# Food relations between coexisting native Hawaiian stream fishes

Michael H. Kido
*University of Hawaii, Hawaii Stream Research Center, 7370A Kuamoo Road, Kapaa, HI 96746, U.S.A.*

## Synopsis

In this study, an ecomorphological perspective is used to examine the role of feeding morphology in shaping patterns of food resource use and coexistence for *Awaous guamensis* and *Sicyopterus stimpsoni*, two native gobies (Gobiidae) which inhabit mountainous streams of the high Hawaiian Islands. Using data from underwater census, gut content analysis, and benthic sampling, I determined that *A. guamensis,* the generalist, had nearly unchallenged use of invertebrate foods. Overlap in fitness for algal use, however, resulted in a partitioning of benthic algae, with *A. guamensis* having domain over most green algae (43.0% of diet), whereas *S. stimpsoni* the algal specialist, fed predominantly on blue-green algae (22.6% of diet) and diatoms (54.2% of diet). *Cladophora* sp. (Chlorophyta) and pennate diatoms (Chrysophyta) were determined to be the 'primary algal foods' of *A. guamensis* and *S. stimpsoni,* respectively, and were utilized in a mutually exclusive manner with other 'secondary algal foods' depending upon availability. Heterogeneity, found in the abundance and composition of algal and invertebrate foods in the benthic landscape both spatially and seasonally, may be regulated by stream flow and periodic disturbance. This changing mosaic of foods is suggested as having provided opportunities for minimizing competitive conflicts and enhancing the potential for stream species to coexist. Competition for preferred foods, created by inter-specific overlap in ecomorphology and spurred by constraints placed on food diversity by the extreme geographic isolation of the Hawaiian Islands, is hypothesized as having played an evolutionary role in shaping resource use patterns which facilitate coexistence.

## Introduction

Ecomorphologists examine the structure and form (morphology) of animals as a means of understanding their ecology and evolution (Wainright & Reilly 1994). With fishes, this idea has been commonly applied to their diet, as feeding morphology is expected to influence feeding ability and subsequently resource use (Wainright & Richard 1995). The adaptive significance of a specific feeding morphology, however, will depend upon the 'realized niche' (Reilly & Wainright 1994) provided to fishes, in relation to community structure and the existing array of available foods in their ecological setting. The 'fitness' (Reilly & Wainright 1994) potential conveyed to interacting species, in terms of their survival and ultimate reproductive success, is influenced by equilibrial and non-equilibrial forces (Wiens 1984) at work affecting the availabilities of resources in the environment. How do coexisting species, each with species-specific 'performance capacities' (Reilly & Wainright 1994), interact within a variable landscape to obtain resources such as food and space? Understanding such interactions in terms of the tradeoffs made to promote survivorship, will provide insight into the role of perform-

ance capacity in shaping resource use patterns and community structure.

In this study, I examine these interactions between two native Hawaiian stream gobies (Gobiidae), *Sicyopterus stimpsoni* (Gill) and *Awaous guamensis* (Valenciennes). These species are often syntopic in mountainous streams throughout the Hawaiian Islands (M. Kido unpublished data) and have evolved in a demanding torrential environment subjected to periodic extremes of flood and drought, where geographical isolation has severely limited taxonomic diversity. Resource use by each species was found to coincide with feeding morphology (Kido 1996b). *Sicyopterus stimpsoni* tricuspid teeth, poorly developed gill raker system, highly convoluted gut, and large gut-length to body-length ratio were superbly matched to the herbivory it exhibited (Kido 1996b). Similarly, the highly developed gill raker system and sharply pointed conical teeth of *A. guamensis* coincided with its extensive use of stream invertebrates as food (Kido 1996b). Despite its distinctly carnivorous mouth features, however, *A. guamensis* also possessed a highly convoluted gut with a relatively large gut-length to body-length ratio (Kido 1996b) which coincided with the preponderance of algae in its diet (Kido et al. 1993). Given that native food diversity in Hawaiian streams is largely confined to algae and a limited invertebrate fauna, interesting questions arise as to the roles of inter-specific fitness, behavioral and performance capacities, and competition in shaping styles which enable species coexistence.

Styles for partitioning food resources [Hutchinson's (1959) 'food relations' a term which I choose to dust off and adopt] are fundamental to species coexistence and important in the structuring of natural communities (Tilman 1982). Species coexistence requires the balancing of styles for the acquisition of resources such as food or space (Cody & Diamond 1975) and functions in a variable environment (May & MacArthur 1972). Species must interact to acquire food according to their performance capacities and accomodate differences in resource availability as it relates to the degree of environmental heterogeneity and thus the diversity of available resources (Levin 1992). Landscape complexity can slow competitive exclusion and poten-

tially increase the number of coexisting species (Palmer 1992). Disturbance regimes regulate food availability by influencing the temporal and spatial patchiness of resources in the environment (Sousa 1984). Given their overlap in fundamental and realized niches (Reilly & Wainright 1994), what are the 'food relations' between *A. guamensis* and *A. stimpsoni*? What role has morphology played in shaping food resource use patterns and how have these patterns facilitated species coexistence in the rigorous environment of Hawaiian streams? Such understanding provides interesting insight into the forces shaping adaptation, fitness, and evolution (Reilly & Wainright 1994). From a more pragmatic viewpoint, this information is also essential for resource managers who must understand how human perturbations are causing the accelerating decline in populations of these native Hawaiian species.

The following objectives were addressed in this study in relation to understanding styles which facilitate the coexistence of *A. guamensis* and *S. stimpsoni* in Hawaiian streams: (i) to compare densities of each species in two sites at different elevations and, at these densities, evaluate the strength of association between species, (ii) to determine the manner and degree to which different foods are preferred and subsequently partitioned between species in relation to the availability of foods; (iii) to determine which factors influence food selection; and (iv) to assess the extent of spatial heterogeneity of foods in the benthos in relation to physical factors like stream flow.

## Materials and methods

### Study area

Two sites were selected for this investigation in the Wainiha River which discharges into the ocean on the northern shore of the Hawaiian island of Kaua'i. This fourth order stream descends about 21 km to the ocean from an elevation of 610 m beginning at the base of the island's eroded central caldera, Mt. Wai'ale'ale. Mean daily discharge records for 1992 measured by a permanent USGS gauge at 300 m elevation was 3.5 m$^3$ sec$^{-1}$. A hydro-

electric diversion weir at ca. 213 m elevation diverts water to a power plant at ca. 30 m where it is subsequently returned to the stream. Both study sites were located below the diversion weir. Each site was ca. 100 m in length and consisted of riffle-run habitat with stretches of large exposed boulder. The sites were separated by a distance of about 4 km; the 'lower site' was at an elevation of ca. 37 m and the 'upper site' at ca. 116 m.

