

Morphological Variation in Feeding Traits of Native Hawaiian Stream Fishes¹

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ABSTRACT: The five native species of amphidromous gobioid fishes inhabiting Hawaiian streams were compared for dentition, gut length to body length ratios, intestinal convolution, gill raker morphology, position of mouth, and diet. Based on morphological comparisons, three manipulative modes of feeding are indicated, as follows: picking-biting, rock scraping, and sediment foraging. Comparisons indicated a surprising predominance of algae in the diet of all species despite various degrees of morphological specialization for their use. Avoidance of competition for algae was therefore suggested as a potential factor influencing species interactions and community organization. Differential preference among native gobioids for stream invertebrates may also provide mitigation for competitive interactions. Variation in food availability in the benthic landscape of Hawaiian streams, possibly regulated by stream flow and periodic disturbance, is hypothesized as being an important determinant of fish community structure. Human-induced alteration of factors that regulate food availability could therefore influence stability of native fish populations through disturbance of their food base.

COMPARING SPECIES DIFFERENCES in morphological traits for acquiring food and exploring the relationship of these characters to resource use is a fundamental step toward understanding trophic interactions and patterns of community organization in fish. These traits affect food selection and foraging efficiency and establish a basis for predicting food and habitat use among fish species (Werner 1984). Dietary differences between species should correlate with morphological differences (Schoener 1965, Schluter 1982), and it is expected that species that coexist should be less similar in morphology than

species that do not associate (Grant and Schluter 1984). Of central ecological interest is the role of competition in influencing community organization, and morphological comparisons can provide a "firm base" for such inquiry (Maiorana 1978). In this study, I examine the validity and applicability of these tenets for amphidromous stream fishes native to the Hawaiian Islands.

Only five fish species in two families (Gobiidae and Eleotridae) are native to the steep-gradient mountainous streams of Hawai'i, where the native aquatic food base is largely limited to algae and immature Diptera. It seems plausible that competition for this limited diversity of foods, spurred by the extreme isolation of the Hawaiian Archipelago, has played an evolutionary role in shaping species interactions (Kido, unpubl. data). Dietary studies on these gobioids, however, are incomplete and very little of their basic biology has been studied; thus virtually nothing is known about morphological variation between species or their connection to resource use. Published diet information is only available for two of the gobies (Gobiidae). *Awaous*

¹ This study was made possible through program support to the Kaua'i Research Facility (University of Hawai'i, College of Tropical Agriculture and Human Resources) for environmental research in the Hawaiian Islands from the Agricultural Research Service, U.S. Department of Agriculture and through a grant from the Division of Aquatic Resources, State of Hawai'i, Department of Land and Natural Resources, Award No. L010-PO5910. Manuscript accepted 15 June 1995.

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guamensis (Valenciennes) is described as a generalist that utilizes both algae and invertebrates (Kido et al. 1993), and *Sicyopterus stimpsoni* (Gill) has been shown to specialize on diatoms and blue-green algae (Kido 1996). These two species exhibit a distinct pattern in the partitioning of algal foods and strong preference for the ubiquitous green alga *Cladophora* sp. (Kido, unpubl. data). No published dietary information is available for *Lentipes concolor* Gill and *Stenogobius hawaiiensis* (Cuvier & Valenciennes) (both Gobiidae) or the lone native eleotrid (Eleotridae), *Eleotris sandwicensis* Vaillant & Sauvage.

Population structure of gobioids among Hawaiian Island streams also has been poorly studied both spatially and temporally. *Eleotris sandwicensis* and *S. hawaiiensis* overlap in range and generally are confined to lower elevations and estuaries (Maciolek 1981). The remaining three gobies are less restricted and range farther into mountainous reaches; however little quantitative data on species distribution are available. Coexistence and positive association, which can be influenced by species densities, were found for *A. guamensis* and *S. stimpsoni* (Kido, unpubl. data). Based on studies in three streams on three Hawaiian islands, Kinzie (1988) determined that *L. concolor* did not co-occur with other gobies because of its longitudinal distribution pattern and that *A. guamensis* and *S. stimpsoni* differed in microhabitat utilization pattern in those reaches of streams where they co-occurred. How are these patterns related to resource use and guided by species differences in morphological feeding traits?

