Food Webs and Feeding Dynamics of Coexisting Native Hawaiian Stream Gobies[1]

MICHAEL H. KIDO

The Hawaii Stream Research Center
University of Hawaii—Center for Conservation Research and Training
7370A Kuamoo Rd., Kapaa, HI 96746, USA
email address mkido@hawaii.edu

Abstract—The food webs of *Awaous guamensis* and *Sicyopterus stimpsoni,* two native gobies that commonly coexist in mountainous reaches of Hawaiian streams, were found to be comprised of reticulate connections between a relatively depauperate, but tightly linked, group of native and alien consumers highly dependent on algae. In these webs, the two gobies foraged as omnivores, individuals utilizing a variety of prey types simultaneously. Omnivory provided an adaptive solution for native gobies to cope with spatial and temporal fluctuations in resource abundance. Heterogeneity in resource abundance mediated by variation is streamflow coupled with limitations in the diversity of prey types were suggested as important factors shaping consumer/resource interactions. Nutritional subsidies from terrestrial habitat were weakly linked in the food chains of gobies primarily via two adventive caddisfly species which utilize detritus. Energy subsidies, however, may be important to native Hawaiian gobioids in certain habitat and during periods when resource abundance is low or altered by pertubation.

Introduction

Foods available for the five native gobioid species inhabiting streams on the high Hawaiian Islands are essentially limited to algae and a depauperate community of native invertebrate consumers. Reduced numbers of species native to stream environments are typical of oceanic islands (Covich & McDowell 1996). Conspicuously few, in Hawaiian streams, are native consumers of decaying organic matter (detritivores) which dominate running water ecosystems on continents (Cummins et al. 1973). Absent, for example, are native aquatic insect species in functional roles as detritivores (Williams 1937, Hardy 1960, 1980). This niche in mountainous reaches of Hawaiian streams is apparently only occupied by a single native shrimp species, *Atyoida bisulcata* Randall, that also feeds on algae (Couret 1976). In lower elevation stream habitat and estuaries, a native prawn *Macrobrachium grandimanus* (Randall), utilizes detritus as a generalist bottom

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scavenger (Maciolek 1981). Scanty food habit data available for relatively recent invertebrate species introductions into streams, notably several caddisflies (Insecta: Tricoptera) (Merritt & Cummins 1984), a triclad flatworm (Platyhelminthes: Turbellaria) (Pennak 1991), and an Indo-Pacific prawn (Kinzie 1990), suggest a further filling of this under-utilized niche of decaying organic matter. Still, in regards to trophic components, this "external environment" (Brandon 1995) of Hawaiian stream gobioids provides a relatively simplified framework for studying food web dynamics.

Streamflow and periodic disturbance from unpredictable flood and drought may regulate spatial and temporal patchiness in the abundance and composition of algal and invertebrate foods found in the benthic landscape of Hawaiian streams (Kido, in press). Variation in streamflow, then, may be a predominant force shaping the "ecological environment" (Brandon 1995) of stream gobioids through its influence on food availability. Heterogeneity can provide protection for resources and disrupt consumer regulation (Polis & Strong 1996) as well as decidedly influence the relative "fitness" (Reilly & Wainright 1994) of interacting species in their search for food. Algal-based food chains in aquatic environments often exhibit intense "top-down" forces where consumers can substantially depress populations of resources (recipient-control) the effects of which can initiate "trophic cascades" (Hrbacek et al. 1961) to links lower in the chain (Polis & Strong 1996). Allochthonous subsides of nutrients into streams reduces such control supporting larger consumer populations without affecting resource renewal rates (donor-control) (Rosemond et al. 1993). Within such an "ecological environment", how do native gobioids select and interact over prey? Do individuals of species utilize many foods simultaneously or do they specialize on certain ones? What is the trophic spectrum (Darnell 1961) in Hawaiian stream environments and how are its components connected? What are the dynamics of consumer-resource interactions in these environments and how do they influence community structure?

