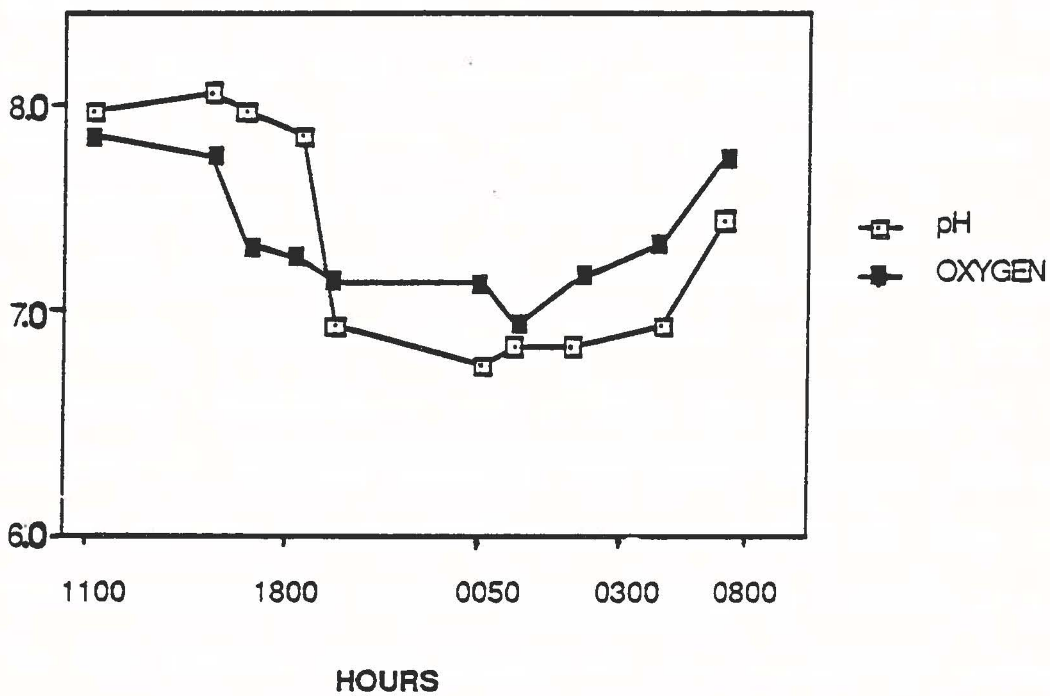

Figure 3. Diel fluctuations of pH and oxygen concentrations at station 4. Oxygen is given in mg/l.

Seasonality

During this investigation, the dry season extended between mid-November and May (Figure 4). Concomitant changes in the composition of the invertebrate fauna occurred (Figure 5). The most notable diference was an increase in the number of taxa during the dry season. Zygopterans, anisopterans, cladocerans, ostracods and copepods were characteristic taxa during the dry season. As the stream flow decreased and pools stabilized, the stream was colonized rapidly by invertebrates more characteristic of lentic environments.

The torrential species were either absent or occurred at lower densities during the dry season. The net-spinning lepidopteran was present only during the rainy season and Atyoida pilipes was more abundant during the rainy season. A temporal replacement of species of Ephemeroptera was found. Pseudocloen sp. occurred during the wet season, while Cloeon sp. was collected during the dry season.

Current Velocity

Current velocity was positively correlated with densities of Atyoida pilipes (P <.05) and negatively correlated with densities of Caridina nilotica (P <.001). Taxa were generally not equally distributed between pool and riffle sites, but occurred predominantly in either pools or riffles. The net-spinning lepidopterans were

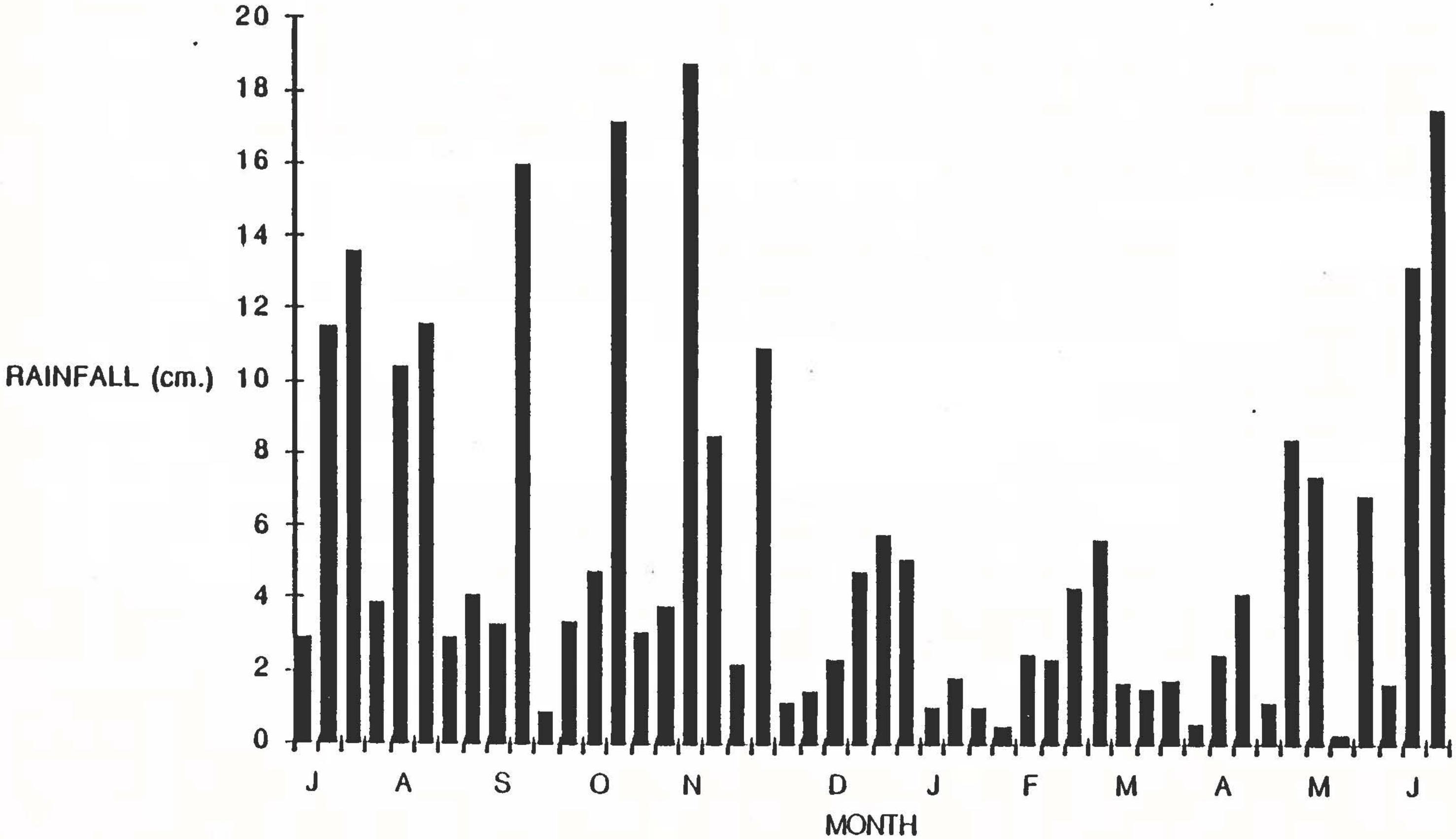

Figure 4. Temporal distribution of rainfall near the mouth of the Pigua River.

TAXA	4 JUL	6AUG	26AU	16SP	28SP	3OCT	1NOV	1DEC	3JAN	1FEB	3MAR	1APR	1MAY
C. TYPUS	G		G		G	G					G	G	
C. NILOTICA	G						G	G		G			
A. PILIPES						G		G	G	G	G		
CLOEON SP.													
PSEUDOCLO. SP.													
LEPIDOPTERA													
ANISOPTERA													
ZYGOPTERA													
CLADOCERA													
ISOPODA													
COPEPODA													
SIMULIDAE													
CERATOPOGONIDS													
OLIGOCHAETA													
CHIRONIMIDAE													

Figure 5. Monthly occurrence of benthic invertebrates in the Pigua River. White regions designate presence and the shaded regions designate absence. Gravid atyids were collected during the months which have a G.

collected only in riffles, whereas odonates were found only in pools. *C. typus* was the only invertebrate which was abundant in both riffles and pools throughout this investigation.

Substrate Particle Size

Substrate particle size was only a minor factor in the distributional patterns of the Pigua River invertebrates. *Caridina nilotica* was negatively correlated with substrate particle size ($P < .01$) and the net-spinning lepidopteran occurred only on consolidated surfaces. No other correlations were found between particle size and distribution or abundance.

CPOM and Invertebrate Distribution

Coarse particulate organic matter (CPOM) inputs were predominantly in the form of leaf litter, represented by bamboo (*Bambusa vulgaris*), pago (*Hibiscus tiliaceus*) and tangen-tangen (*Leucaena leucocephala*). Woody debris was not considered in CPOM calculations and was a rare component of the leaf-litter packs in the Pigua River. In pool sites, CPOM was positively correlated with *Caridina nilotica*, chironomid densities and total number of benthic species (Table 3). In riffles, CPOM and invertebrate denisties were not significantly correlated.

The presence of leaf litter was a major factor in the distribution of benthic invertebrates at station 1 (Figure

Table 3. Results of a multivariate correlation analysis. The product-moment correlation coefficient is given with the significance level noted parantheticaliy below the coefficient. The numbers above the diagonal are pool sites and the numbers below the diagonal are riffle sites.

	C. typus	*C.nilotica*	*A.pilipes*	# Species	Chironimids	CPOM
C. typus		.1478 (.333)	.0697 (.649)	.3097 (.038)	-.0574 (.708)	.0039 (.982)
C. nilotica	-.0860 (.634)		-.0764 (.618)	.3286 (.028)	.4649 (.001)	.6494 (.0001)
A. pilipes	.4933 (.004)	-.1343 (.845)		.2949 (.049)	-.0538 (.726)	-.0930 (.606)
# Species	.1669 (.353)	.3445 (.050)	.0585 (.747)		.3824 (.009)	.4080 (.018)
Chironmidae	.1507 (.402)	-.0551 (.761)	.0481 (.790)	.4479 (.009)		.7118 (.0001)
CPOM	.0738 (.683)	-.0354 (.845)	.0391 (.829)	.2080 (.245)	.2045 (.254)	

6). Densities of Caridina nilotica (t=2.93, P<.05), Caridina typus (t=2.44, P<.05), mayflies (t=5.06, P<.001), and overall invertebrate densities (t=2.66, P<.05) were positively correlated with the amount of bamboo litter in a sample.

Colonization in Litter Bags

Species which colonized leaf-litter bags were dominated by Caridina typus and C. nilotica, the mayfly Cloeon sp., and the damselfly Ischnura aurora auror. Chironomids and oligochaetes were also present but were not included in the ANOVA calculations because they are predominantly sediment dwellers. Additionally, two odonate larvae were recovered from the litter bags. Total numbers of particular taxa found in a litter bag were used for the ANOVA instead of densities. No signifcant variation could be attributed to the differences in substrate present in the bags (Table 4). These results contradict the findings of temperate studies where leaf type and degree of microbial conditioning affect both the community composition and abundance of benthic invertebrates (Petersen and Cummins, 1974; Sedell et al., 1975; Reice, 1980). Although not significant, the greatest variance in invertebrate colonization was attributable to differences between localities of litter bags. The lack of significance in this analysis may result from the low number of replicates.

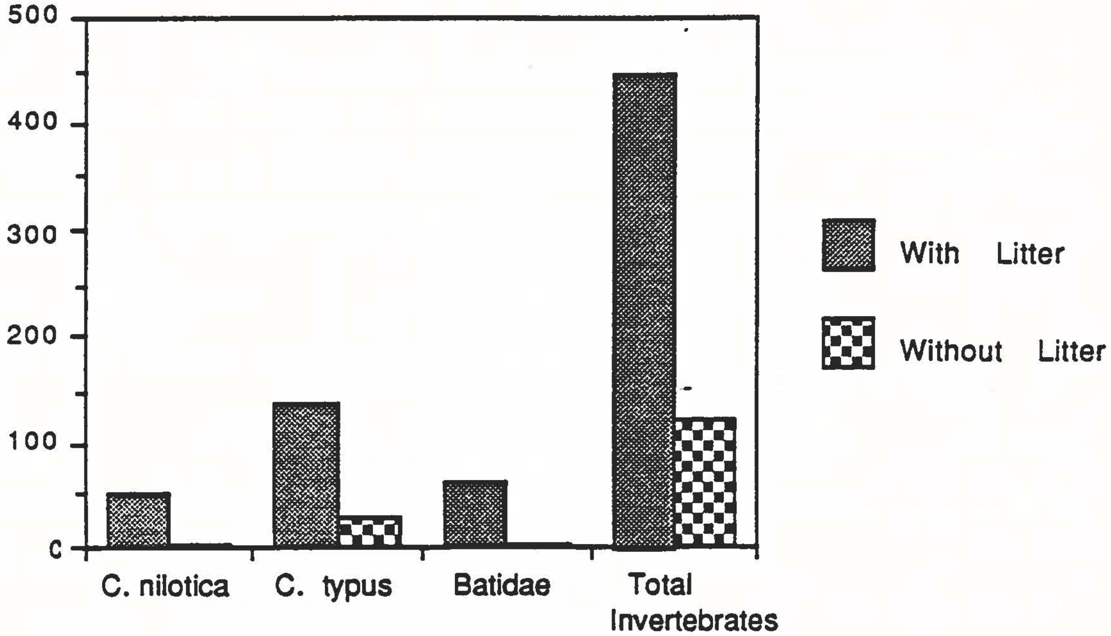

Figure 6. Invertebrate densities at station 1 collected with and without leaf litter.

Table 4. ANOVA table from litter bag experiment.

Variable		d.f.	SS	MS	Fs
A	Site	2	1179.5000	589.7500	
B	Species	3	1172.0833	390.6944	
C	Litter	2	225.1667	112.5834	
AxB		6	1207.8334	201.3056	3.0597 n.s.
AxC		4	219.8333	54.9538	0.4801 n.s.
BxC		6	668.8333	114.4722	1.7399 n.s.
AxBxC		12	789.5000	65.7916	

Secondary production and Atyid Biomass

Monthly standing stock and densities fluctuated asynchronously between the three species of atyid shrimps throughout the year (Table 5). The only similar patterns of the three species were low densities and biomass estimates during July and August of 1984 (Table 5). The dry season of 1984 was extremely dry and in June the Pigua River was reduced to a series of pools with little water flowing between them; only sites 5 through 8 had any flow.

Mean densities and biomass of Atyoida pilipes increased from September through December and then declined during the period from February to May (Figure 7); these times correspond to periods of heavy rainfall and reduced rainfall, respectively (Figure 4). A. pilipes was most common in riffle habitats or where current velocity exceeded 10 cm/sec. Peak standing crop occurred in January, near the cessation of the wet season. Bright (1982) observed peak densites of A. pilipes during February which is also near the end of the wet season in the Palau Islands.

Caridina typus was the most abundant invertebrate throughout this investigation (densities and biomass, Table 5) and was common in both pool and riffle sites. Densities and biomass of C. typus decreased during the rainy season and increased throughout the dry season (Figure 4). This increase in density was probably a

Table 5. Mean monthly density and biomass estimates of the atyid shrimps. Density (D) is given in individuals/m^2 and biomass (B) units are mg dry wt/m^2.

Date	*A. pilipes*		*C. nilotica*		*C. typus*	
	D	B	D	B	D	B
July 84	8.5	2.3	10.2	9.8	127.4	66.8
Aug. 84	61.3	19.3	18.6	3.5	123.1	54.0
Aug. 84	117.5	25.7	71.0	14.8	214.6	65.1
Sept.84	180.1	36.9	73.0	12.7	352.0	29.5
Oct. 84	180.6	34.7	84.4	9.8	243.4	24.4
Nov. 84	120.2	17.8	66.2	13.1	289.3	51.1
Dec. 84	125.4	31.5	117.5	20.4	260.7	39.3
Jan. 85	172.3	40.3	104.0	20.3	543.2	52.2
Feb. 85	73.8	23.1	47.0	10.4	573.3	68.7
Mar. 85	54.0	9.1	42.0	16.7	696.4	96.8
Apr. 85	53.9	7.9	50.0	21.6	652.8	114.7
May 85	108.9	18.8	30.8	19.6	846.0	130.0
June 85	61.1	18.6	35.2	14.1	637.7	114.6

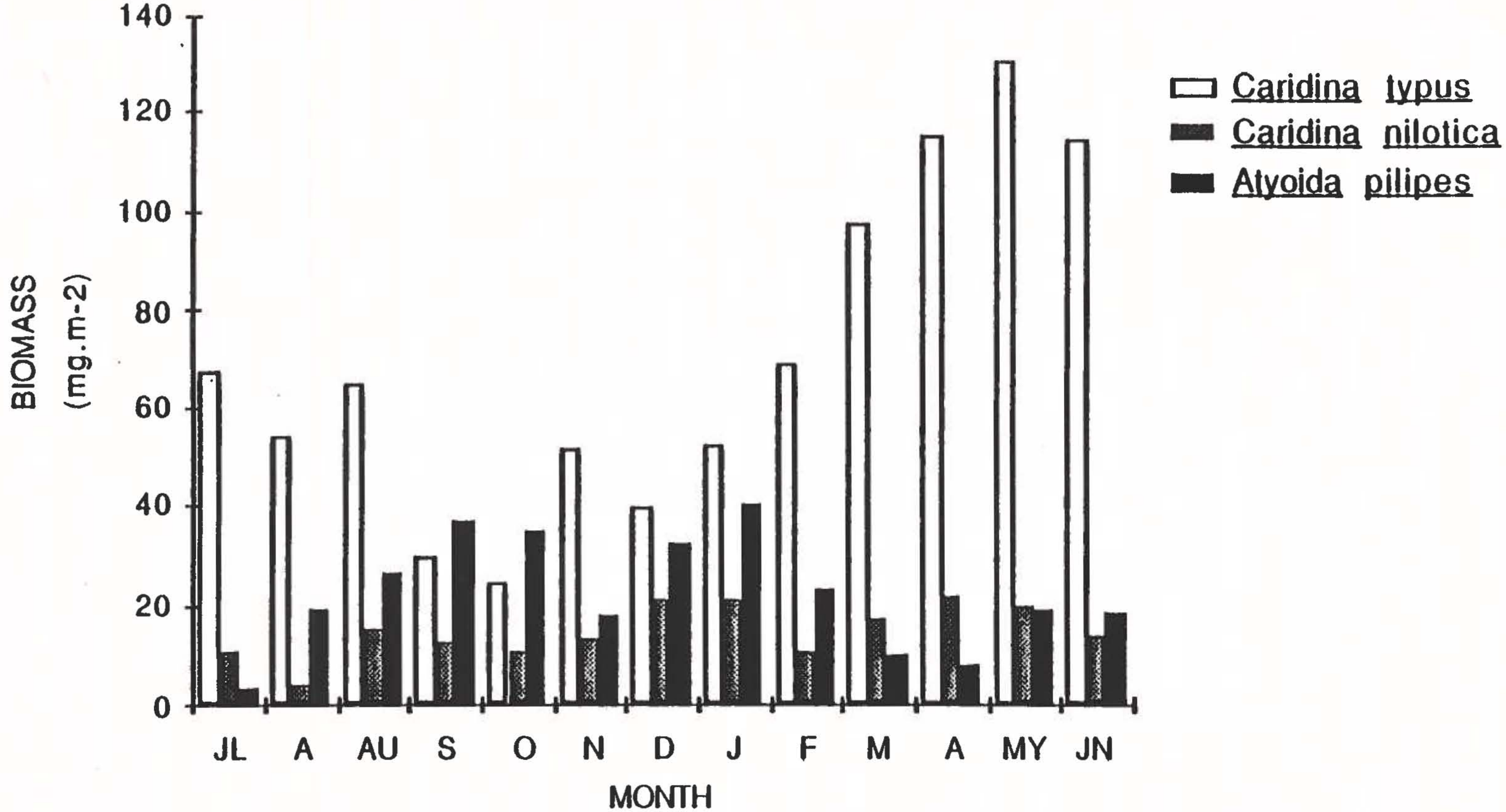

Figure 7. Monthly biomass patterns of atyids in the Pigua River.

function of higher juvenile survivorship during dry periods along with a physical concentration of individuals as the stream channel narrowed.

Caridina nilotica was the least common atyid, which is evident from the low density and biomass estimates (Table 5). Peak densities occurred in December and January, corresponding to a period of increased juvenile abundance. C. nilotica was found almost exclusively in pools and the highest densities occurred in the deepest pools. No general trend was noted for temporal biomass or density fluctuations of C. nilotica.

Annual mean density (all sites) and weight at loss used in production estimates are presented in Table 6. Weight at loss is the difference between the geometric means of successive size classes; this estimate represents the loss of biomass through maturation of a cohort and is used in the secondary production estimates. Weight estimates were derived from length-to-dry-weight curves and geometric means of sequential size class weights represent the weight at loss. Size-to-weight relationships were best described by an exponential equation for all three species. Cohort production intervals (CPI), or the average period required for growth, can have a large influence on production estimates and should be adjusted for in the calculations of secondary production (Benke, 1979; Waters, 1979). The

Table 6. Annual mean density (D) and weight at loss (ΔW) for each size class of atyids. Densities are given in individuals/m^2 and weight at loss is given in mg.

Size Class	*A. pilipes*			*C. nilotica*			*C. typus*		
	D	ΔD	ΔW	D	ΔD	ΔW	D	ΔD	ΔW
1	33.1			16.9			135.8		
2	24.6	8.5	0.032	12.4	4.5	0.071	120.5	15.3	0.049
3	18.9	5.7	0.059	10.9	1.5	0.112	92.7	27.8	0.082
4	7.6	11.3	0.106	5.9	5.0	0.175	32.5	60.2	0.139
5	5.9	1.7	0.191	3.6	2.3	0.237	19.6	12.9	0.235
6	4.8	1.1	0.348	2.9	0.7	0.427	15.3	4.3	0.398
7	3.6	1.2	0.628	2.3	0.6	0.668	8.8	6.5	0.632
8	2.8	0.8	1.137	1.0	1.3	1.050	3.1	6.0	1.137
		2.8	2.059		1.0	1.631		3.1	1.920

time required for _Caridina typus_ to mature from size class 1 to 7 in this study was 270 to 290 days. Estimates of the days required to attain the largest sizes were not possible because densities in the larger size classes were always low. Since the rate of growth decreases gradually with increasing size in crustaceans (Teissier, 1960), another 80 days probably is required for _C. typus_ to attain its largest size. This assumption makes the CPI of _C. typus_ 350 to 370 days or roughly one year. _A. pilipes_ developed from size class 1 to 7 in 180 to 210 days. If it is assumed that another 80 days is required for _A. pilipes_ to attain its largest size, a CPI of 260 to 290 days results; 280 days was used for calculations. The time required for _C. nilotica_ to develop from size class 1 to 5 was 218 to 270 days. Densities of _C. nilotica_ were generally low, and the increase in individuals above size class 5 was difficult to follow, so that the CPI is assumed to be one year.

Overall estimates (all sites combined) fall within the range reported for crustacean species in temperate regions (Waters, 1977); although estimates derived from this study fall on the low end of previously reported rates of crustacean secondary production. _Caridina typus_ had the highest overall secondary production rate of the three species (Table 7). Secondary production of _Atyoida pilipes_ in the Pigua was similar to production rates for

Table 7. Standing stock, annual production and turnover ratio of atyids in the Pigua River. Production confidence intervals are noted parenthetically.

Species	Mean Standing Stock, mg/m^2	Production mg/m^2/yr	Annual P/B
A. pilipes	21.54	100.09 (26.61)	4.70
C. nilotica	13.62	45.48 (8.94)	3.34
C. typus	70.49	259.60 (65.12)	3.68

A. pilipes in the Palau Islands (Bright, 1982), and the turnover ratio was higher than the ratio (3.7) reported by Bright (1982). Confidence intervals represented 20 to 25 percent of production estimates (Table 7), indicating high variability in the production estimates.

Table 8 lists secondary production of each species by site. Production differences between sites were high and mirrored the heterogeneous distribution of the atyids. Site 4 had the highest production of Caridina typus and Atyoida pilipes and also supported the highest overall secondary production. The fine rooted substrate of site 4 supported high densities of many benthic invertebrates. Confidence intervals of site production estimates (Table 8) were 3 to 20 percent, 6 to 15 percent and 2 to 26 percent of the production rates for A. pilipes, C. nilotica and C. typus, respectively.

Comparisons of production rates for each species in pool and riffle sites were made using paired-comparison t-tests (Table 9). Production of Atyoida pilipes was significantly higher ($P<.05$) in riffles, whereas Caridina nilotica production was significantly higher ($P<.05$) in pools. No significant difference was noted for C. typus production in pools or riffles.

No significant correlations were found between particle size and production for any species, although production of Atyoida pilipes was at least an order of

Table 8. Annual secondary production for eight sampling sites on the Pigua River. Production values are given in $mg/m^2/yr$. Confidence intervals are given parenthetically below site production estimates.

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site Mean
<u>A</u>. <u>pilipes</u>	0.4	76.8	0.4	273.1	8.9	109.5	113.2	251.9	82.9
	(1.90)	(18.22)	(1.90)	(12.61)	(2.38)	(22.14)	(21.46)	(25.62)	
<u>C</u>. <u>nilotica</u>	53.0	6.2	140.0	33.6	39.8	1.8	74.1	8.6	44.6
	(4.63)	(0.68)	(8.27)	(5.60)	(5.26)	(3.89)	(7.30)	(2.99)	
<u>C</u>. <u>typus</u>	99.8	135.3	7.2	1379.8	153.8	277.1	25.2	33.4	264.0
	(5.22)	(8.82)	(2.62)	(21.58)	(3.43)	(8.09)	(6.77)	(4.25)	
Total	153.2	202.5	147.5	1620.8	200.7	365.9	89.2	242.1	

Table 9. Results of paired-comparisons t-test for production estimates in pool and riffle habitats. Sampling site is noted parenthetically beside production estimates. Estimates are given in $mg/m^2/yr$.