The following objectives were addressed in this study: (1) to compare the morphological feeding traits of the five native Hawaiian stream fishes and determine the availability of feeding modes; (2) to determine the degree to which these differences are reflected in resource use; and (3) to assess the role of food competition in structuring native stream fish populations. This information is of broad ecological interest but is also useful for developing effective management strategies for declining native stream fish populations in the Hawaiian Islands.

MATERIALS AND METHODS

The study was conducted in the Wainiha River, which drains the Alaka'i Swamp atop the ancient caldera of Mount Wai'ale'ale on the island of Kaua'i. Discharging into the ocean on the island's northern shore, Wainiha River descends to sea level from an elevation of 610 m, traveling a distance of ca. 21 km. Mean discharge for 1992 measured by a permanent U.S. Geological Survey gauge at 300 m elevation was $3.5 \text{ m}^3 \text{ sec}^{-1}$. Four fish collection sites were used, at sea level (estuary), ca. 37 m elevation (site 2), ca. 116 m elevation (site 3), and in the steeply graded tributary, Maunahina, at ca. 190 m elevation (site 4). Stored specimens of *S. stimpsoni* and *A. guamensis*, collected previously in sites 2 and 3 (February 1992 to January 1993) (Kido, unpubl. data), were utilized for morphological comparisons. *Lentipes concolor* was collected in Maunahina (site 4) and *E. sandwicensis* from site 2 in August 1992, whereas *S. hawaiiensis* was collected in Wainiha estuary in July 1993.

Adult fishes were captured using hand-nets in the estuary and with electrofishing gear in the mountainous sites. Fishes were anesthetized in the field with MS-222 (tricaine methanesulphonate), measured for standard length, weighed to the nearest 0.1 g, and preserved in 10% buffered formalin. In the laboratory, fishes were examined externally for morphological features related to feeding (Lowe-McConnell 1978). The digestive system was dissected, examined for arrangement of folds, and sketched using a dissecting microscope (Leica-Wild M37). All gut drawings were made viewing the organ ventrally (Fukusho 1969). The pattern of convolution was diagnosed and compared by indicating positions of turning or bending (Fukusho 1969). The gut subsequently was removed from esophagus to anus and stored in 10% buffered formalin. Digestive systems were later unraveled and measured for total length to calculate gut length to standard length ratios (Lowe-McConnell 1978). The gut was opened and the animal and plant portions of the contents were sorted, identified to lowest possible taxonomic category

(as in Kido 1996), dried at 60°C for 48 hr, and weighed to the nearest 0.0001 g.

Five morphological feeding traits were compared in the study. For comparisons of bony internal features of the mouth, fishes were cleared and stained with alizarin red using an enzyme method (Taylor 1967) that removes flesh with minimal damage to bony structures. Gut length to standard length ratios were normalized using a log ($x + 1$) transformation and compared using analysis of variance (ANOVA) (GLM Procedure [SAS Institute 1992]). Means were separated at $P < 0.05$ using Duncan's multiple range test. Longer gut lengths (larger ratios) are typical of herbivores that ingest fibrous plant foods that resist digestion, whereas carnivores have shorter systems (smaller ratios) adapted to processing mostly high-quality foods (Wootton 1990). The pattern of intestinal convolution was compared because it is a standard diagnostic character used in comparative fish studies (Fukusho 1969). Gill rakers, forward-directed projections on the inner margins of the gill arches, vary in size and number depending on a fish's diet (Wootton 1990) and were used as a third comparative trait. Bony, cartilaginous, and fleshy toothlike projections on gill rakers were compared and sketched viewing the mouth from an anterior to posterior perspective. A fourth diagnostic character was the position of the mouth because it influences foraging efficiency. Finally, the shape, density, and pattern of teeth in the marginal bones of the jaw, gill margins, and pharynx were compared and sketched.

