HABITAT USE BY AN ASSEMBLAGE OF TROPICAL OCEANIC ISLAND STREAMFISH

by

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Visual surveys were made of the fish assemblage of the Asmafines River, Guam, to discern possible habitat use patterns in relation to abiotic and biotic variables. The fish assemblage contained *Stiphodon elegans*, *Stiphodon caeruleus*, *Sicyopterus macrostetholepis*, *Sicyopus leprurus*, *Awaous guamensis*, *Stenogobius* sp., *Eleotris fusca*, *Kuhlia rupestris*, and *Anguilla marmorata*. Abiotic environmental variables considered were the location of the first waterfall, habitat type, flow regime, substrate, elevation, distance from the ocean and bed slope; biotic variables included the densities of each fish species and the density of the river prawn *Macrobrachium lar* present at 135 sites within the perennial portion of the river. Factor analysis revealed a break in the fish assemblage distribution at the first major waterfall, and placed the Sicydinae gobies (*Stiphodon elegans, Stiphodon caeruleus, Sicyopterus macrostetholepis, Sicyopus leprurus*) into a distinct group. Additionally, visual surveys were used to assess microhabitat usage and to determine the extent of habitat segregation between fish species. Factor analysis showed water velocity, proximity to cover, depth, and substrate to be important factors. Species separation along these factors was differentiated with niche breadth and niche overlap analysis. This microhabitat examination combined with known trophic information allowed the construction of an ecological key to habitat use. Habitat use was determined to be non-random at distributional and microhabitat levels with segregation of habitat occurring on both abiotic and biotic factors.

TO THE OFFICE OF GRADUATE SCHOOL AND RESEARCH

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This work is dedicated to my parents, Walter and Lenore Parham, whose guidance, support, and encouragement have opened new horizons throughout my life, and whose wisdom and achievements inspire me to reach new heights.

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Table of Contents

List of Tables

List of Figures

Introduction

Information on habitat use is important to the understanding of the ecology of streamfishes. Habitat use by streamfishes has been shown to be influenced by many factors, including abiotic factors such as the variability (Schlosser 1985, Bain et al. 1988, Poff and Allen 1995), persistence (Capone and Kushlan 1991) and seasonality (Baltz et al. 1991) of water flow, and differences in habitat structure (Gorman and Karr 1978). Also, biotic factors such as predation (Werner et al. 1983, Prejs 1987, Schlosser 1987, Brown and Moyle 1991, Gilliam et al. 1993, Fraser et al. 1995), competition (Zaret and Rand 1971), and reproduction (Nesler et al. 1988) have been shown to affect habitat use.

The life cycle of streamfishes on tropical oceanic islands may influence their habitat use (Kinzie 1988). All of the fishes on the oceanic islands in the Pacific are considered secondary freshwater fishes, having invaded the freshwater from ancestral marine stocks; and all retain a portion of this marine heritage in their diadromous life cycle (Myers 1938). All of Guams' indigenous freshwater fishes are amphidromous, except the catadromous genus *Angullia*. Amphidromous fishes live and breed in freshwater, and their larvae develop in the ocean (Myers 1949). Larval fish metamorphose into juveniles upon contact with freshwater. Once settled in a given stream, a juvenile fish migrates upstream to reach adult habitats. This obligate upstream movement of juveniles to adult habitats provides the juveniles with a wide choice of habitats.

Potential differences in habitat utilization by an assemblage of streamfishes may be observed in distributional and microhabitat patterns. On a broad scale, patterns of habitat use are manifested as within-stream distributional patterns. Patterns of streamfish distribution have been linked to physiographic zones within the stream. In the Republic of Palau (Micronesia), Fehlmann (1960) divided the streams into four zones: the mangrove zone, a lower graded zone, a cascade zone, and a source zone, and described the fish assemblages characteristic of each zone. In Hawaiian streamfishes, assemblage composition and its members relative densities change in relation to elevation and distance from the stream mouth (Kinzie and Ford 1982, Kinzie 1988, Nishimoto and Kuamoo 1991). These zonation patterns may be the result of abiotic stream conditions or the result of morphological differences affecting upstream movement. For example, the fused pelvic fins of the Hawaiian gobies *Lentipes concolor* (Gill) and *Sicydium stimpsoni* (Gill) aid in "climbing" of vertical surfaces, allowing colonization of stream reaches above large waterfalls (Kinzie and Ford 1982). Similarly, the lack of fused pelvic fins of sleeper gobies, such as in *Eleotris sandwicensis* (Vaillant and Sauvage), restrict their upstream ranges to the base of the first substantial waterfall (Kinzie 1990). Additionally, *Macrobrachium lar* (Fabricius), the Tahitian prawn, has been speculated to affect streamfish habitat use through predation or competition (Kinzie and Ford 1982). Determination of distributional patterns in streamfish assemblages is one important component to understanding habitat use.

Another important component of habitat use by a streamfish assemblage is their microhabitat use. Habitat segregation within a group of co-occurring species may be observed in differences in microhabitat selection. The Hawaiian streamfish assemblage showed resource segregation with regard to velocity, depth, substrate, distance from the streambank, and location within pools, runs and riffles (Kinzie 1988). Additionally, in morphological studies of Japanese stream gobies, Sakai and Nakamura (1979) differentiated streamfishes based on degree of morphological adaptation to steep, fast flowing waters and hypothesized that habitat segregation would occur in relation to current velocity. The combination of distributional patterns and microhabitat use may show where members of a streamfish assemblage are found within a stream, and how the fish utilize their habitat at that location.

To determine habitat use by an assemblage of tropical oceanic island streamfishes, I used visual surveys in the Asmafines River, Guam to answer the following questions. First, in the broad sense, is there a pattern to the distribution of the streamfish within the Asmafines River, and if so, does this pattern relate to the major abiotic and biotic factors within the stream? And second, in the narrow sense, what microhabitats do individual fish species select, and is there microhabitat segregation between fish species?

Materials and Methods

Study Site

This study was conducted on Guam, the southernmost island in the Marianas Archipelago, located in the western Pacific Ocean. The focus of the study was the Asmafines River in southwestern Guam (Figure 1). The perennial channel length is 1,341 m and drains a watershed of approximately 96 ha. The highest elevation of the perennial channel is 134 m and the average slope is 10.0% (Best and Davidson 1981). The Asmafines River has three intermittent tributaries, and drains into Sella Bay. The watershed is located within a governmentally zoned recreational area, and so it contains no human development except for a road and a scenic overlook. The placement of the sites, during both sampling periods, and a map of the Asmafines River including the position of the major waterfalls and the road are shown in Figure 2.

The warm climate and high yearly rainfall on Guam has weathered the watershed's volcanic rock and given rise to a highly impermeable clay-rich soil. Isolated patches of limestone from ancient uplifted coral provide calcium carbonate to the stream and support the development of numerous stromatolite formations. Bedrock forms the bottom of much of the steep, upper streambed. A ravine forest borders the stream and provides shade and is the origin of large quantities allochthonous material in the form of leaves and woody debris. Most of the hillsides within the watershed are covered in sword grass (*Miscanthus*