To address these questions, I will attempt to explore in this article the food webs (Pimm 1982) and feeding dynamics of *Sicyopterus stimpsoni* (Gill) and *Awaous guamensis* (Valenciennes) (Fig. 1) using previously published diet data for these two native Hawaiian gobies (Gobiidae) (Kido, in press). These species commonly coexist in mountainous reaches of Hawaiian streams (Kido, unpublished data), are morphologically distinct in their adaptations for feeding (Kido 1996b), yet exhibit considerable overlap in fitness for algal use (Kido, in press). Their coexistence was facilitated by a partitioning of algal and invertebrate foods that was influenced by temporal and spatial changes occurring in the food mosaic of their benthic landscape (Kido, in press). My purposes here are to: i) compare the feeding strategies of coexisting *S. stimpsoni* and *A. guamensis* in terms of their "total niche width" (Giller 1984); ii) point out the features of their food webs; and iii) speculate on the trophic dynamics functioning at the species-level. If I am successful in achieving my purposes, I will have provided information on the "selective environment" (Brandon 1995) of native gobioid phenotypes relative to their adaptativeness for feeding in Hawaiian stream habitat. This description also provides a basis for understanding consumer-resource relations and its influence on

Awaous guamensis (Valenciennes)   *Sicyopterus stimpsoni* (Gill)
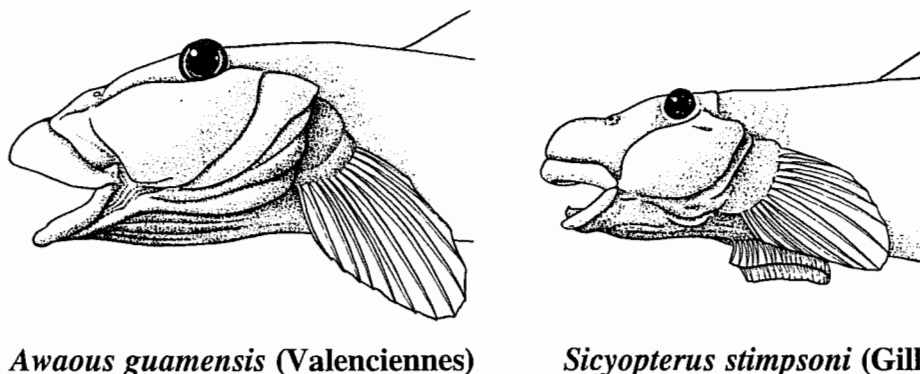
Figure 1.   Head morphologies of native Hawaiian stream gobies (Gobiidae),
Awaous guamensis and *Sicyopterus stimpsoni*.

population and community dynamics. Such understanding is central to the development of strategies for managing Hawaiian streams as "environments".

Materials and Methods

FEEDING STRATEGIES

In this paper a graphical approach, never before applied to diet data of native Hawaiian stream fishes, was used to obtain information about prey importance, feeding strategy, and niche width for *A. guamensis* and *S. stimpsoni*. This approach plots the "prey-specific abundance" (Amundsen et al. 1996) of a particular prey item against its "frequency of occurrence" (% F) (Hynes 1950). Prey-specific abundance is "the percentage a prey taxon comprises of all prey items in only those predators in which the actual prey occurs" (Amundsen et al. 1996) while the "frequency of occurrence" gives the sample proportion of individuals in the population having a particular food item in the gut (Hynes 1950). Previously published biomass data of food items in the gut of *A. guamensis* (N = 59) and *S. stimpsoni* (N = 94) collected in the Wainiha River on the Hawaiian island of Kaua'i were used in this study (Kido, in press). Frequency of occurrence data (% F) were used directly and prey-specific abundance data were recalculated from dry biomass data of food items (% DW) (Zander 1982) found in the gut. Fish were collected in two 100 m long stream reaches (37 m and 116 m elevation) from Feb 1992 to Jan 1993.