RESULTS

In total, six *S. hawaiiensis* (50.0% male and female), five *L. concolor* (40.0% male, 60.0% female), and seven *E. sandwicensis* (42.9% male, 57.1% female) were collected from Wainiha River and used for morphological comparisons. Mean standard length for these fishes was 52.1 ± 3.35 , 67.2 ± 3.03 , and 89.1 ± 5.23 mm, respectively. Ten specimens each of *A. guamensis* and *S. stimpsoni* (50.0% male and female) were selected at

random from all size classes from stored material. Mean standard length of these fishes was 95.1 ± 2.91 and 74.9 ± 1.67 mm, respectively. All species except *E. sandwicensis* had ventroterminal mouths with the lower jaw closing posterior to the upper jaw. *Eleotris sandwicensis* differed in having a terminal mouth with a wide gape that opened somewhat dorsally, the lower jaw closing well anterior to the upper jaw. No indication of abilities to protrude the jaw was observed in any of the species, and no differences between sexes were observed for this or any other trait.

The five native stream gobioids differed significantly in gut length relative to body length and in the pattern of intestinal convolution. Comparisons of log-transformed gut length to standard length ratios with ANOVA indicated significant interspecific differences ($F = 199.12$, $df = 4$, $P < 0.0001$). *Sicyopterus stimpsoni* had significantly larger mean ratios (2.73 ± 0.041) than the other species ($P < 0.05$). Mean ratios for *A. guamensis* (1.27 ± 0.036) were lower than those for *S. stimpsoni* but significantly larger than those of the remaining gobioids ($P < 0.05$). *Stenogobius hawaiiensis* and *L. concolor* had similar gut to length ratios (0.93 ± 0.032 and 0.82 ± 0.036 , respectively) ($P < 0.05$). *Eleotris sandwicensis* had significantly shorter ratios (0.65 ± 0.039) than the other species ($P < 0.05$). *Sicyopterus stimpsoni* had the most convoluted gut, with 14 bends or turns, followed by *A. guamensis* (nine), *L. concolor* (six), *S. hawaiiensis* (three), and *E. sandwicensis* (two) (Figure 1).

Distinct differences in dentition of the marginal bones of the jaw were found between certain species; however, certain characteristics were also shared. Marginal teeth in upper and lower jaw were most similar for *A. guamensis* and *E. sandwicensis*, consisting of sharply pointed conical teeth curved inward and patterned randomly, not in rows (Figure 2A,B). Tooth densities in fishes of equal size were similar (two teeth per mm^2). *Stenogobius hawaiiensis* differed in dentition in having a single row of fused bluntly pointed teeth in the upper jaw (16 teeth per 0.1 mm^2) with sharply pointed conical teeth widely in-