## Sampling methodology and analyses

### Visual estimation

To assess the species composition, size class characteristics, and densities of fishes in the two study sites, a visual estimation method was used which capitalized on the benthic-dwelling nature of native Hawaiian stream fishes (M. Kido unpublished method). This method employed a series of abutting square meter observation cells placed horizontally from bank to bank across the stream. These cells were delineated by a line which was flagged at meter intervals and was secured on both banks to rest just at the stream's surface. The line was positioned according to a randomized set of predetermined numbers which were matched against a sequentially numbered grid flagged on the stream's bank. Random placement of a minimum of ten lines during each observation period within each study site based the density estimates on approximately 20% of available habitat. A diver, approaching the line slowly from downstream, recorded the species, numbers and total lengths of all fishes in each cell. Upon completion of visual sampling, depth and mean velocity (three readings minimum) in each cell were measured by using a standard Swoffer flow meter and rod (Swoffer Instrument Co., Seattle, WA). All data were identified by cell and position within the sampling grid. Because of time and manpower constraints, monthly visual sampling was only targeted for the initial phase of the study (January to March) but was continued as personnel became available.

### Diet composition and benthic heterogeneity

For the evaluation of 'feeding relations', *S. stimpso-* *ni* and *A. guamensis* were collected with electrofishing gear monthly from mid-February 1992 to late January 1993 at the two sites. A scissors net (1 m width) was held in the stream and fish were collected from an area of about 1 sq m upstream of the opening. Fishes were anesthetized in the field with MS-222 (tricane methanesulphonate), measured for standard length, weighed to the nearest 0.1 g, and preserved in 10% buffered formalin. Fish collection locations within each study site were chosen randomly, and fish captured were identified by location with individual tags. Digestive systems of preserved fishes were removed from esophagus to anus and subsequently dissected. Gut contents were sorted, identified to lowest possible taxonomic category, and processed as described previously (Kido 1996a).

To assess the availability of food items in the benthos over the study period, each fish capture location was identified with a weighted ribbon and subsequently sampled in a randomized fashion (Kido 1996a) using Surber samplers (250 μ mesh) (Surber 1937). Systematic sampling of the benthos was conducted in the lower site in Aug 1994 to evaluate the degree of spatial patchiness of food resources in the benthos existing at a given time. A line used in the visual estimation study was secured across the stream (from bank to bank) in a representative riffle segment. As before, the line delineated abutting square-meter observation cells. Within each cell (across the width of the stream), randomized benthic sampling (Kido 1996a) was carried out and followed by depth and flow measurements. Samples were identified by cell position across the stream and fixed in 10% formalin in the field. Invertebrates and algae collected were processed and dried as previously described for the gut samples.

### Statistical analyses

Mean densities of fishes in the two study sites were calculated from visual estimation data for each line and summed across lines to obtain an overall mean for the sampling period. Data were normalized by using a $\sqrt{\chi}$ transformation and analysis of variance (ANOVA) (GLM procedure, SAS Institute Inc., 1992) applied to test for differences in species densities within and between sites. Combined presence-

absence data from the observation cells were used to calculate the Dice (1945) index as a measure of association. The variance of this statistic was calculated as in Janson & Vegelius (1981). A chi-square test (Ludwig & Reynolds 1988) with one degree of freedom was used to determine if the two species were associated in the microhabitat sampled. A non-significant chi-square value would indicate that the two species were not sharing available microhabitat. The number of unoccupied observation cells summed over all lines provided a means of evaluating the extent of unused habitat. The non-parametric Spearman coefficient (Proc Corr procedure, SAS Institute Inc. 1992) was used for relationship comparison of species density, depth and flow.

Diet data were compared by using an analysis of covariance procedure (ANCOVA)(GLM procedure, SAS institute Inc. 1992) in which the covariate, fish standard length, was incorporated into the model to increase precision. Initially, main food categories (algae, aquatic invertebrates, terrestrial invertebrates) were compared between species and site to determine if species differed in their use. Diet data were subsequently analyzed separately within main food categories (e.g. only within algal foods). Biomass of food items consumed were then compared between species and site within each of the three main food categories. Data were sorted into seasonal categories (Dec–Feb, Mar–May, Jun–Aug, Sep–Nov) and compared for seasonal dietary differences between species. Means were separated at $p < 0.05$ by using the Duncan option (GLM procedure, SAS Institute Inc. 1992), and only means adjusted for fish length are reported. Per cent dietary abundances of food items (calculated by dividing food item weight by total sample weight) were used in plotting and comparing seasonal trends between goby. Spearman's correlation coefficient (Proc Corr procedure, SAS Institute Inc. 1992) was applied to per cent abundance data to assess the relationship between food items within the diet of each species and their availability within the benthos.

Benthic biomass data (g m$^{-2}$) collected for algae and invertebrates in square meter cells across the width of the lower stream site were normalized using a log ($\chi + 1$) transformation. Overall, group, and species differences in mean algal and invertebrate biomass between-cells were compared using ANOVA (GLM procedure). Means were separated at $p < 0.05$ using Duncan's multiple range test. Flow data (m s$^{-1}$) taken within cells were normalized by using a $\sqrt{\chi}$ transformation and ANOVA (GLM procedure) used to compare mean flows between cells. Means were separated as described previously for benthic data.

### Diet, overlap and selectivity indices

To compare the numbers of *S. stimpsoni* and *A. guamensis* feeding on a particular food, a frequency of occurrence index (% F) (Hynes 1950) was calculated which gives the sample proportion of individuals in the population having a particular food item in the gut. The relative importance of a food item in the diet is expressed as a percentage of its dry weight to total dry weight of all foods found in the gut (% DW) (Zander 1982). Per cent abundance data were used to evaluate the similarity in pattern of resource usage between species by calculating a 'general overlap' value as in Ludwig & Reynolds (1988). This value ranges from 0.5 to 1.0 and quantifies the degree to which species overlap in the use of available foods. General overlap (GO) values were calculated for monthly comparisons and for combined diet data for the study. For the latter, a chi-square statistic with 22 degrees of freedom was calculated as in Ludwig & Reynolds (1988) to determine whether or not overlap in diet between species was complete.