Diet data plotted in this manner provides information on several aspects of the feeding strategies of individuals of each species foraging on the stream bottom through examination of distribution points of prey items along the diagonals and axes (Amundsen et al. 1996) (Fig. 2). The diagonal from lower left to upper right provides a measure of prey importance, dominant prey being plotted at the upper right and rare or unimportant prey at the lower left. The position of prey along the vertical axis elucidates the feeding strategy of the gobies in terms of specialization or generalization. Foods which plot in the far upper right corner reflect resource
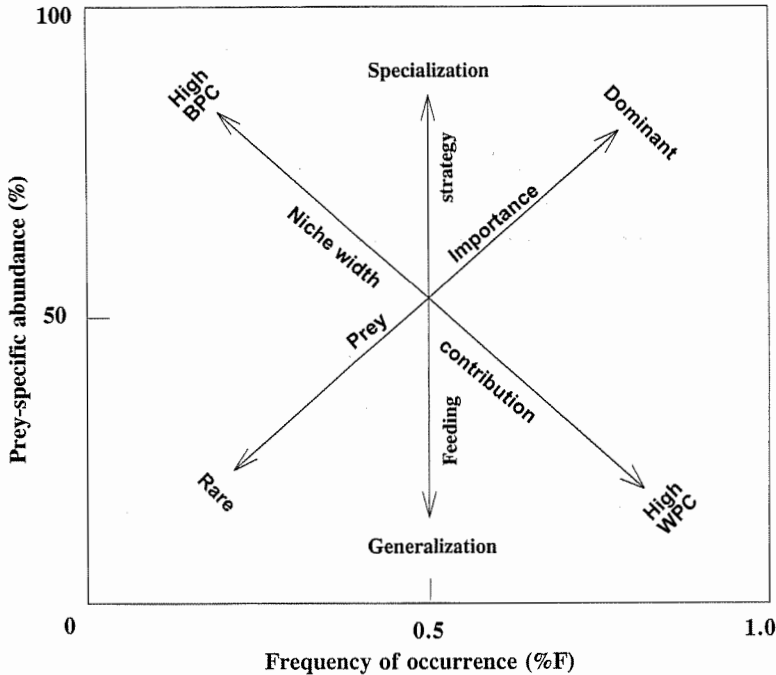
Figure 2.   Interpretation of feeding strategy, niche width contribution and prey
             importance in frequency of occurrence vs prey-specific abundance plot of
             stomach content data (Amundsen et al. 1996).

use of a predator population with a narrow niche width as all individuals in the
population have diets restricted to a small number of prey types. The niche width
contribution of a prey item is evaluated along the diagonal from upper left to lower
right. A population in which different individuals specialize on different resource
types exhibit a high "between-phenotype component" (BPC) (Giller 1984); thus
prey items in their diets have high specific abundance but low occurrence (upper
left). Individuals in this population would be specialists with little or no overlap in
resource use (Giller 1984) and food items would concentrate in the upper left cor-
ner of the diagram. Populations in which individuals utilize many resources simul-
taneously exhibit a high "within-phenotype component" (WPC) (Giller 1984) and
consists of generalists each exploiting a wide range of overlapping resources
(Giller 1984). Prey points, in this instance, would be distributed in the lower right
of the diagram.

FOOD WEBS

For the evaluation of the food webs and web dynamics of coexisting *A. gua-
mensis* and *S. stimpsoni,* I abandoned the "trophic-level ideal" (Polis & Strong
1996) of a straight, linear food chain. Instead, I adopted the more realistic view of
food webs (Pimm 1982) as consisting of species "reticulately connected via multi-

ple links of various strength to species in the autotrophic and saprophagaous chan-
nels, in the same and different habitats" (Polis & Strong 1996). In my analysis,
consumer-resource species in the benthic environment of *A. guamensis* and *S.
stimpsoni* were assembled in a food web based on the limited life history data
available for aquatic invertebrates in Hawaii. Food chain length was assessed using
Pimm's (1982) convention which places a species at a trophic level corresponding
to the most common (modal) number of prey connections. For convenience, the
strength of a nutritional link was arbitrarily determined to be weak for a particular
prey if its dietary frequency of occurrence (% F) or its mean dietary abundance
(% DW) in the population sampled was less than 1 %. A value for connectance, a
common measure of trophic complexity, was calculated by using the actual, di-
vided by the total possible number of interspecific interactions (Pimm 1982).

Results

Both *A. guamensis* and *S. stimpsoni,* to various degrees, were omnivorous
consumers feeding on both plants and animals across the trophic spectrum; how-
ever both gobies were dependent on algae for the mainstay of their food supply.
Counting pennate diatoms and the Oscillatoriaceae as single groups of algae (al-
though many species were eaten), both *A. guamensis* and *S. stimpsoni* utilized ten
groups of algae; however *Rhizoclonium* sp. and *Calothrix* sp. were not utilized by
each goby respectively (Table 1). For invertebrates (chironomids and terrestrial
arthropods each counted as one group), *A. guamensis* utilized eleven groups and *S.
stimpsoni* only seven. For most foods, prey-specific abundance values were several
times that of their corresponding % DW values (Table 1); therefore groups of indi-
viduals had similar prey in their diet. This was most pronounced in both gobies for
the algae, *Rhizoclonium* sp., Oscillatoriaceae, and the centric diatom *Hydrosera*
sp., and for the invertebrates, *Limonia* spp., *Hemerodromia stellaris* Melander, and
Cheumatopsyche pettiti (Banks) (Table 1).