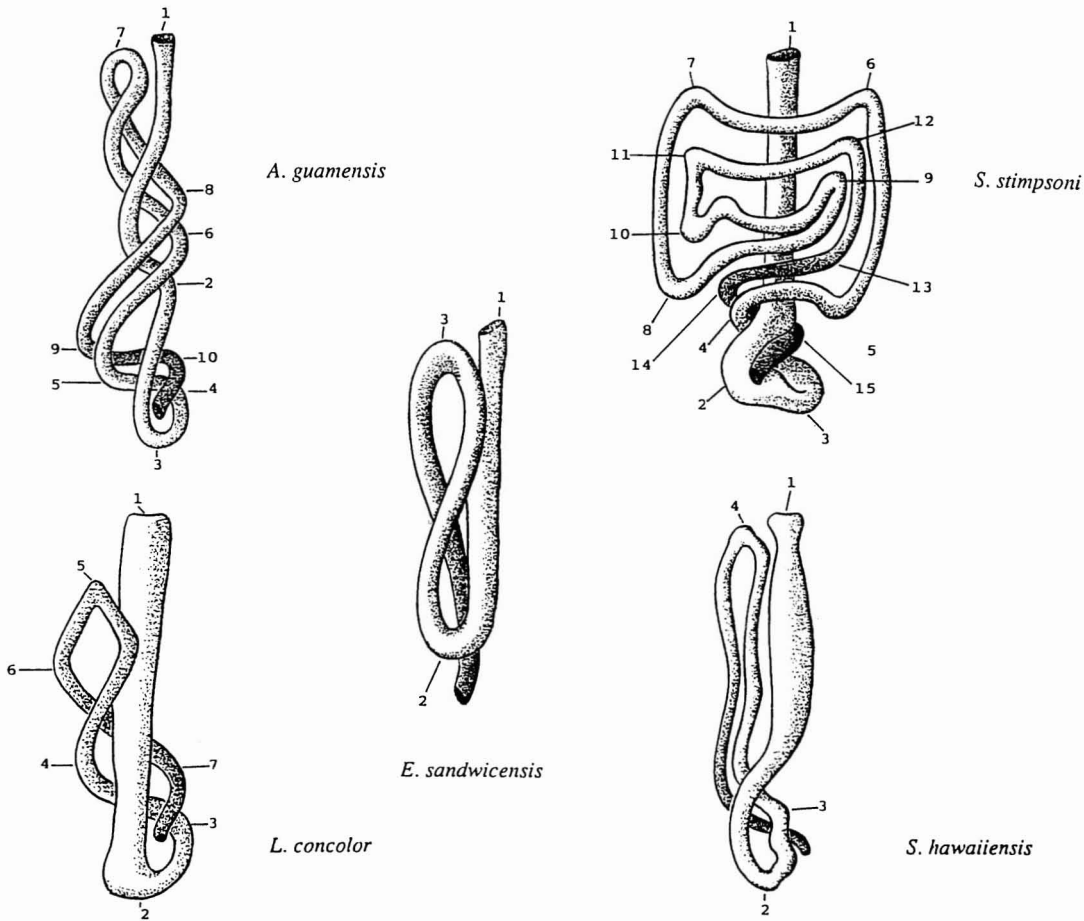


FIGURE 1. Comparison of patterns in gut convolution of native Hawaiian stream gobioids. The organ is viewed ventrally, and bends or turns are numbered from esophagus to anus.

terspersed within (three teeth per 0.1 mm²). Teeth in the lower jaw were conical, sharply pointed, and curved inward in two uneven rows (10 teeth per 0.1 mm²) (Figure 2A). In *S. stimpsoni* and *L. concolor*, upper marginal teeth were straight, in a single row (10 and six teeth per 0.1 mm², respectively), with tricuspid tips bent slightly inward. Tooth structure differed in tricuspid design, with lateral edges having higher points in *S. stimpsoni* as compared with a single central high point in *L. concolor* (Figure 2A). Both species displayed a two-tiered arrangement of teeth in the lower jaw. A single row of labial teeth on the jaw's anterior margin was oriented at right

angles to sharply pointed conical teeth on the jaw's dorsal margin (Figure 2A). Labial teeth in both species were similarly spaced (eight teeth per 0.1 mm²); however, conical dorsal teeth were uniformly spaced in a single row (four teeth per 0.1 mm²) in *L. concolor* but reduced in number and generally confined to the medial and lateral edges of the lower jaw in *S. stimpsoni* (Figure 2A). All the gobioids had four gill arches but differed in arch and raker morphology. Only *A. guamensis* and *E. sandwicensis* had bony teeth on the gill arch. In *A. guamensis*, these teeth were found only on the arch closest to the operculum and were sharply pointed,

