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Microhabitat use in an assemblage of native and introduced stream fishes in Wailoa Stream, Island of Hawaii

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MICROHABITAT USE IN AN ASSEMBLAGE OF NATIVE AND INTRODUCED
STREAM FISHES IN WAILOA STREAM, ISLAND OF HAWAII

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The Department of Biological Sciences

by
Mark G. McRae
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ABSTRACT

To date, most research on the ecology of Hawaiian stream fishes has taken place in the middle and upper reaches of streams. In the terminal reaches of streams in Hawaii, the ecological aspects of the relatively more diverse fish assemblages are largely unknown. This study investigated patterns of microhabitat use in an assemblage of native and introduced stream fishes living in the terminal reach of Wailoa Stream on the Island of Hawaii. Multivariate and univariate analyses of microhabitat data collected through underwater visual surveys indicated that differences in microhabitat preferences were an important factor in the structure of this assemblage. Strong differences in three-dimensional microhabitat use patterns appear to allow native gobioids and introduced poeciliids to coexist in Wailoa Stream with little competition for spatial resources. However, high overlap in the microhabitat use patterns of juvenile *Kuhlia xenura* and introduced *Poecilia mexicana* and *Xiphophorus helleri* is cause for concern.

INTRODUCTION

The information in the following thesis represents an investigation into the spatial ecology of an assemblage of stream dwelling fishes in Hawaii. Specifically, the patterns of microhabitat use, selection, and interspecific overlap for eight species of fishes in Wailoa Stream on the Island of Hawaii were observed, analyzed, and presented herein.

The extreme isolation of the Hawaiian Islands has resulted in a depauperate freshwater fish fauna consisting of five indigenous species of gobioid fishes (four gobies and one eleotrid) (Kinzie 1990). Collectively known as 'O'opu, these fishes share an amphidromous life cycle. The term amphidromy refers to a form of diadromy, a life cycle that includes both freshwater and marine environments (Meyers 1949).

Amphidromous fishes spend their adult lives in streams where spawning takes place. Newly hatched larvae are swept downstream to the sea and become part of the oceanic zooplankton community where they develop and return to streams as juveniles.

Several investigators have noted a general pattern of zonation among stream-dwelling fishes throughout Oceania where species-specific instream distributions are affected by natural barriers to upstream penetration, specifically waterfalls (Nelson et al. 1991, Nishimoto and Kuamo'o 1991, Parham 1995). Many species of amphidromous gobies have evolved the ability to climb vertical waterfalls through the use of pelvic fins that are fused to form a suction disc. Nelson et al. (1991) noted that the differences in the composition of the fish community upstream and downstream of waterfalls in streams on Pohnpei and in Palau correspond to differences in the climbing abilities of member species. The same pattern was observed in an assemblage of diadromous fishes in the Asmafines River in Guam (Parham 1995). A similar distributional relationship is found

in Hawaiian streams. Areas above terminal waterfalls in Hawaii have, at most, three species of indigenous gobies, as only three of the five Hawaiian stream fishes can climb waterfalls (Nishimoto & Kuamoo 1991). Polhemus et al. (1992) classified stream reaches on tropical Pacific islands based partly on this unique faunal arrangement: The term “Midreach” refers to the portion of stream above sharp gradient (e.g., a waterfall) that bars upstream migration of vagrant marine and non-climbing diadromous fishes. The watercourse below such a barrier is classified as the “Terminal Reach”.

The streamfish assemblages in the terminal reaches of Hawaiian streams are often more diverse than in the midreaches due to the presence of itinerant marine and euryhaline estuarine fishes, non-indigenous freshwater animals, as well as amphidromous gobioids. Due to the scarcity of true estuaries throughout the Pacific islands, terminal stream reaches are an important habitat for estuarine species such as fishes in the genus *Kuhlia* and the striped mullet *Mugil cephalus* (Yamamoto and Tagawa 2000). These areas also provide important nursery habitats for several species of near-shore marine fishes such as trevally (*Caranx* sp.) and goatfishes (Archer et al. 1980). Of particular concern, however, is the fact that introduced species are now the predominant component of many terminal reach streamfish assemblages throughout the Hawaiian Islands (Englund and Filbert 1999).

The introduction of non-native freshwater fishes into streams and rivers throughout the Hawaiian Islands has been taking place since the early 1800’s (Devick 1991). One of the most widespread and abundant groups of exotic freshwater fishes in the islands are fishes in the family Poeciliidae (Maciolek 1984). Intentional and accidental releases of poeciliids as agents of mosquito control, unwanted or escaped

aquarium specimens, or as escaped or released baitfishes have resulted in the establishment of poeciliids in all major fresh and brackish water habitats present in Hawaii (Maciolek 1984).

Poeciliids are poorly adapted for the large fluctuations in streamflow that are common in unaltered, high gradient midreaches of Hawaiian streams (Brown et al. 1999) and are often controlled naturally in areas that experience frequent flash floods (Meffe 1984, Fitzsimons et al. 1997). Most terminal reaches in Hawaii, however, are relatively low in gradient and affected to some extent by anthropogenic channel and flow alteration. These conditions allow poeciliids to maintain high population densities, as they can easily find low water velocity refugia during flash floods (Englund and Filbert 1999).

To date, most research on the ecology of Hawaiian stream fish communities has focused primarily on species that can be classified as midreach fishes. The three species of 'O'opu that are able to climb waterfalls appear to exhibit distinct microhabitat preferences and longitudinal distributions which may facilitate their coexistence (Kinzie 1988). Few studies have examined the ecology of terminal reach stream fish assemblages in Hawaii. My study examined similarities and differences in habitat use by an assemblage of fishes including introduced poeciliids, native amphidromous gobioids, and a native kuhliid fish in the terminal reach of Wailoa Stream in Waipio Valley on the Island of Hawaii. Underwater visual surveys were conducted to identify patterns of microhabitat use and availability with the goal of answering the following research questions: Are the microhabitats occupied by the fishes in the terminal reach of Wailoa Stream significantly different from those randomly available to them? Do the

microhabitats of introduced poeciliids and native stream fishes overlap, and, if so, what is the nature of that overlap?

MATERIALS AND METHODS

Study site

Wailoa Stream is located on the windward side of the northern tip of the Island of Hawaii (Figure 1). Flowing through Waipio Valley, Wailoa is the second largest stream on the island, with an average discharge of 49 million gallons per day (MGD) (USDA 1998). Five major tributaries flow into Wailoa Stream; Waima, Koiawe, Alakahi, and Kawainui streams enter Wailoa's midreach and Lalakea enters the terminal reach. A small human population, consisting mostly of traditional taro farmers, resides in the valley.

Flow in Wailoa Stream is altered by three main systems of water diversion. The Lower Hamakua Ditch system diverts water from three of Wailoa's tributaries: Koiawe, Alakahi, and Kawainui streams. Stream flow is diverted to provide water for agricultural irrigation south of Waipio Valley. The second water diversion mechanism in the Wailoa watershed is the Upper Hamakua Ditch which removes water from Lalakea Stream. The third system of diversions consists of a series of weirs constructed of stream stones for the purpose of irrigating taro patches (lo'i) located in lower Waipio Valley. These weirs and their accompanying channels are known as auwai, and are very similar to the system of water diversion utilized by native Hawaiians in Waipio Valley since ancient times. Water removed from Wailoa Stream flows through various networks of lo'i and is returned to the stream.

Only the Lower Hamakua Ditch (LHD) has a significant impact on stream flow in Waipio Stream. The LHD diverts as much as 32 MGD of surface runoff, and essentially limits flow volume in Wailoa Stream near its baseflow level of 22 MGD. This limiting

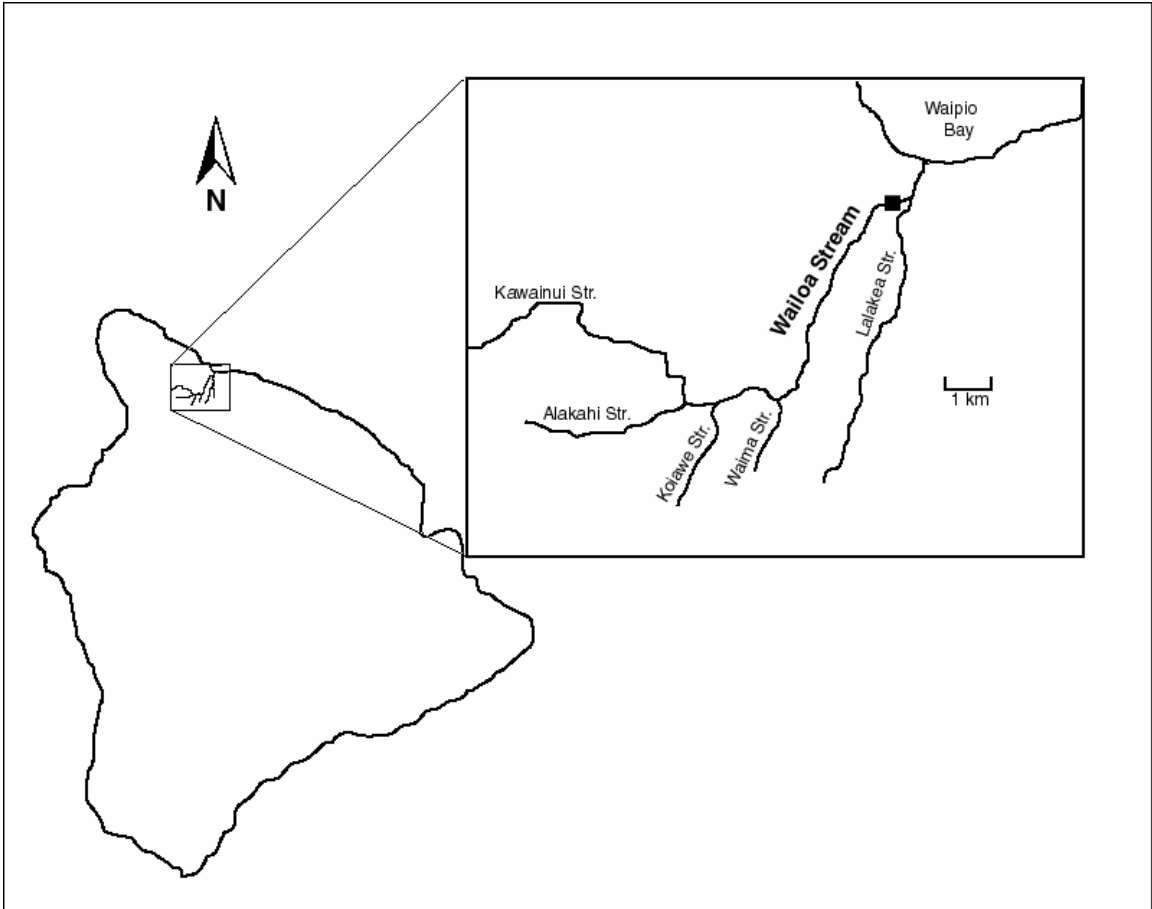


Figure 1. Location of study site. Black square indicates exact location of the study reach.

effect has little noticeable impact during severe storms, during which the 50 MGD threshold of the LHD diversions is exceeded (USDA 1998). The LHD does, however, significantly reduce the normal rise and fall of Wailoa Stream that results from frequent but less severe rain events (USDA 1998).

The study reach was 200 m in length and located in the terminal reach of Wailoa Stream approximately 1.8 km from the mouth. At the point where the study reach was located, Waipio Valley is about 1 km wide with an overall gradient near zero. Two main habitat types dominate Wailoa's terminal reach: deep, slow run (hereafter referred to as "run") and deep riffle (hereafter referred to as "riffle") (Baker and Foster 1992). Run habitats in Wailoa Stream are characterized as having depths > 1m with water velocities between 20 and 75 cm/sec, and substrata dominated by sand and gravel. Riffle habitats are characterized as having depths between 10 and 50 cm with water velocities usually greater than 75 cm/sec, and substrates dominated by cobble and gravel (Baker and Foster 1992). The study reach consisted of two riffles with a combined length of 82 m and an average width of 12.5 m, and one run with a length of 120 m and an average width of 18.5 m. Seven species of fish were observed in the riffle habitat and eight in the run habitat (Table 1). Two additional species, striped mullet *Mugil cephalus* and Tilapia *Oreochromis mossambicus*, were present in the terminal reach of Wailoa Stream, but few observations were made of these species in the study reach.

Table 1. Density (± 1 standard error) of fishes in the terminal reach of Wailoa Stream.

Species	Density (No./m ²)	
	Riffle	Run
<i>Awaous guamensis</i>	0.65 \pm 0.16	1.13 \pm 0.21
<i>Kuhlia xenura</i>	0.42 \pm 0.17	1.38 \pm 0.53
<i>Sicyopterus stimpsoni</i>	1.86 \pm 0.42	0.06 \pm 0.03
<i>Eleotris sandwicensis</i>	0.15 \pm 0.07	0.23 \pm 0.05
<i>Gambusia affinis</i>	0.12 \pm 0.52	1.78 \pm 0.77
<i>Poecilia mexicana</i>	0.13 \pm 0.08	0.87 \pm 0.28
<i>Xiphophorus helleri</i>	0.18 \pm 0.29	4.55 \pm 0.91
<i>Stenogobius hawaiiensis</i>	---	0.93 \pm 0.19

Field methods

Fish observations were made during daylight hours on the following dates: June 1 – 10, and August 3 – 5, 1999; January 26 – February 2, and March 15 and 16, 2000. Stream height was monitored on these dates to ensure that availability measurements did not change over the course of the observation efforts.

Sampling of fish microhabitats took place in randomly located, variable-sized quadrats by way of direct underwater observation (Baker and Foster 1992). The location of quadrat points was determined by using a two-column random number table, with the first column of numbers representing intervals along the length of the survey reach and the second column representing a proportion of the stream width at each interval. Thus, the numbers nine and seven would result in a quadrat that was nine meters upstream of either the starting point or the previous quadrat and at a spot seven tenths of the stream width measured from either side of the stream (Baltz 1990). The size of individual quadrats depended on the field of view ascertained by the observer (Baker and Foster 1992). Each quadrat was approached slowly from downstream in such a way as to

minimize disturbance to the fish. Quadrats that were located in water too shallow to snorkel were observed from the bank with the use of polarized sunglasses.