In their use of algal and invertebrate prey, both *A. guamensis* and *S. stimpsoni*
were generalists as nearly all prey items were concentrated in the lower half of the
prey-abundance vs prey-occurrence diagram (Fig. 3). Both gobies therefore exhib-
ited broad niche widths feeding occasionally on an array of different prey. Use of
diatoms by *S. stimpsoni,* came closest to specialization as 97% of individuals sam-
pled had 53% of their stomachs full of free-living and epiphytic pennate species
(Fig. 3); however a broad range of other foods were also exploited concurrently
with diatoms. Considering prey importance, algae were more important prey than
invertebrates for both gobies although different algal and invertebrate species were
selected between-goby. For *A. guamensis, Cladophora* sp., diatoms, chironomids,
and caddisflies were more important prey while diatoms, *Rivularia* sp., *Cla-
dophora* sp., *Spirogyra* sp., and chironomids were more important prey to *S.
stimpsoni* (Fig. 3). The remaining prey species were concentrated in the "rare" sec-
tion (lower left) of the diagram (Fig. 3) and thus utilized only occasionally as food.
Both gobies also exhibited a high "within-phenotype" component thus most indi-
viduals utilized many resources simultaneously. Important prey for both gobies

Table 1. Dietary frequency of abundance (%F)(Hynes 1950), total dry biomass (%DW) (Zander 1982), and prey-specific abundance (Amundsen et al. 1996) for combined plant and animals found in the gut of 59 *Awaous guamensis* and 94 *Sicyopterus stimpsoni* collected in Wainiha River, Kaua'i, from June 1992 to January 1993 (diet data from Kido, in press).