For comparisons of selection (Manly et al. 1993), a 'selectivity index' ($B_i$) was used which permits comparisons of the relative probabilities of selection of available foods. For calculation of this index (Manly et al. 1993), combined per cent abundance data of foods in the diet of both species were compared with their availability as estimated by benthic sampling. A chi-squared statistic with one degree of freedom was used to test for selection of available food items against a hypothesis of no selection (Manly et al. 1993). A non-significant chi-square test would indicate that animals were randomly selecting food items in proportion to their availability in the habitat. Through the use of ANCOVA, the quantities of foods consumed were compared between individuals of either species captured simul-

taneously or alone to assess if presence of the other species influenced food selection.

Spearman's correlation coefficient was applied to per cent abundance data (Proc Corr procedure) to evaluate the type and degree of temporal covariation in the dietary and benthic abundance of algae. Borrowing from Margalef's (1968) ideas about 'negative or stabilizing feedback', the 'sign' of the correlation (i.e. positive or negative) a particular algal food had with other available algae was compared as an overall percentage of algae selected in a negatively correlated manner. A high percentage (set arbitrarily at 60%) would indicate that a food was selected more often in a mutually exclusive manner and a low percentage (less than 60%) that it was selected more often in a complementary fashion. Per cent abundance data of algae collected in the benthos were analyzed in a similar fashion to follow the changing composition of available algal foods within-site and the degree to which inter-specific interactions over algal foods were influenced by temporal variation in their availabilities.

## Results

### Population dynamics

From the visual census, it was confirmed that only two gobies, *A. guamensis* and *S. stimpsoni*, coexisted in the two stream reaches studied. A total of 1125 square meter observation cells were examined by divers in both study sites. *Sicyopterus stimpsoni* occurred alone in 10.6% and *A. guamensis* in 35.9% of the observation cells. In 9.6% of the cells the two species were found together, 43.9% of the cells were unoccupied. Densities of *A. guamensis* were significantly higher overall (p < 0.05). Only in the lower site, however, did species densities differ significantly (F = 52.08, df = 1, p = 0.0001) with *A. guamensis* being found in significantly higher densities than *S. stimpsoni* (p < 0.05) (Figure 1). This was not true of the upper site where population densities were similar. Mean total length for *A. guamensis* was also higher than *S. stimpsoni* in both lower (8.04 ± 0.575 cm and 6.61 ± 0.698 cm, respectively)
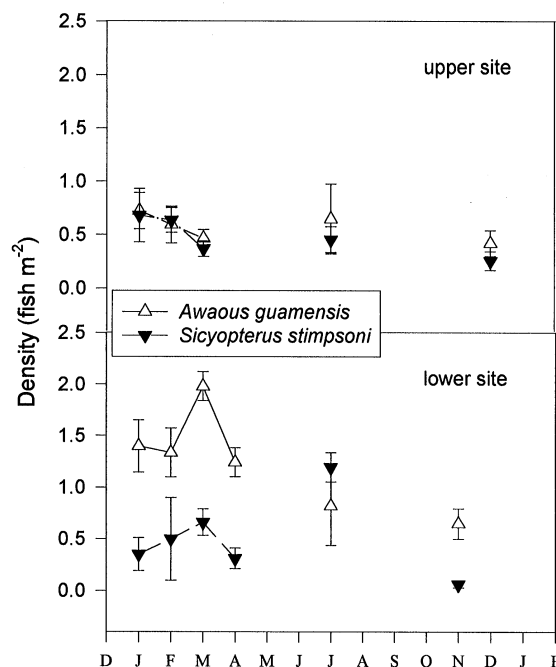


*Figure 1.* Densities (fish m⁻²) of *A. guamensis* and *S. stimpsoni* in study reaches as estimated by visual census from Feb 1992 to Jan 1993.

and upper study sites (8.06 ± 0.771 cm and 6.58 ± 0.436 cm, respectively).

In addition to differences in species densities, the strength of association between *A. guamensis* and *S. stimpsoni* differed within these two sites. Based on the chi-square test utilizing combined observations, the two species did not associate in the lower site where *A. guamensis* was found in significantly higher densities. The measure of this association, based on the Dice index, was 0.26 ± 0.001. In the upper site, however, where both species occurred in similar densities, their association was significant (df = 1, chi square = 4.65, p < 0.05). The Dice index calculated for this association was 0.37 ± 0.002. The depth and velocities at which both species were found within cells were positively correlated (r = 0.463, p = 0.0007 and r = 0.374, p = 0.0074, respectively).

### Feeding relations

Algae were the larger component of the diet of *S.*

*stimpsoni* (94.6% DW) as compared to *A. guamensis* (80.7% DW); however the reverse was found for invertebrates (5.4% DW and 19.4% DW, respectively). In comparisons of mean biomass eaten, these differences were significant (F = 35.51, df = 1, p = 0.0001) with *S. stimpsoni* consuming more algae (df = 1, F = 34.18, p = 0.0001) and *A. guamensis* more invertebrates (F = 6.95, df = 1, p = 0.0084). The gobies also differed in the types of algae (F = 46.49, df = 11, p = 0.0001) and invertebrates (F = 115.45, df = 1, p = 0.0001) eaten over the study period.

Algae from three plant divisions (Chlorophyta, Cyanophyta and Chrysophyta) were consumed by the two gobies (Figure 2) (Table 1); however these were partitioned between them according to algal group. Within the main algal divisions, *A. guamensis* consumed proportionately greater quantities of chlorophytes (F = 13.25, df = 1, p = 0.0003) while *S. stimpsoni* consumed greater amounts of cyanophytes (F = 53.34, df = 1, p = 0.0001) and chrysophytes (F = 93.54, df = 1, p = 0.0001). Five species of

Chlorophyta made up 45.2% of the diet of *A. guamensis* and 17.8% of *S. stimpsoni's* with *Cladophora* sp. and *Spirogyra* sp. contributing the bulk of the chlorophyte biomass for both species (43.0% DW and 17.1% DW, respectively). Of the cyanophytes, which made up 6.8% and 22.6% of the diet of *A. guamensis* and *S. stimpsoni*, respectively, *Rivularia* sp. was the predominant component but was six times more abundant in the diet of *S. stimpsoni* (Table 1). Diatomaceae were consumed by both species and contributed 28.7% and 54.2% to the diet of *A. guamensis* and *S. stimpsoni*, respectively. Both *Hydrosera* sp. (Centrales) and a highly diverse array of pennate (Pennales) species, including both free-living (e.g. *Synedra* sp., *Fragilaria* sp., and *Nitzschia* sp.) and epiphytic forms (e.g. *Gomphosepatum sp., Cymbella* sp., and *Gomphoneis* sp.) were in greater abundance in the diet of *S. stimpsoni*.