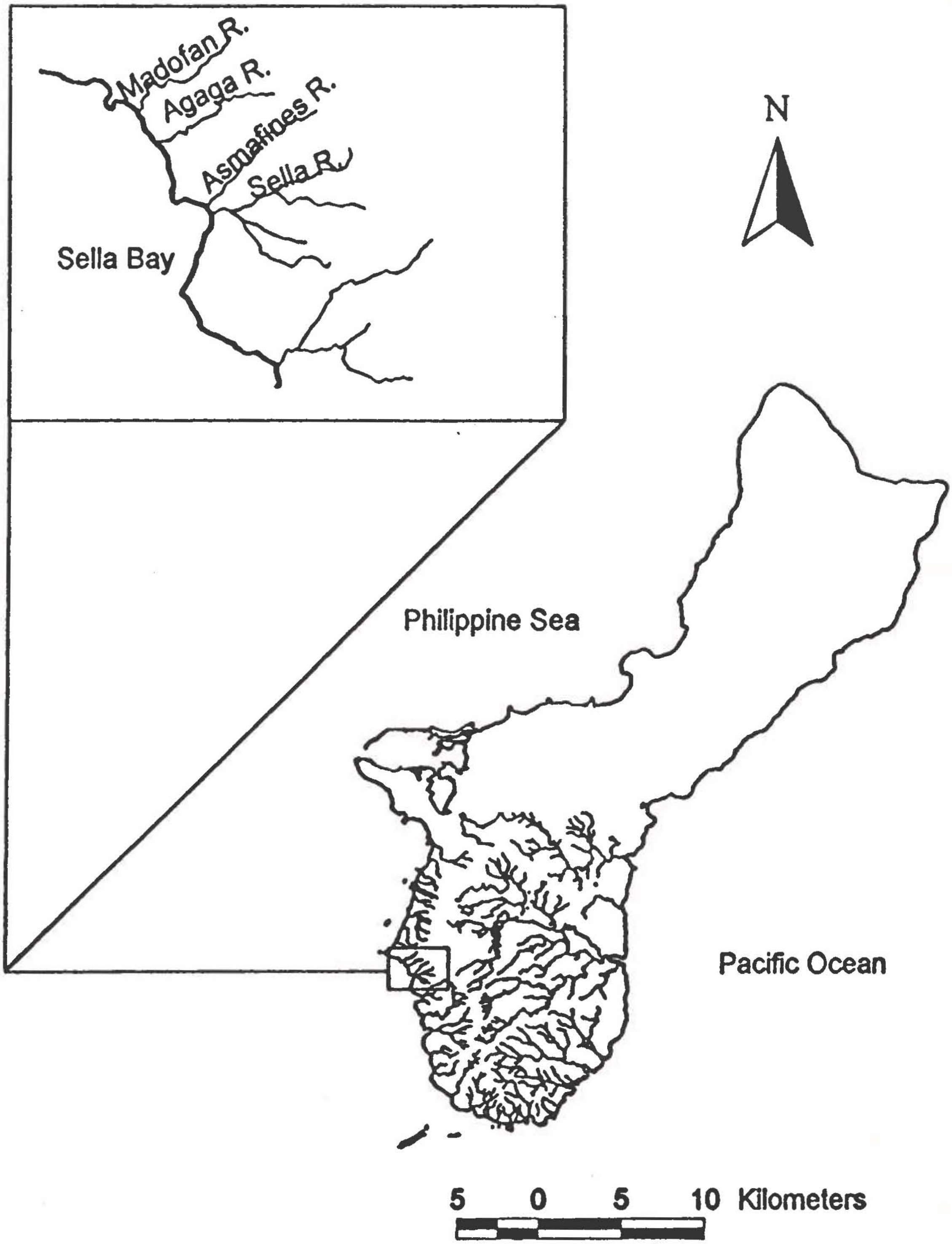

Figure 1. Guam and an expanded view of the Asmafines River area

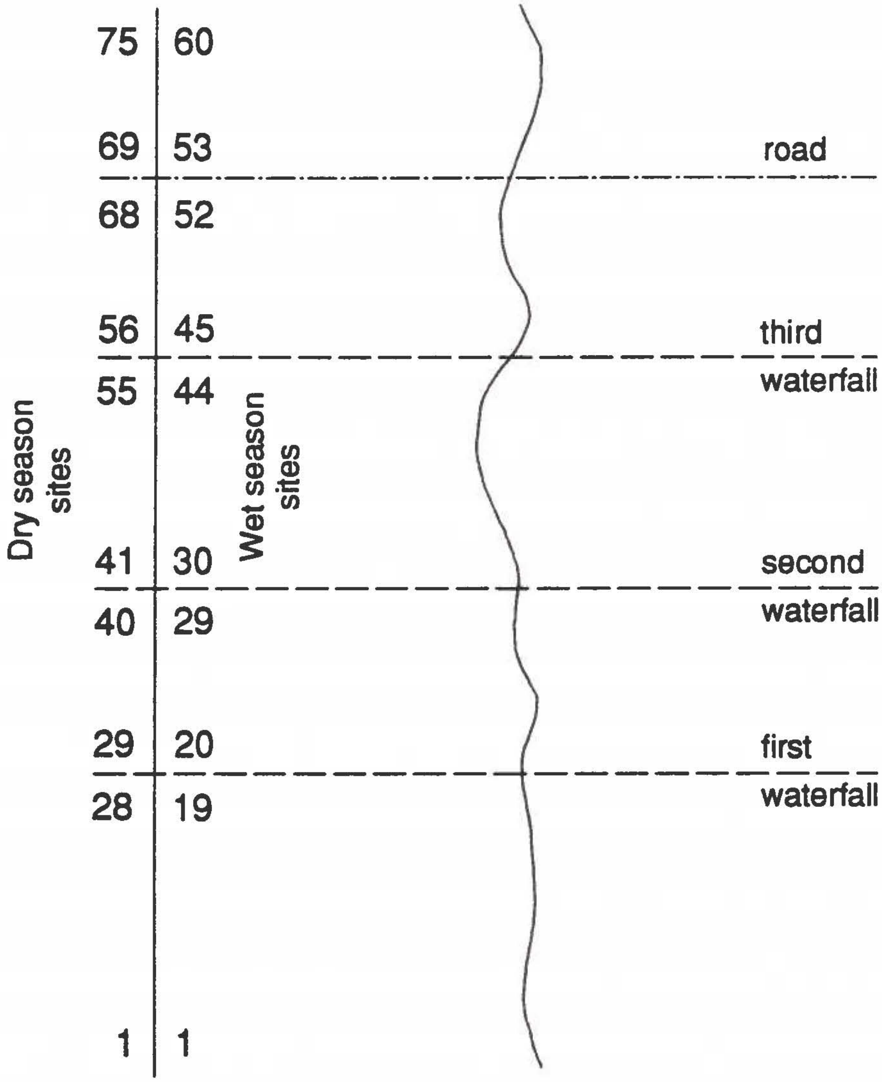

Figure 2. Map of site locations on the Asmafines River. The relative position of the major waterfalls and the road are represented by the dashed lines.

floridulus); however, there are some barren areas that are subjected to severe erosion during heavy rains.

Field Methods

For field sampling, the Asmafines River was divided into three large sections based on access points to the stream. To reduce temporal bias, the particular section surveyed each day was randomly determined. Sampling began at the lowest point of each section, and proceeded upstream, with samples taken at all pool and run sites. Riffles were not sampled because of the inaccuracy of visual survey techniques in extremely shallow, turbulent water. (Baker and Foster 1992 and personal observation).

To include changes in distribution and microhabitat use possibly related to seasonally variable factors such as flow regime, the timing of the two sampling periods was chosen to coincide with the historical peaks of the wet and dry season. Wet season sampling was done in September 1994, and the dry season sampling was done in March 1995.

The locations of individual streamfish were determined by direct observation. Observations were made from the stream bank or in the water with the aid of a mask and snorkel. Water clarity was sufficient to allow accurate species identification and counts of individual fish within each quadrat. Observations were suspended during heavy rain showers and resumed when water clarity permitted.

A modified quadrat method involving variable-sized quadrats was used to determine sampling units (Baker and Foster 1992). The quadrat areas vary with the observer's visual ability to count fish accurately from a single position (Baker and Foster 1992). The observer approached the sample site slowly to avoid disturbing the fish. In preliminary observations, and during the course of this investigation, many of the fish appeared to ignore the observer when approached slowly, and disturbed fish resumed normal behavior (e.g. feeding, courting) within minutes. Once the observer was in position, all of the fish were counted and the locations of undisturbed fish were marked.

To determine distributional patterns for the streamfishes of this assemblage the following information was recorded at each site: the date, time, observer's name, site code number, a site description and a pool or run classification. The site description included sufficient information to allow the site to be positioned with respect to the nearest waterfall. The information collected for a quadrat within a site included: the numbers of each fish species present, the dominant substrate within the quadrat, the length of each side of the quadrat, and a hand-drawn representation of the quadrat. The dominant substrate within the quadrat was recorded with a numerical code representing substrate categories (bedrock=1, boulder=2, cobble=3, gravel=4, and sand/sediment=5) combined with a visual estimate of the substrate available to the nearest 10% for each of the two most common substrate types. A single score for dominant substrate code represented the one dominant substrate code or, if adjacent, a weighted combination of two substrates codes (Moyle and Baltz 1985). The length of quadrat sides were measured, and these measurements were used to calculate area (m^2) and then combined with the number of fish counted to determine fish densities. The quadrat map included the major structural elements (e.g. boulders, logs or overhanging vegetation). The elevation and distance from the ocean of each site was determined from a topographic map.

To determine microhabitats of this fish assemblage, the locations of undisturbed fish were marked within the quadrat at the conclusion of each observation period. Recorded information for individual fish, included the marker number, species code, number of individuals represented, estimated total length, focal point substrate, use of cover, fish's position in the water column, water depth, mean water column velocity, focal point water velocity, and notes on the fish behavior. The locations of each fish were marked with number-coded, 6-cm long sections of iron reinforcement bar with fluorescent flagging tape attached for visibility. A single marker was used for more than one fish when fish of the same species were aggregated in close proximity and were located on the same substrate. The fish lengths were visually estimated and used to categorize individuals as either juveniles or adults. Focal point substrate was the substrate directly underneath a marked fish. Fish were considered to be using cover if they remained underneath or against a sheltering object. Position in the water column was visually estimated in tenths from 0 =

bottom to 1 = surface. Water depth, mean column velocity and focal point velocity was measured with a Marsh-McBirney velocity meter. Water depth was read from the rod markings. Mean column velocity was measured at a position six-tenths of the total water depth below the surface and focal point velocity was the water velocity at the marker representing the snout of an undisturbed fish. After completing the count, representative individuals of each new species encountered were collected for taxonomic verification and voucher samples.

Analytical Methods

A data matrix was created to determine if the fish assemblage distribution showed patterns in relation to the measured variables. This matrix used the 135 sites as cases, and 16 variables were created from a combination of six physical measurements (flow regime, position of the first major waterfall, habitat, dominant substrate code, elevation and distance form the ocean) and the densities of the nine fish species and the density of the Tahitian prawn *Macrobrachium lar.* Factor analysis (BMDP statistical software 1993) was run on this matrix to determine the major factors influencing the distributional variation. Scree plot stopping rules were applied to the factor analysis to focus on the main patterns (Jackson 1993). Further elucidation of the distributional patterns was accomplished with a vertical bar graph showing the density distribution of each fish species throughout the river.

To analyze the microhabitats of the fish assemblage, a second data matrix was created that contained the microhabitat measurements taken of individual fish. The six microhabitat measurements of focal point substrate, use of cover, position in the water column, water column depth, mean water column velocity and focal point water velocity were used as variables and each individual fish represented a case. Factor analysis with orthogonal varimax rotation was used to determine the factors that explained the majority of the variance of these six microhabitat variables for the fish assemblage (BMDP statistical software 1993), and used eigenvalues greater than one as a stopping rule (Jackson 1993). To clarify the resultant factors in terms of species utilization, each species niche breadth (B) was calculated for the different microhabitat variables in accordance with the formula $B = 1/\sum P_{ij}^2$ (Levins 1968). Niche overlap (S) was also calculated between each species pair as defined by $S = 100(1-1/2\sum |P_{xi}-P_{yi}|)$ (Schoener 1970). In these equations, the variable P represents the proportion of the microhabitat resource occupied by the species. Species groupings were determined by niche overlap and median population values. The species groupings for each factor were used to construct an ecological key (sensu Moyle and Senanayake 1984) to show the segregation of habitats within the Asmafines River.

Results

Distributional Patterns

The fish assemblage of the Asmafines River contained nine species. In order of abundance, the fish observed were *Stiphodon elegans* (Steindachner), *Kuhlia rupestris* (Lacepede), *Awaous guamensis* (Valenciennes), *Stenogobius* sp. (an undescribed species), *Sicyopus leprurus* (Sakai and Nakamura), *Sicyopterus macrostetholepis* (Bleeker), *Eleotris fusca* (Bloch and Schneider), *Stiphodon caeruleus* (Parenti and Maciolek) and *Anguilla marmorata* (Quoy and Gaimard).

The analysis on broad abiotic and biotic variables revealed two main factors affecting the distributional patterns (Table 1). These two factors were termed a waterfall factor and a Sicydinae goby factor. The first factor had high positive loadings for *Kuhlia rupestris* density and *Stenogobius* sp. density, with moderately high loadings for dominant substrate code and *Awaous guamensis* density. The negative loadings were for elevation, distance from the ocean, position of the first waterfall and *Macrobrachium lar* density. This factor describes the effect of the first major waterfall encountered moving upstream from the ocean. On the Asmafines River, this waterfall was approximately 30 m high. The species *K. rupestris* and *Stenogobius* sp. were found only below the first major waterfall and *Macrobrachium lar* was found above the waterfall. There was also a change in substrates from depositional substrates in the lower reach to erosional substrates above the falls.

The second factor, termed the Sicydinae goby factor, had high positive loadings for *Stiphodon elegans*, *Stiphodon caeruleus*, *Sicyopus leprurus* and *Sicyopterus macrostetholepis*. The sites with high positive factor scores for this factor were placed between the first and third major waterfalls (approximately 80 to 300 m above sea level), contained a heterogenous substrate and were bordered by steep cascades or riffles. Due to the steep slope, water velocity tended to be swift, but broken by many instream obstructions. This factor may indicate that there are specialized microhabitat requirement of the Sicydinae gobies.

In regard to the first factor, three groups of fishes could be distinguished based on their relationship to the first major waterfall. The groups are: (1) fish found below the first major waterfall, (2) fish found throughout the stream, and (3) fish found predominantly above the waterfall. The first group includes *Stenogobius* sp. (Figure 3) and *Kuhlia rupestris* (Figure 4). These two species were found exclusively downstream of the first major waterfall, and apparently lack the ability to surmount large waterfalls. Recruiting juveniles were seen in the spring sampling period. Loose aggregations of juveniles and adults were common in both species, and little of the observed variation in densities or distribution was attributed to juvenile/adult distribution in the high and low water flow periods.

The second group includes *Stiphodon elegans* (Figure 5), *Awaous guamensis* (Figure 6), and *Anguilla marmorata,* species that appear throughout most of the stream. *S. elegans* was the most abundant fish in the stream, with the bulk of the population centered above the first major waterfall. The extreme lower portion of the stream contained few adult *S. elegans*, but many recruiting juveniles were observed in the lower portion of the stream during the spring (low water flow) sample (Figure 5).

Awaous guamensis (Figure 6) was observed in all but the uppermost portion of the stream. In addition, a large aggregation of spawning *A. guamensis* were observed in the tidally influenced stream mouth, downstream of the study sites, during the high water flow period. Many of the larger *A. guamensis* were observed downstream of the first large waterfall during this high water flow sample. During the low water sampling period, recruiting juveniles dominated the observed fish in lower portion of the stream, and the larger individuals were found throughout the stream.

The eel *Anguilla marmorata* was also found throughout the stream, with individuals observed from the estuarine section to intermittent headwater pools. However, very few individuals were seen within our quadrats. Because *Anguilla* species are primarily nocturnal (Tesch 1977), our diurnal surveys may have underestimated the true abundance of *A. marmorata* within the stream.

The third group of species includes *Sicyopus leprurus, Sicyopterus macrostetholepis, Stiphodon caeruleus,* and *Eleotris fusca.* These species were predominantly found upstream of the first major waterfall. *S. leprurus* (Figure 7) was observed more often in the dry season sample, with juveniles and small adults more common than large adults. A group of large males and females was observed in the uppermost perennial pool during each sampling period. This species was found further upstream than any other of the gobies.

S. macrostetholepis (Figure 8) was observed in the middle portion of the stream with a wider distribution in the high flow period than in the low flow period. A wide size range of males and females was observed, but no recruiting juveniles were seen during either sampling period. When approached carefully, *S. macrostetholepis* usually behaved normally (e.g. feeding), but this species was the most secretive of the gobies and when disturbed, frequently fled into shallow riffle areas to hide in cracks and under rocks.

S. caeruleus (Figure 9) was an uncommonly observed species in each sampling period and was concentrated within the same stretch of water in each season. The density measurements for this species were likely underestimated because of the difficulty of distinguishing female *S. caeruleus* from abundant female *S. elegans*. Male *S. caeruleus* were easily distinguished from male *S. elegans* by differences in coloration. Overestimation of *S. elegans* densities was likely, but due to large differences in the two species abundances, the resulting amount of overestimation was probably small.

The sleeper goby *Eleotris fusca* (Figure 10) was observed most frequently in the middle portion of the stream, above the first waterfall, but not in the headwater areas. A large male *E. fusca* was observed guarding eggs below the waterfall during the high water flow period, and although this individual was not

observed within a sampling quadrat, this was the only instance of spawning behavior observed for *E. fusca* in either sampling period. This species was cryptic in its coloration and behavior and was likely underestimated throughout the stream, and our categorization of its distribution should be considered tentative.

Table 1. Sorted rotated factor loadings from analysis of the distributional data matrix. The rows are rearranged showing loadings greater than 0.500 first, and loadings less than 0.250 have been replaced by zero (BMDP 1993). Variables from the matrix that had loadings less than 0.250 for both factors are not shown. VP represents the eigenvalue for the factor.

Variables	**Waterfall factor**	**Sicydinae goby factor**
Kuhlia rupestris density	0.818	0.000
Elevation	-0.811	0.000
Distance from ocean	-0.806	0.000
Position of the first waterfall	-0.804	0.000
Stenogobius sp. density	0.774	0.000
Macrobrachium lar density	-0.630	0.000
Dominant substrate code	0.616	0.000
Awaous guamensis density	0.554	0.000
Stiphodon elegans density	0.000	0.912
Sicyopterus macrostetholepis density	0.000	0.898
Stiphodon caeruleus density	0.000	0.883
Sicyopus leprurus density	-0.259	0.580
VP	3.101	2.883

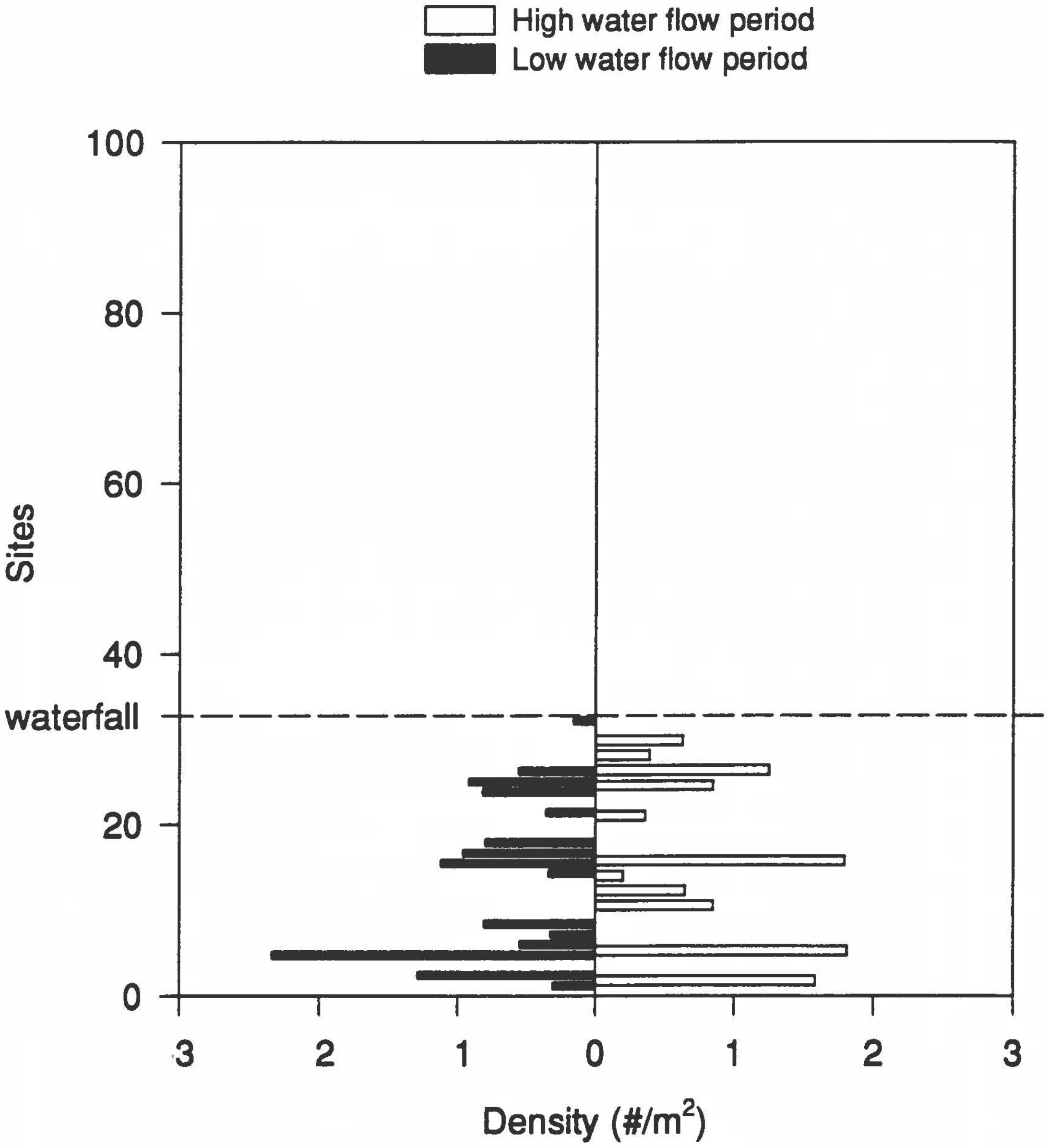

Figure 3. Bar diagram of the density of *Stenogobius* sp. Densities were determined from visual fish counts using the modified quadrat method. Sites have been standardized to allow high and low flow period site positions to be comparable. The Y-axis runs from 0 = downstream of the first site to 100 = upstream of last site. Waterfall notation and accompanying dashed line represent the position of the first major waterfall.

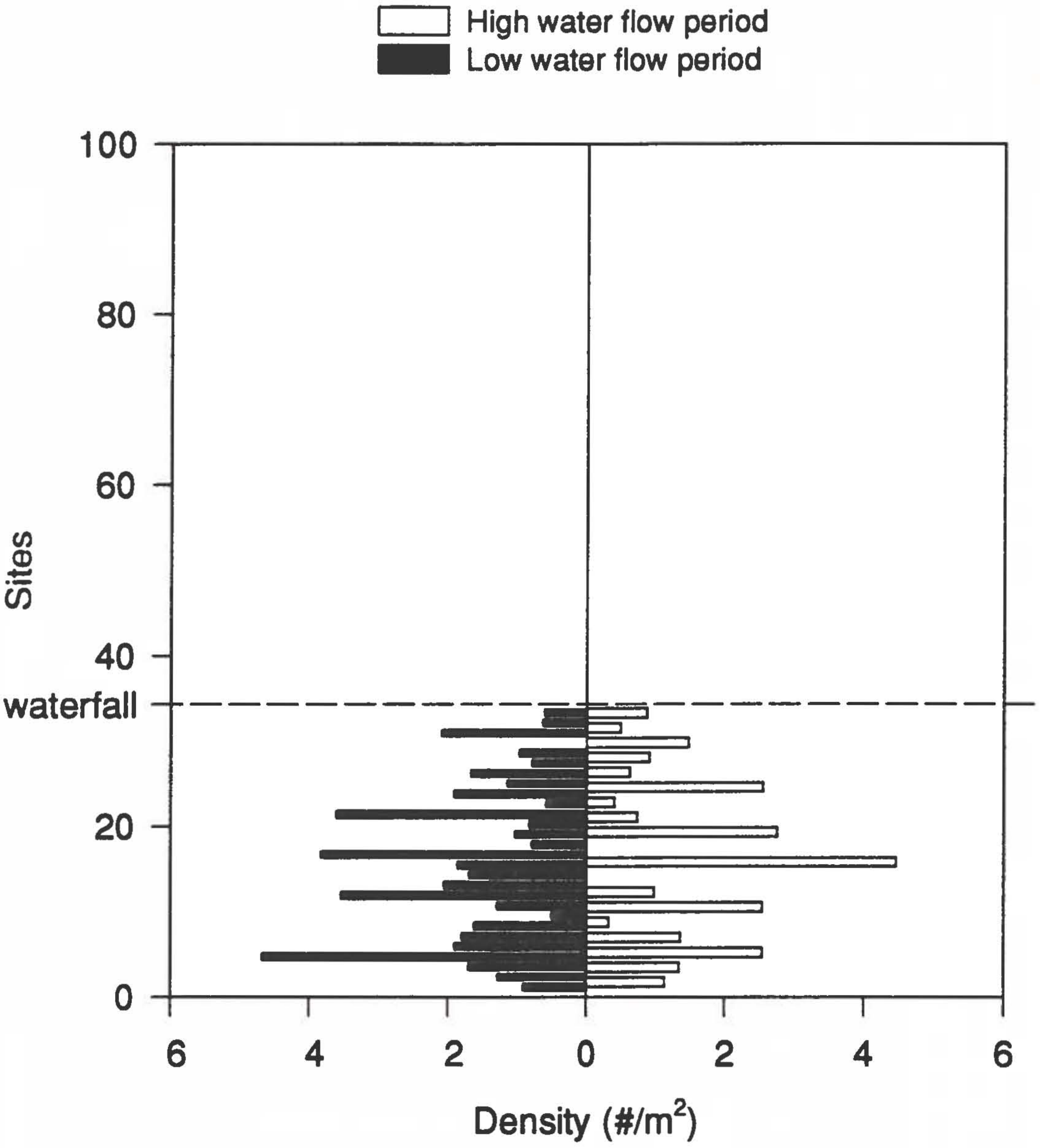

Figure 4. Bar diagram of the density of *Kuhlia rupestris.* Densities were determined from visual fish counts using the modified quadrat method. Sites have been standardized to allow high and low flow period site positions to be comparable. The Y-axis runs from 0 = downstream of the first site to 100 = upstream of last site. Waterfall notation and accompanying dashed line represent the position of the first major waterfall.

