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Insect Introductions and Diet Changes in an Endemic Hawaiian Amphidromous Goby, *Awaous stamineus* (Pisces: Gobiidae)[1]

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ABSTRACT: Data are presented from gut content analysis of 94 *Awaous stamineus* (Edouyx & Souleyet) (*'o'opu nākea*) collected from the Wainiha River on the north shore of the Hawaiian island of Kaua'i during the period from June 1990 to May 1991. Also presented are results from gut analysis of 11 preserved museum specimens captured in Lā'iemalo'o stream, O'ahu, in February 1938 and June 1939. The results suggest that introductions of alien insects into the Hawaiian biota are changing the diet of this endemic fish. Comparison with the results of an earlier study indicate that *A. stamineus* is still dependent primarily on freshwater algae in the genera *Cladophora*, *Rhizoclonium*, *Oedogonium*, and *Spirogyra*; however, aquatic insect foods in the diet have increased from about 6% to nearly 13% in the current study. The findings suggest a reduced reliance on native aquatic chironomids in the genera *Calospectra* and *Telmatogeton* and an increased selection of immature stages of several recent aquatic insect immigrants, most notably two alien caddisfly species, *Cheumatopsyche analis* (Banks) (Tricoptera: Hydropsychidae) and *Hydroptila arctia* Ross (Tricoptera: Hydroptilidae), first reported in Hawai'i in 1967 and 1971, respectively.

THREE ENDEMIC GOBIID species compose the major portion of the native fish fauna found in Hawaiian streams at higher elevations. These benthic gobies, or *'o'opu* as they are known in Hawai'i, are remarkably adapted for life in torrential Hawaiian streams and are characterized by fused pelvic fins that function as sucking disks. These fishes are amphidromous, spending their adult lives in running freshwater habitat but having marine larval stages. *Awaous stamineus* (Edouyx & Souleyet) or the *'o'opu nākea*, which is the focus of the present study, is known to make seasonal migrations to river areas close to the ocean where spawning takes place (Ego 1956, Kido and Heacock 1991). Larvae hatch within 24 to 28 hr after spawning (Ego 1956, Kido and Heacock 1991) and are passively swept out into the ocean where they remain as part of the marine plankton for an estimated 150–169 days (Radtke et al. 1988) before returning to fresh water.

All three endemic *'o'opu* species have been cited as requiring special protection (Deacon et al. 1979); however, currently only *Lentipes concolor* (Gill), the *o'opu alamo'o*, is listed in the National Register for Endangered Species, where it is given Category I status (Dodd et al. 1985). Critical to effective management for preservation of these unique native Hawaiian fishes is a sound understanding of their basic ecology. Central to such understanding is research directed at elucidating their food and feeding habits. As several authors have pointed out (Hynes 1950, Pillay 1952, Berg 1979), diet studies are of great importance in understanding the ecology of fishes, and analysis of gut contents is often an effective method of determining a fish's diet.

The primary purpose of this study was to quantify the contemporary main foods of the endemic *'o'opu nākea*, a subject that has not been seriously studied in many years. In 1936, entomologist F. X. Williams opened

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the guts of three unidentified gobies (likely *'o'opu nākea*) from O'ahu and reported a range of food items from *Megalagrion* nymphs to "*Lymnaea*-like" snails. Ego (1956) examined the digestive tracts of 320 *A. stamineus* from the Wainiha River on Kaua'i and concluded, based on numerical as well as volumetric counts, that filamentous green algae accounted for 84% of the total food ingested, while 16% by volume consisted of animal matter. Comparison of previous with current data on the foods of *A. stamineus*, as well as examination of museum specimens, gave interesting insight into changes occurring in the fish's diet relative to the rapid influx of immigrant species into the Hawaiian biota.

MATERIALS AND METHODS

Study Sites

The field study was conducted in the Wainiha River on the north shore of the Hawaiian island of Kaua'i. This relatively pristine river system is fed by the Alaka'i Swamp, a broad summit plateau, once part of the ancient caldera of Mount Wai'ale'ale, where rainfall can exceed 15 m annually (Stearns 1985). The river descends to the ocean from an elevation of ca. 610 m, in a distance of about 21 km. Two collection sites in the Wainiha River were used, each ca. 100 m long and located in the lower portion of the valley separated by a distance of ca. 2 km. The location designated in the study as "upper site" was a pocket pool habitat characterized by a high percentage of exposed boulders at an elevation of ca. 37 m. The "lower site," a run or glide habitat with very few exposed boulders, is found at an elevation of ca. 5 m.