Aquatic insects and other invertebrates were more important foods to *A. guamensis* than *S. stimpsoni* (19.4% DW and 5.4% DW of diet, respec-
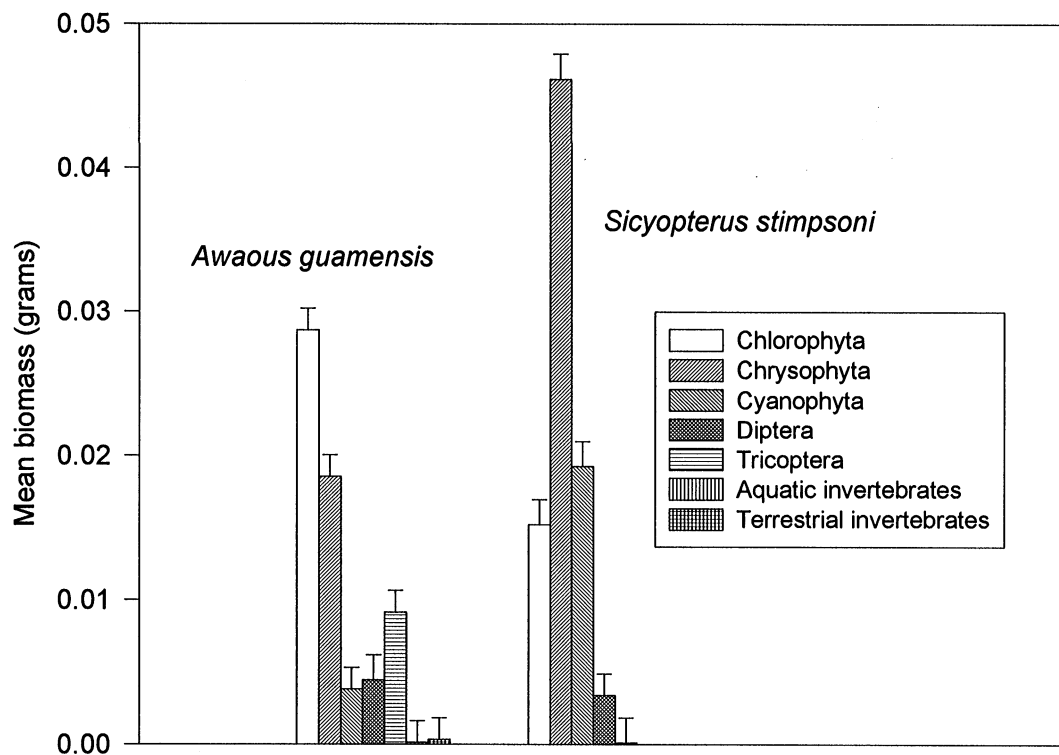


*Figure 2.* Comparisons of mean biomass of major food groups consumed by *A. guamensis* and *S. stimpsoni* (data are adjusted for the covariate fish standard length).

*Table 1.* Benthic abundance (% availability), dietary frequency of occurrence (% F), total dry biomass (% DW), and relative probabilities of selection ($B_i$) for combined plant and animal foods found in the gut of *Awaous guamensis* (N = 59) and *Sicyopterus stimpsoni* (N = 94) collected from June 1992 to January 1993 (* indicates selection greater than expected based on availability as determined by a chi-squared statistic, p < 0.05).

| Food resources | % availability | % F | | % DW | | Selectivity ($B_i$) | |
|---|---|---|---|---|---|---|---|
| | | A. guamensis | S. stimpsoni | A. guamensis | S. stimpsoni | A. guamensis | S. stimpsoni |
| **Plant foods** | | | | | | | |
| Chlorophyta (Chlorophyceae) | | | | | | | |
| *Cladophora* sp. | 42.19 | 94.92 | 71.90 | 33.09 | 13.28 | *0.000239 | *0.000263 |
| *Rhizoclonium* sp. | 0.76 | 0.00 | 5.20 | 0.00 | 0.44 | 0.000000 | 0.000497 |
| *Ulothrix* sp. | 0.08 | 2.54 | 7.30 | 2.21 | 0.14 | 0.003094 | 0.000136 |
| *Oedogonium* sp. | 0.01 | 1.70 | 2.10 | 0.02 | 0.17 | 0.001659 | 0.000000 |
| *Spirogyra* sp. | 2.34 | 52.50 | 67.70 | 9.87 | 3.80 | 0.000404 | 0.000915 |
| Cyanophyta | | | | | | | |
| Oscillatoriaceae | 11.08 | 3.40 | 18.20 | 0.14 | 3.00 | 0.000003 | 0.000206 |
| *Nostoc* sp. | 5.24 | 35.60 | 21.90 | 1.64 | 1.11 | 0.000045 | 0.000084 |
| *Calothrix* sp. | 0.00 | 15.25 | 0.00 | 1.93 | 0.00 | *0.705848 | 0.000000 |
| *Rivularia* sp. | 14.95 | 25.42 | 67.20 | 3.08 | 18.45 | 0.000026 | 0.000448 |
| Chrysophyta (Diatomaceae) | | | | | | | |
| Diatoms (Pennales) | 14.65 | 96.61 | 95.80 | 21.63 | 49.28 | 0.000327 | *0.001855 |
| *Hydrosera* sp. (Centrales) | 0.27 | 13.56 | 17.20 | 7.10 | 4.89 | 0.002844 | 0.006454 |
| **Animal foods** | | | | | | | |
| Diptera | | | | | | | |
| Chironomidae | 1.71 | 96.61 | 93.80 | 5.36 | 5.12 | 0.000637 | 0.002094 |
| *Scatella* spp. (Ephydridae) | 0.04 | 27.12 | 8.30 | 0.04 | 0.01 | 0.000196 | 0.000023 |
| *Hemerodromia stellaris* (Empididae) | 0.08 | 57.63 | 29.20 | 0.18 | 0.03 | 0.000531 | 0.000151 |
| *Procanace* spp. (Canacidae) | 0.06 | 25.42 | 48.40 | 0.09 | 0.08 | 0.000223 | 0.000545 |
| *Limonia* spp. (Tipulidae) | 0.00 | 11.86 | 5.20 | 0.03 | 0.01 | 0.003697 | 0.000971 |
| Tricoptera | | | | | | | |
| Cheumatopsyche pettiti (Hydropsychidae) | 5.17 | 74.58 | 15.60 | 9.36 | 0.01 | 0.000573 | 0.001590 |
| *Hydroptila arctia* (Hydroptilidae) | 0.83 | 84.75 | 38.00 | 2.89 | 0.11 | 0.000812 | 0.068550 |
| *Oxyethira maya* (Hydroptilidae) | 0.00 | 0.07 | 0.00 | 0.03 | 0.00 | 0.013577 | 0.000000 |
| Lepidoptera (Cosmopterigidae) | | | | | | | |
| *Hyposmocoma* spp. | 0.08 | 0.14 | 0.00 | 0.09 | 0.00 | 0.000408 | 0.000000 |
| Turbellaria (Planariidae) | | | | | | | |
| *Dugesia* sp. | 0.47 | 0.07 | 0.00 | 0.52 | 0.00 | 0.000217 | 0.000000 |
| Terrestrial arthropods | 0.00 | 0.54 | 0.00 | 0.77 | 0.00 | 0.249946 | 0.000000 |