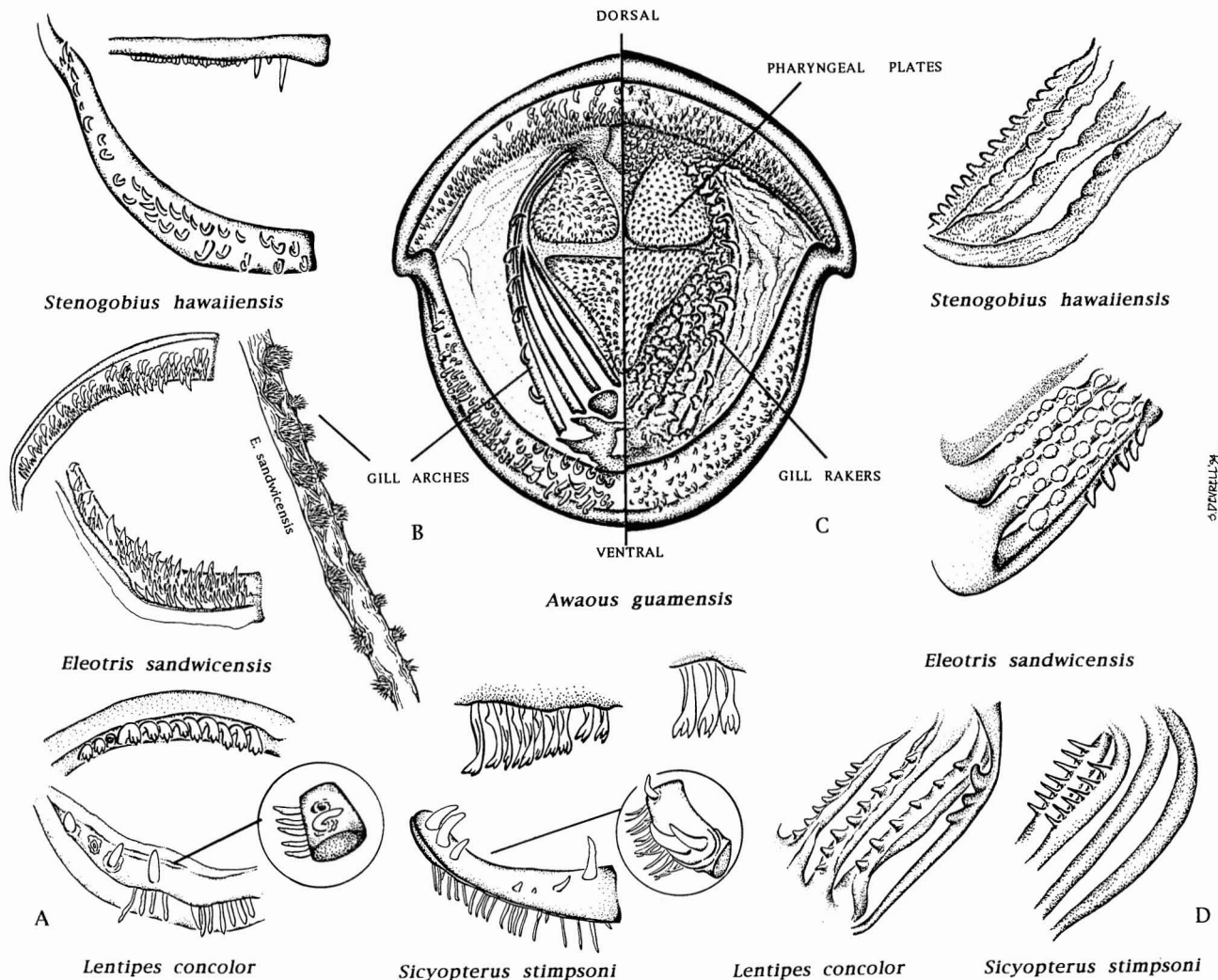


FIGURE 2. Position and morphology of internal structures in the mouth of native Hawaiian stream gobioids as viewed anterior to posterior. Comparisons of: (A) marginal teeth in upper and lower jaw; (B) bony features of jaws, gill arches, and pharyngeal plates of *A. guamensis* and middle gill arch of *E. sandwicensis*; (C) fleshy features of the feeding structures in the mouth of *A. guamensis*; and (D) fleshy gill rakers on the left side of the body in *S. hawaiiensis*, *E. sandwicensis*, *S. stimpsoni*, and *L. concolor*.

directed medially, and widely spaced (one tooth per mm^2) (Figure 2B). In *E. sandwicensis*, clumps of sharply pointed teeth (8–14 teeth per clump) were placed opposingly on either side of the arch (Figure 2B) but most dense on the two center arches. On the gill arch closest to the operculum, these toothed clumps were only present on the medial side; cartilaginous teeth lined its outer edge (Figure 2D). Flesh covered these hard structures and integrated into elaborate networks of fleshy toothlike gill rakers. The gill arch structures formed a sievelike basket in combination with fleshy pharyngeal projections. All five species possessed this food-filtering apparatus; however, it was most highly developed in *A. guamensis* (Figure 2C) and *E. sandwicensis* (in that order) and least developed in *S. stimpsoni* (Figure 2D). Cartilaginous teeth were found on the medial three gill arches in *L. concolor* (three to four teeth

per 0.1 mm^2) and the medial two arches in *S. stimpsoni* (three to four teeth per 0.1 mm^2). This cartilage supported thin, fleshy gill rakers in both species (Figure 2D). In *S. hawaiiensis*, no cartilage was found, but fleshy gill rakers lined the inner two arches and were densest on the inner gill arch (five teeth per 0.1 mm^2) (Figure 2D).