Sampling Methodology

Fish were collected monthly from June 1990 to May 1991 from the two study sites using electrofishing apparatus. Fish were anesthetized in the field with MS-222 (tricaine methanesulphonate), measured for standard length, weighed to the nearest 0.1 g, and preserved in the field in 10% formalin. In the laboratory, the entire gut from esophagus to anus was removed and transferred to 70% alcohol for analysis. The preserved gut was dissected and the contents sorted, identified, and counted. Each food group was subsequently dried at 60°C for 24 hr and weighed to the nearest 0.0001 g.

Data Analysis

Over the years many methods and indices have been developed for quantifying the foods of fishes and evaluating their feeding preferences (Berg 1979). Of these methods, four stand out for their effectiveness and therefore were adopted for use in this study. First, for comparison of gut material that includes both plant and animal matter, dry weight of the food items, used to calculate "% dry weight" (% DW), was selected to provide information on the overall composition of the fish's food. Second, numerical counts of individual food items found within a food group when compared to total numbers of food items yielded a value referred to by Berg (1979) as "% N." Third, the number of times an item appeared in the total sample of fish was used to calculate an index for frequency of occurrence of food items, designated by Berg (1979) as "% F." These indices provide valuable information on the prevalence of foods selected by a fish species and give some basis for further study of food preference. Finally, a Main Food Index (MFI), which is calculated as in equation 1, was adopted from Zander (1982).

$$\text{MFI} = \sqrt{\frac{\%\,\text{N} + \%\,\text{F}}{2}}\ \%\ \text{DW} \qquad (1)$$

The MFI utilizes the three indices above but places a greater emphasis on % DW. A calculated value of 100 indicates that a food item is fed on exclusively. Zander (1982) used four categories of MFI values: >75 = primary food; 51–75 = main food; 26–50 = secondary food; <26 = insignificant food.

Analysis of variance (ANOVA) was performed on dry weights of main food groups by sample site to determine if significant differences existed in diets between fish in the two sections of stream. In addition, to evaluate differences in diet by size class of fish

within a site, ANOVA was performed on dry weights of food ingested by fish with standard lengths in the following three size classes: <76 mm, 76 to 125 mm, and >125 mm.

Museum Specimens

Digestive tracts of 11 formalin-preserved *A. stamineus* held in the ichthyology collection of the Bishop Museum were examined for their content. Collection dates for these fish ranged from January 1902 to February 1938. Intact gut tubes were removed and transferred to 70% alcohol for analysis. The gut tubes were subsequently dissected and the contents sorted, identified, and counted. Volume estimates were made using a graduated cylinder.

RESULTS

In total, 94 *A. stamineus* were collected from the two study sites. For the 70 fish collected in the lower site (37% male, 63% female), mean standard length was 103.3 mm (range, 61–157 mm); mean weight was 24.5 g (range, 3.5–64.3 g). In the upper site, 24 fish were collected (58% male, 42% female), mean standard length was 89.0 mm (range, 13–129 mm), and mean weight was 19.1 g (range, 5.2–55.0 g).

Results from analyses of total dry weight of the gut material are presented in Table 1. Three main food categories were found for *A. stamineus*. The bulk of the diet was plant material, accounting for 86.2% of total food intake as dry weight. The high % F value (88.3%) for plant material indicates that it is frequently selected as a food item. Dominating the plant food category were green algae identified as *Cladophora* spp.; however, other algae in the genera *Rhizoclonium*, *Oedogonium*, and *Spirogyra* were common. Filamentous diatoms and diatom/sediment/detritus mixtures also appeared regularly in the gut samples. Terrestrial mosses that commonly occur on the surfaces of exposed boulders within the stream were found in trace quantities.