tively) and indicated a distinct partitioning of available (mostly non-native) animal food resources in the stream (Figure 2). Unlike *A. guamensis, S. stimpsoni* did not utilize triclad flatworms (*Dugesia* sp.) or drifting terrestrial anthropods and consumed less than 0.01% the quantity of two adventive species of caddisflies (Tricoptera), *Cheumatopsyche pettiti* (Banks) and *Hydroptila arctia* Ross (Table 1). This difference in caddisfly dietary abundance was highly significant (F = 66.35, df = 1, p = 0.0001. *Awaous guamensis* captured simultaneously with *S. stimpsoni* also had significantly greater quantities in its gut (F = 5.96, df = 1, p = 0.0178) as compared to individuals captured alone. No comparable difference was determined for aquatic Diptera which consisted primarily of midge larvae of introduced *Cricotopus bicinctus* (Meigen) with lesser amounts of native *Micropsectra* spp.

With a few notable exceptions, selection of foods by both gobies was primarily random and based upon their availability in the stream (Table 1). Preference was demonstrated for only algal species. *Cla-*

*dophora* sp. was the most abundant food in the benthos (42.2%) and was selected non-randomly by both fish species (p < 0.05). Overall consumption of this alga, however, differed significantly (F = 9.06, df = 1, p = 0.0028) with greater consumption by *A. guamensis* (p < 0.05). No significant differences in *Cladophora* sp. (or any other alga) eaten, however, were found between individuals of either species captured syntopically or alone. Spatial factors may also interact with food choice as exemplified by the non-random selection (p < 0.05) of the relatively rare cyanophyte *Calothrix* sp. by *A. guamensis*. This alga is found floating at the surface in the still-water of shallow, isolated pools some distance from swift-water habitat. It was not eaten by *S. stimpsoni* or collected in the sampling of the benthos which was focused in the swift-water where fish were electro-fished. The two native gobies may therefore differ in their range of microhabitat exploited. Pennate diatoms, many of which are epiphytic on chlorophytes and cyanophytes, may also add a spatial component to food selection as their distribution is influenced by the demographics of their host plants. Pennate diatom selection by *S. stimpsoni* was non-random (p < 0.05) and demonstrated their dietary importance to this goby (Table 1).

*Awaous guamensis* and *S. stimpsoni* tracked temporal changes in algal abundance and consumed seasonally different quantities of chlorophytes (F = 4.07, df = 3, p = 0.0087 and F = 8.63, df = 3, p = 0.0001, respectively), cyanophytes (F = 9.45, df = 3, p = 0.0001 and F = 12.53, df = 3, p = 0.0001, respectively), and chrysophytes (F = 10.89, df = 3, p = 0.0001 and F = 5.19, df = 3, p = 0.0018, respectively) (Figure 3). The gobies did not differ in the seasonal pattern of chlorophyte and cyanophyte consumption which was highest in fall (Sep-Nov) (p < 0.05) and spring-summer (Mar–Aug) (p < 0.05), respectively. The two gobies, however, had peak consumption of chrysophytes in opposing seasons (*A. guamensis* in spring-summer and *A. stimpsoni* in fall-winter) (p < 0.05) although *S. stimpsoni* always consumed significantly greater amounts (p < 0.05).

Accompanying this seasonal variability were corresponding changes in dietary overlap between the coexisting gobies (Figure 4). Based on chi-square tests, diet overlap never reached complete levels during the study but ranged from 0.641 to 0.936 and 0.660 to 0.882 in lower and upper sites, respectively. A decline in the dietary abundance of the predominant cyanophyte, *Rivularia* sp., from high levels in summer to low levels in fall was correlated with dramatic increases in the predominant chlorophyte, *Cladophora* sp., in the diet of fish from both lower (r = − 0.670, p = 0.0001) and upper sites (r = − 0.625, p = 0.0001). This dietary increase was likely associated with a bloom of *Cladophora* sp. which was induced by the return of diverted water to the stream after high winds from a Category V hurricane destroyed the Wainiha hydropower plant. This storm, which struck Kauai in September 1992, also denuded the stream's riparian vegetation and increased ambient light levels on the water's surface. Both gobies responded to the *Cladophora* bloom by increased selection of this alga as food (Figure 3). General overlap (GO) values reached high levels during this period in both lower (GO = 0.852) and upper (GO = 0.936) sites (Figure 4). Both species, therefore, capitalized on the disturbance-induced overabundance of this alga by switching rapidly to it as their major source of food. A series of spates beginning in early October preceded the decline in *Cladophora* sp. abundance and subsequent increases in the abundances of other algal species (Figure 3).