Little difference in the morphologies of the pharyngeal bones were observed between the gobioids. Two irregularly shaped pharyngeal plates in the dorsal roof of the mouth interfaced over a single triangular plate in the lower jaw, creating a viselike grinding surface in the closed position (Figure 2C). Sharply pointed, slightly curved teeth covered the surface of both upper and lower plates; however, tooth densities varied slightly between species. Teeth were most dense in the pharyngeal bones of *S. hawaiiensis* (12 teeth per 0.1 mm^2) followed by *A. guamensis* (10 teeth

TABLE 1

COMPARISON OF GUT CONTENT ANALYSIS BY PERCENTAGE DRY BIOMASS (% DW) FOR *Eleotris sandwicensis*, *Lentipes concolor*, AND *Stenogobius hawaiiensis* COLLECTED IN WAINIHA RIVER, KAUA'I

FOODS	<i>E. sandwicensis</i> % DW	<i>L. concolor</i> % DW	<i>S. hawaiiensis</i> % DW
Animal foods	56.201	6.560	0.400
Arthropoda	15.701	6.560	0.400
Branchiopoda (Cladocera)	0.000	0.000	0.400
Malacostraca (Isopoda)	0.000	1.100	0.000
Decapoda- <i>Atyoida bisulcata</i>	0.000	1.400	0.000
Chilopoda	0.876	0.000	0.000
Insecta	14.825	4.060	0.000
Diptera	0.205	1.455	0.000
Chironomidae	0.152	1.435	0.000
<i>Hemerodromia stellaris</i> Melander (Empididae)	0.053	0.020	0.000
Tricoptera	14.620	1.405	0.000
<i>Cheumatopsyche pettiti</i> (Banks) (Hydropsychidae)	13.450	1.301	0.000
<i>Hydroptila arctia</i> Ross (Hydroptilidae)	1.060	0.104	0.000
<i>Oxyethira maya</i> Denning	0.110	0.000	0.000
Hymenoptera-Formicidae	0.000	1.200	0.000
Miscellaneous animal parts	40.500	0.000	0.000
Plant foods	43.700	93.100	91.000
Chlorophyta	31.100	71.500	27.700
Cladophoraceae- <i>Cladophora</i> sp.	28.700	43.000	0.000
Ulotrichaceae- <i>Ulothrix</i> sp.	0.500	0.000	2.400
Zygnemataceae- <i>Spirogyra</i> sp.	1.900	28.500	25.300
Chrysophyta-Diatomaceae	4.400	10.700	4.500
Cyanophyta-Oscillatoriaceae	8.200	10.900	58.800
Detritus	0.000	0.300	8.600

per mm^2), *S. stimpsoni* (10 teeth per 0.1 mm^2), *L. concolor* (seven teeth per mm^2), and *E. sandwicensis* (five teeth per mm^2).

The results of gut content analysis revealed that algae composed a major portion of the diet of the three species examined; however, the gobioids differed in the types and quantities of animal foods consumed (Table 1). Algae were most abundant (by dry biomass) in the diet of *L. concolor* (93.1% dry weight [DW]) and *S. hawaiiensis* (91.0% DW). Both species ate similar quantities of the chlorophyte *Spirogyra* sp. (28.5 and 25.3% DW, respectively), but of the two, only *L. concolor* utilized the chlorophyte *Cladophora* sp. (Table 1). *Stenogobius hawaiiensis* had a substantial quantity of blue-green algae (Cyanophyta-Oscillatoriaceae) in its diet (58.8% DW) composed primarily of *Lyngbya* sp., which was not found in the gut of other species. *Eleotris sandwicensis* also consumed a large proportionate amount of algae (43.7% DW), most of which was *Cladophora* sp., but had more animal foods in its gut (56.2% DW). Remnants of fish and benthic invertebrates in the eleotrid's gut contributed 40.5% to total dry biomass, but alien caddisfly immatures (Tricoptera) were also found in substantial proportions (14.6% DW). *Lentipes concolor* was the only species found to feed on *Atyoida bisulcata* (Randall), the endemic shrimp found more commonly in the higher elevation reaches of Wainiha River. The appearance of centipedes in the gut of *E. sandwicensis* and isopods and ants in the gut of *L. concolor* (Table 1) illustrates their dietary use of drifting invertebrates as well as their opportunistic nature.