Once at the observation point, the observer recorded the number of each fish species present, the habitat type in which the quadrat was located, and the length and width of the quadrat. This information was used to calculate the relative density of each species (number of fish / m² – see Table 1) and their distributions in the run and riffle habitat types.

To describe the microhabitat use patterns of the fish species observed in the study reach, the locations of undisturbed fish within the quadrat were marked with flagged fishing weights. Information recorded at each marked fish location included the species, life history stage (juvenile or adult), total depth of the water column, focal point position, focal point substrate, focal point velocity (measured at the fish's snout), bottom velocity (water velocity measured 1 cm above the focal point substrate), surface water velocity (water velocity measured 1 cm below the surface), mean water column velocity (water velocity at 0.6 of the total depth), channel position, percent algae, and percent vegetation. Total water column depth was measured with a top-set wading rod. Focal point substrate was recorded by using a numerical code which represented substrate categories and corresponded to the size of an individual particle in each category (1 = decaying plant detritus, 2 = silt or mud, 3 = sand, 4 = gravel, 5 = cobble, and 6 = boulder). Focal point position was a visual estimate of each fish's relative elevation in the water column and was recorded as a proportion of the water column, with zero representing the stream bottom and one representing the water surface (e.g., a fish estimated to be located halfway between the bottom and the surface would be recorded as having a focal point

position of 0.5). All water velocity measurements were made by using a Marsh-McBirney flow meter. Channel position was a proportional estimate of the fish's location in the stream channel relative to the stream bank, with zero representing a channel position immediately adjacent to one of the stream banks, and 0.5 representing a channel position in the middle of the channel. Percent algae was a visual estimate of the percent of the focal point substrate covered in filamentous algae, and percent vegetation was a visual estimate of the percent of the water column comprised of aquatic macrophytes at each marked fish location.

To obtain information on microhabitat availability in the study reach, three flagged markers were tossed randomly over the shoulder of the observer into each quadrat. The same set of variables that were measured or estimated for each marked fish location was measured or estimated at each of the marked random locations with the exception of focal point position and focal point water velocity, both of which were variables that required the presence of a fish.

Statistical methods

Due to the large differences between riffle and run habitats, data analysis was stratified by habitat type. Data from all sampling periods were pooled due to low number of fish observations made during each of the survey periods and because stream heights did not vary markedly between sampling dates (due to the diversion of stream flow through the Lower Hamakua Ditch – see study site description).

To test the null hypothesis of no difference between fish microhabitat use and microhabitat availability, a principal component analysis (henceforth PCA) was conducted on the random availability data to extract independent component axes that

described patterns of microhabitat variation within the stream. Observations of fish microhabitat use were then scored and superimposed on the component axes extracted from the availability data by multiplying each fish's microhabitat use data by the eigenvectors associated with the microhabitat variables on each component axis (Grossman and Freeman 1987). The microhabitat use principal component (PC) scores for each species were then compared to the random microhabitat availability PC scores, and a Mann-Whitney test was used to test for significant differences. When significant differences between fish microhabitat use and random microhabitat availability were detected on a component axis, a univariate inspection of the variables which loaded significantly on that axis was performed: frequency distributions for fish microhabitat use and microhabitat availability were plotted and tested for significant differences by using a Komolgorov-Smirnov Chi-squared goodness of fit test (Zar 1999). Electivity values were calculated for each variable with Jacobs' formula (1974):

$$D = \frac{r - p}{(r + p) - 2rp}$$

where r is the proportion of the resource utilized by each species and p is the proportion available in the environment. The values produced by this index vary continuously between -1 (strong avoidance) and $+1$ (strong selection). This range was subdivided to describe the magnitude of microhabitat selection (Baltz 1990) as follows:

-1.00 to -0.50	strong avoidance;
-0.49 to -0.26	moderate avoidance;
-0.25 to $+0.25$	neutral preference;
$+0.26$ to $+0.49$	moderate preference;
$+0.50$ to $+1.00$	strong preference.

To test the null hypothesis of no significant interspecific overlap in the microhabitat use patterns of the species comprising the Wailoa Stream terminal-reach

streamfish assemblage, a separate PCA was performed on all the fish microhabitat observations. Data were transformed by either ln (linear measurements) or arcsine (percentages) to stabilize variances. Biplots of the two most important principal components (i.e., two highest eigenvalues) were constructed, and the 95% confidence ellipses around the centroid of each species' PC scores were plotted on the new PC axes. Multiple analysis of variance (MANOVA) was performed to test for differences among and between the PC scores for assemblage species.

RESULTS

Riffle

The PCA performed on the random microhabitat availability data (n = 182) gathered in the riffle habitat type produced three component axes that explained 69.7 percent of the total variance in the dataset. Principal Component 1 was a linear combination of the mean water column, surface, and bottom velocities, total water column depth and focal point substrate variables (Table 2). Principal Component 2 only had one variable with a significantly high loading value: percent vegetation. Principal Component 3 represented a linear combination of the percent algae and channel position variables.

Table 2. Eigenvalues and component loadings for the PCA performed on the riffle microhabitat availability data. Component loadings ≥ 0.50 are included.

	PC1	PC2	PC3
Eigenvalue	3.26	1.21	1.11
Mean water column velocity	0.95	---	---
Surface velocity	0.93	---	---
Bottom velocity	0.75	---	---
Total water column depth	0.74	---	---
Substrate	0.54	---	---
Percent vegetation	---	0.78	---
Percent algae	---	---	-0.74
Channel position	---	---	-0.70

The riffle-dwelling assemblage of fishes in the terminal reach of Wailoa Stream was dominated by three indigenous species: *Kuhlia xenura*, *Awaous guamensis*, and *Sicyopterus stimpsoni* (Table 1). All species showed nonrandom microhabitat use on PC axis 1 (Figure 2). A more detailed, univariate examination of the microhabitat use for

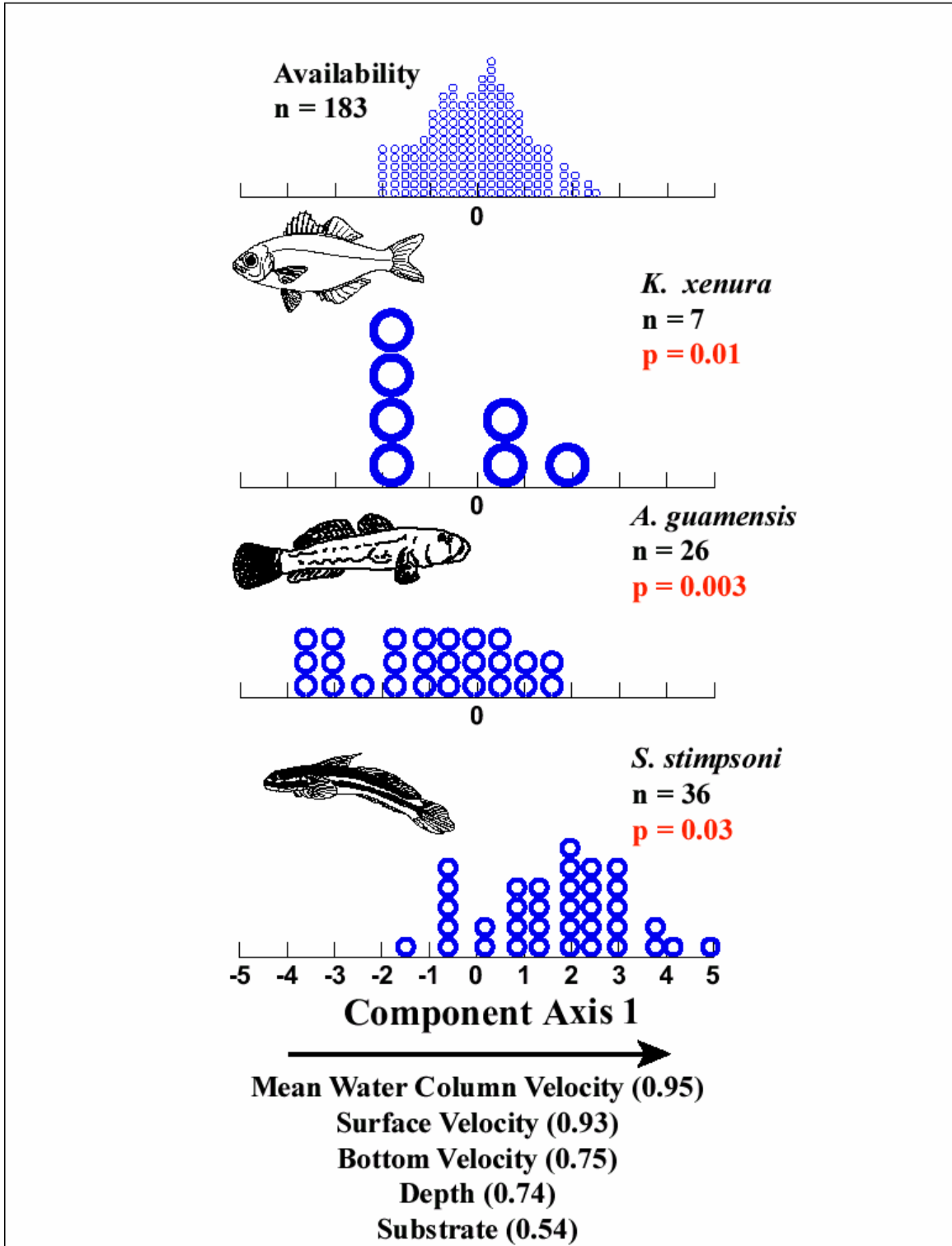


Figure 2. Test of non-random microhabitat use in the riffle habitat type for Component Axis 1. Diagrams represent distributions of component scores for both microhabitat availability and species use data.

these three species (Figure 3) with respect to the individual variables that loaded significantly on PC1 showed that *K. xenura* did not exhibit any significant non-random microhabitat use patterns (possibly attributable to low sample size). The electivity index values, however, indicated that *K. xenura* exhibited moderate to strong preference for areas with relatively low mean water column velocity, strong preference for moderately shallow and very deep areas, and areas with boulder substrata (Figure 3). *Awaous guamensis* also did not show statistically significant non-random use for the three PC1 variables. Electivity scores indicated some moderate preference for mean water column velocities between 30 and 60 cm/sec, moderate to strong preference for water column depths between 10 and 20 cm, and strong preference for areas with sand substrata (Figure 3). Of the three riffle dwelling species, *S. stimpsoni* showed the most non-random microhabitat use pattern with respect to the same three variables (Figure 3). *Sicyopterus stimpsoni* had a highly significant, strong preference for areas with higher mean water column velocities, greater depths, and larger substrata (specifically cobble) than were randomly available. All three riffle-dwelling fishes failed to show any significant non-random use with respect to PC2 (Figure 4) or PC3 (Figure 5).

The results of the PCA of all the microhabitat use observations for the three riffle-dwelling fishes in Wailoa Stream's terminal reach were used to construct the biplot in Figure 6. A MANOVA of the PC scores confirms the lack of microhabitat overlap in these fishes ($p = 0.001$). The two benthic gobies show very different microhabitat use patterns with respect to PC1 which explained 29.4% of the variance in the data, with *S. stimpsoni* using the deeper areas of the riffle habitat that had higher water velocities and larger substrates than *A. guamensis*. There was very little microhabitat overlap between

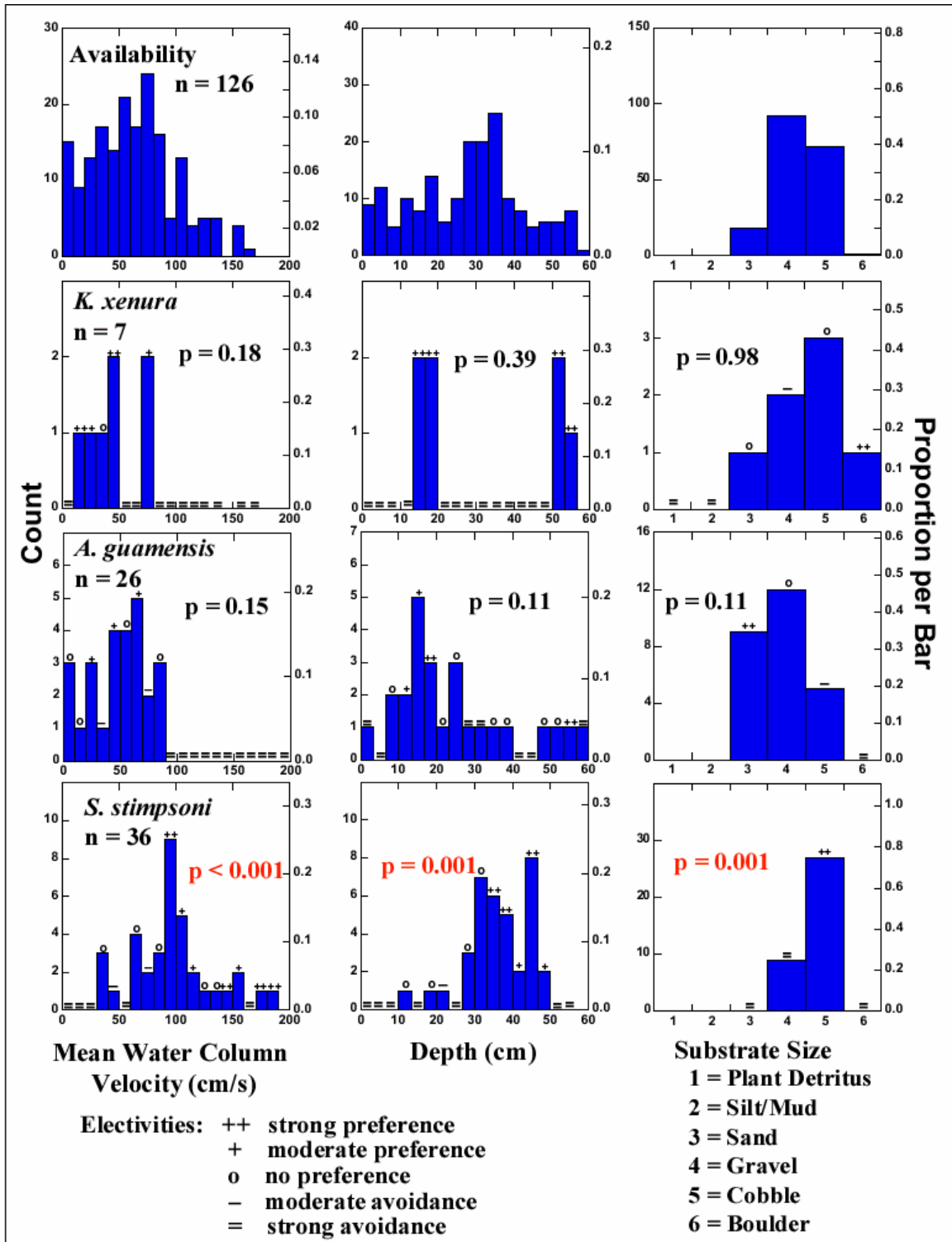


Figure 3. Test of non-random microhabitat use in the riffle habitat type for the variables that loaded on principal component 1.