Correlation comparisons of algal dietary abundance with benthic availability yielded interesting insight into feeding styles and trade-offs. Each goby utilized one alga as a 'primary algal food' in a mutually exclusive fashion with other algae regardless of variation in its availability. This alga was *Cladophora* sp. for *A. guamensis* and pennate diatoms for *S. stimpsoni* (Table 2). Other algae were treated as 'secondary algal foods' and used in either a complementary or exclusionary manner. The availability of most of these 'secondary' algae was inversely related to *Cladophora* sp. abundance in both sites and diatom abundance in the upper site only. The use by the two gobies of 'secondary algal foods' changed as the proportionate availability of these algae changed over time. Use of *Cladophora* sp. as food by *A. guamensis*, in relation to other algae, did not differ temporally between site; however, *S. stimpsoni* was less reliant on *Cladophora* sp. in fa-
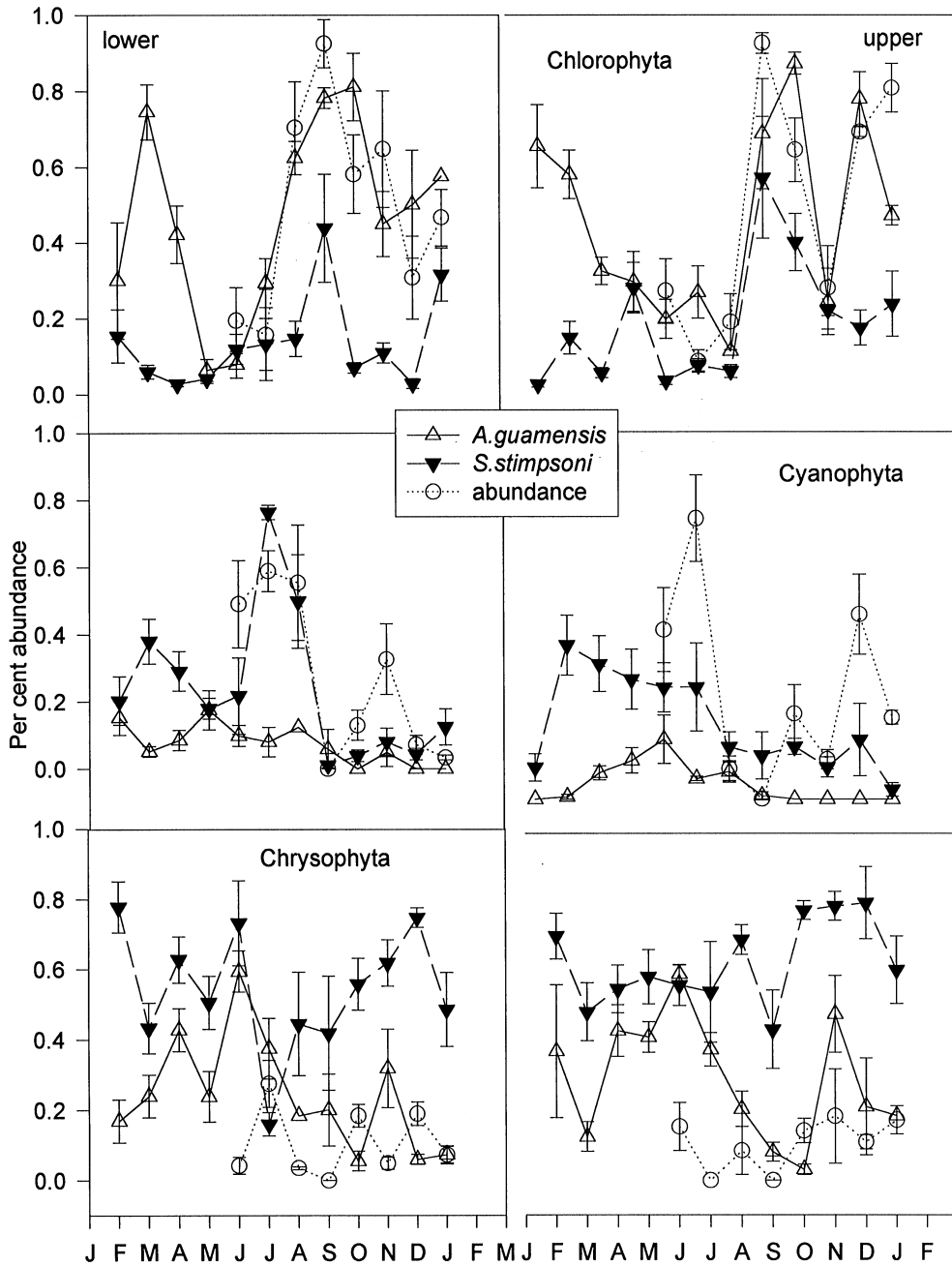
*Figure 3.* Comparisons of temporal and between-site variation in the dietary abundances of chlorophytes, cyanophytes, and chrysophytes for *A. guamensis* and *S. stimpsoni* with their overall availabilities as estimated by benthic sampling.
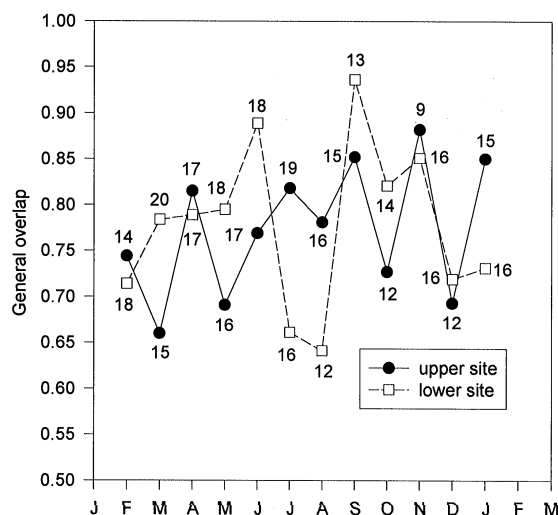
*Figure 4.* Comparison of overlap in food utilization curves for *A. guamensis* and *S. stimpsoni* over the study period based on computations of 'general overlap' indices (Ludwig & Reynolds 1988). Values adjacent to data points indicate the number of available food types, overlap values range from 0.5 (no overlap) to 1.0 (complete overlap).

vor of cyanophytes in the lower site. Interestingly, *Cladophora* sp. was negatively correlated in the diet of the two gobies (r = − 0.59881, p = 0.0025) in the upper site but positively correlated in the diet of fish captured in the lower site (r = 0.42102; p = 0.0018). The two gobies therefore differed between-site in the manner in which this alga was utilized over time.