DISCUSSION

The five native Hawaiian stream fishes cannot be accurately described as morphologically similar yet certain feeding traits are shared or uniquely adapted to perform similar functions. *Awaous guamensis* and *E. sandwicensis*, for example, are similarly equipped as carnivorous feeders possessing sharply pointed bony teeth on pharyngeal plates, gill arches, and jaw margins. These traits

are most highly developed in *E. sandwicensis*, which preys on native stream fishes (unpubl. data). Elaborate fleshy gill raker systems, especially in *A. guamensis*, extend their prey range by making them efficient foragers of bottom sediments. In morphological contrast, *S. stimpsoni* and *L. concolor* were similarly adapted for scraping algae from rock substrate using tricuspid teeth that differed slightly in tooth design. Maciolek (1977) reported irregularly interspersed conical teeth in the upper jaw margin of *L. concolor*; however, none were observed in the specimens I examined. On the anterior margin of the lower jaw, both species possessed labial teeth that may assist in climbing; however, they differed in the dentition of the dorsal margin of the mandible. *Lentipes concolor* had a single row of sharp, conical teeth, giving it a rudimentary capacity to pick or bite, whereas *S. stimpsoni* had fewer teeth that may only serve to anchor and support the upper jaw as it is scraped over algae-covered substrate. In this trait, *L. concolor* was more similar to *S. hawaiiensis*, which had a double row of conical teeth in the lower jaw. The fused set of serrated upper teeth of *S. hawaiiensis* was morphologically unique among the five species, but, like the tricuspid design of *L. concolor* and *S. stimpsoni*, is likely functionally suited to scraping. In gill arch comparison, both *L. concolor* and *S. stimpsoni* were similar in having cartilaginous teeth that supported thin, fleshy gill rakers, whereas *S. hawaiiensis* lacked cartilaginous support but still possessed fleshy gill rakers. The five gobioids therefore have various abilities to sieve food particles through the gill raker system.

Based on the above morphological comparisons, three general manipulative modes of feeding are suggested: picking-biting, rock scraping, and sediment foraging. Of the five species, *S. stimpsoni* is solely restricted to rock scraping, although it has a limited ability to filter food particles. In comparison, *L. concolor* and *S. hawaiiensis* are able to scrape algae from rocks but also have improved abilities to pick-bite and filter food particles. *Awaous guamensis* and *E. sandwicensis* are both highly adapted for picking-biting and sediment foraging, but only the eleotrid is

likely morphologically capable of ingesting and killing large fish using its extensively toothed gill arch system. Bony teeth on the outer gill arches in *A. guamensis* may be a piscivorous ancestral trait. Based on these morphological comparisons, *S. stimpsoni* is predicted to be strictly herbivorous, but *L. concolor* and *S. hawaiiensis* (in that order) would likely feed substantially on algae and occasionally on invertebrates as well. *Awaous guamensis* should feed primarily on invertebrates picked off of stones or filtered through gravel, whereas *E. sandwicensis* would be expected to prey exclusively on fishes and invertebrates.

Comparisons of gut length to body length ratios, which are indicative of a fish's physical ability to digest fibrous plant or high-energy animal material, agreed with the above predictions except in the case of *A. guamensis*. The long, convoluted gut (high ratio) of *S. stimpsoni* coincided with its specialization for herbivory. Similarly, the short, straight gut (small ratio) of *E. sandwicensis* matched its specialization for carnivory. Intermediate ratios and gut convolution patterns for *L. concolor* and *S. hawaiiensis* coincided with adaptation for consuming both plant and animal foods. It is surprising that *A. guamensis* was most similar in gut convolution and gut length to body length ratios to *S. stimpsoni*, indicating adaptation for efficient use of plant foods despite its otherwise carnivorous features.