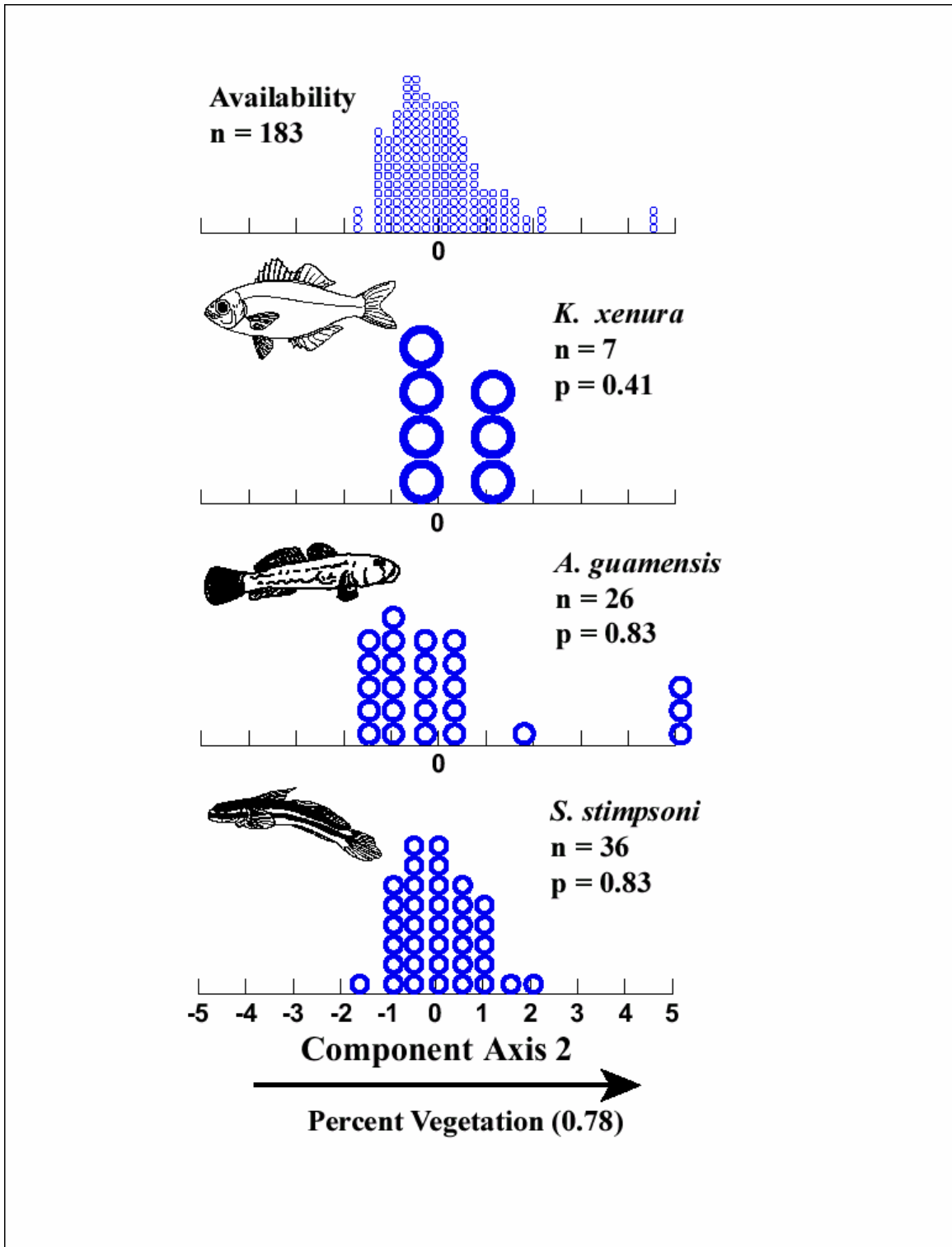


Figure 4. Test of microhabitat use in the riffle habitat type for Component Axis 2. See Fig. 2 for explanation

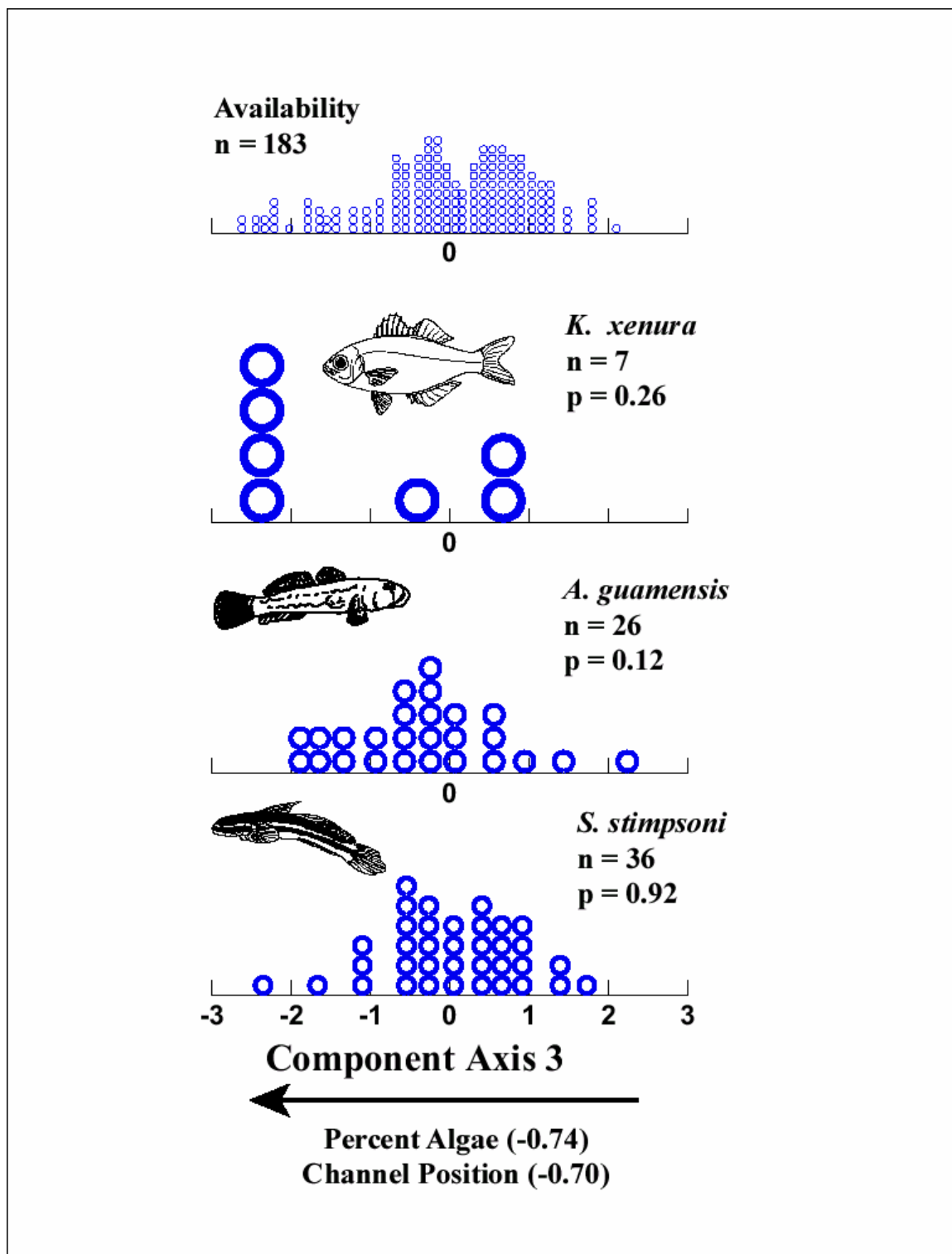


Figure 5. Test of microhabitat use for Component Axis 3 in the riffle habitat type. See Fig. 2 for explanation.

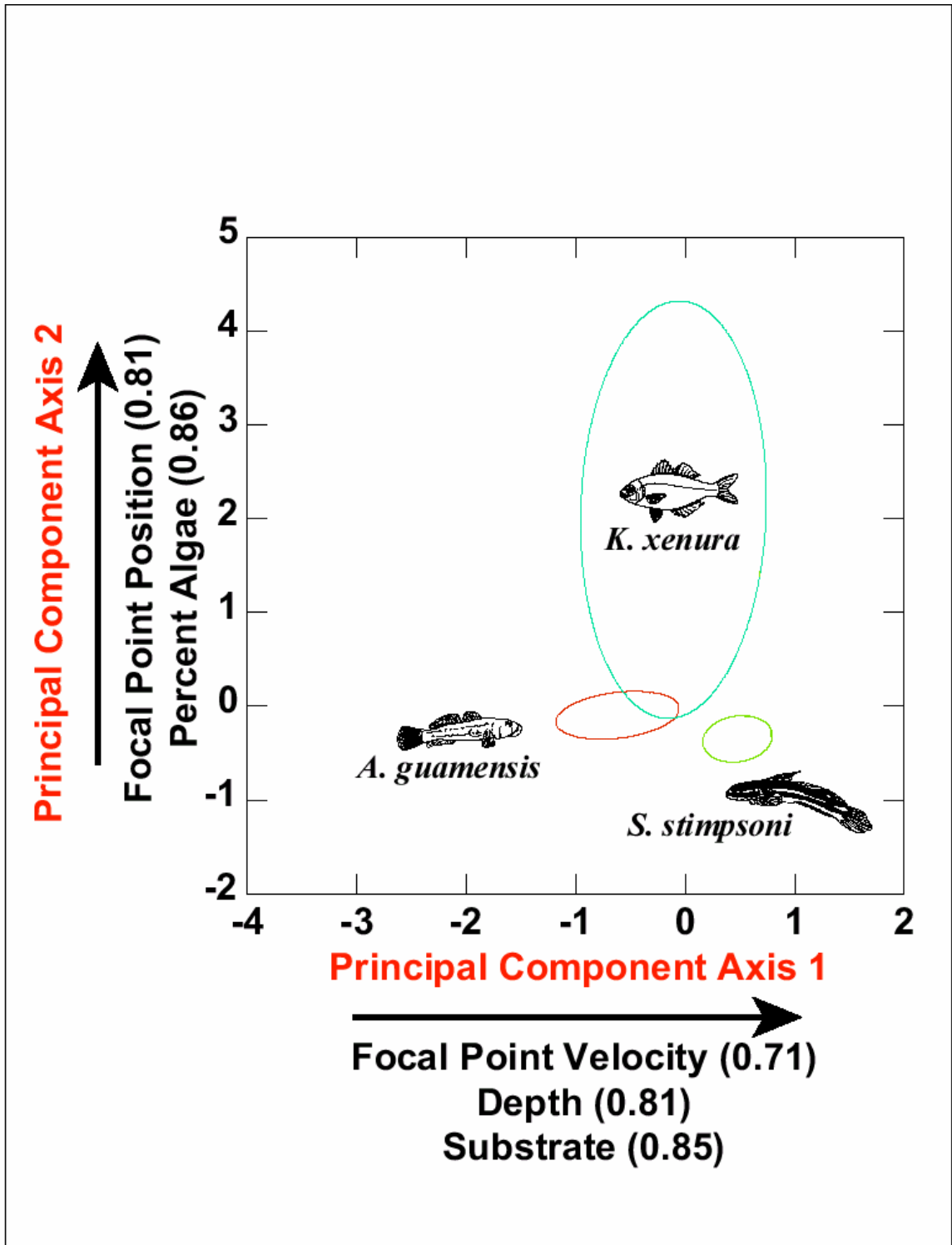


Figure 6. Interspecific microhabitat overlap on Principal Component 1 (Eigenvalue = 3.96) and Principal Component 2 (Eigenvalue = 1.63) in the riffle habitat type.

the two gobies and *K. xenura* with respect to PC2 which explained 22.7% of the variance in the data. *Kuhlia xenura* were using areas that were higher in the water column and areas with more algae covering the substrate than were the two gobies.

Run

The PCA that was performed on the random microhabitat availability data gathered in the run habitat type yielded three principal components which accounted for 71.7% of the variance in the data set (Table 3). Principal Component 1 represented a linear combination of the mean water column, surface and bottom velocities, substrate, and percent vegetation variables. Principal Component 2 represented a combination of the depth and channel position variables, while PC3 corresponded to the percent algae variable only.

Table 3. Eigenvalues and component loadings for the PCA performed on the run microhabitat availability data. Component loadings ≥ 0.50 are included.