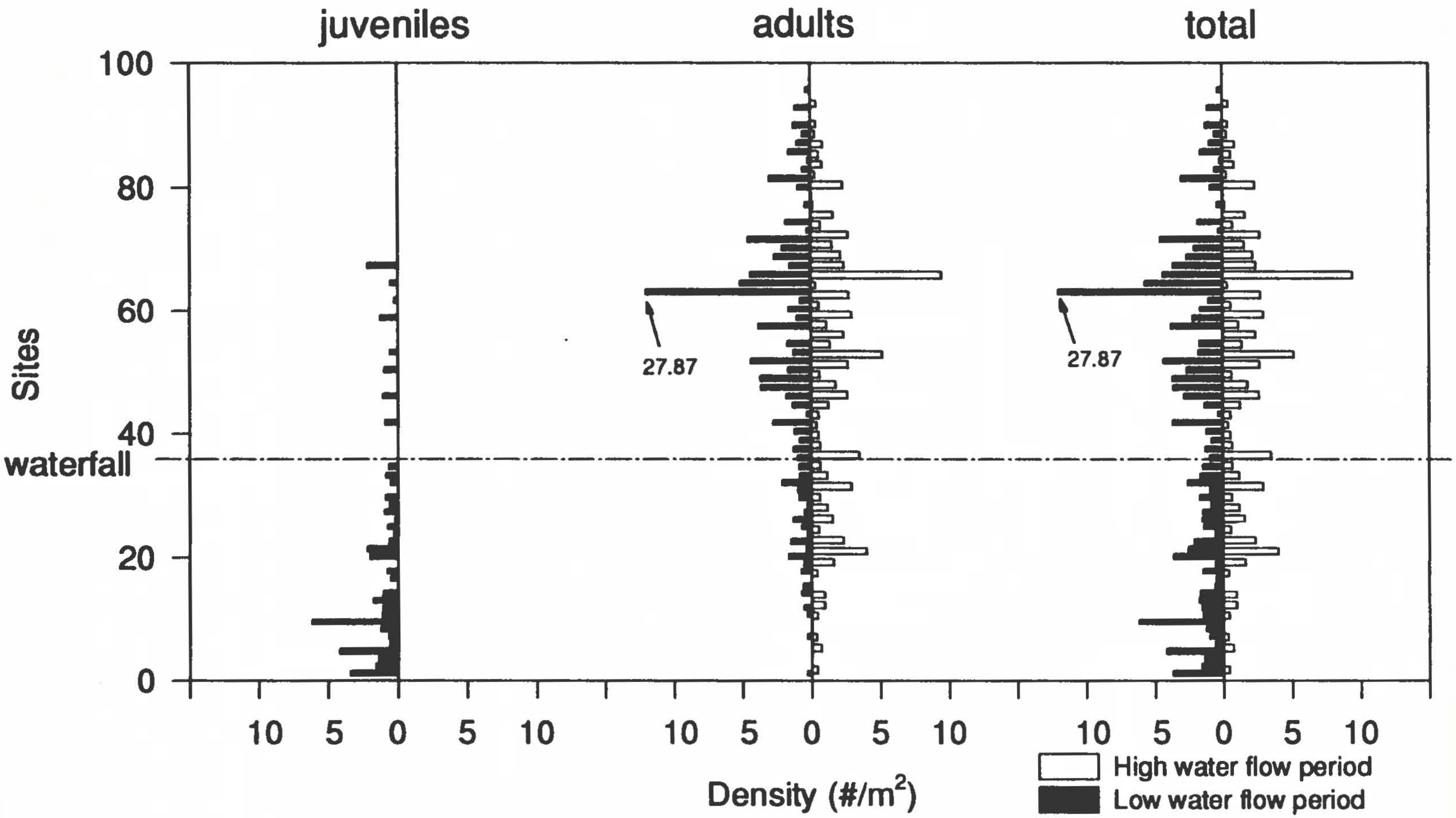

Figure 5. Bar diagram of the density of *Stiphodon elegans.* Densities were determined from visual fish counts using the modified quadrat method. Sites have been standardized to allow high and low flow period site positions to be comparable. The Y-axis runs from 0 = downstream of the first site to 100 = upstream of last site. Waterfall notation and accompanying dashed line represent the position of the first major waterfall.

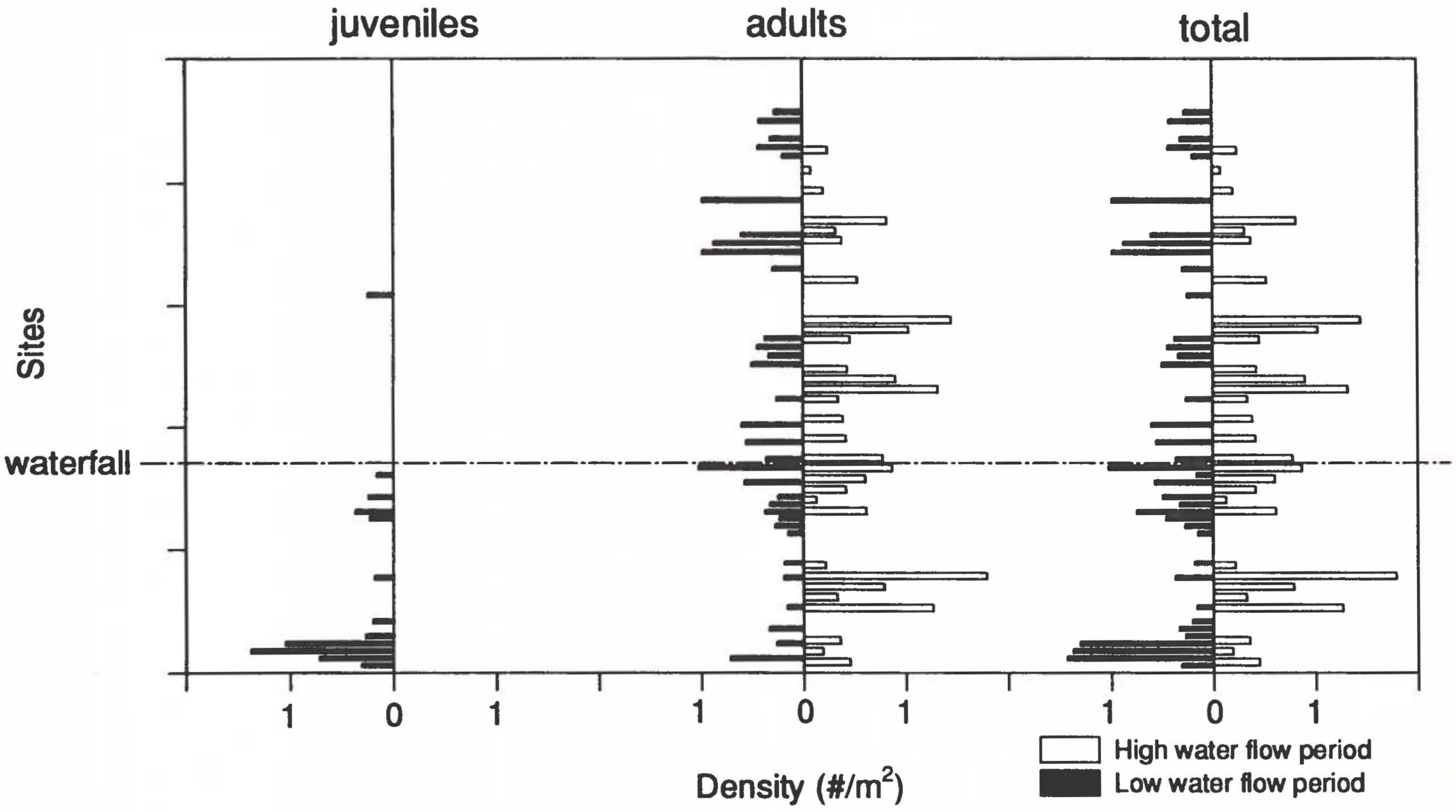

Figure 6. Bar diagram of the density of *Awaous guamensis*. Densities were determined from visual fish counts using the modified quadrat method. Sites have been standardized to allow high and low flow period site positions to be comparable. The Y-axis runs from 0 = downstream of the first site to 100 = upstream of last site. Waterfall notation and accompanying dashed line represent the position of the first major waterfall.

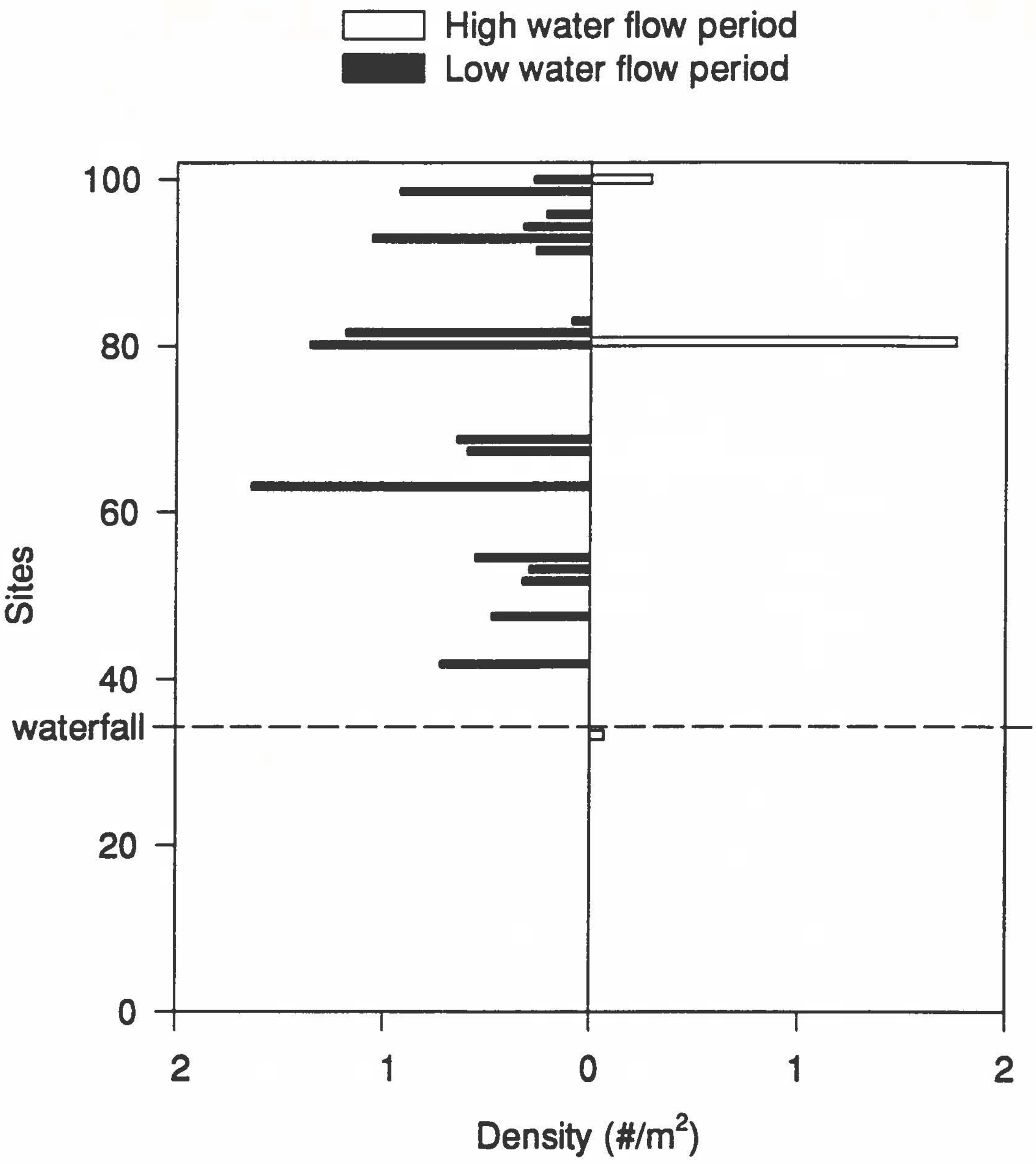

Figure 7. Bar diagram of the density of *Sicyopus leprurus.* Densities were determined from visual fish counts using the modified quadrat method. Sites have been standardized to allow high and low flow period site positions to be comparable. The Y-axis runs from 0 = downstream of the first site to 100 = upstream of last site. Waterfall notation and accompanying dashed line represent the position of the first major waterfall.

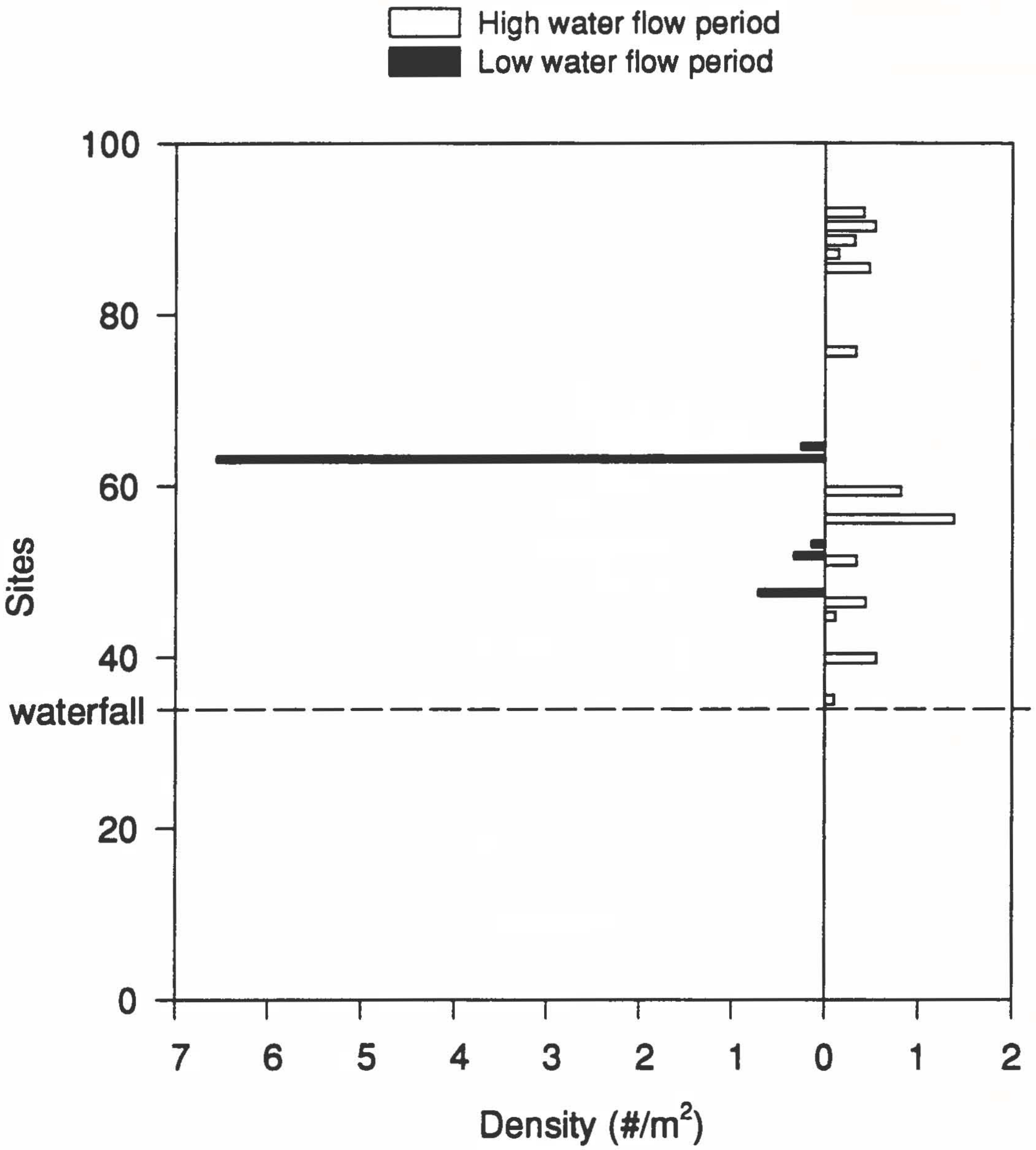

Figure 8. Bar diagram of the density of *Sicyopterus macrostetholepis.* Densities were determined from visual fish counts using the modified quadrat method. Sites have been standardized to allow the high and low flow period site positions to be comparable. The Y-axis runs from 0 = downstream of the first site to 100 = upstream of last site. Waterfall notation and accompanying dashed line represent the position of the first major waterfall.

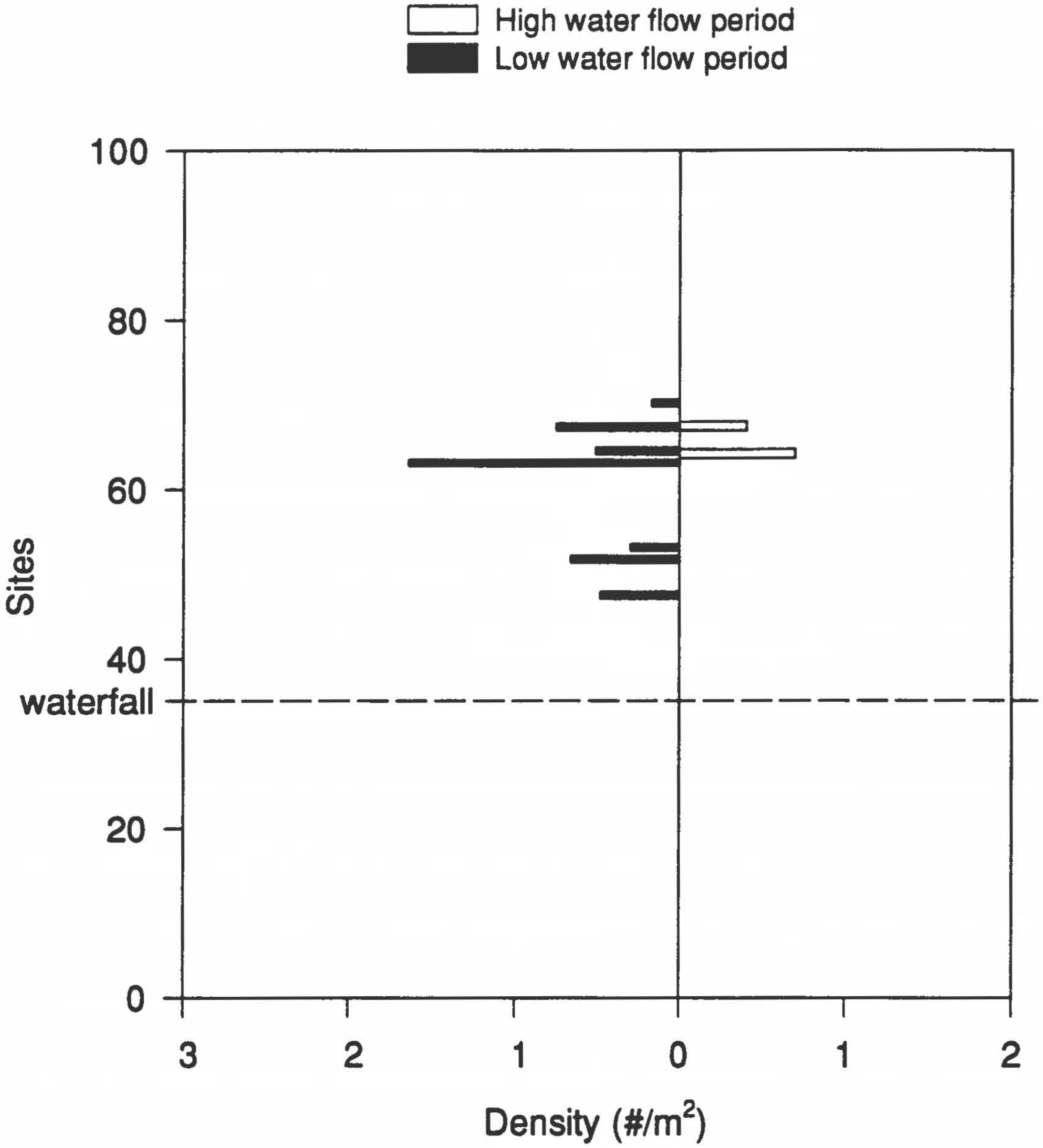

Figure 9. Bar diagram of the density of *Stiphodon caeruleus.* Densities were determined from visual fish counts using the modified quadrat method. Sites have been standardized to allow high and low flow period site positions to be comparable. The Y-axis runs from 0 = downstream of the first site to 100 = upstream of last site. Waterfall notation and accompanying dashed line represent the position of the first major waterfall.

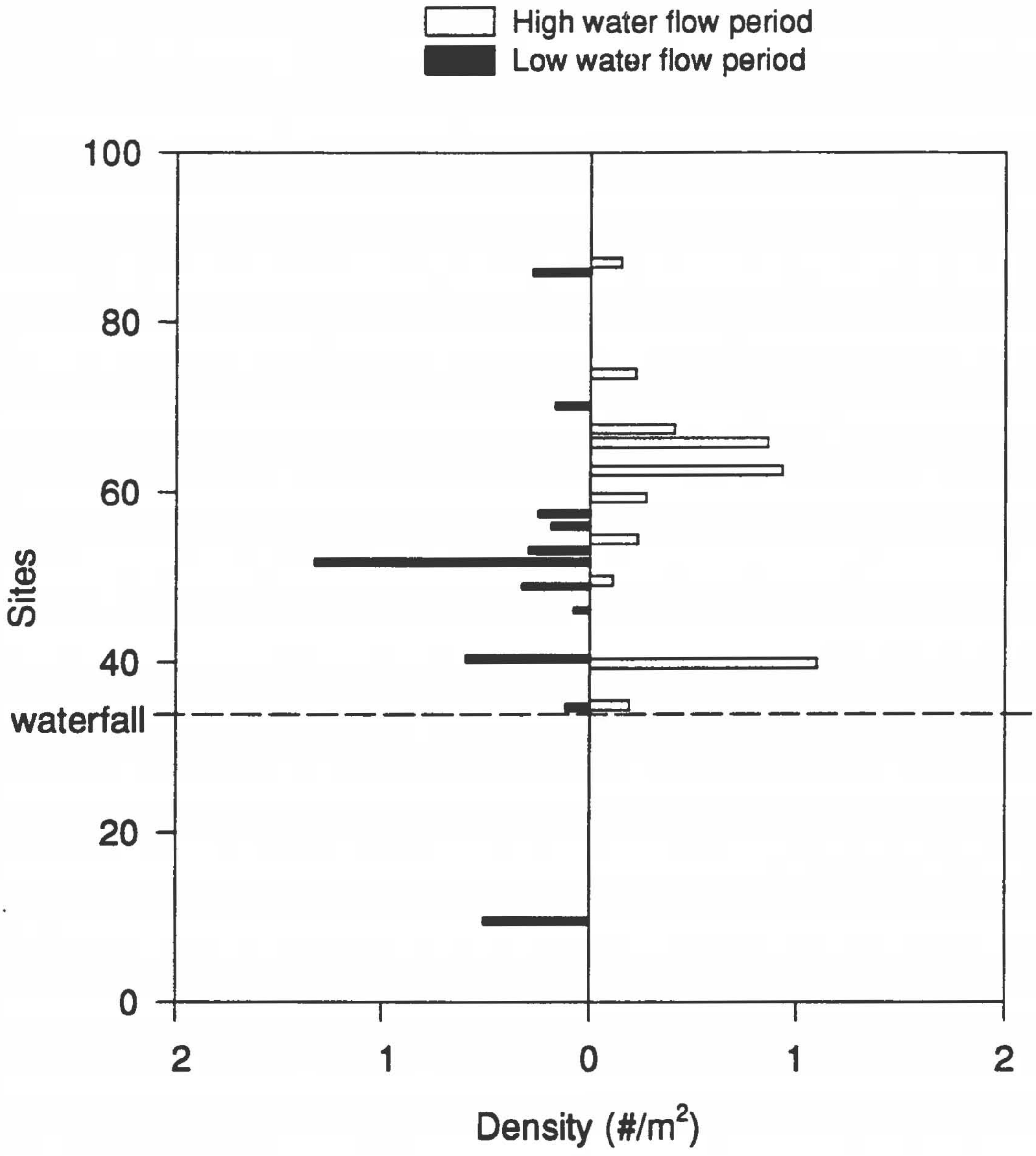

Figure 10. Bar diagram of the density of *Eleotris fusca.* Densities were determined from visual fish counts using the modified quadrat method. Sites have been standardized to allow high and low flow period site positions to be comparable. The Y-axis runs from 0 = downstream of the first site to 100 = upstream of last site. Waterfall notation and accompanying dashed line represent the position of the first major waterfall.

Microhabitat Patterns

Microhabitat use was determined for *Stiphodon elegans, Kuhlia rupestris, Awaous guamensis, Stenogobius* sp., *Sicyopus leprurus, Stiphodon caeruleus,* and *Sicyopterus macrostetholepis.* The sleeper goby *Eleotris fusca*, which was cyptic and easily distrubed, and the eel *Anguilla marmorata,* which was rarely observed within a survey quadrat, were not included in the microhabitat analysis due to insufficient data.

Factor analysis revealed three factors that explain 72% of the variance within the data set. These factors were a velocity factor, a proximity factor, and a depth/substrate factor (Table 2). For each of these factors, Levin's niche breadth and Schoener's niche overlap indices were calculated for the component microhabitat variables. The results were combined with median values to determine species resource use groups for each factor.

Factor one was termed the water velocity factor. Variables that loaded heavily on this factor were focal point water velocity and mean water column velocity. Niche breadth analysis showed varying degrees of use for these two components, as can be seen in Table 3 for focal point water velocities and Table 5 for mean water column velocities. *Awaous guamensis* had the widest tolerance of mean water column velocity but a relatively narrow use of focal point velocities. *Sicyopterus macrostetholepis* had a wide niche breadths in regard to focal point water velocity and mean water column velocity. *Stiphodon elegans* and *Kuhlia rupestris* had moderate scores for both indices. *Stenogobius* sp. had a moderate niche breadth in regard to mean water column velocity but the narrowest niche breadth with regard to focal point water velocity. *Stiphodon caeruleus* and *Sicyopus leprurus* each had much lower niche breadth scores for mean column water velocity than for focal point water velocities.

A combination of niche overlap and median scores was used to determine species grouping patterns for the water velocity factor. The niche overlap analysis showed two groups with respect to focal point velocity (Table 4). *Sicyopterus macrostetholepis, Stiphodon caeruleus*, and *Sicyopus leprurus* utilizated relatively high focal point water velocities (medians>1 cm/sec), while *Stiphodon elegans, Awaous guamensis, Kuhlia rupestris,* and *Stenogobius* sp. used relatively low focal point water velocities (medians<1 cm/sec). With respect to mean water column velocity (Table 6), different groups emerged. The first group contained *Awaous guamensis, Sicyopterus macrostetholepis, Kuhlia rupestris, Stiphodon elegans,* and *Stenogobius* sp.; these fish tended to use higher mean water column velocities (medians>1 cm/sec). The second group contained *Stiphodon caeruleus* and *Sicyopus leprurus,* both of which used habitats of low mean water column velocity (medians<1 cm/sec). The combination of these two groups revealed three differing strategies of water current use. Fish that use higher mean water column velocities than focal point water velocities use current shelters closely associated with the main current. Included in this group were *Awaous guamensis, Stenogobius* sp., *Kuhlia rupestris* and *Stiphodon elegans.* Fish that use high mean water column velocities and high focal point water velocities are fish that position themselves in the main current, not in a current shelter. This group contained one species, *Sicyopterus macrostetholepis.* Finally, fish that used low mean water column velocities, but high focal point water velocities are fish that are found away from the main currents (e.g. eddies, side pockets), but still oriented to the local bottom currents. This group contains *Stiphodon caeruleus* and *Sicyopus leprurus.*

Factor 2, termed the proximity factor, had high positive loadings for use of cover and had a high negative loading for postion in the water column. The term proximity is used to denote nearness to cover or to the bottom. Niche breadth and niche overlap analysis for use of cover, Tables 7 and 8 respectively, and for postion in the water column, Tables 9 and 10 respectively, resulted in similiar groupings. Niche breadth showed narrow resource use for the goby assemblage and wide resource use for *Kuhlia rupestris* for both components. Niche overlap analysis for use of cover showed high overlap for the goby assemblege as a group that was rarely observed using cover. This group was segregated from *Kuhlia rupestris*, of which 65% were using cover. A school of *Kuhlia rupestris* was usually focused around a sheltering object (i.e. root wad, undercut bank, fallen tree) from which the fish continuously range out to patrol their home range. Niche overlap analysis on position in the water column had a consistent grouping pattern. The bottom dwelling gobies had high overlap with each other and low overlap with *K. rupestris*, which had a mean position of .36 of the total depth off the bottom. Observations for *Stiphodon elegans* in the water column were adult males in breeding colors displaying. *Awaous guamensis* and *Sicyopus leprurus* were occasionally seen feeding on drifting particles in the water column. The proximity factor separated the goby assemblege from *K. rupestris.*

Factor three, the depth/substrate factor, had high positive loadings for the water column depth and focal point substrate variables. This factor may reflect the general trend of deeper waters having lower velocites and ,therefore, finer substrates on the bottom. Niche breadth analysis for water column depth (Table 11) showed *Awaous guamensis* had the widest depth use and *Stiphodon caeruleus* had the most narrow resource use. *Kuhlia rupestris, Stiphodon elegans, Sicyopus leprurus, Sicyopterus macrostetholepis*, and *Stenogobius* sp. had moderate breadth scores to the depth component. Niche breadth for focal point substrate showed two groups (Table 13). The fish with moderate width for depth use included *Kuhlia rupestris, Stiphodon elegans, Awaous guamensis,* and *Sicyopterus macrostetholepis.* The second group had narrow depth use and included *Stenogobius* sp., *Stiphodon caeruleus,* and *Sicyopus leprurus.*

Niche overlap for water column depth (Table 12) showed *Kuhlia rupestris* and *Awaous guamensis* used relatively deep waters, while *Sicyopterus macrostetholepis*, *Sicyopus leprurus*, *Stenogobius* sp., and *Stiphodon caeruleus* used shallow waters. *Stiphodon elegans* had wide overlap with all species. Niche overlap for focal point substrate use (Table 14) differentiated species that used erosional substrates (bedrock, boulder) including *Stiphodon caeruleus*, *Sicyopus leprurus*, *Sicyopterus macrostetholepis*, and *Stiphodon elegans*, from species that utilized depositional substrates (sand, gravel), which included *Stenogobius* sp. and

Awaous guamensis. *Kuhlia rupestris* used all available substrates and had medium overlap with *Stiphodon elegans, Stenogobius* sp. and *Awaous guamensis.*

Niche overlap and median resource use values were combined to determine grouping patterns. This led to the formation of five groups differentiated by this factor. Group one used shallow depths and hard substrates, and included the species *Sicyopterus macrostetholepis*, *Stiphodon caeruleus*, and *Sicyopus leprurus*. Group two utilized shallow water and soft substrates. This group included one species, *Stenogobius* sp. The third group used deep depths and soft substrates, and included *Awaous guamensis.* The final two groups separated on one component. In group four, *Stiphodon elegans* used hard substrates and a wide range of depths and in group five, *Kuhlia rupestris* used deeper water depths and a wide ranges of substrates.

The three factors descerned by factor analysis provided enough information to separate six of the seven species on their physical microhabitat utilization. The final species pair, *Stiphodon caeruleus* and *Sicyopus leprurus*, were able to be differentiated by the trophic status as determined from earlier published work (Sakai and Nakamura 1979). Figure 11 showed the resource segregation for the fish assemblage in the form of an ecological key constructed from this microhabitat analysis.

Table 2. Sorted rotated factor loadings from analysis of the microhabitat data matrix. The rows are rearranged showing loadings greater than 0.500 first, and loadings less than 0.250 have been replaced by zero (BMDP 1993). VP represents the eigenvalue for the factor.

Variables	**Velocity factor**	**Proximity factor**	**Depth/substrate factor**
Focal point velocity	0.920	0.000	0.000
Mean column velocity	0.915	0.000	0.000
Use of cover	0.000	0.844	0.000
Position in water column	0.000	-0.808	0.000
Water column depth	0.000	0.000	0.811
Focal point substrate	0.000	0.000	0.677
VP	1.687	1.443	1.175

Table 3. Proportional resource use and niche breadth for focal point water velocities. B is the niche breadth calculated by $B=1/\sum P_{ij}^2$, where P_{ij} represents the observed proportional use of each category (Levins 1968). N = sample size and StDev = standard deviation.

upper bound of velocity category (cm/sec)	*Stiphodon elegans*	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
1.00	0.53	0.29	0.64	0.69	0.44	0.33	0.54
2.00	0.23	0.43	0.09	0.10	0.47	0.33	0.19
3.00	0.04	0.14	0.10	0.13	0.06	0.17	0.02
4.00	0.03	0.00	0.03	0.00	0.00	0.08	0.15
5.00	0.05	0.07	0.03	0.00	0.03	0.00	0.03
6.00	0.02	0.00	0.03	0.08	0.00	0.00	0.00
7.00	0.01	0.07	0.04	0.00	0.00	0.00	0.00
8.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00
9.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
>10.00	0.06	0.00	0.03	0.00	0.00	0.08	0.07
B	2.94	3.38	2.31	1.98	2.40	3.79	2.84
N	440	14	97	48	32	11	185
median	0.91	1.22	0.91	0.61	1.22	1.37	0.91
mean	2.99	1.83	1.89	1.19	1.14	2.63	2.50
StDev	6.66	1.73	3.01	1.54	0.93	3.35	3.74

Table 4. Niche overlap for focal point water velocities. Niche overlap calculated from Schoener (1970), where niche breadth variables are compared between species pairs with the formula $S = 100(1-1/2\sum|P_{xi}-P_{yi}|)$. Similarity values are chosen to be $S < 33.33$ as low overlap (L), $33.33 < S < 67.67$ as moderate overlap (M), and $S > 67.67$ as high overlap (H).

	Stiphodon elegans	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
Stiphodon elegans	-	61.53	77.96	69.28	73.92	69.24	85.92
Stiphodon caeruleus	M	-	55.38	51.49	80.80	76.19	52.90
Awaous guamensis	H	M	-	86.60	62.37	59.11	74.23
Stenogobius sp.	H	M	H	-	60.42	56.25	66.09
Sicyopus leprurus	H	H	M	M	-	72.92	67.96
Sicyopterus macrostetholepis	H	H	M	M	H	-	69.77
Kuhlia rupestris	H	M	H	M	H	H	-

Table 5. Proportional resource use and niche breadth for mean water column velocities. B is the niche breadth calculated by $B=1/\sum P_{ij}^2$, where P_{ij} represents the observed proportional use of each category (Levins 1968). N = sample size and StDev = standard deviation.

upper bound of velocity category (cm/sec)	*Stiphodon elegans*	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
1.00	0.47	0.71	0.30	0.31	0.72	0.27	0.40
2.00	0.18	0.07	0.21	0.40	0.25	0.27	0.34
3.00	0.09	0.00	0.10	0.04	0.00	0.27	0.13
4.00	0.06	0.07	0.11	0.17	0.03	0.00	0.00
5.00	0.05	0.07	0.05	0.00	0.00	0.00	0.06
6.00	0.01	0.00	0.03	0.00	0.00	0.00	0.00
7.00	0.01	0.07	0.03	0.00	0.00	0.00	0.00
8.00	0.02	0.00	0.08	0.08	0.00	0.09	0.00
9.00	0.01	0.00	0.01	0.00	0.00	0.00	0.00
10.00	0.02	0.00	0.01	0.00	0.00	0.00	0.00
>10.00	0.08	0.00	0.06	0.00	0.00	0.09	0.07
B	3.68	1.88	5.86	3.44	1.72	4.17	3.32
N	440	14	97	48	32	11	185
median	1.22	0.91	1.83	1.22	0.61	1.37	1.22
mean	3.44	1.74	3.51	2.01	0.90	3.60	2.24
StDev	6.59	1.88	4.17	1.96	0.67	5.68	3.15

Table 6. Niche overlap for mean water column velocities. Niche overlap calculated from Schoener (1970), where niche breadth variables are compared between species pairs with the formula $S = 100(1-1/2\sum|P_{xi}-P_{yi}|)$. Similarity values are chosen to be $S < 33.33$ as low overlap (L), $33.33 < S < 67.67$ as moderate overlap (M), and $S > 67.67$ as high overlap (H).

	Stiphodon elegans	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
Stiphodon elegans	-	66.23	80.68	60.78	67.44	64.55	79.53
Stiphodon caeruleus	M	-	52.43	45.54	81.70	34.42	53.09
Awaous guamensis	H	M	-	72.27	53.64	72.64	72.16
Stenogobius sp.	M	M	H	-	59.38	67.05	69.47
Sicyopus leprurus	M	H	M	M	-	52.27	65.00
Sicyopterus macrostetholepis	M	M	H	H	M	-	74.55
Kuhlia rupestris	H	M	H	H	M	H	-

Table 7. Proportional resource use and niche breadth for use of cover. B is the niche breadth calculated by $B = 1/\sum P_{ij}^2$, where P_{ij} represents the observed proportional use of each category (Levins 1968). N = sample size and StDev = standard deviation.

	Stiphodon elegans	*Stiphodon caeuleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
Cover	0.02	0.07	0.03	0	0	0	0.65
No Cover	0.98	0.93	0.97	1.00	1.00	1.00	0.35
B	1.04	1.15	1.06	1.00	1.00	1.00	1.84
N	440	14	97	48	32	12	185
Median	1.00	1.00	1.00	1.00	1.00	1.00	0.00
Mean	1.98	1.93	1.97	2.00	2.00	2.00	1.35
StDev	0.14	0.27	0.17	0	0	0	0.48

Table 8. Niche overlap for use of cover. Niche overlap calculated from Schoener (1970), where niche breadth variables are compared between species pairs with the formula $S = 100(1-1/2\sum|P_{xi}-P_{yi}|)$. Similarity values are chosen to be $S < 33.33$ as low overlap (L), $33.33 < S < 67.67$ as moderate overlap (M), and $S > 67.67$ as high overlap (H).

	Stiphodon elegans	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
Stiphodon elegans	-	94.90	98.95	97.95	97.95	97.95	37.18
Stiphodon caeruleus	H	-	95.95	92.86	92.86	92.86	42.28
Awaous guamensis	H	H	-	96.91	96.91	96.91	38.23
Stenogobius sp.	H	H	H	-	100.00	100.00	35.14
Sicyopus leprurus	H	H	H	H	-	100.00	35.14
Sicyopterus macrostetholepis	H	H	H	H	H	-	35.14
Kuhlia rupestris	M	M	M	M	M	M	-

Table 9. Proportional resource use and niche breadth for position in the water column. B is the niche breadth calculated by $B=1/\sum P_{ij}^2$, where P_{ij} represents the observed proportional use of each category (Levins 1968). N = sample size, StDev = standard deviation, 0.00 = the bottom, and 1.00 = surface.

upper bound of category	*Stiphodon elegans*	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
0.00	0.98	1.00	0.97	1.00	0.91	1.00	0.01
0.25	0.01	0.00	0.01	0.00	0.00	0.00	0.23
0.50	0.02	0.00	0.02	0.00	0.06	0.00	0.64
0.75	0.00	0.00	0.00	0.00	0.03	0.00	0.12
1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
B	1.05	1.00	1.06	1.00	1.21	1.00	2.11
N	440	14	97	48	32	12	185
Median	0.00	0.00	0.00	0.00	0.00	0.00	0.37
Mean	0.01	0.00	0.01	0.00	0.05	0.00	0.36
StDev	0.06	0.00	0.06	0.00	0.15	0.00	0.15

Table 9. Proportional resource use and niche breadth for position in the water column. B is the niche breadth calculated by $B=1/\sum P_{ij}^2$, where P_{ij} represents the observed proportional use of each category (Levins 1968). N = sample size, StDev = standard deviation, 0.00 = the bottom, and 1.00 = surface.

upper bound of category	*Stiphodon elegans*	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
0.00	0.98	1.00	0.97	1.00	0.91	1.00	0.01
0.25	0.01	0.00	0.01	0.00	0.00	0.00	0.23
0.50	0.02	0.00	0.02	0.00	0.06	0.00	0.64
0.75	0.00	0.00	0.00	0.00	0.03	0.00	0.12
1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
B	1.05	1.00	1.06	1.00	1.21	1.00	2.11
N	440	14	97	48	32	12	185
Median	0.00	0.00	0.00	0.00	0.00	0.00	0.37
Mean	0.01	0.00	0.01	0.00	0.05	0.00	0.36
StDev	0.06	0.00	0.06	0.00	0.15	0.00	0.15

Table 10. Niche overlap for position in the water column. Niche overlap calculated from Schoener (1970), where niche breadth variables are compared between species pairs with the formula $S = 100(1-1/2\sum|P_{xi}-P_{yi}|)$. Similarity values are chosen to be $S < 33.33$ as low overlap (L), $33.33 < S < 67.67$ as moderate overlap (M), and $S > 67.67$ as high overlap (H).

	Stiphodon elegans	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius sp.*	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
Stiphodon elegans	-	97.73	99.18	97.73	92.22	97.73	2.81
Stiphodon caeruleus	H	-	96.91	100.00	90.63	100.00	0.54
Awaous guamensis	H	H	-	96.91	92.69	96.91	3.63
Stenogobius sp.	H	H	H	-	90.63	100.00	0.54
Sicyopus leprurus	H	H	H	H	-	90.63	9.92
Sicyopterus macrostetholepis	H	H	H	H	H	-	0.54
Kuhlia rupestris	L	L	L	L	L	L	-

Table 11. Proportional resource use and niche breadth for water column depth. B is the niche breadth calculated by $B=1/\sum P_{ij}^{2}$, where P_{ij} represents the observed proportional use of each category (Levins 1968). N = sample size and StDev = standard deviation.

depth (m)	*Stiphodon elegans*	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
0.10	0.06	0.00	0.00	0.02	0.03	0.00	0.00
0.20	0.21	0.29	0.14	0.48	0.13	0.09	0.10
0.30	0.18	0.21	0.14	0.17	0.31	0.27	0.19
0.40	0.29	0.36	0.21	0.06	0.19	0.36	0.18
0.50	0.12	0.00	0.15	0.13	0.06	0.00	0.13
0.60	0.06	0.14	0.07	0.02	0.06	0.09	0.23
0.70	0.02	0.00	0.11	0.06	0.00	0.00	0.06
0.80	0.02	0.00	0.04	0.06	0.13	0.18	0.02
0.90	0.01	0.00	0.05	0.00	0.03	0.00	0.05
1.00	0.01	0.00	0.02	0.00	0.06	0.00	0.03
>1.00	0.01	0.00	0.05	0.00	0.00	0.00	0.00
B	5.46	3.63	7.49	3.50	5.63	3.90	6.30
N	440	14	97	48	32	11	185
median	0.30	0.27	0.43	0.24	0.30	0.30	0.43
mean	0.33	0.29	0.47	0.30	0.40	0.37	0.44
StDev	0.21	0.14	0.29	0.19	0.26	0.19	0.20

Table 12. Niche overlap for water column depth. Niche overlap calculated from Schoener (1970), where niche breadth variables are compared between species pairs with the formula $S = 100(1-1/2\sum|P_{xi}-P_{yi}|)$. Similarity values are chosen to be $S < 33.33$ as low overlap (L), $33.33 < S < 67.67$ as moderate overlap (M), and $S > 67.67$ as high overlap (H).

	Stiphodon elegans	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
Stiphodon elegans	-	74.09	75.39	64.13	68.92	64.32	70.04
Stiphodon caeruleus	H	-	56.70	53.57	58.93	75.32	61.85
Awaous guamensis	H	M	-	60.07	67.49	55.48	78.06
Stenogobius sp.	M	M	M	-	52.08	40.34	55.88
Sicyopus leprurus	H	M	M	M	-	73.86	68.06
Sicyopterus macrostetholepis	M	H	M	M	H	-	57.64
Kuhlia rupestris	H	M	H	M	H	M	-

Table 13. Proportional resource use and niche breadth for focal point substrate. B is the niche breadth calculated by $B=1/\sum P_{ij}^2$, where P_{ij} represents the observed proportional use of each category (Levins 1968). N = sample size and StDev = standard deviation.

substrate category	*Stiphodon elegans*	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius sp.*	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
Bedrock	0.57	0.79	0.19	0.06	0.81	0.58	0.07
Boulder	0.06	0.21	0.04	0.00	0.13	0.17	0.00
Cobble	0.14	0.00	0.13	0.00	0.00	0.08	0.17
Gravel	0.10	0.00	0.05	0.15	0.06	0.17	0.43
Sand/Sediment	0.13	0.00	0.59	0.79	0.00	0.00	0.33
B	2.65	1.51	2.49	1.53	1.47	2.48	3.04
N	440	14	97	48	32	12	185
Median	1.00	1.00	5.00	5.00	1.00	1.00	4.00
Mean	2.15	1.21	3.81	4.60	1.31	1.83	3.95
StDev	1.50	0.43	1.60	1.01	0.78	1.19	1.06

Table 14. Niche overlap for focal point substrate. Niche overlap calculated from Schoener (1970), where niche breadth variables are compared between species pairs with the formula $S = 100(1-1/2\sum|P_{xi}-P_{yi}|)$. Similarity values are chosen to be $S < 33.33$ as low overlap (L), $33.33 < S < 67.67$ as moderate overlap (M), and $S > 67.67$ as high overlap (H).