How did resource use coincide with morphology? Diet comparisons suggested that algae were an important dietary component for all species. *Sicyopterus stimpsoni*, shown to be morphologically adapted to scraping algae, is known to be nearly entirely herbivorous (94.6% of diet biomass is algae [Kido 1996]). Algae are also known to be a substantial dietary component of *Awaous guamensis* (86.2% of diet biomass [Kido et al. 1993]), which was indicated by its complex gut morphology. The goby also ingests significant quantities of swift-water insect immatures and drifting terrestrial invertebrates (12.8% of diet biomass [Kido et al. 1993]) with its picking-biting mouthparts. In aquaria, *A. guamensis* readily filters sediment

through its gill raker system in search of food (unpubl. data) and therefore likely ingested some of the smaller invertebrates found in its gut through such sediment foraging in streams. Diet data from this study showed that, as was expected, *L. concolor* fed substantially on algae (93.1% DW) but also ingested invertebrates including isopods, atyid shrimp, and drifting terrestrial insects (6.6% DW). *Stenogobius hawaiiensis*, however, used less invertebrate and more algal foods than was expected. The species apparently fed in an environment with high quantities of detritus because it was present in the gut in substantial proportions (8.6% DW); however, it is debatable that this material is used as food. Surprisingly large proportionate quantities of algae (43.7% DW) were found in the diet of *E. sandwicensis* despite its morphological predisposition for carnivory. It is not clear, however, if these algae were ingested incidentally during foraging excursions for invertebrates because the eleotrid's short gut does not indicate that it could efficiently process plant material. Diet comparisons of *E. sandwicensis*, *S. hawaiiensis*, and *L. concolor* in this study were based on very small numbers of individuals; therefore, further comprehensive dietary studies on these species are needed.

In general, functional similarities in morphological feeding traits and overlap in diet suggest that forced coexistence of the five species would result in some competition for food. *Stenogobius hawaiiensis* and *E. sandwicensis* perhaps avoid this potentially competitive existence by spatial separation from the other species and limitation in their range. The remaining three species would likely compete for algae in reaches of streams where they all co-occurred and actively coassociated, particularly if algal availability were limiting. Avoidance of this situation might explain Kinzie's (1988) habitat partitioning data. *Awaous guamensis* and *S. stimpsoni* coexist by partitioning algae so that the former has primacy over the ubiquitous green alga *Cladophora* sp. and the latter dominates diatoms and blue-green algae (Kido, unpubl. data). The high proportionate abundance of *Cladophora* sp. in the diet of *L. concolor*

determined in this study thus suggests that *S. stimpsoni* could coexist comfortably with either *A. guamensis* or *L. concolor* but not both in native stream habitat. If the diet data are accurate, *A. guamensis* and *L. concolor* would be predicted to compete for both *Cladophora* sp. as well as invertebrates and therefore should avoid association; however, a potential mitigating factor might be the abundance and availability of invertebrate foods for which the two species may show differential preference. Increasing use of nonnative aquatic insect immatures such as larval caddisflies (Kido et al. 1993) by *A. guamensis* may thus play an increasingly important role in influencing fish community structure in Hawaiian streams. These ideas require further detailed field and experimental studies for validation.

Food availability is obviously an important factor affecting fish community structure in Hawaiian streams. Elucidation of the mechanisms that govern the spatial and temporal variability of foods in the benthic landscape of Hawaiian streams is thus an essential prerequisite for understanding species interactions. I have previously suggested that this variability is largely regulated by stream flow and periodic disturbance (Kido 1996). If this is valid, then the degree to which these two regulatory factors are influenced by human-based activities may have substantial long-term consequences on the stability of native stream fish populations. Of the five native species, *S. stimpsoni* is perhaps most affected by food availability because of its morphological specialization for algal feeding. The other gobioids have greater ranges in potential prey but are limited by the low diversity of native foods and thus may still be dependent to varying degrees on algal availability. *Awaous guamensis* is perhaps best capable of compensating for variation in food availability because it can efficiently process algae, forage in sediment, and adroitly pick off both benthic aquatic insects and drifting terrestrial invertebrates.

In this article I offer several hypotheses that relate feeding morphologies to resource use and subsequently to species interactions

and fish community structure in Hawaiian streams. Further study is badly needed to test these ideas and I have made several suggestions as to our gaps in knowledge. Without these data, it is nearly impossible for resource managers to set policy aimed at protecting native stream species or for decision-makers to resolve controversies arising over the allocation of Hawai'i's finite water resources.

ACKNOWLEDGMENTS

I sincerely thank Robert Kinzie III for reviewing the manuscript. My great appreciation to Julia Devrell and Anna Asquith for their superb illustrations and also to Melissa Pacheco-Agan for her assistance in the field and laboratory.

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