Aquatic insects accounted for 12.8% of the gut material by dry weight. An overall % F value of 97.4% (higher than that for plant material) shows that nearly all the fish sampled consumed insect foods (Table 1). Dominating this food category were immature aquatic stages of two recently introduced species of caddisfly (Tricoptera) accounting for 9.8% of the total material by dry weight. The larger species, *Cheumatopsyche analis* (Banks) (Hydropsychidae), reaches larval lengths of >1 cm in late instars and builds pebbled web cases on the undersides of stones in swift-flowing riffle areas. *Cheumatopsyche analis* immatures contributed 6.8% to total food weight, and a % F value of 68.8% indicates that it was frequently ingested by *A. stamineus* (Table 1). The other species ingested was *Hydroptila arctia* Ross (Hydroptilidae), a case-building micro-caddisfly also found in swift-flowing riffle areas. Larvae and cases were ingested. *Hydroptila arctia* was selected nearly as often as *C. analis* (% F = 61.0%), but smaller numbers were taken (% N = 8.9%) when compared with *C. analis* (% N = 23.1%) (Table 1). Because of the

TABLE 1

TABULATED VALUES[a] CALCULATED FROM ANALYSIS OF GUT MATERIAL OF *A. stamineus*

FOOD ITEM	% N	% F	% DW	MFI
Plant matter	88.3[b]	88.3	86.2	86.7
Aquatic insects	86.0	97.4	12.8	34.3
Tricoptera	32.0	85.7	9.8	24.0
C. analis	23.1	68.8	6.8	17.6
H. arctia	8.9	61.0	3.0	10.2
Chironomidae	52.5	89.6	2.4	13.0
Calospectra sp.	51.6	88.3	++[c]	++
Telmatogeton sp.	0.9	14.3	++	++
Ephydridae	1.2	31.2	0.4	6.0
N. cilipes	0.7	15.6	++	++
E. milbrae	0.5	15.6	++	++
Gelechiidae				
Hyposmocoma sp.	0.1	2.6	0.1	0.3
Empididae				
Hemerodromia sp.	0.2	9.1	0.1	0.3
Aquatic mites	6.8	59.7	0.6	4.6
Prawn larvae	0.1	9.1	0.1	0.6
Worms	0.2	2.1	0.2	0.6
Eggs	6.9	6.5	0.1	0.9

[a] % N, numerical % of food items; % F, frequency of occurrence of food items; % DW, % dry weight of food items; MFI, Main Food Index.
[b] Estimated.
[c] ++, not weighed individually.

significantly smaller size (<4 mm) of *H. arctia* immatures, their contribution to the total weight of insect food was only 3.0%.

Native aquatic midges (Diptera: Chironomidae) dominated the insect material by number (% N = 52.5%) and appeared frequently (% F = 89.6%), but because of their microscopic size (<3.5 mm) made a smaller contribution to total food weight (% DW = 2.4%) (Table 1). Lack of taxonomic keys for immature Hawaiian chironomids prevented specific identification; the dominant genus appeared to be *Calospectra* (Chironominae). Also appearing in the gut material on occasion were larvae of the endemic torrential chironomid *Telmatogeton* spp. (Clunioninae).

Contributing in only a minor way to the diet of *A. stamineus* were immature stages of three other groups of aquatic insects. Remnants of pupae of two species of aquatic shoreflies (Diptera: Ephydridae), *Neoscatella cilipes* Wirth (endemic), and what appeared to be *Ephydra milbrae* Jones (introduced), were found regularly in the gut (% F = 31.2%). Immature ephydrids were relatively few in number (% N = 1.2%) and accounted for only 0.4% of the total gut material by dry weight (Table 1). Larvae of an unidentified introduced species of aquatic dance fly (Diptera: Empididae), likely in the genus *Hemerodromia*, occurred infrequently (% F = 9.1%) in small numbers (% N = 0.2%) and made only a minor 0.1% contribution to total weight. Also occurring infrequently (% F = 2.6%) and in minor numbers (% N = 0.1%) were cases of native semiaquatic Microlepidoptera (Gelechiidae: Cosmopteriginae) in the genus *Hyposmocoma*, adding a relatively insignificant 0.1% to total food weight.

Representing a relatively minor component of the fish's total diet (% DW = 1.0%) were diverse food items that support the view that the fish are highly opportunistic. Common in this material were tiny aquatic mites adding in only a minor way to weight (% DW = 0.6%) and number (% N = 6.8%) but occurring frequently (% F = 59.7%) (Table 1). Found infrequently (% F = 9.1%) and in minor numbers (% N = 0.1%) were larvae of freshwater crustaceans, either the endemic Hawaiian prawn *Macrobrachium grandimanus* (Randall) or the introduced Tahitian prawn, *Macrobrachium lar* (Randall). Terrestrial diet items included one earthworm and one moth caterpillar (% DW = 0.2%). Appearing intermittently in the gut material (% F = 6.5%) but sometimes in great numbers (% N = 6.9%) were what appeared to be fish eggs, accounting for only 0.1% of the total dry weight.