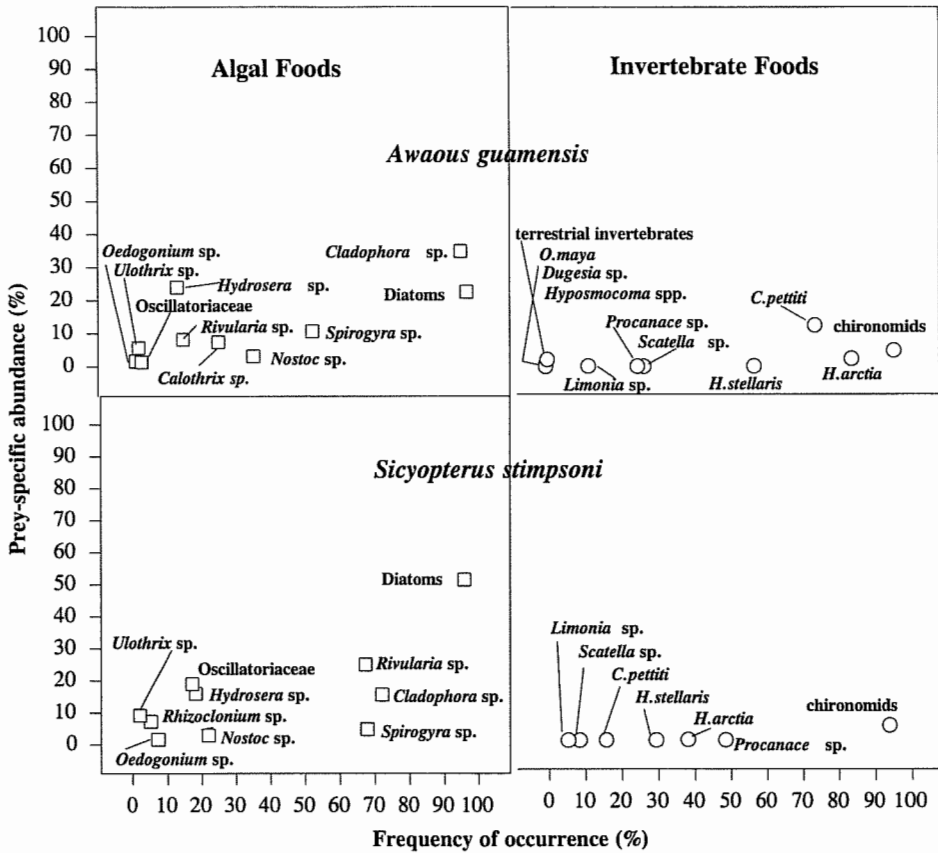|	% F		% DW		% Prey-spec. abundance	
	A. guamensis	*S. stimpsoni*	*A. guamensis*	*S. stimpsoni*	*A. guamensis*	*S. stimpsoni*
Plant food resources						
Chlorophyta (Chlorophyceae)						
Cladophora sp.	94.915	71.900	33.089	13.280	34.950	15.682
Rhizoclonium sp.	0.000	5.200	0.000	0.440	0.000	7.305
Ulothrix sp.	2.5400	7.300	2.213	0.140	5.739	1.657
Oedogonium sp.	1.700	2.100	0.015	0.170	1.669	9.214
Spirogyra sp.	52.500	67.700	9.865	3.800	10.692	4.855
Cyanophyta						
Oscillatoriaceae	3.400	18.200	0.142	3.000	1.448	15.980
Nostoc sp.	35.600	21.900	1.640	1.110	3.107	2.932
Calothrix sp.	15.254	0.000	1.932	0.000	8.255	0.000
Rivularia sp.	25.424	67.200	3.081	18.450	7.446	25.062
Chrysophyta (Diatomaceae)						
Diatoms (Pennales)	96.610	95.800	21.627	49.280	22.630	51.574
Hydrosera sp. (Centrales)	13.559	17.200	7.096	4.890	24.076	19.003
Animal food resources						
Diptera						
Chironomidae	96.610	93.800	5.360	5.120	5.033	4.807
Scatella spp. (Ephydridae)	27.119	8.300	0.040	0.010	0.123	0.072
Hemerodromia stellaris (Empididae)	57.627	29.200	0.184	0.030	0.269	0.113
Procanace spp. (Canacidae)	25.424	48.400	0.089	0.080	0.218	0.175
Limonia spp. (Tipulidae)	11.864	5.200	0.032	0.010	0.195	0.072
Tricoptera						
Cheumatopsyche pettiti (Hydropsychidae)	74.576	15.600	9.356	0.010	12.635	0.107
Hydoptila arctia (Hydroptilidae)	84.746	38.000	2.891	0.110	2.544	0.315
Oxyethira maya (Hydroptilidae)	0.068	0.000	0.026	0.000	0.125	0.000
Lepidoptera (Cosmopterigidae)						
Hyposmocoma spp.	0.136	0.000	0.087	0.000	0.678	0.000
Turbellaria (Planariidae)						
Dugesia sp.	0.068	0.000	0.517	0.000	0.141	0.000
Terrestrial arthropods	0.542	0.000	0.774	0.000	2.256	0.000

Figure 3.   Use of algal and invertebrate foods by *Awaous guamensis* and
Sicyopterus stimpsoni in terms of feeding strategies, niche width contribu-
tions, and prey importance.

were found to be concentrated in the lower right of the diagram (Fig. 3) indicating
relatively low to moderate prey-specific abundance but high occurrence.

Using modal number of connections to assess trophic level (Pimm 1982) and
counting individual algae and invertebrates as single prey, trophic level differed be-
tween goby. *Sicyopterus stimpsoni* was placed at the second trophic level and *A.
guamensis,* by virtue of greater (numerical and by-biomass) use of invertebrate
species, was placed at the third trophic level. Food chains for both gobies were pri-
marily based on energy pathways leading to algae directly or through invertebrate
species utilizing algae (Fig. 4). Both gobies were also connected to detrital channels
through consumption of adventive hydropsychid and hydroptilid caddisflies which
utilize detritus (Merritt & Cummins 1984); however, so few were consumed by *S.
stimpsoni* that this link could be described as "weak" at best. (Table 1) The same,
essentially, was true of all invertebrates except chironomids for *S. stimpsoni* and
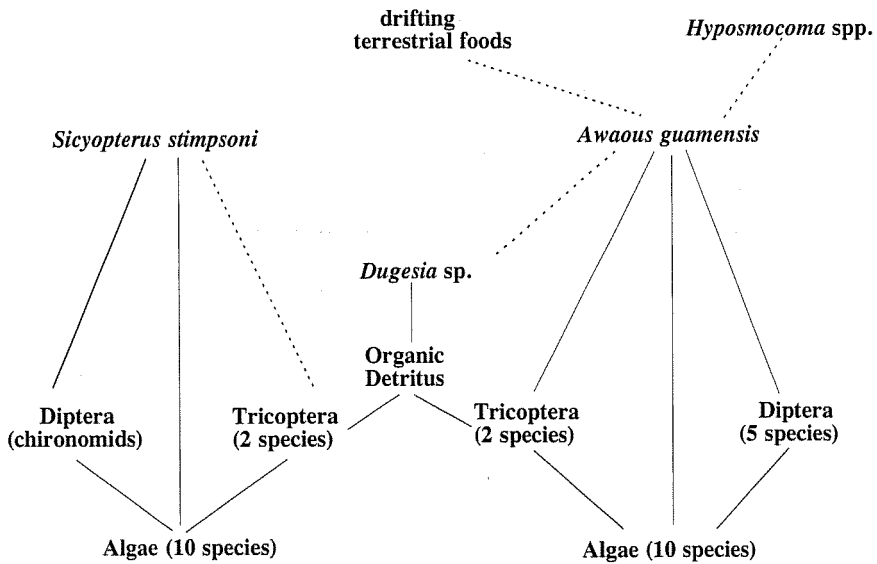*Cheumatopsyche pettiti, Hydroptila arctia* Ross, and chironomids for *A. guamensis*