	PC1	PC2	PC3
Eigenvalue	3.47	1.23	1.03
Mean water column velocity	0.92	---	---
Surface velocity	0.90	---	---
Bottom velocity	0.84	---	---
Total water column depth	---	-0.76	---
Substrate	0.58	---	---
Percent vegetation	-0.64	---	---
Percent algae	---	---	-0.74
Channel position	---	-0.67	---

Microhabitat observations were made on seven species encountered in the run habitat and included the natives *Awaous guamensis*, *Eleotris sandwicensis*, *Stenogobius*

hawaiiensis, and *Kuhlia xenura* as well as the non-indigenous poeciliids *Gambusia affinis*, *Poecilia mexicana*, and *Xiphophorus helleri*. None of the native gobies showed any non-random microhabitat use on Principal Component axis 1 (Figure 7). Both juvenile and adult *K. xenura* showed significantly non-random microhabitat use on PC axis 1 (Figure 8). Adult *K. xenura* were using microhabitats with mean water column velocities (Figure 9) that were significantly higher than were randomly available and showed a strong preference for velocities between 45 and 50 cm/sec. With respect to the percent vegetation and substrate variables, adult *K. xenura* were not using microhabitats that were significantly different from what was randomly available to them (Figure 9). Based on the electivity values, however, adult *K. xenura* did show some strong preferences for microhabitats that had between 20 and 70% vegetation and a moderate preference for cobble substrata. Although juvenile *K. xenura* did not exhibit any significant non-random microhabitat use with respect to these individual variables, based on electivity values they showed strong preference for areas that had a mean water column velocity around 5 cm/sec, and 50 to 70% vegetation, but no preference for a particular substrate (Figure 9).

All three poeciliid species showed highly significant non-random microhabitat use on Component Axis 1 (Figure 10). *Gambusia affinis* showed highly significant, strong preference (Figure 11) for areas that had lower water velocities and more vegetation than was randomly available and, based on the electivity values, a strong preference for areas with decayed plant detritus substrate although their substrate use did not differ significantly from what was randomly available. *Poecilia mexicana* also used microhabitats with mean water column velocities that were lower than was randomly

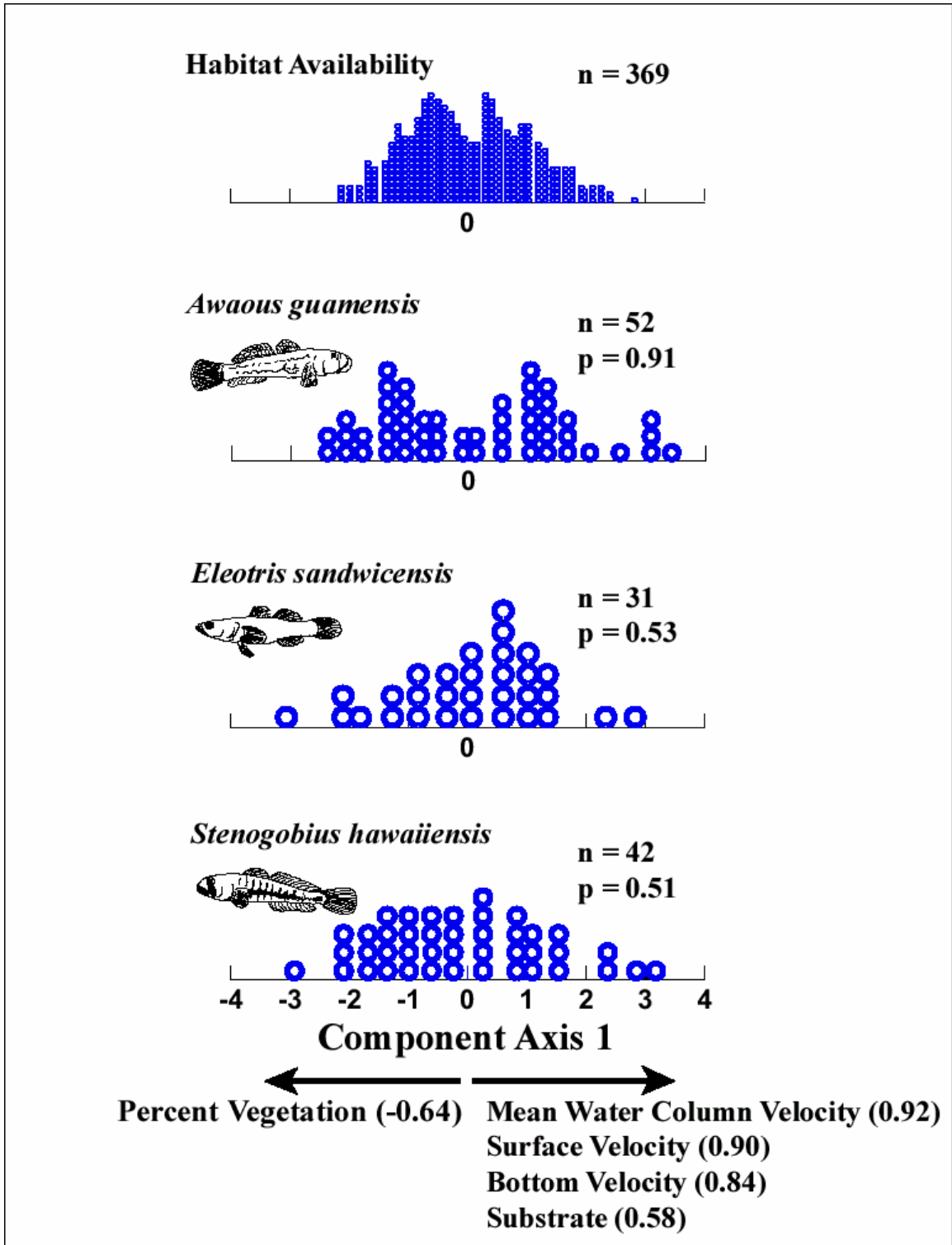


Figure 7. Test of microhabitat use by native gobies for Component Axis 1. See Fig. 2 for explanation.

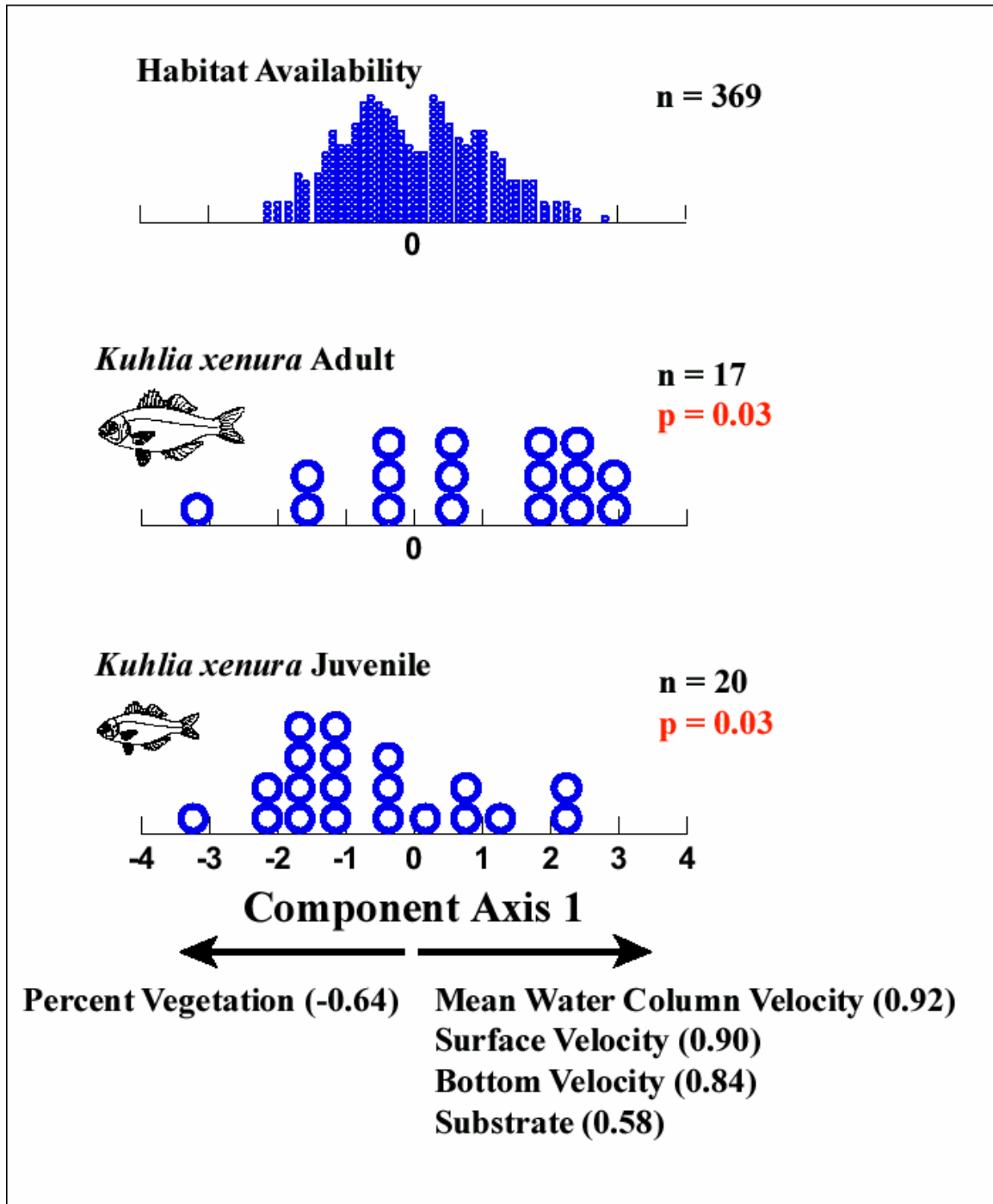


Figure 8. Test of microhabitat use by adult and juvenile *K. xenura* for Component Axis 1. See Fig. 2 for explanation.

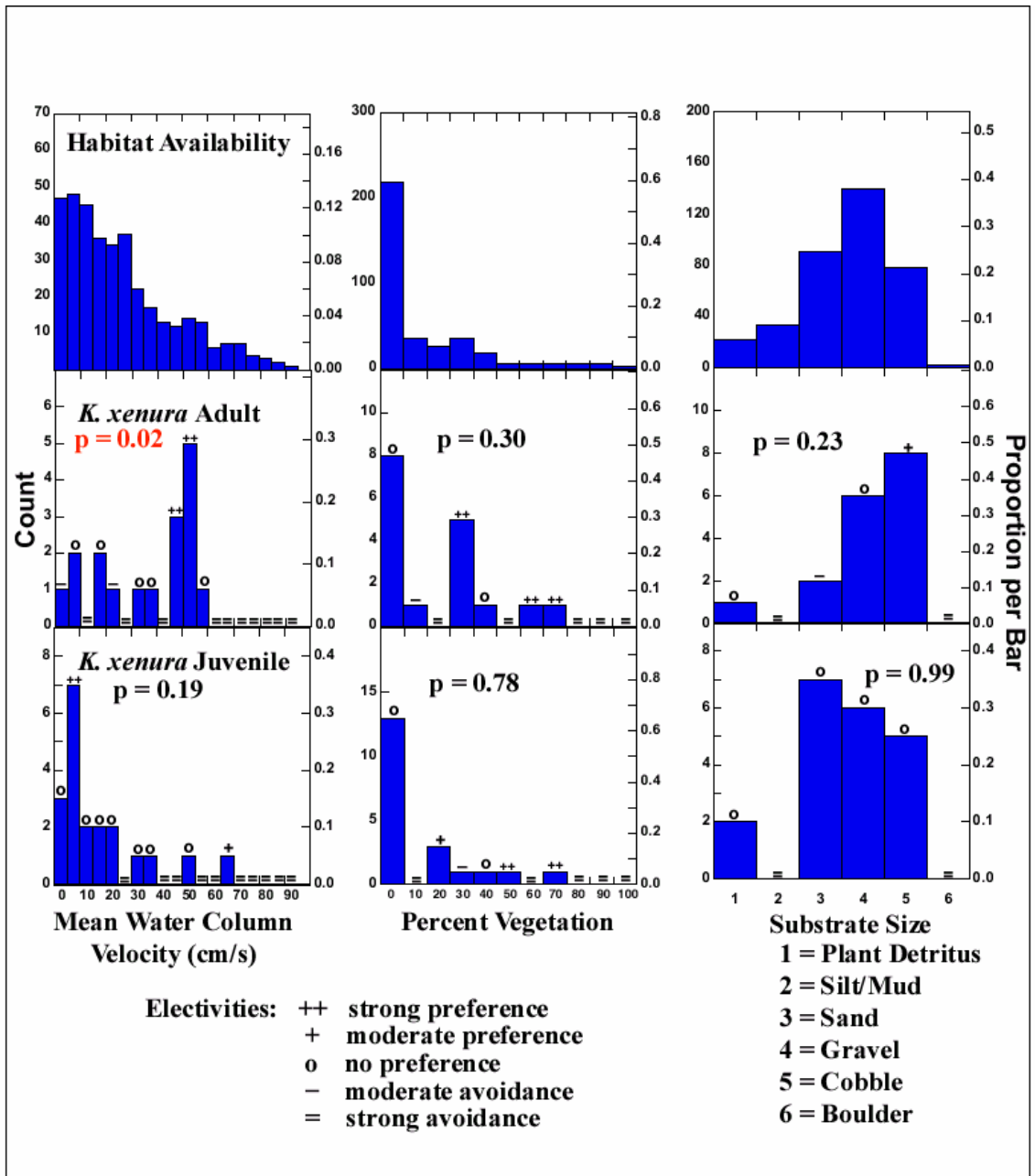


Figure 9. Test of non-random microhabitat use by adult and juvenile *K. xenura* in the run habitat for the variables that loaded on Principal Component 1.