A Main Food Index (MFI) value of 86.7 for plant matter (primarily algae) (Table 1) signifies that it is a "primary food" of *A. stamineus* based on Zander's (1982) classifications. According to these standards, aquatic insects would be considered "secondary foods" (MFI = 34.3) and all other food items as "insignificant foods" for the species.

Based on ANOVA, fish in the lower station consumed a significantly greater quantity of plant matter ($F = 3.99$; df = 1,75; $P < 0.05$) and ate a significantly smaller quantity of aquatic insects ($F = 7.84$; df = 1,75; $P < 0.01$) than fish in the upper station based on total dry weight. No significant differences in food composition by size class were shown by ANOVA within the respective sample stations. It should be noted, however, that fish in the <76 mm and >125 mm size classes were poorly represented in the samples from both stations.

Results from analysis of preserved *A. stamineus* in the Bishop Museum collection are summarized in Table 2. For the 11 fish examined (36% male, 64% female), mean standard length was 78.4 mm (range, 11–143 mm). Five intact gut tubes with distinguishable contents were obtained from the collection. All five specimens were collected in Lā'iemalo'o stream on O'ahu on 26 February 1938 and 27 June 1939 by G. B. Mainland. For these five fish (40% male, 60% female), mean standard length was 87.2 mm (range, 60–143 mm). Based on volume estimates, plant matter accounted for 95.8% of their diet. Much of this material appeared to be filamentous algae; however diatom/sediment/detritus mixtures were common. The remainder of the gut content was insect material

TABLE 2

SUMMARY OF GUT CONTENT OF FIVE *A. stamineus*[a] IN BISHOP MUSEUM COLLECTION

FOOD GROUPS	ESTIMATED % OF TOTAL VOLUME INGESTED	% FREQUENCY (% N)
Plantae		
Algae/diatoms/detritus	95.8	NA
Arthropoda: unidentified fragments		++[b]
Insecta		
Pheidole megacephala (Formicidae)	4.0	92.8
Calospectra sp. (Chironomidae)	0.2	7.2

[a] 40% male, 60% female; mean standard length, 87.2 mm; range, 60–143 mm; collected from Lā'iemalo'o stream, O'ahu, 26 Feb. 1938 and 27 June 1939.

[b] ++, insignificant weight or volume.

(4.2%). Dominating this animal food component (% N = 92.8) was the bigheaded ant, *Pheidole megacephala* (F.). In minor numbers (% N = 7.2) were native chironomids likely in the genus *Calospectra*.

DISCUSSION AND CONCLUSIONS

Our overall results agree well with Ego's (1956) feeding study on *A. stamineus* done some 36 yr earlier in the Wainiha River. Ego (1956) provided a value for plant food material ingested of 84% by volume and described this material as "green filamentous algae." Clearly, our data indicate that algae are still the primary food of *A. stamineus*. This is shown by their dominance in the gut material by weight (86.2%), high % F (88.3%), and significant MFI value (86.7). *Cladophora* spp. appear to be the dominant algae in both feeding studies; however, our results indicate that other algal species as well as diatomaceous mixtures may also be important plant components in the diet of *A. stamineus*.

Despite the lower MFI values for animal foods, their importance in the diet of *A. stamineus* should not be overlooked. More fish, for example, had aquatic insect material in the gut (% F = 97.4) than plant material (% F = 88.3). The MFI index calculated for plant foods utilizes a subjective value for % N and should therefore be interpreted carefully, as it may overemphasize their importance. In this study % N is estimated for comparison purposes as equivalent to % F; however, it is not a truly applicable index for plant foods. Animal foods may also have a greater caloric content than plant foods and therefore may be nutritionally preferable. Cummins and Wuycheck (1971), for example, reported a caloric content of 0.64 kcal/g for aquatic invertebrates as compared with a reported value of 0.33 kcal/g for bottom algae (Mizuhara et al. 1955). The lower MFI values for animal foods may also be contributed to in part by significant reductions in food item weight of some food groups due to advanced stages of digestion (Berg 1979).

