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Larval drift of amphidromous shrimp and gobies on the island of Oahu, Hawai‘i

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Abstract—As is typical of aquatic macrofauna on tropical and subtropical montane islands, Hawaii’s native stream fauna exhibit a migratory life cycle. In this life cycle, called amphidromy, newly hatched fish and shrimp larvae drift downstream to the ocean, recruit back to stream mouths as juveniles, and then migrate upstream to live as adults. On Oahu, urbanization has led to widespread habitat degradation, especially in lower stream reaches, that can potentially disrupt the amphidromous life cycle of the native stream fauna. In this study, we collected drifting larvae from 19 sites in 8 streams on the island of Oahu to examine larval presence/absence and distribution. In addition, in one watershed (Manoa-Palolo) we compared composition and abundance of drifting larvae to that of adult populations. The most frequently collected larval species were those that, as adults, are tolerant of a wider range of environmental conditions. Degraded streams produced the fewest drifting fish larvae, and the least altered stream produced the most. Abundances of larval species did not correlate with abundances of adults. As a management strategy, drift sampling may be most useful when used in conjunction with other monitoring methods, such as surveys of adult populations or monitoring returning post-larvae.

Introduction

Although diadromy is a relatively uncommon life history strategy, macrofauna inhabiting tropical continental and oceanic island streams frequently have migratory life cycles (McDowall 1988, 1996, Flecker 1992, Bell & Brown 1995, Pringle & Ramirez 1998). Fishes and crustaceans of tropical and subtropical freshwater systems are often amphidromous (Fig. 1), a type of diadromy where adult lives are spent in streams, and larval periods are spent as marine or estuar-

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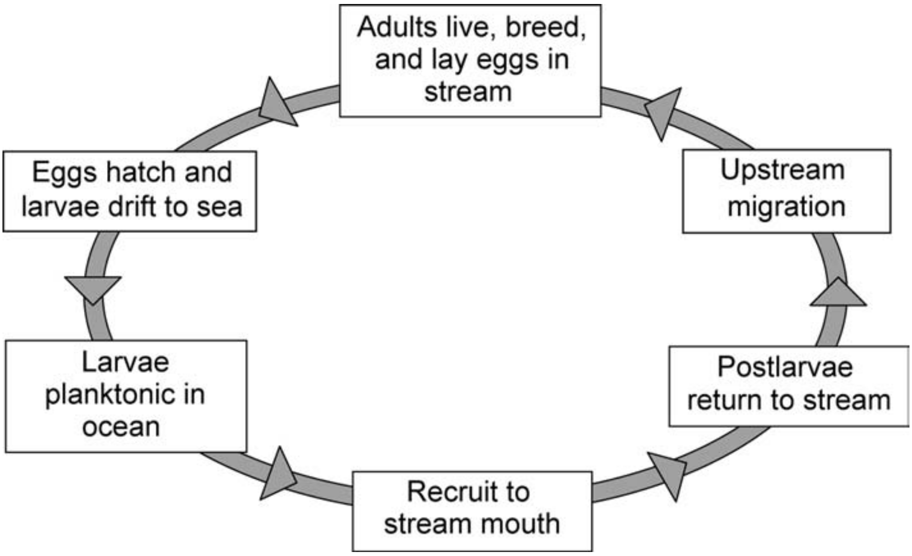

Figure 1: Stages of the amphidromous life cycle.

ine zooplankton (Ford & Kinzie 1982, Kinzie 1988, McDowall 1988, 2003). Such stream assemblages appear to be structured by the differing upstream colonization abilities (Joy & Death 2001, Benbow et al. 2002) and habitat preferences of the various species (Lyons & Schneider 1990), as well as the unpredictable recruitment by post-larvae (Kinzie 1988). A critical feature of the amphidromous life cycle is the requirement for unimpeded access to and from the ocean for downstream dispersal of larvae and upstream migration of post-larvae (Resh et al. 1992, McDowall 1995, Brasher 1996, Benstead et al. 1999, Joy & Death 2001).

Amphidromous species spawn in the stream and, with the possible exception of the goby *Awaous guamensis* (Ego 1956, Kinzie 1990, Ha & Kinzie 1996), there is little evidence that the adults in Hawaiian streams make a downstream migration to spawn. Newly hatched fish and shrimp larvae drift downstream and maintain position in the water column by alternatively swimming upward and passively sinking back down as they are carried toward the sea (Bell & Brown 1995, Lindstrom 1998). This behavior makes collecting drifting larvae a potentially viable method for assessing populations of amphidromous gobioid fishes and crustaceans (Lindstrom 1998, Pringle & Ramirez 1998).

Goby and crustacean larvae that have successfully drifted to the ocean spend from 1 to 5 months as plankton before recruiting back to fresh water (Radtke & Kinzie 1987, Radtke et al. 1988, Benstead et al. 1999). This relatively long oceanic larval stage may be due to the amount of time required to locate a freshwater settlement site as well as the developmental complexities required to complete the marine-to-freshwater transition (Bell et al. 1995, Radtke et al. 2001).

Studies on some of the Hawaiian amphidromous gobies indicate that adult populations are genetically undifferentiated throughout their range, recruitment is from a well-mixed pool of larvae, and that larvae do not return to their natal streams (Fitzsimons et al. 1990).

Macrofauna can be primary controllers in tropical stream systems exhibiting top down trophic cascades (Covich 1988, Flecker 1992, Pringle & Hamazaki 1998). Because of this, larval drift of migratory macrofauna represents an important functional linkage between upper stream reaches and the ocean (March et al. 1998, Benstead et al. 1999). Human modifications of island streams have typically been most intensive at lower elevations, which may have the greatest impact on the migrations of seaward moving larvae and returning juveniles (Maciolek 1972, Kinzie & Ford 1982, Kinzie 1990, Resh et al. 1992, Pringle 1997, Fievet et al. 2001). An understanding of the dynamics of larval drift and recruitment is thus critical for the conservation and management of tropical stream systems inhabited by amphidromous fauna. Although a few studies have addressed spatial and temporal patterns of downstream larval dispersal (Iguchi & Mizuno 1990, Lindstrom 1998, March et al. 1998), some with reference to disruption of the amphidromous cycle by hydrologic alteration (Benstead et al. 1999, Fievet et al. 2001, March et al. 2003), little information exists concerning anthropogenic impacts on larval drift of native species in relatively degraded watersheds.

Urbanization and agricultural practices have previously been shown to have deleterious effects on Oahu's streams (Brasher 2003). For example, approximately 60% of the streams on Oahu had been channelized and/or diverted by 1978 (Timbol & Maciolek 1978). The result has been fragmentation of stream habitat through degradation of instream and riparian areas. These conditions, along with a proliferation of non-native fishes and crustaceans, have led to a decline in native freshwater macrofauna on Oahu (Kinzie 1990). Of the five native amphidromous fishes *(Eleotris sandwicensis, Stenogobius hawaiiensis, Awaous guamensis, Sicyopterous stimpsoni,* and *Lentipes concolor),* only the two species most tolerant of large variations in environmental conditions, *E. sandwicensis* and *S. hawaiiensis* (Hathaway 1978), are numerous in some Oahu streams (Hawaii Stream Assessment 1990, Kinzie 1990). The native fishes least tolerant to habitat degradation (Hathaway 1978, Kinzie 1990), *L. concolor* and *S. stimpsoni,* are rarely observed on Oahu (Timbol et al. 1980, Fitzsimons et al. 1990, Higashi & Yamamoto 1993). The two native *(Macrobrachium grandimanus* and *Atyoida bisulcata)* and one introduced *(Macrobrachium lar)* amphidromous shrimp are commonly collected from Oahu's streams (Brasher et al. 2004).

In light of the increasing human population on all of the main Hawaiian islands, as well as in developing areas of the tropics globally, an effort to characterize the direct or indirect effects of habitat degradation resulting from urbanization on migratory freshwater fauna is critical for maintaining sustainable freshwater aquatic communities. The purpose of this study was to determine the composition and relative abundance of gobioid fish and crustacean larvae drifting in Oahu streams.

Methods

STUDY SITES

Sampling was conducted from May 1999 to March 2001. Larval drift was collected at 19 sites on 8 streams (n = 48): Manoa, Palolo, Maunawili, Waihee, Kaluanui, Waiahole, Opaeula, and Punaluu. These streams were chosen to encompass the range of drainage area and land use present on Oahu (Fig. 2). Downstream sites were selected as near to the mouth of the stream as possible, and upstream sites were chosen based on distance from the stream mouth and accessibility. Land use was categorized as agricultural, forest, or urban (Table 1) and was quantified within the drainage area of each stream (Klasner & Mikami 2003). The land-use category of forest includes undeveloped areas vegetated by shrubs and/or grasses.

DRIFT SAMPLING

Drift samples were collected using a 200-µm mesh net measuring 1 m in length with a 28.8-cm x 18.5-cm rectangular mouth and a 1-liter collection bottle at the cod end. Drift sampling sites were located at bridge crossings whenever possible. The net was placed in the thalweg and attached to the bridge with a length of rope that stabilized the top of the net just below the water surface. In the absence of a bridge, the net was anchored to the stream bottom and floats were attached to the top of the net. In cases of uniform channelization where no thalweg was discernable the net was placed in the middle of the stream channel.

Previous studies in Hawaii and elsewhere have shown that peak larval drift for both fishes and crustaceans begins post-sunset and continues for approximately 3–4 hours (Kuboto 1972, Couret 1976, Barnes & Shiozawa 1985, Iguchi & Mizuno 1990, Lindstrom 1998, March et al. 1998, Benstead et al. 1999). We confirmed this for Oahu with two 24-hour sampling periods at Punaluu Stream. Consequently, nets were placed in the stream at sunset (as reported by the U.S.

Table 1. Characteristics of the streams selected for sampling. Drainage area, land cover, and stream length modified from Klasner and Mikami (2003). Discharge data were obtained from U.S. Geological Survey streamflow-gaging station records.

	Percent land cover					
Stream	Urban	Agricultural	Forest	Drainage area (km^2)	Total stream length (km) above lowest sampling site	Average annual discharge (m^3/s) 1999–2000
Manoa-Palolo	38	3	59	26.51	33.18	0.38[a]
Maunawili	26	3	71	29.69	45.1	n/a
Waihee	10	6	84	4.34	5.97	0.13
Kaluanui	0	0	100	9.16	14.17	0.09
Waiahole	0	0	100	10.01	9.82	1.35[b]
Opaeula	0	20	80	15.98	44.41	0.28
Punaluu	0	0	100	15.65	36.47	0.22

[a] Average of values for the year 2000 only.

[b] Average of values from October 2001 to October 2002.

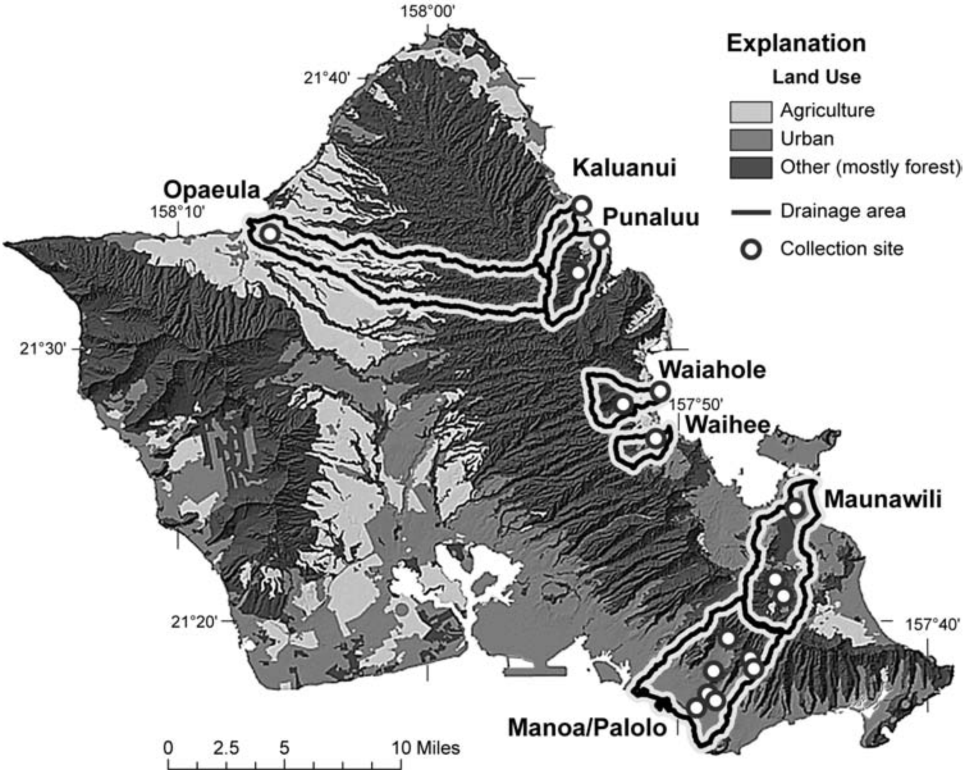

Figure 2: Land use, drainage-basin boundaries, and sampling sites on the island of Oahu, Hawaii. Base map modified from Klasner & Mikami (2003).

Naval Observatory, http://aa.usno.navy.mil/data/) and a continuous sample was collected for a period of 3 hours. During elevated discharges and in streams carrying large amounts of suspended material, the net was periodically cleaned to prevent backwelling. Water velocity was measured at the mouth of the net at least once for each site sampled.

At the end of the sampling period, nets were removed from the stream, the contents were rinsed into a collection bottle and then poured into a 1-liter glass jar. Samples were preserved in 10% formalin for later sorting. Some samples were stained with alizarin-S red to help discern larvae from other materials contained in the sample. Fish larvae were counted and identified to species under a dissection microscope by using a key developed by Lindstrom (1999). Crustacean larvae were identified to the genus level for *Macrobrachium* and to the species level for *A. bisulcata.*

Larval density (larvae per m^3) was estimated by using measured water velocity at the sampling net and discharge data obtained from U. S. Geological Survey streamflow-gaging stations. Mean larval density per stream was calculated using all samples collected from that stream.

SAMPLE SITE DISTANCE FROM STREAM MOUTH

To examine larval drift along a longitudinal gradient, drift samples from five watersheds were collected from sites close to the stream mouth as well as from sites farther upstream. Punaluu, Waihee and Waiahole Streams each had one site near the mouth and one upstream site. Manoa and Palolo Streams shared one site near the mouth, and both had two upstream sites above the convergence. Samples from all sites along a stream were collected at the same time of day (during 3 hours following sunset). Data from all sample sites were analyzed for species composition and included in calculations of relative species abundance and total larval abundance per stream.

SIMULTANEOUS SAMPLES AMONG STREAMS

A subset of drift samples were collected from either two or three streams simultaneously on six occasions. This subset of samples, which was collected from the sites nearest to the stream mouth, was examined for temporal larval drift patterns among streams. