AN ABSTRACT OF THE THESIS OF Catherine J. Leberer for the Master of Science in Biology presented August 29, 1997.

Title: Factors Affecting the Abundance and Distribution of Atyid Shrimps in Two Tropical Insular Rivers.

Approved: Stephen G. Nelson, Chairman, Thesis Committee

Several abiotic and biotic variables were measured to determine the extent to which they influence atyid shrimp densities in two streams on the western Pacific island of Guam. Thirty-six randomly selected sites, composed of three habitat types (riffles, runs, and pools), were surveyed in the rainy and dry seasons. Visual counts of instream fauna were made in 2-square-meter quadrats within each site. Additional abiotic and biotic variables were also evaluated at each site. To test the effect of predators on atyid distribution directly, a transplant experiment involving the jungle perch *Kuhlia rupestris* was conducted in the field. The results of various statistical analyses suggest that habitat and river are major factors affecting atyid distribution on Guam. However, the results of the transplant experiment were striking: no atyids remained in pools containing transplanted *Kuhlia*. The experiment illustrated the major effect of predation by *Kuhlia* on the distribution of atyid shrimp. Both abiotic factors and biotic interactions are important influences of atyid distribution.

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The members of the Committee approve the thesis of Catherine J. Leberer presented

August 29, 1997.

Stephen G. Nelson, Chairman

Charles E. Birkeland

Charles E. Birkeland, Member

John Jenson, Member

Gustav Paulay, Member

ACCEPTED:

Joyce Marie Camacho

JOYCE MARIE CAMACHO
Dean, Graduate School and Research

DATE 9/10/97

FACTORS AFFECTING THE ABUNDANCE AND DISTRIBUTION OF ATYID SHRIMPS IN TWO TROPICAL INSULAR RIVERS

by

CATHERINE J. LEBERER

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

MASTER OF SCIENCE

IN

BIOLOGY

UNIVERSITY OF GUAM

AUGUST 1997

ACKNOWLEDGMENTS

I thank Frank Camacho, Michelle Gaither, and Brent Tibbatts for all their assistance in the field and for their much appreciated senses of humor. I wish also to express my gratitude to the faculty, staff, and my fellow graduate students at the University of Guam Marine Laboratory. I would like to thank Rosemary Leberer for her support and for all the time she spent in libraries locating references unavailable to me. Finally, I would especially like to thank Greg Fulcher for all his support.

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INTRODUCTION

Atyid shrimps are common in the freshwater habitats of oceanic islands and ideally suited for use as bioindicators for lotic ecosystems that are subjected to various forms of disturbance. They are small, numerous, easy to collect, and sensitive to water quality (Jalihal et al., 1994). There are seven recorded species of atyids on the western Pacific island of Guam: *Atyoida pilipes* (Newport), *Atyopsis spinipes* (Newport), *Caridina longirostris* (Milne-Edwards), *Caridina nilotica* (Roux), *Caridina serratirostris* de Man, *Caridina typus* Milne-Edwards, and *Caridina weberi* de Man. All except *Atyopsis spinipes* were seen during this study. *Caridina longirostris* and *C. weberi* are new records for Guam. Voucher specimens of each species (except *A. spinipes*) are deposited in the USNM (United States National Museum, Department of Invertebrate Zoology) and all but *A. spinipes* and *C. longirostris* in the University of Guam invertebrate collections. Adults of *Atyoida pilipes* can be easily identified in the field, but adults of the five species of *Caridina* resemble one another (Bouvier, 1925) and cannot be distinguished without the aid of a microscope. Like most other atyids (Benzie, 1982; Shokita, 1985), those that occur on Guam have numerous small eggs and pelagic larvae. Such atyids are amphidromous, with their larvae drifting downstream to the ocean, developing in the plankton, and migrating back upstream as juveniles.

Few previous studies have addressed the post-larval ecology of atyids. Dudgeon (1985) found temperature fluctuations to affect the distribution of two atyid species in Hong Kong. Ellis-Neill (1987) concluded that current velocity and abundance of leaf litter are important influences of atyid distribution on Guam. Furthermore, Crowl and Covich (1994) determined that the predatory prawn *Macrobrachium carcinus* affects atyid distribution in Puerto Rico. In order to establish effective bioassessment and monitoring programs based on atyids as indicators, more information on the physical and biotic factors affecting their densities and distribution is necessary.

This study addressed the following question: Which abiotic and biotic factors affect the distribution of atyids on Guam? Several abiotic and biotic variables were analyzed including: season, river, reach, habitat, pH, water temperature, maximum depth, canopy cover, substrate composition, abundance of aquatic vegetation, current velocity, and densities of other riverine fauna. These variables were examined with factor analysis, ANOVA (and nonparametric equivalents), and correlation analysis.

Preliminary observations suggested that predation was an important biotic factor influencing atyid distribution. Predation was examined in two ways. First, densities of atyid species were compared with potential predator densities in a correlation analysis. In the streams of Guam, potential predators include the jungle perch *Kuhlia rupestris* (Lacepède), the freshwater eel *Anguilla marmorata* (Quoy and Gaimard), the sleeper goby *Eleotris fusca* (Bloch and Schneider), the Mariana goby *Awaous guamensis* (Valenciennes), and the Tahitian prawn *Macrobrachium lar* (Fabricius). Stomach contents of these species (except *M. lar*) have been found to contain atyids (R.B. Tibbatts, personal communication). Second, to test the effect of predators on atyid distribution directly, a transplant experiment involving *Kuhlia rupestris* was conducted in the field. *Kuhlia* are free-swimming, visual predators, occurring only in the lower reaches of rivers, below barrier waterfalls. If predation by *Kuhlia* is important in determining the distribution of atyids in the streams of Guam, then densities of atyid species would be expected to be lower in pools containing transplanted *Kuhlia rupestris* than in control pools containing no *K. rupestris*.

METHODS

Study Area

Data were collected from two rivers on Guam, the Asmafines River and the Ugum River (Fig.1). The Asmafines River (lat. 13°19′ N; long. 144°39′ E) is a high-gradient stream located in the south on Guam's steeper western slope. The Ugum River (lat. 13°20′ N; long. 144°45′ E) is a long, low-gradient stream located in one of the large drainage basins characteristic of the southeast. The Asmafines has a perennial channel length of 1,341 m and an elevation of 134 m (Best and Davidson, 1981). The Ugum is a major tributary of the Talofofo River and has a main channel length of 11,460 m and an elevation of 183 m (Best and Davidson, 1981). Both rivers are considered relatively undisturbed, but the lower reaches of the Ugum are obstructed by a weir. The weir was built in 1992 by the Public Utility Agency of Guam and is estimated to supply between 7 and 11 million liters of water per day to villages in the southeast (Wiles and Ritter, 1993). The effect of this water removal on current velocity, which may be an important factor in determining atyid densities and distribution, is poorly understood.

Study Sites and Field Methodology

The method for site selection was modified from the stratified random sampling method of Baker and Foster (1992). Habitat types were classified qualitatively as riffles (areas with current, surface turbulence and emergent rocks), runs (areas with current, no surface turbulence and no emergent rocks), and pools (areas with little or no current and no surface turbulence). Both the Asmafines River and the Ugum River were divided into three reaches: upper, middle, and lower, with the intention of choosing 6 sites for each

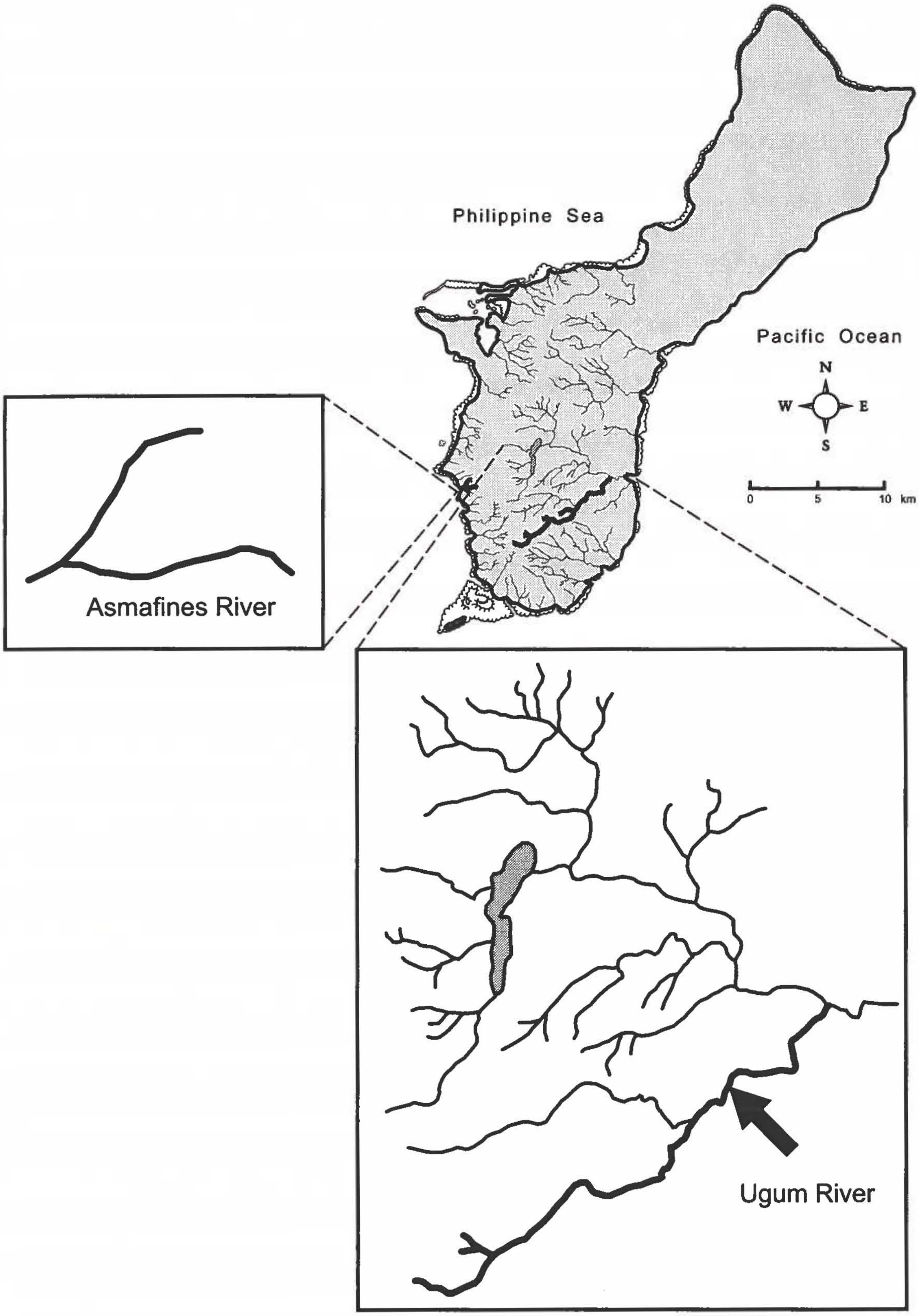

Figure 1. Map of Guam indicating geographic location of study areas.

reach (i.e. 2 of each habitat type). However, no pools were encountered in the lower reach of the Ugum, and there was a paucity of riffles in both the lower reach of the Ugum and the upper reach of the Asmafines. Additionally, during the period of high flow, one run on the lower reach of the Ugum was impossible to survey. Extra riffles and extra runs (one in place of the missing pool) were surveyed in the middle and upper reaches of the Ugum. Therefore, 5 riffles, 6 runs, and 6 pools were surveyed on the Asmafines River, and 7 riffles, 7 runs, and 5 pools were surveyed on the Ugum River, for a total of 36 sites. Because preliminary observations indicated that current velocity may have a major effect on atyid distribution (Ellis-Neill, 1987), data were collected during periods of low flow (March 1996-May 1996) and high flow (September 1996-January 1997) for a total of 72 quadrats. This sample size provided a power of approximately 0.8 (the probability of rejecting the null hypothesis when it is false) in comparisons between species and habitats.

Sites on both rivers were chosen with the aid of a random numbers table. Numbers selected represented the number of habitat types upstream from access points to the reach. For example, for pools, selection of 3 and 5 indicated that the third and fifth pools encountered upstream from the point of access to the reach were surveyed. Sets of numbers were selected for each type of habitat.

Counts were made in 2-square-meter quadrats within the sites. The parameters of each quadrat (1.4 m x 1.4 m) were measured with a tape measure before the counts were made. One quadrat per site was surveyed. In order to provide the most representative estimate of atyid densities, quadrats were not chosen randomly within the sites. Instead, they were determined for each site in a uniform way. Because adults of all atyid species are found more frequently near the edges of rivers, quadrats were located along the right bank (when facing upstream) of the river, at the upstream end of the habitat type. Visual counts were made while snorkeling in the stream or by observations from the bank. Atyids were identified to genus. The quadrat was approached from downstream so as not to disturb the shrimp.

In order to standardize the visual surveying technique, regression analyses were performed, regressing densities determined by visual counts on collection-based density estimates for each genus. In pools and deep runs, collection-based densities were determined by screening off a 0.25-square-meter section in each quadrat surveyed and collecting all individuals within the screened area with a dipnet. However, both the contours of the streambed and the shallow depths of riffles made screening difficult. In these situations the area within the 0.25-square-meter section was swept rapidly and repeatedly with a dipnet while the observer watched with mask and snorkel to insure that all atyids (or very nearly so) were collected. Individuals were fixed on site in vials containing 80% ethanol for later identification in the lab. The position of the 0.25-square-meter section was selected with the use of random numbers chosen between 0 and 10 (i.e. 1-9), representing tenths of the distance across the center of the 2-square-meter quadrat. This point acted as the approximate center of the 0.25-square-meter quadrat.

Data Collection

In addition to atyid density, the following variables were evaluated at each site: 1) pH; 2) water temperature (°C); 3) maximum depth in quadrat (cm); 4) % canopy cover; 5) % cover of bedrock; 6) % cover of boulders; 7) % cover of rubble; 8) % cover of gravel; 9) % cover of sand; 10) % cover of silt; 11) abundance of aquatic vegetation; 12) current velocity (cm/s); 13) *Kuhlia rupestris* density; 14) *Anguilla marmorata* density; 15) *Awaous guamensis* density; 16) *Eleotris fusca* density; 17) *Macrobrachium lar* density; and 18) density of all other gobies combined including: *Sicyopterus macrostetholepis* (Bleeker), *Sicyopus leprurus* Sakai and Nakamura, *Stenogobius* sp., *Stiphodon caeruleus* Parenti and Maciolek, and *Stiphodon elegans* (Steindachner).

The variables were measured in the following ways. pH was measured with a Sper Scientific Digital pH meter® and temperature was measured with a mercury thermometer, both on site. The canopy cover directly over the quadrat was estimated visually to the nearest 10%. This method was tested against a Model-C Robert E. Lemmon forest densiometer® and found to be accurate and more expedient. The percent cover of each substratum type was also visually estimated. Substrata were categorized as bedrock, boulders (>256 mm; i.e. "head-sized"), rubble (>64 mm-256 mm; i.e. "fist-sized"), gravel (>2 mm-64 mm; i.e. "thumb-sized"), sand (>0.2 mm-2 mm; i.e. "grain-sized"), and silt (material 2μ-0.2 mm that can be suspended in the water column) (modified from Baker and Foster, 1992). The % cover of each substratum type was estimated in one-quarter increments and assigned the following values: 0= absent; 1= approximately 25%; 2= approximately 50%; 3= approximately 75%; and 4=100%. Aquatic vegetation was categorized qualitatively as 0= absent, 1= present (found in <50% of quadrat), or 2= abundant (found in >50%). Current velocity was measured at the center of the quadrat, at 0.6 x the total depth, by a Marsh-McBirney® velocity meter. Population densities of other species (variables 13-18) were determined with visual counts, in the same way as atyid densities.

Transplant Experiment

In addition to examining the data with various statistical analyses, a transplant experiment was conducted to test the effect of predation directly. Three pairs of pools, each containing comparable atyid densities, were identified above the barrier waterfall on the Asmafines River. The upstream and downstream access points of these pools were then fenced with 3-cm mesh wire. Atyid densities were again measured after the screens were in place. *Kuhlia* were captured from the lower reaches of the Asmafines, transferred to the pools in 20-l buckets, and released. One to two *Kuhlia* were placed in each of three randomly selected pools. One each was placed in two pools (area=5.22 square meters, *Kuhlia* density=0.19 per square meter; area=7.30 square meters, *Kuhlia* density=0.11 per square meter). Two *Kuhlia* were placed in another pool (area=17.55 square meters, *Kuhlia* density=0.14 per square meter). These densities fell within the range of *Kuhlia* densities determined for this study (0.0-5.0 per square meter). Pools were checked after 24 hours (the pool with two *Kuhlia*) and 48 hours (the other two pools). At that time, atyid densities were determined again for all pools.

Data Analyses

Data analyses were performed with the SOLO® Statistical System for Windows and BMDP New System for Windows®, both published by BMDP Statistical Software, Inc.© (12121 Wilshire Blvd., Suite 300, Los Angeles, CA, 90025). The factor analysis was performed using a correlation matrix factored with orthogonal varimax rotation and eigenvalues greater than one as a stopping rule (Jackson, 1993). For all parametric tests, Levene's test for homogeneity of the variances was conducted and appropriate transformations were performed as needed. When data did not meet the assumptions of ANOVA, even after the transformations, Kruskal-Wallis 1-way ANOVA on ranks and Brown-Forsythe equality of means tests were conducted.

RESULTS

Regression Analyses

The visual surveying technique was standardized to collection-based densities by conducting regression analyses. Figure 2 shows the results of a regression analysis, with *Atyoida* densities determined by visual surveys regressed on collection-based densities of *Atyoida* (r=0.47). Figure 3 illustrates the same type of regression analysis for *Caridina* (r=0.84).

Factor Analysis

Factor analysis identified three major factors that can be referred to as: a "river" factor, a "habitat" factor, and a "season" factor (Table 1). Abiotic variables loaded most heavily on all three factors. River and pH loaded most heavily on the river factor (Table 1). Habitat, depth, and current velocity loaded most heavily on the habitat factor (Table 1). Temperature and season loaded most heavily on the season factor (Table 1). *Caridina* loaded on the habitat factor but not very heavily, and *Atyoida* did not have a loading on any of the factors.

Univariate Analyses

Each variable was compared with densities of *Atyoida* and densities of *Caridina* in a series of univariate analyses. Although many relationships were not found to be significant (i.e. *Atyoida* and *Caridina* vs. pH, temperature, canopy cover, depth, current velocity, and all types of substrata; *Caridina* vs. season and aquatic vegetation), some variables proved to be important influences of atyid distribution. The distribution of atyid species in each river is shown in Figure 4. Although comparable densities of

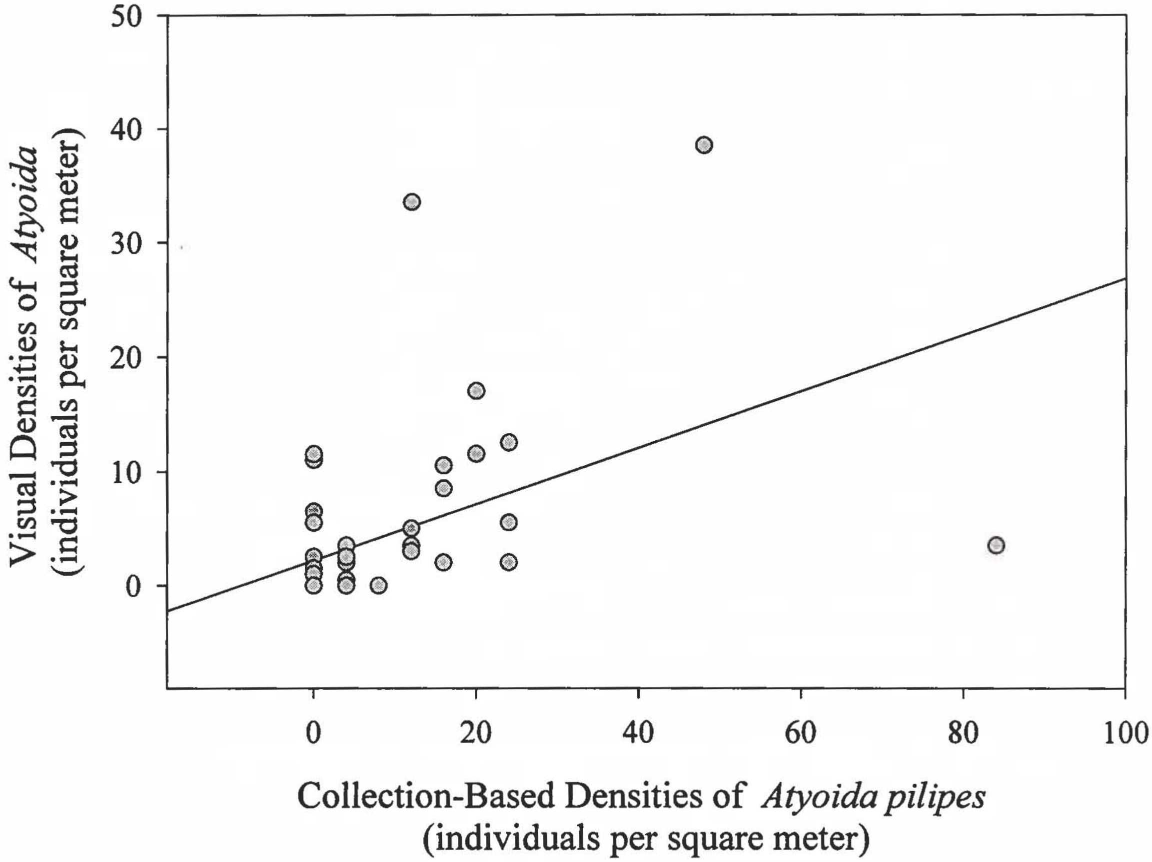

Figure 2. Regression of densities of *Atyoida* determined by visual counts on collection-based densities of *Atyoida*.

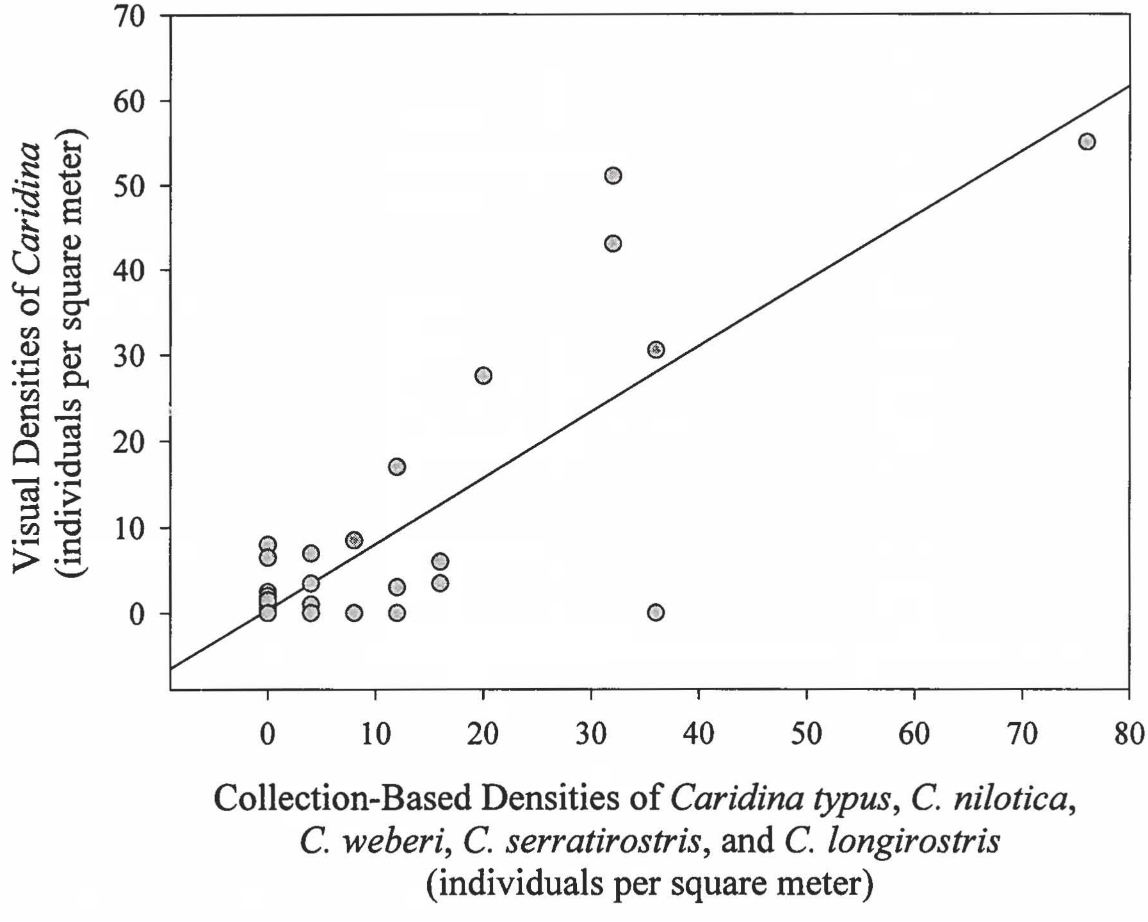

Figure 3. Regression of densities of *Caridina* determined by visual counts on collection-based densities of *Caridina*.

Table 1. Sorted rotated factor loadings from analysis of the distributional data matrix. Only variables with loadings greater than 0.4 are shown.

Factor	Variables	Factor Loadings
River Factor	River	-0.79
	pH	0.66
	Gravel	0.49
	Kuhlia density	0.47
	Canopy cover	0.46
	Aquatic vegetation	-0.46
	Bedrock	-0.42
Habitat Factor	Habitat	0.86
	Depth	0.73
	Current velocity	-0.65
	Macrobrachium density	0.46
	Caridina density	0.43
Season Factor	Temperature	0.80
	Season	-0.65
	Aquatic vegetation	0.59

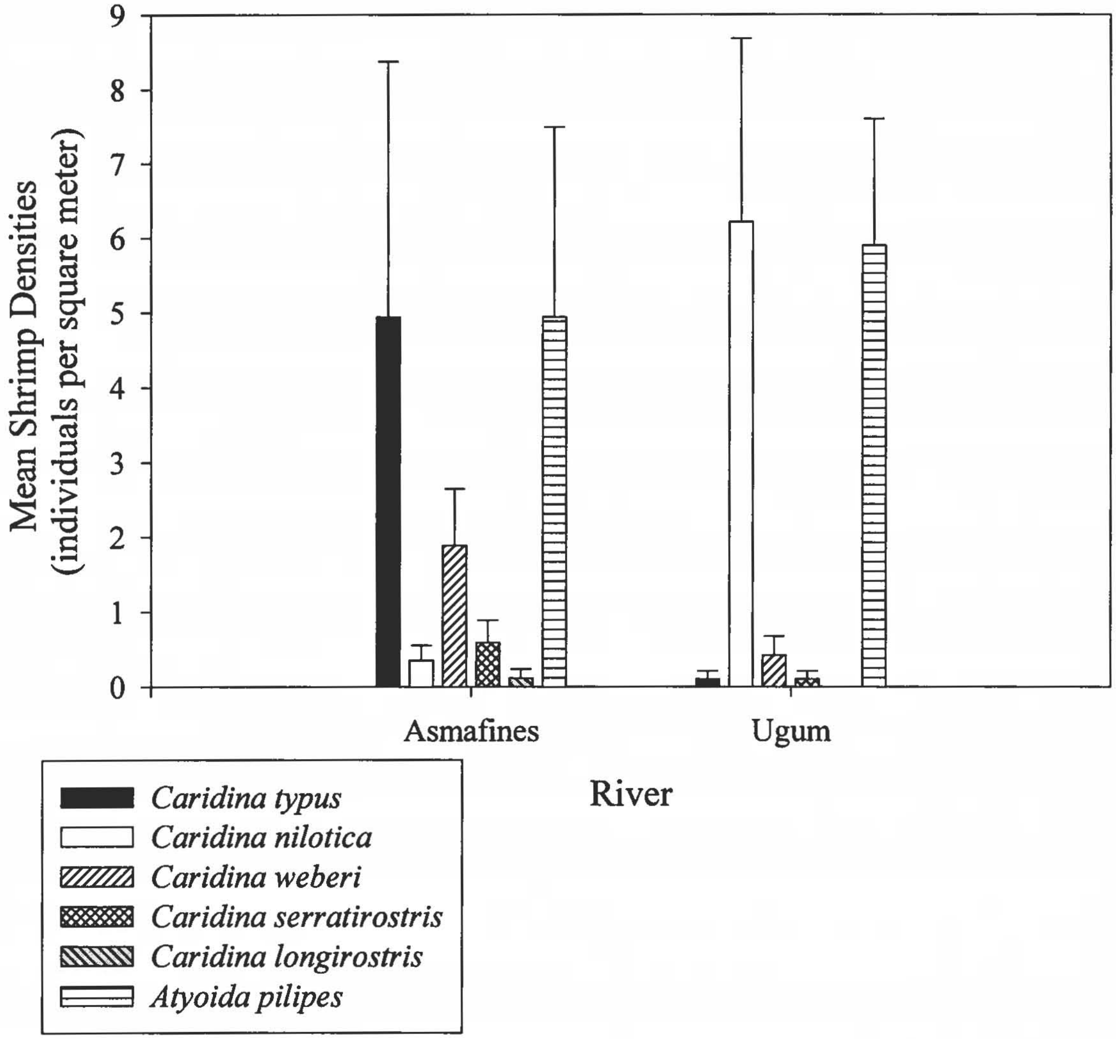

Figure 4. Histogram of mean densities of six species of atyid shrimp grouped by river. Mean densities were determined from collections of specimens within 0.25-square-meter areas with a dipnet. Capped bars represent standard errors of the means.

Atyoida pilipes occur in both rivers, different species of *Caridina* predominate in each river. *Caridina typus* and *C. weberi* occur in higher densities in the Asmafines River, whereas *C. nilotica* is the dominant species in the Ugum River. Atyids were not randomly distributed among habitats either. Densities of *Atyoida* were significantly higher in riffles than in runs and pools (Brown-Forsythe, $P<0.01$) (Fig. 5). Conversely, densities of *Caridina* were significantly higher in runs and pools than in riffles (Brown-Forsythe, $P<0.05$) (Fig. 5). There was no shift in atyid densities between habitats during periods of low and high flow, but densities of *Atyoida* were significantly lower for all three habitat types in the rainy season than in the dry season (Brown-Forsythe, $P<0.05$). As was stated above, *Atyoida* are found in significantly higher densities in riffles, which are characterized by significantly higher current velocities than other habitats (Kruskal-Wallis, $P<0.001$). Densities of the two genera were not correlated (Fig. 6). In fact, the two genera do not frequently cooccur, which corresponds with their preponderance in different habitats.

Densities of atyids are not correlated with predator densities, neither separately nor when all potential predators are combined. However, it is clear that atyids are not seen where *Kuhlia* occur, in the lower reaches, below the barrier waterfalls (Fig. 7). Atyids found in habitats containing *Kuhlia* are juveniles, found only buried within gravelly substrata. Figure 8 shows that mean shrimp carapace length is significantly larger above the barrier waterfalls than below in both rivers and for both genera (1-way ANOVA, $P<0.001$). Additionally, the carapace lengths (of each atyid genus) from sites nearest the top of the barrier waterfalls on each river were compared with those from sites farther

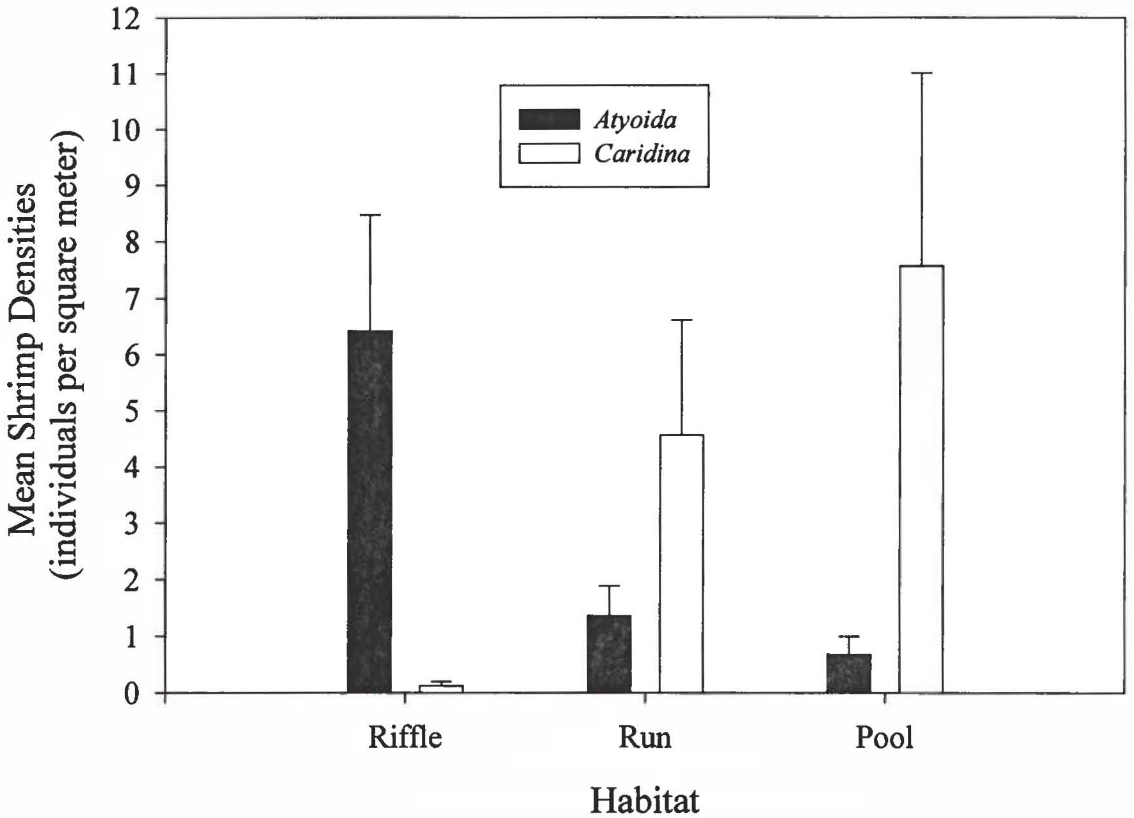

Figure 5. Histogram of mean densities of *Atyoida* and *Caridina* grouped by habitat. Densities were determined by visual counts. Capped bars represent standard errors of the means.

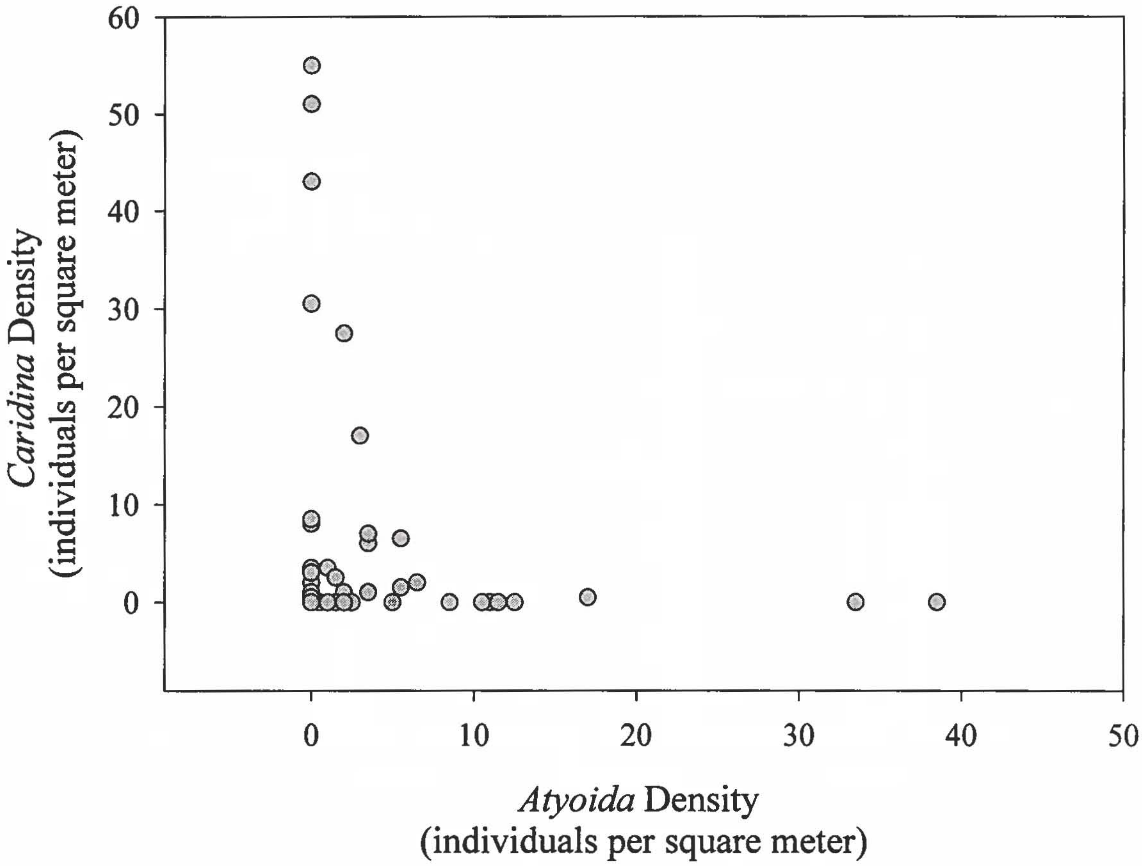

Figure 6. Scatterplot of density of *Atyoida* versus density of *Caridina*. Densities were determined by visual counts.

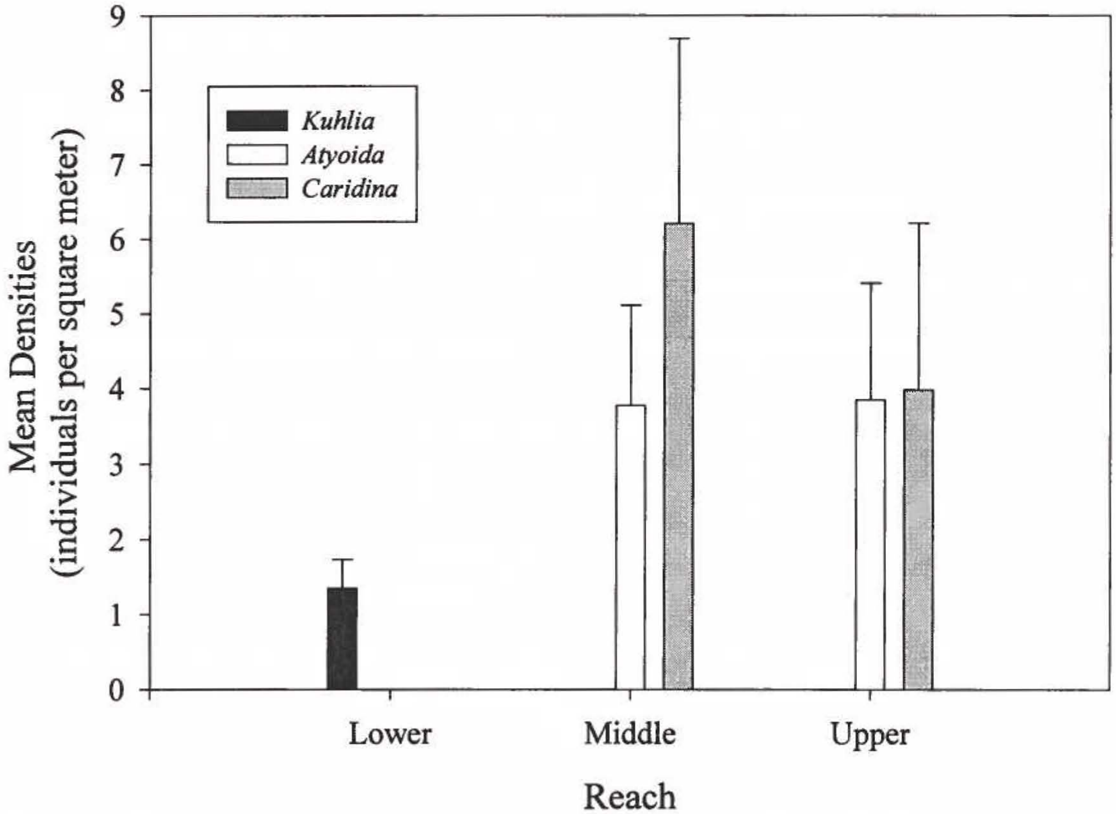

Figure 7. Histogram of mean densities of *Kuhlia rupestris*, *Atyoida*, and *Caridina* grouped by reach. Densities were determined by visual counts. Capped bars represent standard errors of the means.

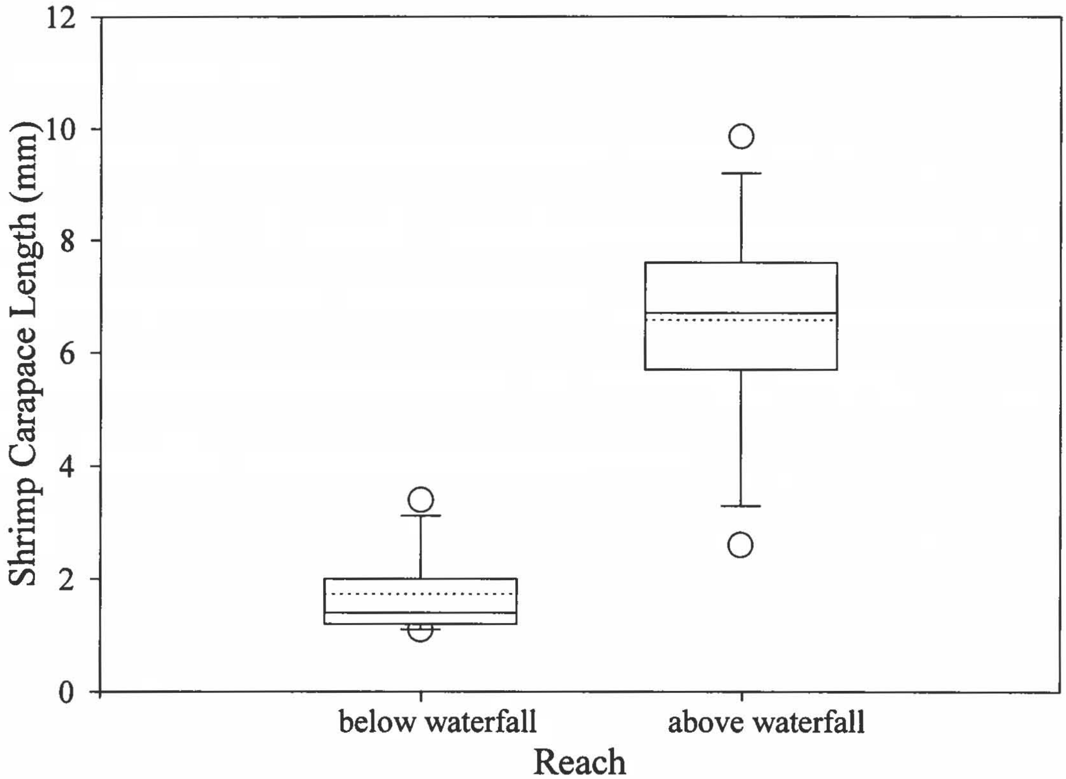

Figure 8. Boxplot comparing atyid carapace lengths from below and above the barrier waterfalls of the Asmafines and Ugum Rivers on Guam. Carapace lengths were measured to the nearest tenth of a millimeter. The upper and lower boundaries of the box represent the 75th and 25th percentiles, respectively. Capped bars above and below the box indicate the 90th and 10th percentiles. The filled circles indicate the 95th and 5th percentiles. The solid line within the box marks the median and the broken line represents the mean.

upstream. There was no significant difference except for *Atyoida* in the Asmafines River. In this case, the carapace lengths from sites farther upstream from the barrier waterfall were significantly shorter than those closest to the top of the waterfall (1-way ANOVA, $P<0.001$).

Transplant Experiment

A transplant experiment involving *Kuhlia* directly tested their importance as a predator of atyids. Before transplanting *Kuhlia*, experimental and control pools all contained atyids at densities from 0.92-1.32 per square meter. No atyids were seen in pools containing transplanted *Kuhlia* (Fig. 9). Conversely, atyid densities in control pools did not differ significantly during the experiment.

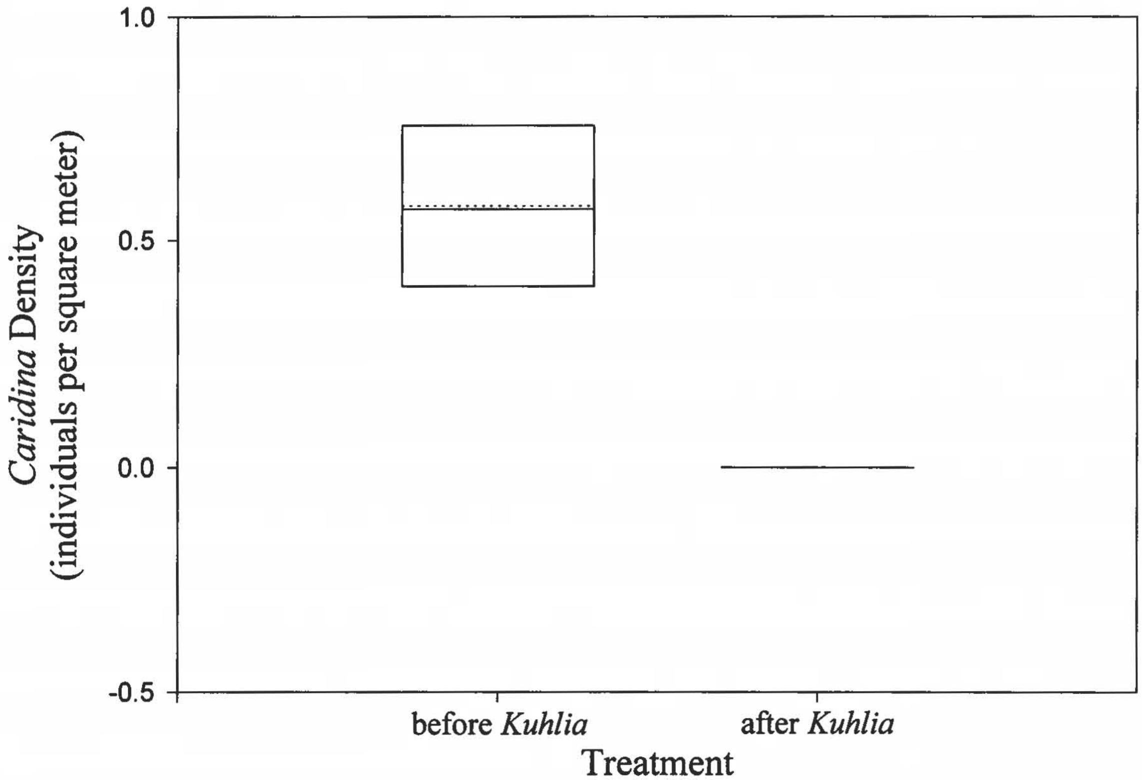

Figure 9. Boxplot of densities of *Caridina* in treatment pools before and after *Kuhlia* were transplanted. Densities were determined by visual counts. The upper and lower boundaries of the box represent the 75th and 25th percentiles, respectively. Capped bars above and below the box indicate the 90th and 10th percentiles. In this case, both capped bars correspond with the upper and lower boundaries of the box. The solid line within the box marks the median and the broken line represents the mean. During the transplant experiment, only species of *Caridina* were seen, probably because the experiment took place in pools.

DISCUSSION

Regression Analyses

The relationship between visual and collection-based densities of *Atyoida* is not strong (Fig. 2). This is most likely due to the less accurate method of obtaining collection-based densities in riffles (i.e. sweeping the 0.25-square-meter section rapidly and continuously), where *Atyoida* is primarily found (Fig. 5). Conversely, the relationship between visual and collection-based densities of *Caridina* is stronger (Fig. 3), reflective of the better method for obtaining collection-based densities in pools and runs (i.e. screening the area off), where *Caridina* are mainly found (Fig. 5). These results illustrate that visual surveys of atyid shrimp, especially in runs and pools, might be quite precise representations of collection-based densities. The relationship may prove just as strong for riffles if a better method of obtaining collection-based densities in this habitat can be identified.

Factor Analysis

The factor analysis explored all the variables collectively and revealed three tenable factors: a river factor, a habitat factor, and a season factor. The river and habitat variables, which had high loadings on the first two factors listed above (Table 1), were shown to be important influences of atyid distribution by univariate analyses. The loading of river and pH on the river factor corresponds with the presence of a limestone cap on Mt. Lamlam above the Asmafines River, which could serve to raise its pH. The loading of temperature and season on the season factor is easily deducible. Finally, the loading of habitat, depth, and current velocity on the habitat factor is also logical since current velocity tends to decrease as depth increases (i.e. in pools and runs). The loading of *Caridina* on the habitat factor supports its propensity for runs and pools (Fig. 5). However, *Atyoida* was found significantly more often in riffles than in other habitats (Fig. 5) and did not have a loading on the habitat factor. This may be because riffles have less variability in depth and current velocity, both of which had high loadings on the habitat factor.

Univariate Analyses

Different species of *Caridina* predominated in different rivers (Fig. 4). They rarely cooccurred at each site. As stated before, it is very difficult to differentiate them in the field with visual surveys. For these reasons, a mean ratio of their densities (determined by visual counts) was impossible to calculate. Thus, visual surveys on Guam are accurate in identifying atyid shrimps only to genera. In areas where other genera occur, preliminary observations, in conjunction with laboratory identifications, should be conducted in order to ensure the accuracy of visual surveys.

Atyoida and *Caridina* are found in different habitats (Fig. 5). This is unlikely to be the result of competition. The two genera are not obviously aggressive toward each other in areas where they coexist. They are detritivores and thus, their food supply is probably not limited. Additionally, their predominance in different habitats corresponds with morphological differences in their apical tufts. *Atyoida* possess longer setae appropriate for filter-feeding in higher flowing water (Chace, 1983) while *Caridina* have both short and long setae appropriate for filtering or scraping in a wider range of habitats (Bouvier, 1925).

There was no shift in densities of genera between habitats during periods of high and low flow. This may be due to the similarity in conditions between the two seasons. Guam experienced an uncharacteristically rainy "dry" season in 1996. Thus, variables such as current velocity, substrate composition, and depth did not differ significantly with season. The reduction of *Atyoida* densities in all habitats during the rainy season may be due to an increase in habitat area, with shrimp number remaining the same, resulting in decreased density. This phenomenon may not affect *Caridina* in the same way because they are normally found more closely associated with each other (personal observation). Alternatively, because *Atyoida* are primarily found in a habitat characterized by higher current velocities (i.e. riffles), they may be more vulnerable to being washed downstream during heavy rains, whereas species of *Caridina* may be able to find refuge in the more protected areas of pools.

Predation by *Kuhlia* appears to be a major biological factor influencing atyid densities. Although there was no negative correlation between atyid and individual or combined predator densities, two known predators, *Anguilla marmorata* and *Eleotris fusca*, were almost certainly under-represented in the visual surveys. *Anguilla marmorata* is more active at night and *E. fusca* is highly cryptic, specializing in ambushing its prey. Although atyids have been found in the stomach contents of *Awaous guamensis*, these fish mainly feed on interstitial organisms in the sand and are not considered to be a serious predator of atyids (Watson, 1992). But all of these predatory fishes are present throughout the river, cooccurring with atyids. Wellborn and Robinson (1991), through predator exclusion experiments in a Texas reservoir, concluded that predation by fish does not substantially affect abundances of macroarthropods that naturally cooccur with them. They suggested that these macroarthropods possess some kind of antipredator defenses. Atyids may escape predation by *Anguilla marmorata*, *Eleotris fusca*, and *Awaous guamensis* to a great extent by reducing activity at night and by occupying only exposed hard substrata during the day. The prawn *Macrobrachium lar* also occurs with both genera of atyids in high densities and has never been seen to consume them, both in the field and in laboratory aquaria. This contrasts with the results of Crowl and Covich (1994), which demonstrated that the prawn *Macrobrachium carcinus* preys upon the atyid *Atya lanipes* in Puerto Rico.

Transplant Experiment

The jungle perch *Kuhlia rupestris* is the only predator that does not cooccur with adult atyids, and it was shown to have a dramatic effect on atyids in the transplant experiment. This is especially striking when compared to the results of other exclusion/inclusion experiments. For example, Allan (1982) found that a reduction in trout densities in streams in Colorado did not result in a significant increase in densities of benthic invertebrates, even though examination of trout stomach contents demonstrated intensive grazing on certain aquatic insect taxa. He surmised that, either trout are consuming only a small fraction of total invertebrates, or prey are highly adapted to trout predation and thus, unsusceptible to a reduction in fish densities. Similarly, Reice and Edwards (1986) conducted both exclusion and inclusion experiments in two Canadian streams (one that naturally contains fish and one that does not) and concluded that brook trout do not have a major effect on the distribution of benthic invertebrate communities in these streams. Gilinsky (1984) reported mixed results from exclusion and inclusion experiments with bluegill sunfish in a North Carolina pond. She found that the effect of fish predation on benthic macroinvertebrates was dependent on season and habitat complexity. However, Fraser et al. (1995) performed both inclusion and exclusion experiments in streams on the tropical island of Trinidad and found that in areas split by barrier waterfalls, predators can produce disjointed prey distributional patterns, by both consumption and by causing prey to ascend cascades.

The results of the transplant experiment in this study suggest either a behavioral response by the atyids, such as hiding or migrating to adjacent areas, or consumption by *Kuhlia*, or both. Analysis of stomach contents of recaptured *Kuhlia* would have been helpful in confirming the latter. Unfortunately, *Kuhlia* proved impossible to recapture within a reasonable amount of time and with methods that are non-destructive to the stream ecosystem. Laboratory experiments involving *Kuhlia* and atyids might prove useful in determining to what extent shrimp can hide or escape and to what extent they are eaten.

The influence of *Kuhlia* on atyid distribution is also supported by the difference in shrimp carapace length from below and above the waterfalls (Fig. 8). Only small atyids that stay buried within substrata are found to occur with *Kuhlia*. If differences in carapace length are reflecting the amphidromous lifestyle of atyids instead of the influence of *Kuhlia*, a gradual increase in size would be expected as distance from the mouth of the river increases. However, carapace length is not significantly larger in sites further from the top of the waterfalls than in sites closest to the top of the waterfalls. This suggests that *Kuhlia* are a major influence on atyid size distribution.

Conclusions

This study is among the few quantitative studies of the ecology of atyid shrimp on tropical islands. Although habitat and river characteristics appear to be major factors affecting the distribution of atyid shrimps in tropical streams, the transplant experiment illustrated the striking effect of predation by the jungle perch *Kuhlia rupestris* on atyid distribution. Thus, it is essential to explore biotic interactions and survey all habitat types in various rivers when developing and implementing biomonitoring programs for stream ecosystems on oceanic islands.

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