Species	Production Pools	Production Riffles	Difference	t_s
A. pilipes	0.4 (1)	76.8 (2)	76.4	3.359*
	0.4 (3)	273.1 (4)	272.7	
	8.9 (5)	109.5 (6)	100.6	
	113.2 (7)	251.9 (8)	138.7	
C. nilotica	53.0 (1)	6.2 (2)	46.8	4.222*
	140.0 (3)	33.6 (4)	106.4	
	39.8 (5)	1.8 (6)	38.0	
	74.1 (7)	8.6 (8)	65.5	
C. typus	99.8 (1)	135.3 (2)	35.5	1.166 n.s.
	7.2 (3)	1379.8 (4)	1372.6	
	153.8 (5)	277.0 (6)	123.2	
	25.2 (7)	33.4 (8)	8.2	

* $p < .05$

magnitude lower in sites with particle sizes smaller than 0 (phi scale).

DISCUSSION

Seasonality

Within the Pigua River, seasonal changes in invertebrate abundance and community composition were apparent throughout this study. Seasonality within tropical streams has also been documented in many other geographic regions (Zaret and Rand, 1971; Bishop, 1973; Felgenhauer and Abele, 1983). Bishop (1973) attributed the seasonal differences in abundance of invertebrates to scouring of the streambed during flooding periods. Scouring of the streambed was probably an important factor in the seasonal trends within the Pigua River; this is supported by the fact that invertebrates characteristic of slower waters were collected only during the dry season.

Reproduction of the atyids did not follow a seasonal periodicity however. Bright (1982) also reported no sychronization of reproduction with seasonal discharge in atyid populations. On the other hand, Abele and Blum (1977) found that atyids of the Perlas Archipelago, Panama reproduced throughout the wet season. Additionally, clear seasonal reproductive patterns within the paleomonid shrimps of the Central Amazon have been reported (Walker and Ferreira, 1985). The significance of continual versus seasonal reproduction of the atyids is not clear. Larval dispersal and survivorship may influence the periodicity of reproduction of atyids. The low densities and biomasses of all three atyid species during the onset of this investigation were probably a result of the extensive drought of 1984. Although low water levels would tend to concentrate individuals, the drying of the streambed and elimination of most flowing water were probably the causes of the low densities. During years of higher rainfall, densities and production rates may be greater than those reported in this investigation.

Distributional Factors

The distributional dynamics of benthic invertebrates was a function of several factors and probably a result of the interactions between these factors. Current velocity, substrate particle size and the amount of CPOM were all important distributional parameters. Additionally, each species uniquely responded to environmental gradients and should be considered independently in any distributional study. Physical and chemical water characteristics did not influence the distribution of benthic invertebrates in this study. Alternatively, Hunte (1978) found that oxygen, temperature and current velocity were influential in the distribution of Jamaican freshwater shrimps. The difference in these findings is probably a matter of scale, as the Jamaican study compared regional and altitudinal distributions.

Some patterns of distribution did emerge from this investigation. The presence of leaf litter was a major factor in distribution within pools, but not in riffles. Taxa characteristic of riffles were either filter feeders or grazers, whereas those of pools were scrapers or collector-gatherers. Riffle communities are clearly dependent on seston or algal production for nutrition and are thus independent of large particles of detritus entering the stream. In temperate streams, species assemblages associated with leaf litter are often dominated by shredder guilds (Cummins et al., 1973; Petersen and Cummins, 1974; Anderson and Sedell, 1979). The direct utilization of leaf litter as a food source is an obvious proximal reason for the association with leaf litter. In the Pigua River, shredders are absent. The similar colonization patterns of inorganic and organic substrates in the litter bags support the idea that the role of litter in distribution is in the provision of structure to an associated flora and fauna. Bishop (1973) found that substrate characteristics were important in governing invertebrate distributions in a Malayan stream and suggested that the microfauna associated with the leaf materials may be more important than the leaf products. Walker (1985) found an abundant microfauna associated primarily with submerged leaf litter in the Amazon and high densities of macroinvertebrates in the leaf packs (Walker and Ferreira, 1985).

The abundances and distributions of atyids in the Pigua River can to a large extent be correlated with their feeding behaviors and degree of specialization. Several studies have described in detail the functional feeding morphology of atyid cheliped setae (Felgenhauer and Abele, 1983; Fryer, 1960; 1977). These studies have delineated two types of cheliped setae; short comb-like setae are often utilized in scraping the substrate and longer feather-like setae are utilized in filtering seston. Filtering is accomplished through the extension of cheliped setae which form a fine sieve in the water column (Couret, 1976). Individual Atyoida pilipes possess only filtering setae on their chelipeds; the absence of scraping setae suggests that A. pilipes feeds by means of filtering seston. Reductions in A. pilipes throughout the dry season result from reduced flow and associated decrease in seston abundance. Caridina typus has both scraping setae and longer filtering setae which would allow feeding in a variety of flow regimes. As mentioned earlier, C. typus was common in both pools and riffles. This indicates that C. typus is a generalist in feeding mode and distribution. Individuals of C. nilotica also possess both scraping setae and longer filtering setae. Setal-to-body-length-ratios of this species are smaller than the ratios of individuals of C. typus, indicating that _C_. _nilotica_ has proportionally shorter filtering setae. Other studies (Fryer, 1960) found _C_. _nilotica_ to be characteristic of standing water, and this species appears to be confined to pools in the Pigua.

Secondary Production

The confidence intervals for site-specific production were relatively smaller by 10 to 15 percent than the overall production confidence intervals for all three atyids. This indicates that the high variability in secondary production can to a large extent be attributed to site differences in production. Any further investigations of tropical secondary production, or nutrient regeneration by invertebrates or other ecological studies should incorporate many sites within a particular river.

Secondary production was highest within the fine roots at station 2. The significance of the root system to the biology of the atyids is not known but conceivably the roots provide both habitat and increased surface area from which to scrape detrital and autochthonous materials. Thus, the roots may be analogous to leaf litter within the stream in terms of their role in the distribution of the shrimps.