Figure 4.   Simplified food webs of *Awaous guamensis* and *Sicyopterus stimpsoni*
showing consumer-resource interactions. Dotted lines indicate weak feeding
links (ie. % F or % DW values of food items in diet were less than 1 %).

(Fig. 4). *Dugesia* sp., an alien triclad flatworm which subsists on dead animal mat-
ter (Pennak 1991), provided a separate (but relatively weak) connection to the
saprophagous channel while drifting terrestrial invertebrates provided nutritional
access across "habitat boundaries" to the terrestrial environment. Only *A. guamen-
sis,* however, utilized these subsidized nutritional channels. Another weak terrestrial
link for *A. guamensis* was provided by its use of *Hyposmocoma* spp., a native case-
bearing moth species (Lepidoptera: Cosmopterigidae), which inhabits the exposed
surfaces of stream boulders and commonly fall (or crawl) into the stream.
Connectance for the food webs of *A. guamensis* and *S. stimposoni* ranged from 0.4
to 0.5 depending upon the number of interspecific interactions counted in the web.
The food webs of the two gobies therefore exhibited comparable (relatively high)
trophic complexity despite differences in trophic level and prey selection.

Discussion

Although simplified in terms of the total numbers of species, the food re-
source environments of native Hawaiian stream fishes exhibited relatively high
connectance and thus trophic complexity, particularly with the additional filling of
niches by adventive invertebrate species. The food webs of coexisting. *A. guamen-
sis* and *S. stimpsoni* were reticulate, highly connected, and primarily based on mul-
tiple links to autochthonous energy production by algae. Energy subsides from de-
trital channels were primarily via consumption of alien net-spinning caddisfly
immatures which collect suspended detritus but likely also utilize algae (Merritt &

Cummins 1984). Additional energy subsidies to *A. guamensis* were provided from the terrestrial environment via relatively large drifting invertebrates including earthworms, amphipods and an assortment of adult insect species.

The two gobies foraged in this environment as omnivores (generalists) preying frequently on both plants and animals. Algae, however, dominated their diets in terms of both frequency of occurrence and total biomass. *Awaous guamensis,* likely aided by its larger size and carnivorous feeding morphology (Kido 1996b), preyed on a wider range of invertebrates than *S. stimpsoni* which consumed primarily immature chironomids. It is still not clear whether this morphological herbivore (Kido 1996b) deliberately or passively ingests these insects which commonly build cases within algal mats (Kido, unpublished data). In terms of feeding strategy, both gobies displayed high within-phenotype components (Giller 1984) thus individuals feeding on the stream bottom utilized a variety of prey types simultaneously. Groups of individuals within-species were found to have similar prey in their diet. This may be attributed to temporal variation in the availability of resources, groups of individuals feeding in patches in close proximity, individuals depleting particular prey within-patches before moving to adjacent patches or a combination of these.