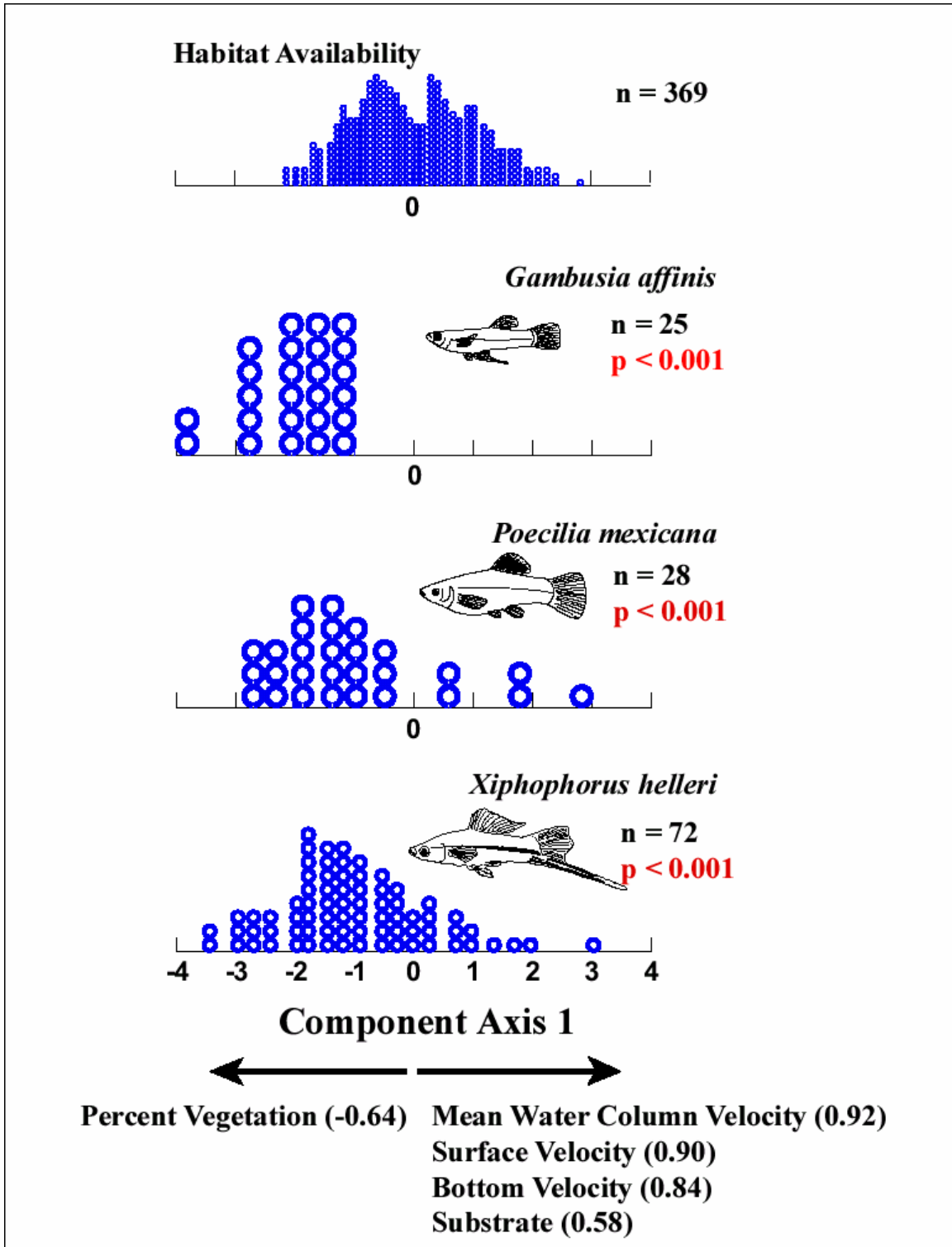


Figure 10. Test for non-random microhabitat use by poeciliid fishes in the run habitat on Component Axis 1. See Fig. 2 for explanation.

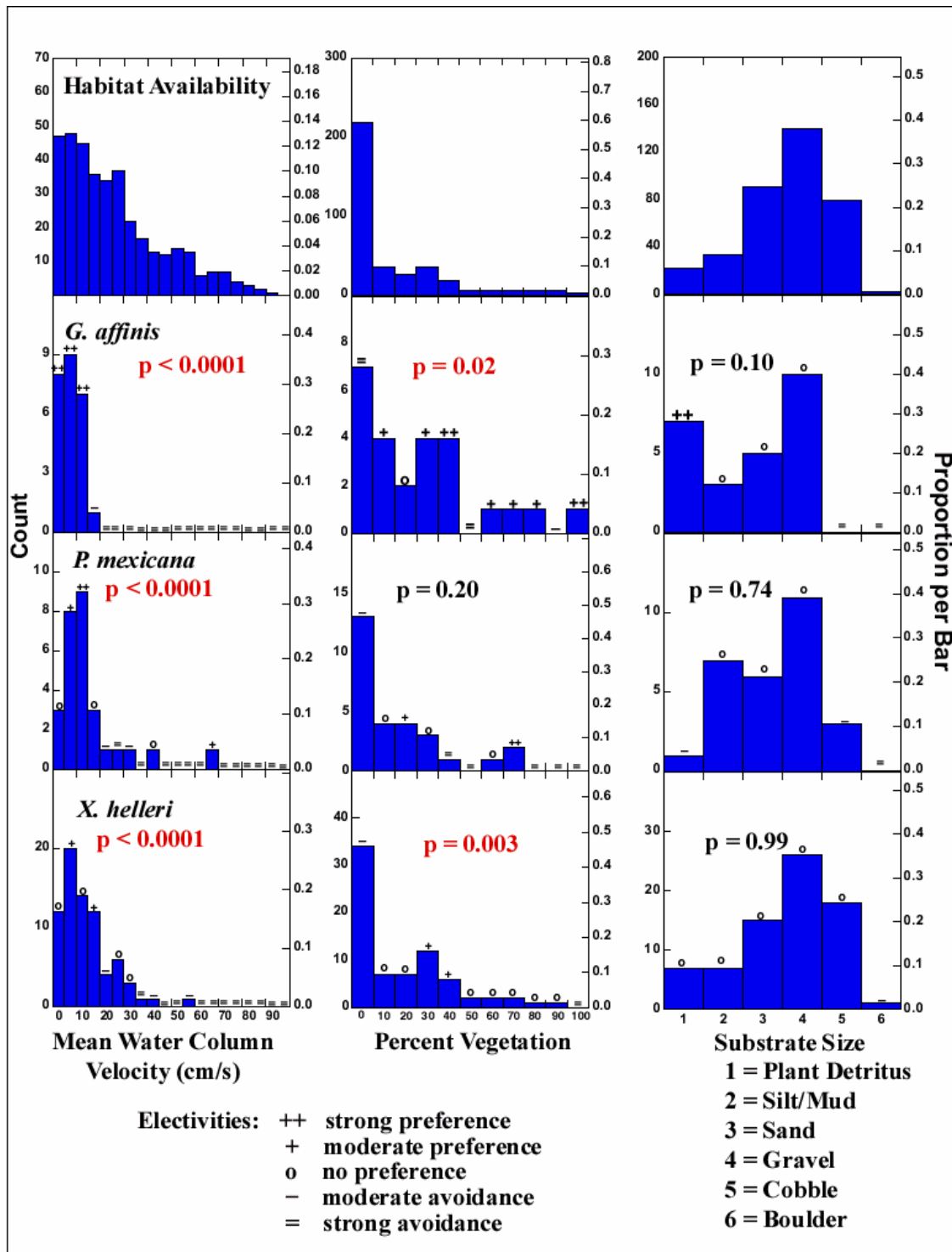


Figure 11. Test for non-random microhabitat use by poeciliids in the run habitat for the variables that loaded on Principal Component 1.

available, and showed strong preference for velocities between 10 and 15 cm/sec. With respect to the percent vegetation variable, *P. mexicana* microhabitats did not differ significantly from what was randomly available in the study reach, but based on the electivity index values, they showed a strong preference for microhabitats that had between 70 and 80% vegetation. With regards to the substrate variable, *P. mexicana* microhabitat use patterns did not differ from what was randomly available. *Xiphophorus helleri* were using microhabitats that had slower mean water column velocities and higher percent vegetation than was randomly available to them, but did not show any non-random use of a particular substrate.

Only *Stenogobius hawaiiensis* and *Gambusia affinis* displayed non-random microhabitat use on Principal Component 2 (Figures 12, 14, and 15). *Stenogobius* showed a strong preference for deep areas (Figure 13), while *Gambusia* were using shallow areas that were close to the bank (Figure 16).

The poeciliids *P. mexicana* and *X. helleri* were the only species that exhibited non-random microhabitat use on Principal Component axis 3 (Figures 17, 18, and 19). Both species were using areas that had more algae than was available at random in the run habitat type (Figure 19).

The PCA that was performed on all of the microhabitat observations for all species present in the run habitat type resulted in the biplot in Figure 20 and provided information on interspecific microhabitat overlap. The assemblage of terminal reach streamfishes in Wailoa Stream appears to have been comprised of two spatial guilds: a benthic guild, which included the three native amphidromous gobioids, and a water column guild that consisted of the three exotic poeciliids and the native *K. xenura*.

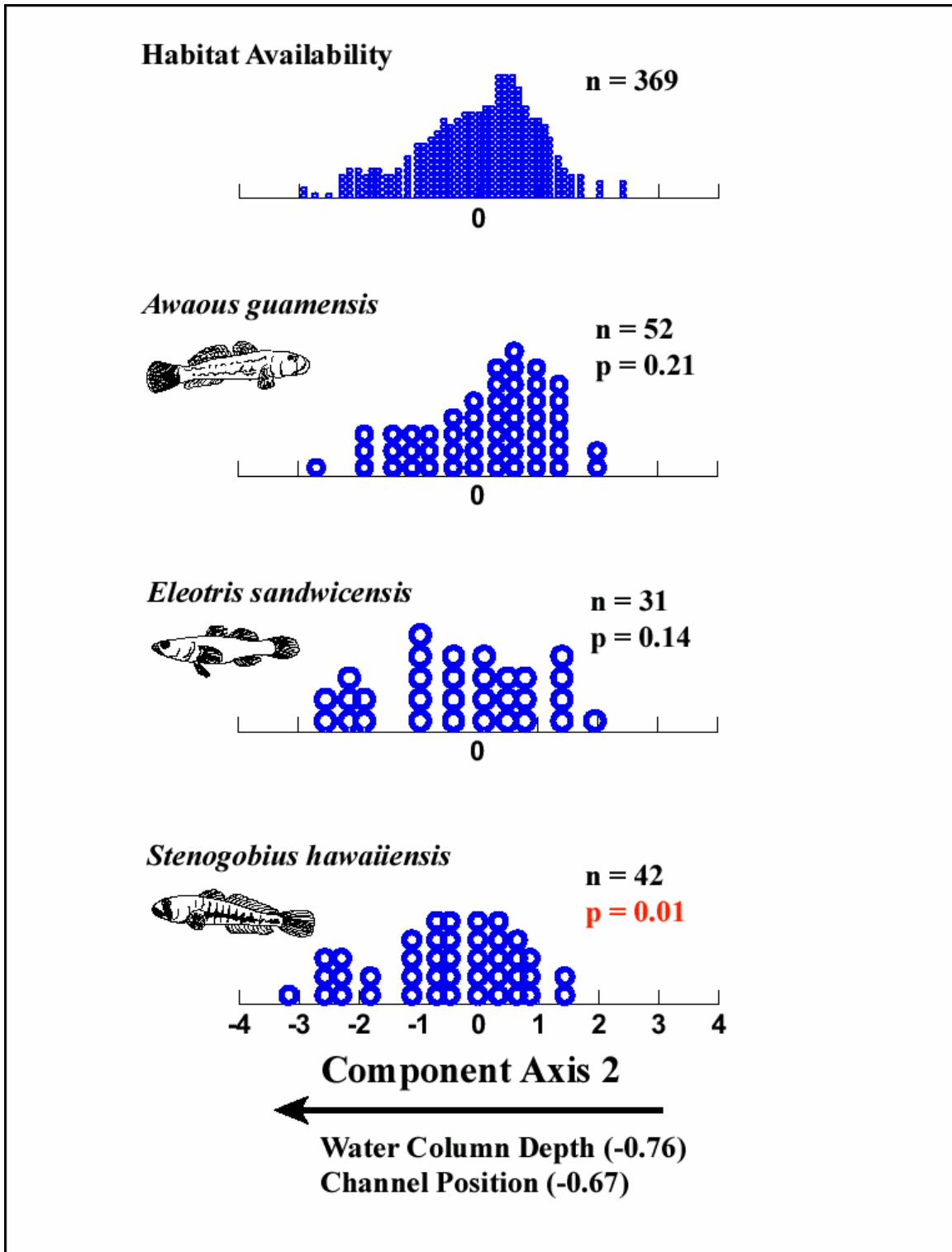


Figure 12. Test of microhabitat use by native gobies in the run habitat type on Component Axis 2. See Figure 2 for explanation.

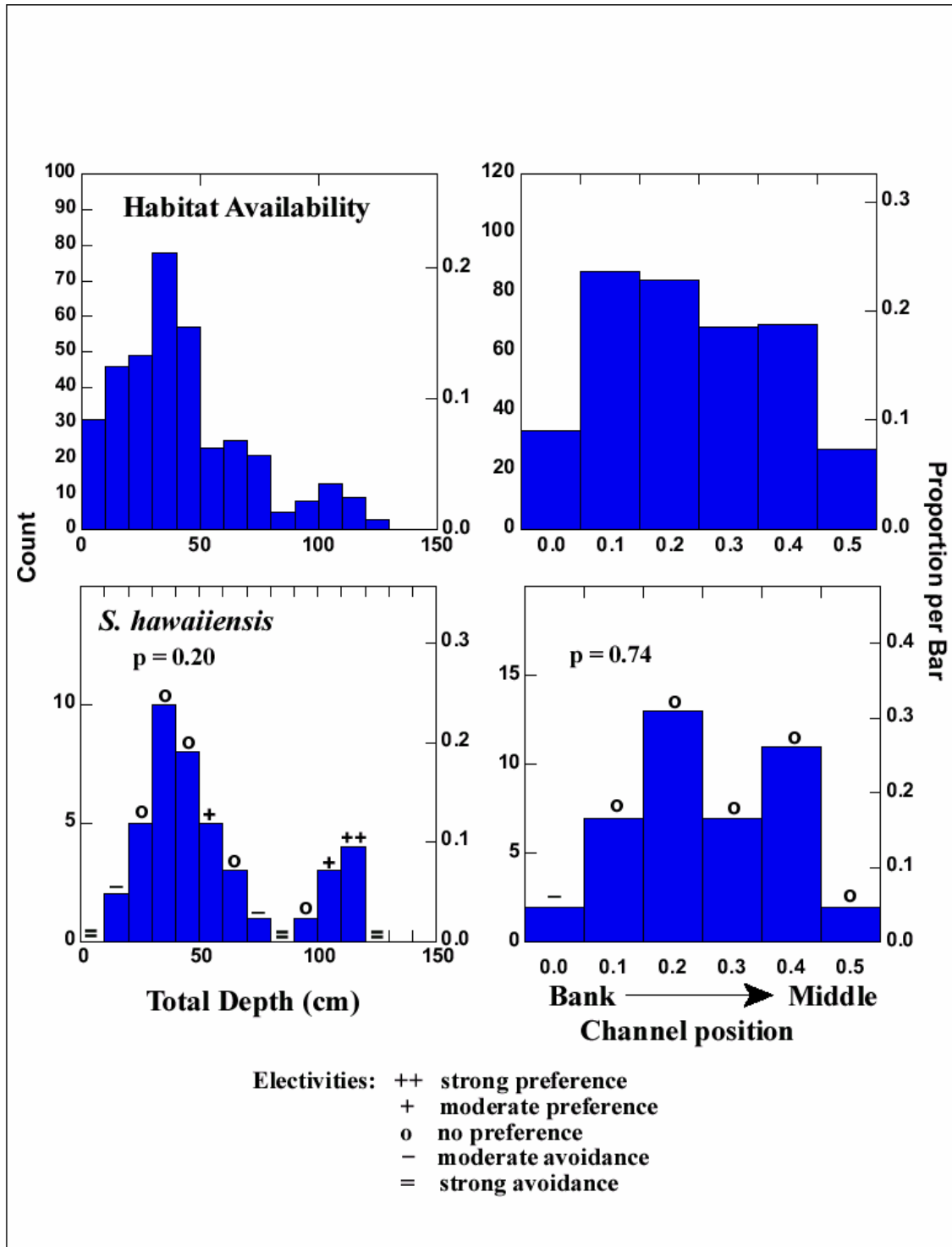


Figure 13. Test for non-random microhabitat use by native gobies in the run habitat for the variables that loaded on Principal Component 2.

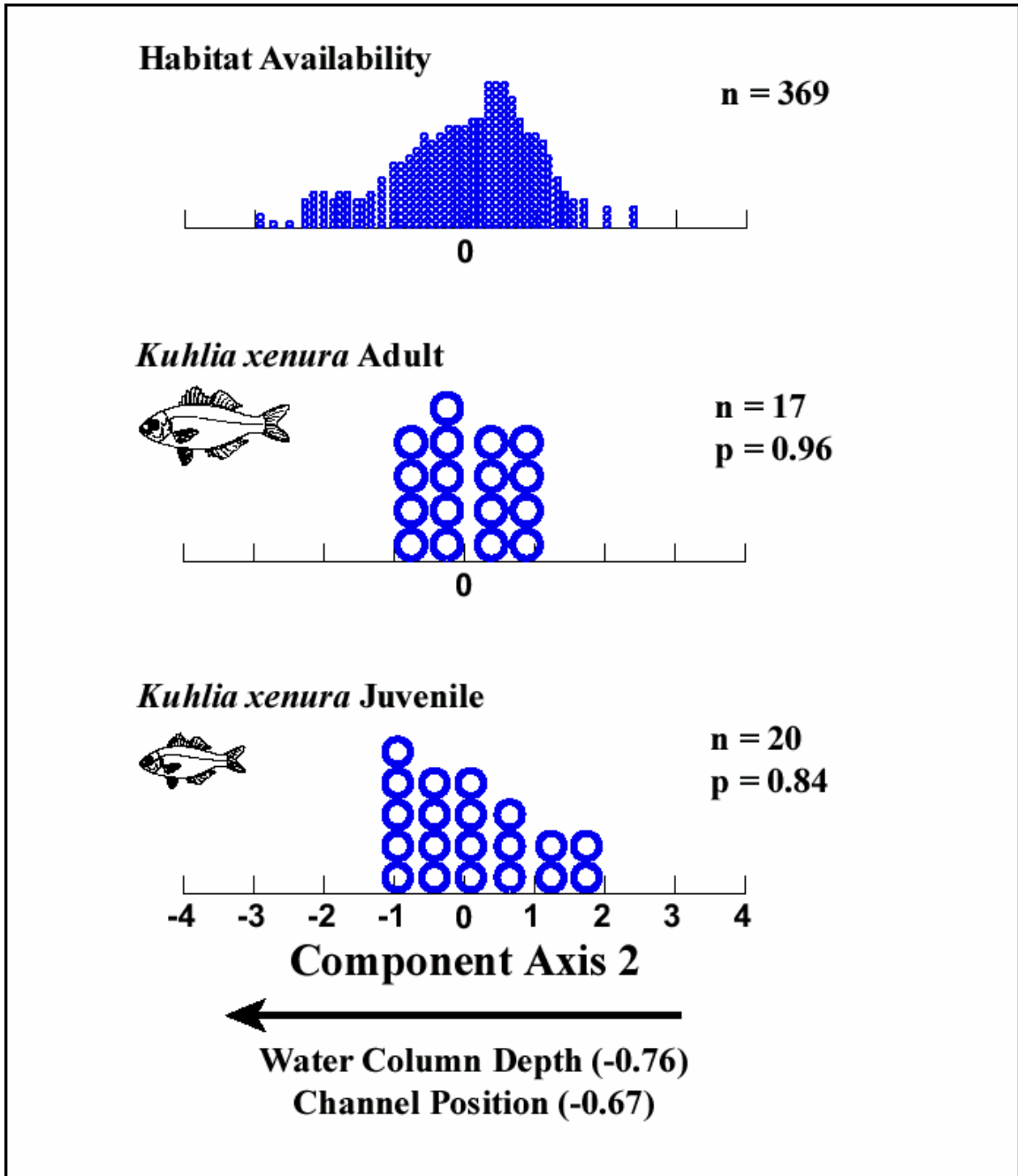


Figure 14. Test of microhabitat use by adult and juvenile *K. xenura* in the run habitat type for Component Axis 2. See Fig. 2 for explanation.

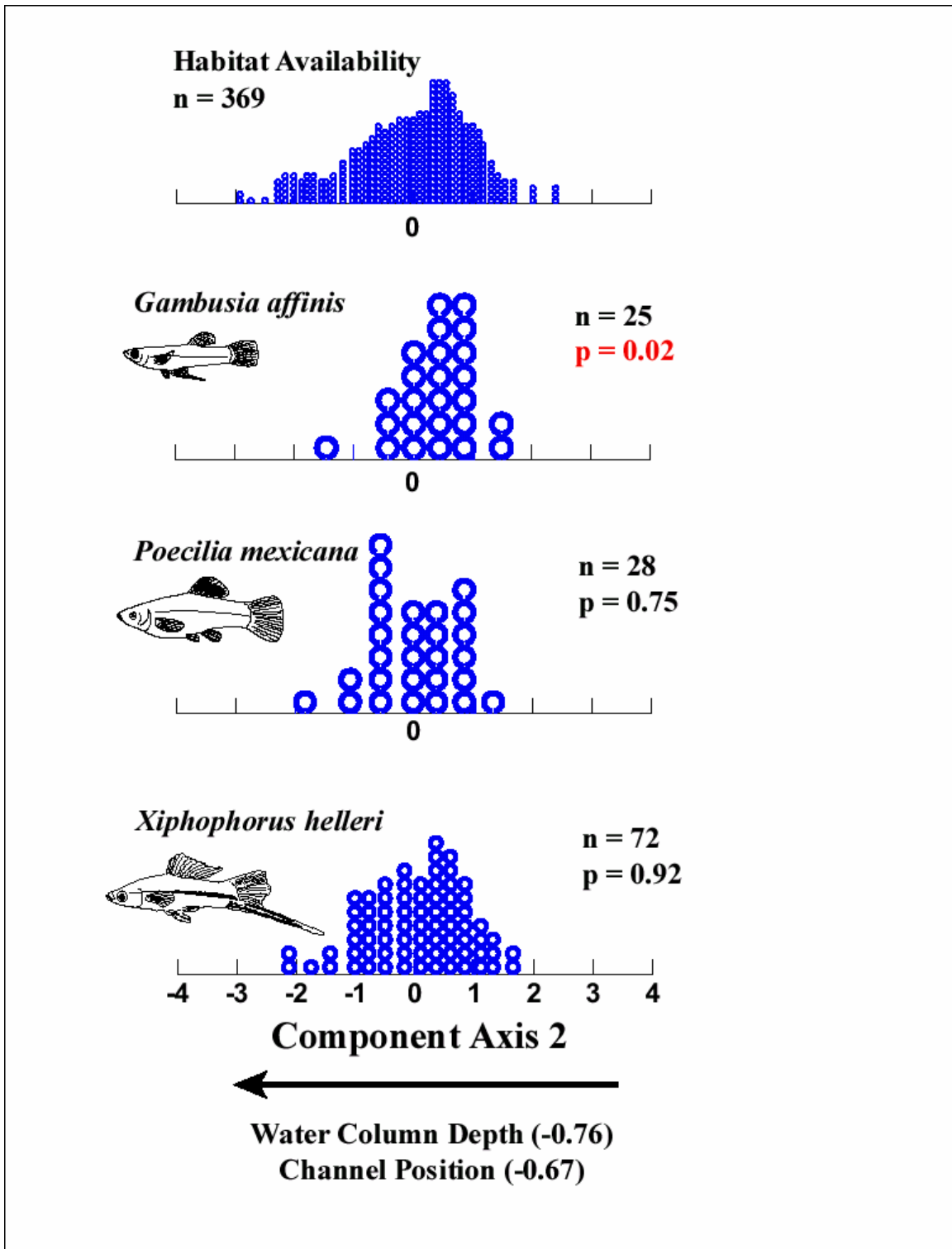


Figure 15. Test of microhabitat use by poeciliids in the run habitat type for Component Axis 2. See Fig. 2 for explanation.

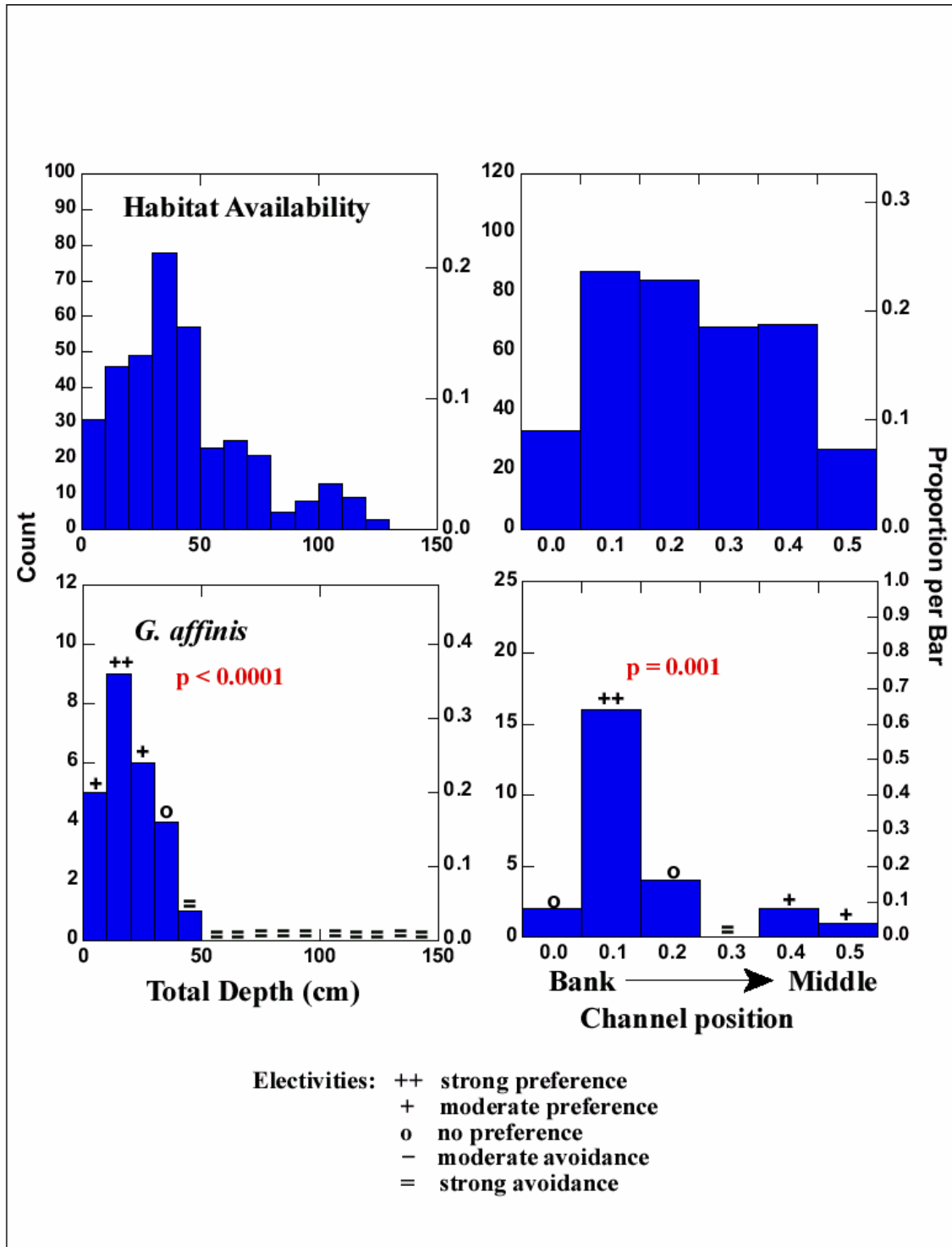


Figure 16. Test of non-random microhabitat use by *G. affinis* in the run habitat type for the variables that loaded on Principal Component 2.

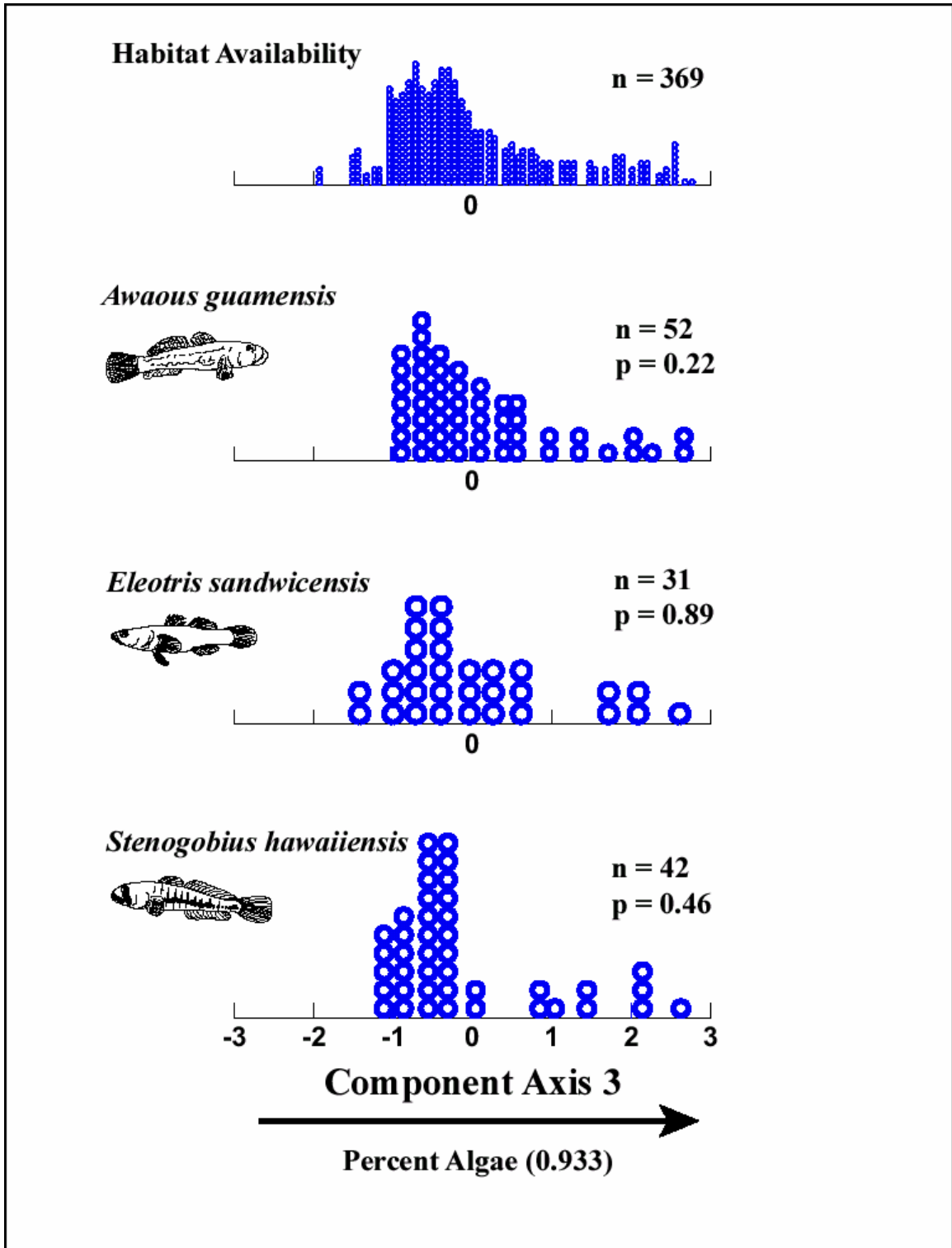


Figure 17. Test of microhabitat use by native gobies in the run habitat type on Component Axis 3. See Fig. 2 for explanation.

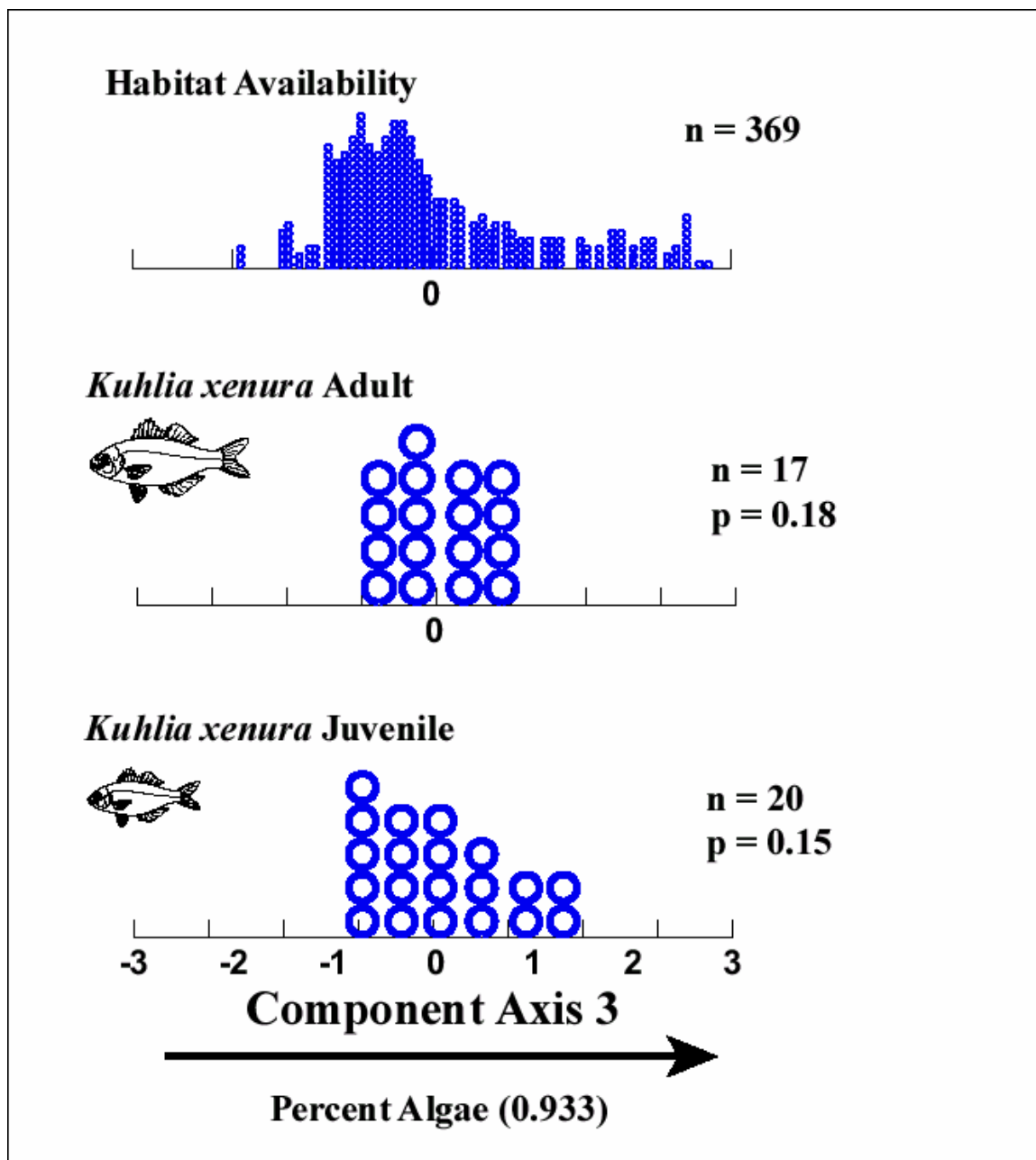


Figure 18. Test of microhabitat use by adult and juvenile *K. xenura* in the run habitat type on Component Axis 3. See Fig. 2 for explanation.

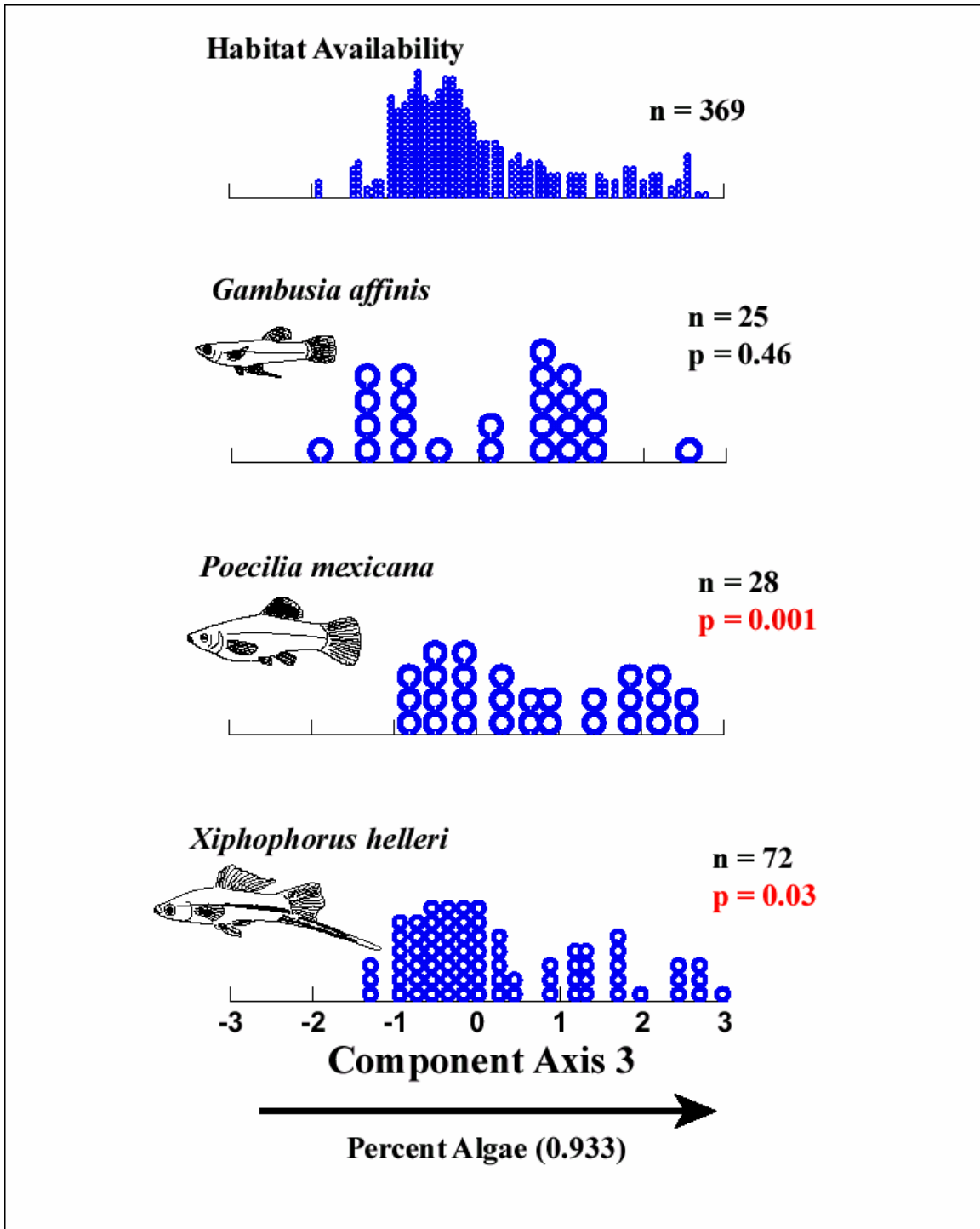


Figure 19. Test of microhabitat use by poeciliid fishes in the run habitat type on Component Axis 3. See Fig. 2 for explanation.

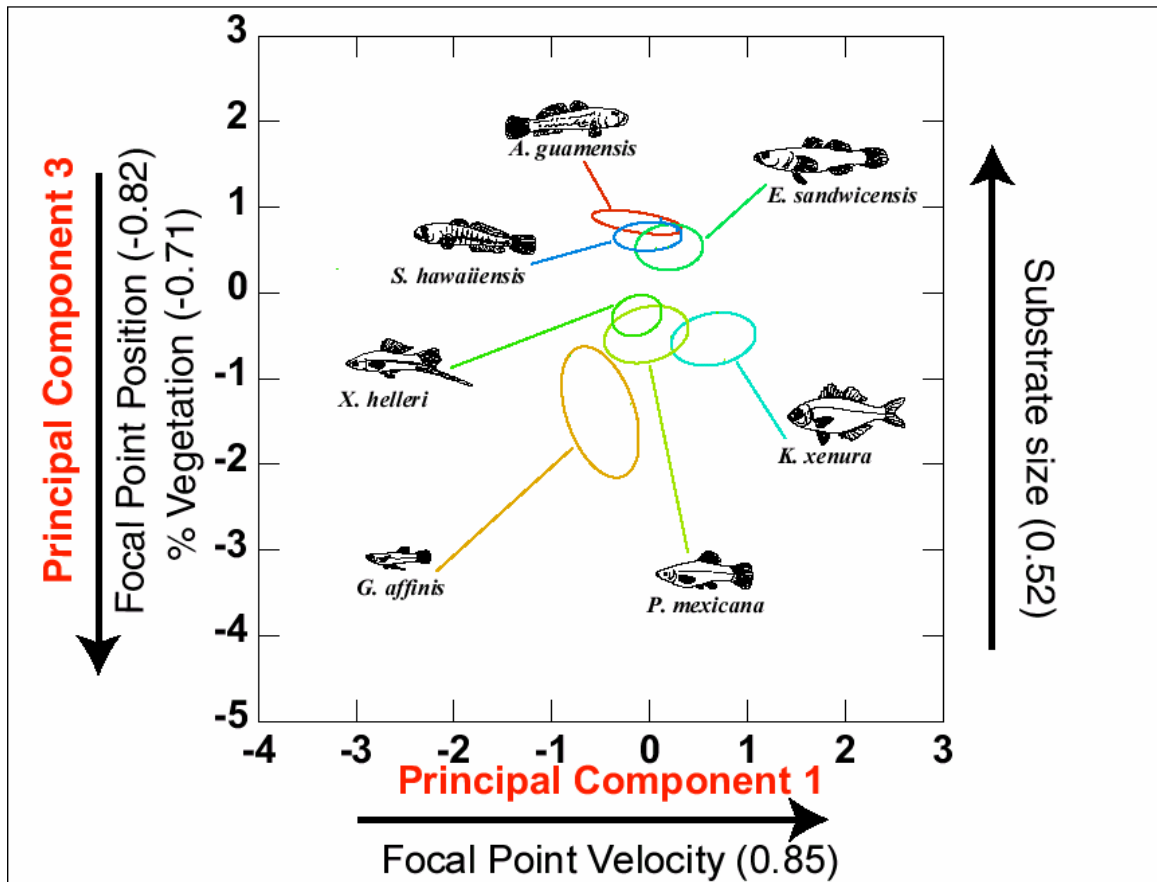


Figure 20. Interspecific microhabitat overlap for all run-dwelling fishes on Principal Component 1 (Eigenvalue = 3.40) and Principal Component 3 (Eigenvalue = 2.05). Numbers in parentheses represent each variables loading value.

A separate PCA performed on the data from just the water column guild (Figure 21) showed that there was considerable overlap in the microhabitat use patterns of juvenile *K. xenura* and the poeciliids *P. mexicana* and *X. helleri*. Adult and juvenile *K. xenura* exhibited very different microhabitat use, with adults using microhabitats that had higher water velocities in greater depths than the microhabitats occupied by juveniles (Figure 21). *Gambusia affinis* showed very little overlap with any of the other species found in the run habitat; this species used microhabitats that were higher in the water column, shallower, with more vegetation, finer substrate, and lower water velocity.

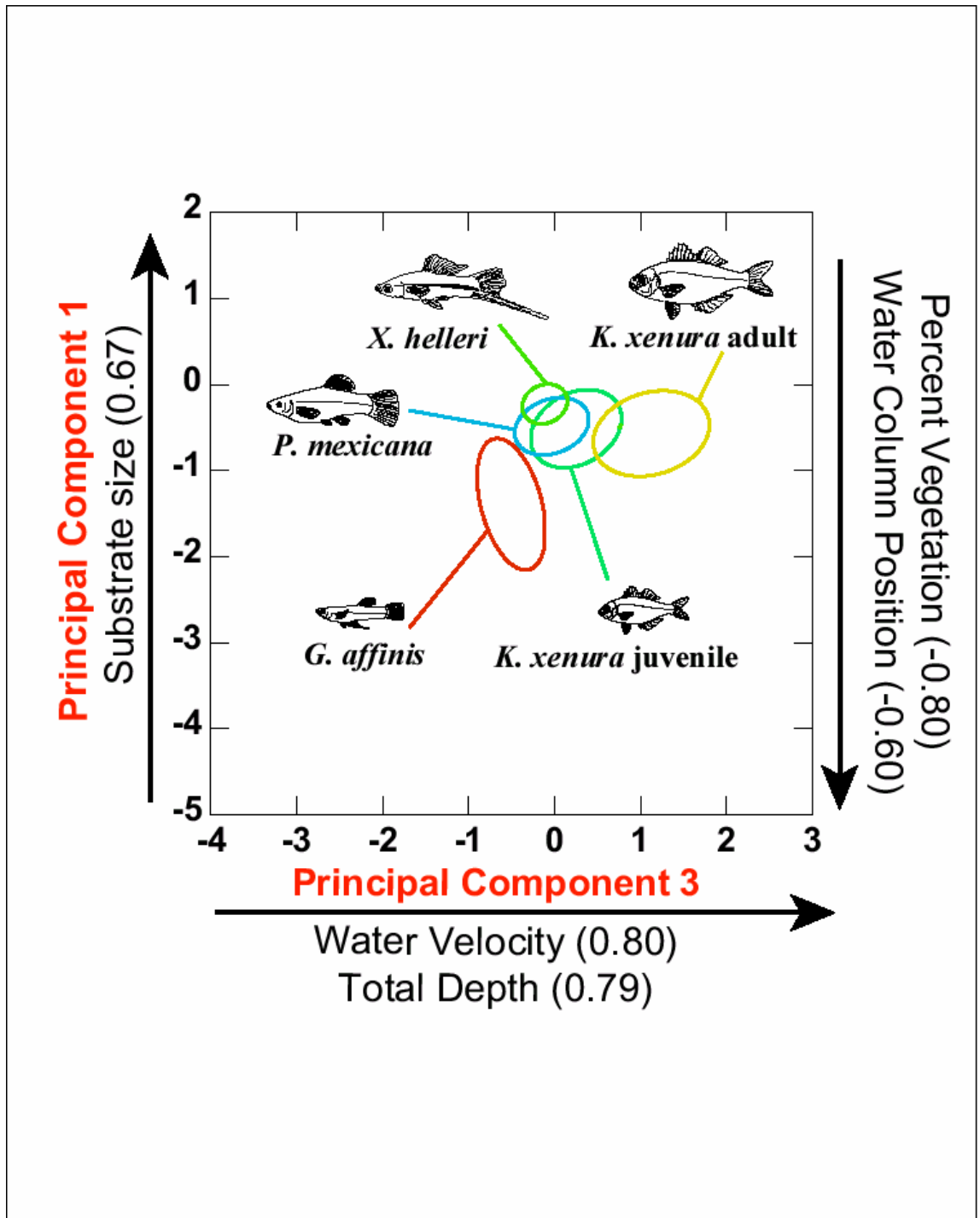


Figure 21. Interspecific microhabitat overlap for the watercolumn guild in the run habitat type on Principal Component 3 (Eigenvalue = 2.98) and Principal Component 1 (Eigenvalue = 2.50).

DISCUSSION

Differences in three-dimensional microhabitat preferences apparently facilitate coexistence of the fishes in the terminal reach of Wailoa Stream. This was particularly evident in the riffle habitat type, where differences in the focal point positions of *K. xenura* and the two benthic gobies *A. guamensis* and *S. stimpsoni* resulted in a very low degree of microhabitat overlap. The high degree of microhabitat differentiation between *A. guamensis* and *S. stimpsoni* in the riffle habitat type is similar to that observed in the mid-reaches of streams in Hawaii where the two species occur sympatrically (Kinzie 1988) and may be related to morphological variations in feeding traits; *Sicyopterus stimpsoni* are strict herbivores with dentition adapted for scraping algae off hard, coarse substrates (e.g., cobble, boulder) while *A. guamensis* is an omnivore morphologically adapted to foraging through fine bottom substrates (e.g., sand) for invertebrates and algae (Kido 1996). The high potential vulnerability of these amphidromous gobies to stochastic events throughout the planktonic and instream stages of their life cycle makes this level of competition-reducing microhabitat specialization somewhat surprising (Sale & Dybdahl 1975, Sale 1978, Grossman et al. 1982). All five genera of amphidromous gobioids present in Hawaii are also present on other islands in the Pacific, and it is presumed that the endemic Hawaiian species evolved from colonists from these faraway islands. It is, therefore, likely that the high degree of microhabitat specialization observed in the mid-reach/riffle dwelling gobies in Hawaii represent remnant behavioral characteristics that evolved in ancestor species living in the much more diverse fish communities found in streams on islands elsewhere in the Indo-Pacific (Kinzie 1988, Nelson et al. 1991, Parham 1995, Fitzsimons pers. com.).

In contrast to the riffle-dwelling gobies, the three amphidromous gobioids that comprised the benthic guild in the run habitat exhibited very high overlap in their microhabitat use patterns, which suggests some potential for competitive interactions. In this case, however, it is likely that slight differences in feeding morphologies and strategies facilitated the coexistence of these spatially overlapping species. *Stenogobius hawaiiensis* are adapted for filtering algae out of fine bottom substrates and detritus while *A. guamensis* exhibits a high degree of omnivory by foraging through the substrate for benthic invertebrates and algae (Kido 1996). *Eleotris sandwicensis* have morphological and physiological adaptations for a predatory feeding strategy, but also show a surprising amount of algae in their diet (Kido 1996). Even though all three species potentially utilize algae as a food source, algal availability is not likely a limiting factor in the run habitat type, and it is unlikely that these species compete for this resource. Thus, even though these three species were using very similar microhabitats in Wailoa Stream's terminal reach, coexistence within those microhabitats was likely facilitated by the lack of competition over food resulting from differences in their feeding strategies.

The fishes that made up the water column guild in the run habitat type exhibited a high level of diversity in the microhabitats they occupied. The single indigenous species in this guild, *K. xenura*, exhibited microhabitat use that varied with life history stage. *Kuhlia xenura* in Wailoa Stream feed primarily on drifting food particles carried downstream by the current (personal observation). As the availability of drifting invertebrates increases with water velocity (Hynes 1970), it is possible that an intraspecific dominance hierarchy exists in which larger, potentially more dominant adults occupy microhabitats in deeper water with higher water velocities in which they

are more likely to encounter drifting food items. Juvenile *K. xenura* are excluded from these “prime” feeding areas by larger and more competitive individuals (personal observation, Benson and Fitzsimons pers. com.). The differences and similarities in microhabitat use between and among the three poeciliid species in the terminal reach run habitat reflects the evolutionary histories of these introduced fishes. *Gambusia affinis* are native to the bayous and backwater swamps of the southeastern region of North America and are adapted to living in shallow, low water velocity habitats with an abundance of aquatic macrophytes. Both *P. mexicana* and *X. helleri* are native to lotic systems in Mexico and Central America, and as a result are more adapted to using deeper, higher velocity microhabitats (Meffe & Snelson 1989).

Of particular concern from a conservation standpoint is the high degree of overlap in the microhabitat use patterns of juvenile *K. xenura* and the introduced poeciliids *P. mexicana* and *X. helleri* within the water column guild. It is apparent that terminal stream reaches are important nursery habitats for the newly identified *K. xenura* (Benson unpublished). Extremely high population densities of these two poeciliids are common in terminal stream reaches throughout the Hawaiian Islands (Englund et al. 2000) and may be resulting in the exclusion and/or displacement of juvenile *K. xenura* from preferred microhabitats. This potential exclusion would represent a serious anthropogenic degradation of the nursery habitat for this species and is an area of research that is in need of attention.

Differences in patterns of three dimensional microhabitat use apparently allow indigenous gobioids and introduced poeciliids to coexist in the terminal reach of Wailoa Stream. Gobioids and poeciliids did occur in areas of similar water velocities in the run

habitat type in lower Wailoa Stream, but strong differences in their focal point positions appear to have kept competition for spatial resources to a minimum. Thus, it can be speculated from the results of this project that the absence of native gobioids from streams with large poeciliid populations is likely a result of human alterations of stream habitats and not a result of spatial displacement of gobioids by the poeciliids. Hawaii's native amphidromous organisms need clean, cold, natural running streams to survive and successfully complete their complex life cycle. Streams that have been significantly dewatered due to water diversions are often reduced to mere trickles characterized by slow or non-flowing waters that have mostly silty or muddy substrates and abundant aquatic vegetation – perfect poeciliid habitat. Much more research is needed, however, to gain a clearer understanding of the full ecological impact of introduced poeciliids on native stream fishes in the terminal reaches of Hawaiian streams. It has already been shown that the non-native pathogenic fish parasites that are now common in native stream fishes were first transferred to them by introduced poeciliids (Font 1998). Predation by poeciliids has also been implicated in the reduction of endemic *Megalagrion* damselfly populations (Englund 1999). But what about other possible ecological impacts of poeciliid introduction on the native amphidromous macrofauna in Hawaiian streams? Are poeciliids preying heavily upon migratory larval and post-larval amphidromous gobioids, decapods, or molluscs? Are there limited food resources for which poeciliids are competing with native stream fishes? Are poeciliid fishes excluding or displacing juvenile native estuarine fishes from critical nursery habitats? Answers to these and many other critical questions regarding potential negative impacts of poeciliid introduction into Hawaiian streams are required to improve conservation efforts centering

on Hawaii's endemic stream biota. This study is the first attempt at understanding the ecological relationships among native and introduced streamfishes and hopefully will serve as a starting point for additional research.

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VITA

Mark G. McRae was born on March 6, 1973 in Hilo, Hawaii to Brenda and Robert McRae. From a very young age, Mark had a strong love of nature and the outdoors. He attended St. Joseph's Elementary and High Schools and graduated in 1991. His passion for the natural world inspired him to major in biology at the University of Hawaii at Hilo where he remained for two years. After his second year at UH-Hilo, Mark transferred to Oregon State University and completed his Bachelor's degree in Wildlife Science in March of 1996. After graduating from OSU, he continued to live in the Pacific Northwest and was employed as a stream surveyor which led to an intense interest in the ecology of streams and stream organisms. In 1998, Mark returned to Hilo, Hawaii to work as a Fishery Aide for the Hawaii Division of Aquatic Resources. While employed there, he met and worked with Dr. Mike Fitzsimons who encouraged Mark to apply to Louisiana State University's Master's program. In August 1998, Mark moved to Baton Rouge, Louisiana to pursue his Master's degree under the direction of Dr. Fitzsimons. Mark will earn his Master of Science Degree in Biological Sciences in December 2001 and plans to pursue a PhD in Biological Sciences at Louisiana State University.