Segregation of site-production rates for each species supported the descriptive results of atyid distribution. In particular, _Atyoida_ _pilipes_ had significantly higher production in riffles, coincident with the positive correlation between density and current velocity of this species. Caridina typus was productive in both riffle and pools and appears capable of exploitation under a variety of conditions. C. typus also was the most productive atyid throughout this investigation. The high production of C. typus may be attributable to the flexibility of feeding modes and an ability to reside in a variety of flow regimes in a stream in which spatial and temporal environmental changes dominate. C. nilotica on the other hand, was significantly more productive in pools. Again, this supports the negative correlation found between C. nilotica and current velocity. Production of C. nilotica has been reported to be as high as $24g/m^2/yr$ in the littoral of Lake Sibaya (Hart, 1981). C. nilotica production in the Pigua River was several orders of magnitude lower ($.045g/m^2/yr$). That there is a large difference in these production rates supports the previous suggestion that C. nilotica is primarily a lentic species and not living in optimal conditions in the Pigua.

Secondary production in the unshaded sites (7 and 8) was not notably higher than those of other sites for any species. These results do not support the results of Behmer and Hawkins (1986) who found secondary production to be higher in open sites as opposed to shaded sites for most taxa in a temperate stream. The disparity in the

Pigua data probably results from the differences in functional feeding groups; atyid shrimps are either filter-feeders, collector-gatherers, or both, but not grazers.

The secondary production rates reported in this study have several potential sources of error. First, sexual size differences exist in all three species and sexes were not differentiated in this investigation. Mean weights used for the largest size classes reflect an average maximum size attained for both sexes. This would probably result in an underestimation of secondary production rates. Partial to total protandry has been described for other species of Atyoida (Carpenter, 1978; 1983); if A. pilipes is protandrous, then this source of error would not apply. Second, The CPI of the Pigua atyids was crudely estimated. If further studies indicate a CPI other than reported in this investigation, corrections of these production estimates will need to be made. The potential sources of error outlined above should not influence the use of secondary production to describe the association of the atyids and their habitat because all sites were treated equally.

Production rates for atyid shrimps in the Pigua were not notably high despite the persistence of warm stream temperatures. It is suggested that the seasonal floods and droughts influence the surivorship and production of atyids in the Pigua. Secondly, the assessments of secondary production rates in an insular tropical stream are largely affected by the choice of habitats in which sampling is carried out. Atyid feeding mechanisms and microdistribution appear to be important considerations in their production dynamics.

CONCLUSIONS

The invertebrates of the Pigua were patchily distributed along several environmental gradients, including current velocity, sediment size and leaf litter. Seasonality in stream flow had the largest effect on community structure; invertebrate community changes included an increase in lentic species during the dry season and a temporal replacement of species in certain taxa. The spatial distribution of atyid secondary production supported the other observations on important distributional factors. Production rates for atyid shrimps in the Pigua River were not notably high despite the persistence of warm stream temperatures. Atyid feeding mechanisms and microdistribution were important considerations in their production dynamics.

LITERATURE CITED

Abele, L., and N. Blum. 1977. Ecological aspects of the freshwater decapod crustaceans of the Perlas Archipelago, Panama. Biotropica 9:239-252.

Anderson, N. H., and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Ann. Rev. Entomol. 24:351-377.

Behmer, D. J., and C. P. Hawkins. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. Freshwater Biol. 16:287-300.

Benke, A. C. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnol. Oceanogr. 24:168-171.

Benke, A. C., T. C. VanArsdall, Jr., and D. M. Gillespie. 1984. Invertebrate productivity in a subtropical blackwater river:the importance of habitat and life history. Ecol. Monogr. 54:25-63.

Best, B. R., and C. E. Davidson. 1981. Inventory and atlas of the inland aquatic ecosystems of the Marianas Archipelago. Univ. Guam Mar. Lab. Tech. Rep. No. 75. 226 p.

Bishop, J. E. 1973. Limnology of a small Malayan river, Sungai Gombak. W. Junk, Publ., The Hague. 431 p.

Bright, G. R. 1982. Secondary benthic production in a tropical island stream. Limnol. Oceanogr. 27:472-480.

Carpenter, A. 1978. Protandry in the freshwater shrimp, Paratya curvirostris (Heller, 1872) (Decapoda:Atyidae), with a review of the phenomenon and its significance in the Decapoda. J. Roy. Soc. N.Z. 3:343-358.

Carpenter, A. 1983. Population biology of the freshwater shrimp Paratya curvirostris (Heller,1862) (Decapoda:Atyidae) N.Z. J. Mar. Freshwater Res. 17:147-158.

Chase, F. A., Jr. 1983. The Atya-like shrimps of the Indo-Pacific region (Decapoda:Atyidae). Smithson. Contrib. Zool. 384:1-54.

Couret, C. 1976. The biology and taxonomy of a freshwater shrimp, Atya bisulcata Randall, endemic to the Hawaiian Islands. M.S. Thesis, Univ. Hawaii. 166 p.

Cummins, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. Am. Midl. Nat. 67:477-504.

Cummins, K. W., and G. F. Lauff. 1969. The influence of substrate particle size on the microdistribution of stream macrobenthos. Hydrobiol. 34:675-692.

Cummins, K. W., R. C. Petersen, F. O. Howard, J. C. Wuycheck, and V. I. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54:336-345.