### Spatial heterogeneity

Data collected through Surber sampling of the benthos across a reach of the lower stream site, indicated high spatial heterogeneity in the microhabitat abundances and therefore availabilities of food resources in the benthos at any given time (Figure 5). Algae and invertebrates differed significantly between cells (F = 13.03, df = 2, p = 0.0002) across the reach of stream sampled. Algal biomass was greater than invertebrate biomass (p < 0.05) and was highest in still-water microhabitat behind large, partially submerged boulders (p < 0.05). Aquatic insect densities differed significantly between cells (F = 7.97, df = 9, p = 0.0001) and were generally higher in areas of moderate to high flow. Immature aquatic midges (primarily alien *Cricotopus bicinctus*) and the alien purse-building micro-caddisfly, *Hydroptila arctia*, were found in the highest densities (p < 0.05) particularly in habitat with moderate to high flows. Motile aquatic insect species were widely distributed but varied in densities in relation to position in stream, depth, and associated flow regime. Algal abundance also differed significantly between cells (F = 8.05, df = 4, p = 0.0001) with cyanophytes found in the highest densities (p < 0.05). The blue-green alga *Nostoc* sp. was found in the highest overall abundance (p < 0.05), widely distributed across the reach of stream sampled. The chlo-

*Table 2.* Benthic availability of algae (% abundance) and per cent comparisons of negatively correlated algal species in the benthos and diet of *A. guamensis* and *S. stimpsoni* captured in the upper and lower study sites of Wainiha River, Kauai. 'None' indicates that the alga did not occur in the diet or benthos.

| Algal foods | Benthic % abundance | Upper site % negative correlation | | | Benthic % abundance | Lower site % negative correlation | | |
|---|---|---|---|---|---|---|---|---|
| | | benthic | *A. guamensis* | *S. stimpsoni* | | benthic | *A. guamensis* | *S. stimpsoni* |
| *Cladophora* sp. | 57.4 | 71.4 | 100.0 | 71.4 | 34.5 | 83.3 | 100.0 | 57.1 |
| *Rhizoclonium* sp. | 0.6 | 44.4 | none | 14.3 | 1.0 | 16.7 | none | 57.1 |
| *Ulothrix* sp. | 0.1 | 33.3 | 57.1 | none | 0.1 | 71.4 | 28.6 | 57.1 |
| *Oedogonium* sp. | 0.0 | 66.7 | 57.1 | none | 0.0 | none | none | 28.6 |
| *Spirogyra* sp. | 3.6 | 51.9 | 28.6 | 42.9 | 1.5 | 28.6 | 14.3 | 28.6 |
| Oscillatoriaceae | 11.7 | 77.8 | none | 71.4 | 12.4 | 28.6 | 28.6 | 85.7 |
| *Nostoc* sp. | 2.8 | 44.4 | 14.3 | 42.3 | 8.8 | 42.9 | 14.3 | 28.6 |
| *Calothrix* sp. | 0.0 | none | none | none | 0.0 | none | 57.1 | none |
| *Rivularia* sp. | 10.6 | 33.3 | 42.9 | 28.6 | 22.3 | 42.9 | 28.6 | 57.1 |
| Diatoms (Pennales) | 12.7 | 66.7 | 28.5 | 100.0 | 19.4 | 42.9 | 66.7 | 100.0 |
| *Hydrosera* sp. (Centrales) | 0.6 | 33.3 | 42.9 | 42.9 | 0.0 | none | 57.1 | none |
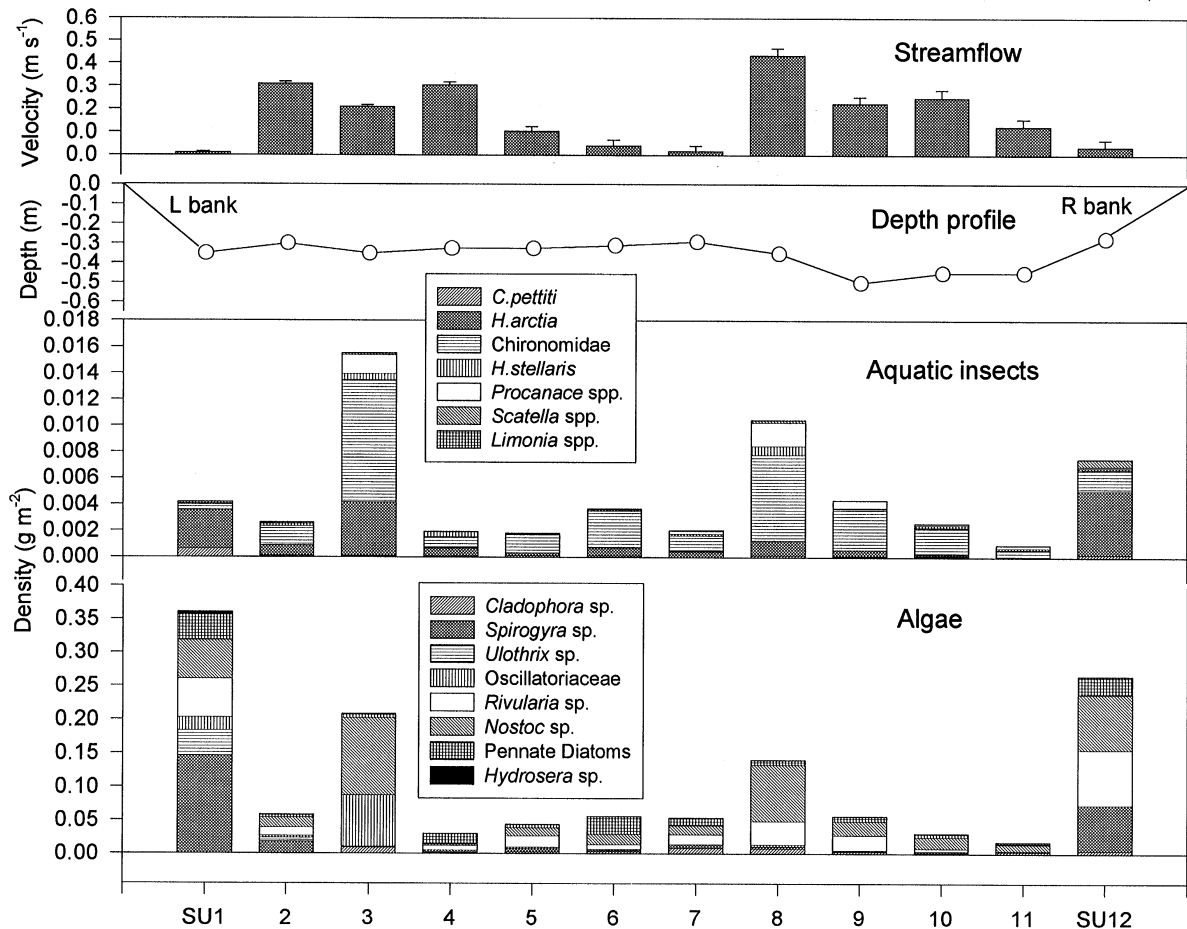
*Figure 5.* Densities (g m⁻²) and species composition of algae and invertebrates in relation to depth (m) and flow (m sec⁻¹) as determined by systematic benthic sampling in twelve adjacent square meter sampling units (SU) across (bank to bank) a randomly selected reach in the lower site.

rophyte *Ulothrix* sp., was restricted by microhabitat type and only found in one still-water cell (cell one) while other algae were more ubiquitously distributed. Little is known, however, about algal or aquatic insect phenologies in Hawaiian streams.