Given the manner in which the two gobies utilized resources, it seems plausible that spatial and temporal heterogeneity in prey availability played an important, perhaps controlling, role in their web dynamics. Heterogenous resource landscapes regulated by streamflow over time may be a feature of the benthic environment in Hawaiians streams and I have previously discussed this as well as its role in influencing feeding interactions between *A. guamensis* and *S. stimpsoni* (Kido, in press). Limitations in prey choices resultant from low species diversity in Hawaiian streams has also previously been discussed as a potential source of competition for food between native gobiid species (Kido, in press). The high connectance observed in the food webs of these two native gobies may be caused by the coupling of these factors so that the direct effects of consumption are spread-out by omnivory throughout the trophic spectrum (Polis & Strong 1996). Omnivory is thought to increase connectance (Strong 1992) and function as such in food web dynamics. Darnell (1967), for example, pointed out that the ability of a species to utilize alternative foods was a primary "buffering factor" which tended to stabilize population levels. Diverse trophic linkages made possible by omnivory improves the ability of native gobiid fish populations to better handle lean times or drastic changes occurring in the abundances of foods caused by perturbations such as flood events.

Detrivory apparently only played a minor role in the food webs of *A. guamensis* and *S. stimpsoni*. If adventive prey are ignored and only native species considered, no nutritional links to detritus would exist for the gobies taken from Wainiha River. This would suggest a lack of accumulating organic material in mountainous reaches of larger Hawaiian streams (like Wainiha) in their native condition. Algae have little or no lignin and cellulose (Polis & Strong 1996) making them vulnerable and nutritious to gobiid herbivores but poor producers of decaying plant material. Low rates of detrital production combined with high DOM from decaying

consumer feces and rapidly recycling nutrients may induce top-down effects that cascade in aquatic ecosystems (Polis & Strong 1996). Trophic cascades (Hrbacek et al. 1961), in fact, may be based on the susceptibility of algae to efficient grazers which themselves are susceptible to predation (Polis & Strong 1996). Based on the trophic structure and food web dynamics developed here *for A. guamensis* and *S. stimpsoni,* the potential for top-down, recipient-control of resources in Hawaiian streams is certainly present. Realistically, however, food web dynamics are likely much more complex involving both donor- as well as recipient-control as influenced by variation in consumer and resource densities over time and space. This is likely to be an important and productive area for future research.

Finally, there are likely high rates of subsidies from terrestrial environments that provide nutrient channels to stream fishes outside the stream environment. While drifting terrestrial invertebrates were found to be fed on by *A. guamensis,* they did not appear to be taken in significant quantities. Such prey do, however, provide an alternate source of food which may be of significance during lean periods, high fish population cycles, or in smaller streams where the riparian canopy is more closed. In such a closed canopy environment, for example, terrestrial insects comprised nearly 7% (by dry biomass) of the diet of *Lentipes concolor* Gill, another native Hawaiian stream goby (Kido 1996b). Allochthonous subsidies from leaf litter fall commonly subsidizes continental stream herbivores which can depress algae (Rosemond et al. 1993). Little is known about such subsidies in Hawaiian streams, although most riparian habitats are today dominated by alien species such as guava (*Psidium gujava* L.), rose apple (*Syzygium jambos* L.), and *hau* (*Hibiscus tiliaceus* L.) which seasonally deposit large quantities of organic biomass into streams (Kido, unpublished data). Such material collects and decays in massive quantities in deep estuaries of streams that have such habitat (M. Kido unpublished data) and it should not be surprising then that this is the typical habitat of the native detritivorous prawn, *Macrobrachium grandimanus*. Nearly 9% (by dry biomass) of the diet of a native estuarine goby, *Stenogobius hawaiiensis* (Cuvier & Valenciennes), was found to be detritus (Kido 1996b). Spatial subsidies then, may be of vital importance in food web dynamics for certain habitats and species. This is then another crucial area for future research.

The food webs within which native Hawaiian stream fishes feed are comprised of reticulate connections between a relatively depauperate, but tightly linked, group of native and alien consumers highly dependent on algae. Omnivory, as in other more complex food webs, seems to be an adaptive solution for coping with spatial and temporal fluctuations in resource abundance induced through equilibrium or non-equilibrium based influences. It is not understood how consumer densities in Hawaiian streams are controlled or how nutritional infusions from outside the stream environment influence food web dynamics. It is apparent, however, that the rapidly changing terrestrial landscape in Hawaiian watersheds coupled with escalating rates of alien species introductions are altering natural functioning of these ecosystems. Experimental manipulations of input from various nutritional channels to assess its effects on consumers-resources and their interactions would be an effective means of understanding these dynamics. Without

such understanding, it will be next to impossible to manage Hawaiian streams as functioning environments and stem the steady decline we are witnessing in native stream fish populations.

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