Edington, J. M. 1968. Habitat preferences in net-spinning caddis larvae with special reference to the influence of water velocity. J. Anim. Ecol. 37:675-692.

Felgenhauer, B. E., and L. G. Abele. 1983. Ultra-structure and functional morphology of feeding and associated appendages in the tropical freshwater shrimp Atya innocous (Herbst) with notes on its ecology. J. Crustacean Biol. 3:336-363.

Fryer, G. 1960. The feeding mechanism of some atyid prawns of the genus Caridina. Trans. R. Soc. Edinb. 64:217-244.

Fryer, G. 1977. Studies on the functional morphology and ecology of the atyid prawns of Dominica. Phil. Trans. R. Soc. London B. 279:57-129.

Hamilton, A. L. 1969. On estimating annual production. Limnol. Oceanogr. 14:771-782.

Harrison, A. D., and J. J. Rawkin. 1975. Forest litter and stream fauna on a tropical island, St. Vincent, West Indies. Verh. Internat. Verein. Limnol. 19:1736-1745.

Hart, R. C. 1981. Population dynamics and production of the tropical and freshwater shrimp Caridina nilotica (Decapoda:Atyidae) in the littoral of Lake Sibaya. Freshwater Biol. 11:531-547.

Holthius, L. B. 1965. The Atyidae of Madagascar. Mem. Mus. Natl. Hist. Nat. 33:1-48.

Hunte, W. 1978. The distribution of freshwater shrimps (Atyidae and Palaemonidae) in Jamaica. Zool. J. Linn. Soc. 64:135-150.

Hynes, H. B. N. 1970. The ecology of running waters. Univ. of Toronto Press, Toronto. 555 p.

Hynes, H. B. N., and Coleman, M. J. 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13:569-573.

Johnson, D. S. 1967. Some factors influencing the distribution of freshwater prawns in Malaya. In Proc. Symp. Crustacea at Ernakulam, Jan. 12 to 15, 1965. 1:428-433.

Krueger, C. C., and F. B. Martin. 1980. Computation of confidence intervals for the size-frequency (Hynes) method of estimating secondary production. Limnol. Oceanogr. 25:773-777.

Lieftnick, M. A. 1962. Insects of Micronesia, Odonata. Bernice P. Bishop Museum. Vol. 5:1-95.

Minshall, G. W., and J. N. Minshall. 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (USA) stream. Hydrobiol. 55:231-249.

Petersen, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biol. 4:343-368.

Reagan, M. K., and A. Meiger. 1984. Geology and geochemistry of early arc-volcanic rocks from Guam. Geol. Soc. Am. Bull. 95:701-713.

Reice, S. R. 1977. The role of animal associations, current velocity and sediments in lotic litter decomposition. Oikos 29:357-365.

Reice, S. R. 1980. The role of substratum in benthic macroinvertebrate microdistribution and litter decomposition in a woodland stream. Ecology 61:580-590.

Resh, V. H. 1977. Habitat and substrate influences on population and production dynamics of a stream caddisfly <u>Ceraclea ancylus</u> (Leptoceridae). Freshwater Biol. 7:261-277.

Ross, H. H. 1963. Stream communities and terrestrial biomes. Arch. Hydrobiol. 59:235-242.

Rzoska, J. 1967. Freshwater productivity in the tropics: notes on secondary level studies. J. Anim. Ecol. 36:15.

Sedell, J. R., R. J. Triska, and N. S. Triska. 1975. The processing of conifer and hardwood leaves in two coniferous forests: I. Weight loss and associated invertebrates. Verh. Internat. Verein. Limnol. 19:1617-1627.

Scott, D. 1958. Ecological studies on the Tricoptera of the River Dean, Cheshire. Arch. Hydrobiol. 54:340-392.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, 2nd edition. Freeman. New York. 859 p.

Stantzer, B., and B. Hilger. 1985. Questions and comments on the River Continuum Concept. Can. J. Fish. Aquat. Sci. 42:1038-1044.

Teisser, G. 1960. Relative growth, p.537-556. In T. H. Waterman [ed.], The physiology of crustacea. Academic Press. 624 p.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Walker, I. 1985. On the structure and ecology of the microfauna in the Central Amazonian forest stream 'Igarape da Cachoeira'. Hydrobiologia 122:137-152.

Walker, I., and M.J.N. Ferreira. 1985. On the population dynamics and ecology of the shrimp species (Crustacea, Decapoda, Natantia) in the Central Amazonian river Taruma-Mirim. Oecologia (Berlin) 66:264-270.

Waters, T. F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 10:91-164.

Waters, T. F. 1979. Influence of benthos life-history upon the estimation of secondary production. J. Fish. Res. Bd. Can. 36:1425-1430.

Waters, T.F., and J. C. Hokenstrom. 1980. Annual production and drift of the stream amphipod *Gammarus dolimnaeus* in Valley Creek, Minnesota. Limnol. Oceanogr. 25:700-710.

Winterbourn, M. J., J. S. Rounick, and B. Cowie. 1981. Are New Zealand stream ecosystems really different? N.Z. J. Mar. Freshwater Res. 15:321-328.

Wolda, H., and R.W. Flowers. 1985. Seasonality and diversity of mayfly adults (Ephemeroptera) in a "nonseasonal" tropical environment. Biotropica 17:330-335.

Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecol. 52:336-342.

Zolan, W. J., and L. Ellis-Neill. 1986. Concentrations of aluminum, iron, and calcium in four southern Guam rivers. WERI Tech. Rep. No. 64. 68 p.