Flow varied markedly both between and within sampling cells (F = 118.23, df = 11, p = 0.0001) (Figure 5). Brief pulses of flow varying in direction in shallow cobble microhabitat contrasted with steady high-velocity pulses in the deeper primary stream channels which accommodated the major volume of discharge. Flow was fastest in cell eight (p < 0.05) and slowest in the cells adjacent to the stream bank (p < 0.05). In the cross-section of stream sampled, 87.5% of algal and 57.1% of the invertebrate abun-

dance was negatively correlated with flow. This can be compared with negative correlations of 71.4% of algal and 55.6% of the invertebrate abundance based on flow data taken with benthic collections in this lower site over the duration of the study. Through its influence on the spatial and temporal abundance of foods, stream discharge may therefore play a central role in mediating the feeding relations of Hawaiian stream fishes.

## Discussion

The distinct partitioning of foods determined between *A. guamensis* and *S. stimpsoni* is a central fac-

tor which facilitates their coexistence in Hawaiian streams. To a large degree, differences in food use were dictated by discrete differences in morphological traits for feeding (Kido 1996b) and it was not unexpected, therefore, that *A. guamensis* would have nearly unchallenged access to stream invertebrates for food. Of greater ecomorphological interest, however, was the manner in which *A. guamensis* and *S. stimpsoni*, each with various fitness for herbivory (Kido 1996a), interacted over algae given the severely limited array of food niches available to them in Hawaiian streams. In this environment, the gobies were found to partition plant foods according to the 'primary dictum' that priority is granted to *A. guamensis* for *Cladophora* sp. and to *S. stimpsoni* for diatoms and cyanophytes. Inter-specific overlap in the dietary use of these 'primary algal foods', however, was decidedly influenced by the proportionate availabilities of the existing array of 'secondary algal foods' in the benthos. Based on the breadth of foods eaten and available, the two gobies appeared to utilize the maximum range of their feeding abilities (i.e. performance capacities) yet were able to lessen the influence of potential competition resulting from the limited diversity in available food types. The role of density-dependent forces in regulating food availability, however, is an important area which requires study to complete our understanding of their 'feeding relations'.

The existence of past competition in shaping present resource use patterns is difficult to assess but should be considered (Schoener 1987). Following Sale's (1974) approach, glimpses of competitive interactions are reflected in the patterns of resource utilization. Both gobies show strong preference for the abundant and ubiquitous stream alga *Cladophora* sp., yet *A. guamensis* is its major consumer, except when the alga becomes super-abundant. Zaret & Rand (1971) use similar phenomenon to invoke the competitive exclusion principle among Panamanian stream fishes based on the idea that the overabundance of foods reduces the intensity of competition. Higher consumption of stream caddisfly immatures by *A. guamensis* in the presence of *S. stimpsoni* is analogous to feeding habit changes observed in Swedish coastal gobioids living under conditions of competitively constrained coexistence (Edlund & Magnhagen 1981). Partitioning of habitat observed for *A. guamensis* and *S. stimpsoni* (Kinzie 1988) is regarded as a common trait of freshwater fishes to reduce interspecific competition (Ross 1986). Association between the two gobies and utilization of similar microhabitat is strongly positive under conditions of equal population densities; however this association breaks down when the densities of *A. guamensis* becomes significantly higher. Such negative density dependence is assumed to be caused by competition (Wilson & Yoshimura 1994) and favors the evolution of specialization (Rosenzweig 1991). These glimpses of competition may be reflections of its past evolutionary role in shaping the 'feeding relations' of these two native gobies. Any disputes over food, however, appear to have been resolved by the supreme court of natural selection long ago as they are seldom observed to exhibit antagonistic interactions over food in aquaria (M. Kido unpublished data) and coexist in streams throughout Hawaii.

Disturbance is typically expected to moderate the overriding influence of competition in ecological communities (Reice 1985). Seasonal and unpredictable flood disturbance is commonplace in Hawaiian streams and has been suggested as an important factor contributing to spatial heterogeneity of foods in the benthos (Kido 1996a). Benthic sampling in this study revealed significant spatial patchiness, albeit at relatively gross resolutions, in both abundance and composition of algae and invertebrates in relation to flow. Variation in flow may be one of the key physical factors mediating species composition and abundance of foods within the stream benthos; however, little attention has been focused on these relationships. Periodic flood disturbance can maintain differences among patches and act as a 'reinitializing mechanism' (Reice 1985). Operation of this mechanism is evidenced in the decreases in abundances of algae correlated with the bloom of *Cladophora* sp. and their subsequent 'reinitialization' after the first spate. This is suggestive of the overriding influence of flow-related disturbance in Hawaiian streams; however, neither the manner in which stream fish select from the benthic mosaic nor the role of disturbance events in regulating succession in this mosaic has been studied.

Greater probabilities of coexistence with increasing environmental variability is predicted from simulation studies of competition (Palmer 1992), and it may have been in the context of such variability that feeding relations which mediated coexistence among Hawaiian stream gobioids evolved.

Hawaiian streams are ecological oddities where evolutionary pressures were derived from a demanding physical environment in which the diversity of colonizing species was severely constrained by geographical isolation. These two interacting factors likely lessened, to various degrees, ecological pressures from predation and inter-specific competition. Limitations in food diversity, on the other hand, likely emphasized the role of morphological variation between-species as a source of potential conflict over food. In the case of *A. guamensis* and *S. stimpsoni*, performance capacities for feeding were found to be strongly linked to food utilization patterns. Overlap in fundamental niches (Reilly & Wainright 1994), juxtaposed over limitations in food diversity, logically may have been an important selective force working to shape these patterns. Elucidating the relative influences of behavior and periodic flow disturbance on these patterns are two important areas of future study. Taxonomic and biogeographical comparisons with related gobioids from other regions may also provide insight into the sequence of species invasion into Hawaiian streams and their ancestral morphologies. The evolutionary outcome for *A. guamensis* and *S. stimpsoni* is a relationship in which competitive interactions have been minimized and, although they may be 'doomed' to associate (Diamond 1992), they may not have to do so as 'enemies'.

## Acknowledgements

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