	Stiphodon elegans	*Stiphodon caeruleus*	*Awaous guamensis*	*Stenogobius* sp.	*Sicyopus leprurus*	*Sicyopterus macrosteth.*	*Kuhlia rupestris*
Stiphodon elegans	-	63.18	54.19	28.98	69.43	81.29	43.85
Stiphodon caeruleus	M	-	22.68	6.25	91.07	75.00	7.03
Awaous guamensis	M	L	-	70.17	27.84	36.17	58.50
Stenogobius sp.	L	L	H	-	12.50	20.83	53.81
Sicyopus leprurus	H	H	L	L	-	77.08	13.28
Sicyopterus macrostetholepis	H	H	M	L	H	-	32.03
Kuhlia rupestris	M	L	M	M	L	L	-

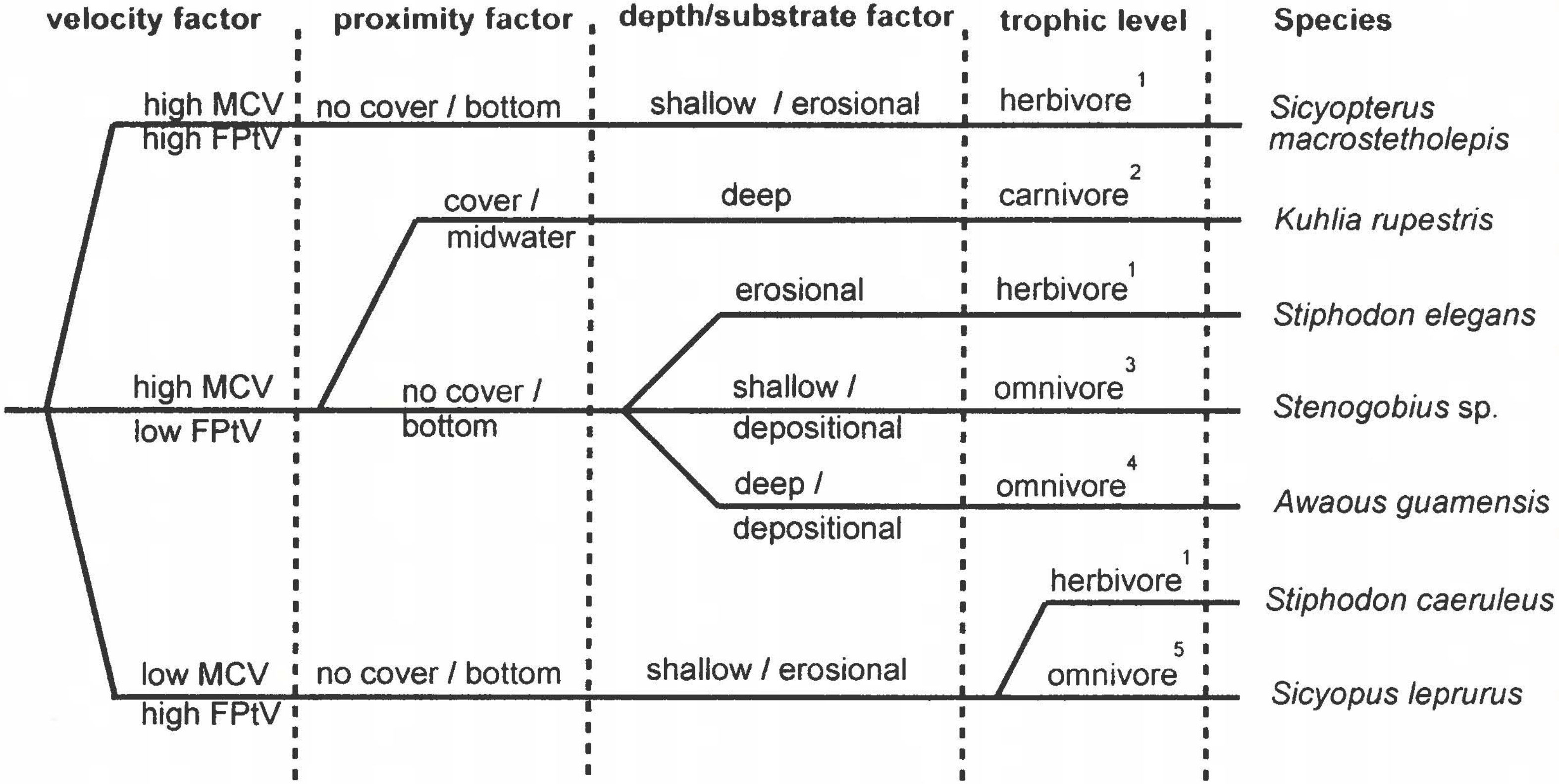

Figure 11. Ecological key to microhabitat utilization for the fish assemblage. MCV = Mean water Column Velocity, FPtV = Focal Point water Velocity. The citations for trophic level categories are: 1 - Parenti and Maciolek 1993, 2 - Lewis and Hogan 1987, 3 - Watson 1992, 4 - Watson 1991, and 5 - Sakai and Nakamura 1979.

Discussion

The fish assemblage of the Asmafines River exhibited non-random habitat utilization at both the distributional and the microhabitat levels. The major factor affecting the distribution of the fish was the position of the first major waterfall. Due to the diadromous life histories of the fish species, barriers to upstream movements of the recruiting juveniles were expected to stop any fish species without morphological adaptation for surmounting the waterfalls, as noted in Palau (Fehlmann 1960), Hawaii (Kinzie and Ford 1982, Kinzie 1988, 1993), Pohnpei (Parenti and Maciolek 1993), and Trinidad (Gilliam et al. 1993, Fraser et al. 1995). If the restriction of upstream movement by the waterfall was the only ecological mechanism at work in the stream, then two grops of fish should be seen: those found below the waterfall and those found throughout the stream. However, we found three groups of fish, those found only below the falls, those found throughout the stream, and those found predominantly above the falls.

Predation or risk of predation may influence the distribution of smaller fishes, especially given the high densities of *Kuhlia rupestris* downstream of the first waterfall. *Kuhlia rupestris* is an active predatory fish and has been observed closely following feeding *Anguilla marmorata,* waiting for the eel to flush hiding prey, and this behavior may further limit potential hiding places for prey species below waterfalls. Predation has been shown to fragment the within stream distributions of tropical fish species in Trinidad (Gilliam et al. 1993, Fraser et al. 1995).

There are three other potential fish predators present in the Asmafines River. The anguillid eels and the sleeper goby *Eleotris fusca* are found throughout the stream at low densities. The Tahitian prawn *Macrobrachium lar* has been hypothesized to be a predator on streamfishes (Kinzie and Ford 1982), but we found the prawn almost exclusively above the waterfall, co-occurring with the stream fish at even high densities. It is likely that predation by *Kuhlia rupestris* limits the distribution of some species primarily to sites above the first major waterfall.

The Sicydinae goby factor, which associates *Stiphodon elegans, Stiphodon caeruleus, Sicyopterus macrostetholepis,* and *Sicyopus leprurus*, probably show the historical legacy of taxonomically similar species that still utilize similar habitats, and indicates that competition between the species is not a major determinant of their distribution. Mixed species aggregations were observed and little interspecific aggression was observed, even where intraspecific territoriality was occurring. In Palau, *Stiphodon elegans* was also common above and below the first major waterfall, while *Stiphodon caeruleus* and many other species of Sicydinae gobies were common above the waterfall only (Nelson et al. 1995). The lack of any physical measurements loading with this group suggests that some unmeasured component, possibly related to food availability, groups these species.

Awaous guamensis also has a streamwide distribution in Hawaii (Ego 1956, Ha 1991) and in throughout its range (Watson 1992). The downstream migration for spawning that has been clearly shown for this species in Hawaii (Ego 1956, Ha 1991) was less pronounced in our observations, but large adult *Awaous guamensis* in breeding colors were observed in the tidally influenced mouth of the stream during much of the rainy season.

Eleotris fusca is able to ascend waterfalls, although it lacks the fused pelvic disk characteristic of gobies, and is found predominantly above the waterfall on the Asmafines River. This may be a result of the higher densities of small gobies, *Macrobrachium lar*, and atyid shrimp in the upper sections of the stream that are probable prey items for this ambush predator. Avoidance of the lower sections due to predation by *Kuhlia rupestris* is unlikely due to the large size of adult *Eleotris fusca*. The distribution above waterfalls is also noted on Yap (Nelson 1989), and the closely related *Bunaka* sp. were found above the waterfalls in Palau (Fehlmann 1960, Nelson et al. 1995). *Eleotris sandwicenes* in Hawaii is not able to ascend waterfalls and possible patterns involving *Eleotris* predation on Sicydinae gobies have been hypothesized, but not substantiated (Kinzie and Ford 1982).

At the microhabitat level, the non-random habitat use by the fishes allowed the formation of the ecological key (Figure 11). While this key shows segregation for all species, high niche overlap and multispecies aggregations were not uncommon. The velocity factor showed segregation of fish position within, near, or away from the main current, and current has been shown to influence microhabitat utilization in many stream fish assemblages (Moyle and Baltz 1985, Schlosser 1985, Grossman and Freeman 1987, Bain et al. 1988, Leonard and Orth 1988, Pearson and Li, 1992). Segregation by the velocity factor for the Sicydinae gobies is consistent with the observations of Sakai and Nakamura (1979) that were supported by data on the morphological differences in the pelvic disk holding power. *Sicyopterus macrostetholepis* did hold in the highest current areas, with *Stiphodon elegans* near the main current and *Sicyopus leprurus* in the lowest current areas. While our study supports the morphological adaptations influencing microhabitat selection, their hypothesis regarding differences in distribution based on increased ability to deal with the torrential nature of the streams was not supported. *Sicyopus leprurus,* the least differentiated species, was found furthest upstream in the extremely steep headwaters.

The segregation of certain goby genera by substrate is consistent with known and observed habits. *Awaous guamensis* (Ego 1956, Ha 1991, Watson 1992) and the *Stenogobius* genus (Watson 1991) use soft substrate for feeding, by sifting sand through their mouths, and for cover, by diving into sand when alarmed. *Stiphodon* (Sakai and Nakamura 1979, Parenti and Maciolek 1993), and *Sicyopterus* (Sakai and Nakamura 1979) feed on epiphytic algae that grow on bedrock and boulders, and seek cover under rocks and in high current.

Thus, variability in productivity and food availability are likely to influence the distribution of these species.

This study shows a pattern of habitat use that is influenced by both abiotic and biotic variables and also shows that segregation of habitats occurs at the distributional and microhabitat level. The broad pattern where *Kuhlia rupestris* dominates below the first major waterfall, replaced by the sicydinae gobies above the waterfall is consistent with observations in other streams of Micronesia (Parenti and Maciolek 1993, Nelson et al. 1995). The microhabitats of these fishes would be expected to be similar in different areas, given the importance of current velocity and substrate availability on aspects of their feeding ecology. Additional studies are needed to see if these patterns of habitat use are consistent over time and in different streams or if variability in recruitment (Sale 1977, 1978) causes changes individual species habitat utilization.

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