The most striking difference between our findings and those of Ego (1956) is the greater role in the diet played today by aquatic insects. Although animal foods still compose 14–16% of the total diet of the species, a recalculation of Ego's (1956) data indicates that aquatic insect foods have increased from about 6% to nearly 13% in the current study. The primary cause of this increase is the ingestion of large quantities of immature stages of swift-water aquatic insect species that are relatively new immigrants into Hawaiian streams. Conspicuously absent from the present animal gut material were endemic atyid shrimp (*Atyoida bisulcata* Randall) and *Megalagrion* nymphs, which were reported by both Ego (1956) and Williams (1935). Today these animals appear to be confined to higher elevations in Wainiha. Whether they are sig-

nificant in the diet of *A. stamineus* in these habitats is unknown.

The change in the diet of this native fish as a result of the introduction of alien insects into the Hawaiian biota is interesting from a community ecology perspective. Our data suggest a reduced reliance on native aquatic insect foods and increased consumption of introduced species. Early evidence of this is seen in the dominance of *Pheidole megacephala* in the gut of museum specimens of *A. stamineus* captured in Lā'iemalo'o stream, O'ahu, in February 1938 and June 1939. According to Reimer et al. (1990), *P. megacephala* was reportedly already well established in Hawai'i by the time the Fauna Hawaiiensis survey (Forel 1899) was conducted in the 1890s. Our gut findings suggest that this pest ant species was fairly common in riparian areas on O'ahu by 1938 and that a change in the natural diet of this endemic fish species had occurred. Ego's (1956) survey showed that about 5.5% by volume of the diet of *A. stamineus* in the Wainiha River consisted of native chironomid species, whereas our results indicate that only 2.4% by dry weight was consumed.

Alien swift-water insects were not reported by Ego (1956) but were common in the fish sampled in our study. Adult caddisflies, *Cheumatopsyche analis*, were reportedly first captured in a light trap on O'ahu in 1965 (Denning and Beardsley 1967). Microcaddisfly adults, *Hydroptila arctia*, were first identified from 'Ōpae'ula Stream on O'ahu and Honakahua Stream on Maui in 1971 (Beardsley 1971). Immature stages of two other immigrant aquatic insect species of interest that appeared in the gut were those of the dance fly *Hemerodromia* sp., which to date has not been formally reported in Hawai'i, and that of the aquatic shorefly *Ephydra milbrae*, a species that is not known to be in the Wainiha River and is more commonly associated with strongly saline or alkaline waters (Williams 1935, Hardy and Delfinado 1980). Benthic samples taken with a Surber net in comparable riffle areas in both study sites (M. H. K., unpublished data) indicate that *C. analis* composed 68%, *H. arctia* 9%, and native chironomids 19% of total numbers of organisms collected. These findings suggest that immature stages of the alien caddisflies may now dominate the swift-water habitat in the lower Wainiha River.

Some general information on the feeding biology of *A. stamineus* was provided by the study. The significant differences in diet detected by ANOVA in fish sampled in the two study sites may be a result of differences in food availability in the two habitats, coupled with the opportunistic feeding behavior of *A. stamineus*. This conclusion is supported in part by observations that indicate greater species diversity and higher numbers of aquatic insects in the upper study site (where a significantly greater quantity of insects were eaten) as compared with the lower (A. Timbol, pers. comm.). It is generally recognized that composition and availability of food are important factors influencing the feeding habits of fishes (Nikolsky 1963). No seasonal shift in food habits was detected during the study period for *A. stamineus* as was reported by Sawara (1978) for *Rhinogobius brunneus* (Temminck & Schlegel) (Gobiidae), where an abrupt change was found. No significant size-related differences in diet for *A. stamineus* were found in the study; however, small (<75 mm) and large (>125 mm) size classes may have been insufficiently sampled. Such differences have been reported for other gobies and were attributed to factors such as changing growth requirements and interspecific competition (Sawara 1978, Villiers 1980).

Our findings characterize *A. stamineus* as an omnivorous benthic feeder, dependent primarily on algae and other plants, but opportunistic in taking aquatic and occasionally terrestrial invertebrates when available. Food availability may vary according to the habitat and thereby influence diet. Introduction of alien swift-water aquatic insects into Hawaiian stream ecosystems (which were once characterized by relatively low species diversity) has had a marked influence on the feeding ecology of this native fish. The results suggest a greater role of aquatic insects in the diet of *A. stamineus* in the lower Wainiha River

today; however, there may be a reduced consumption of native species and an increased selection of alien forms.

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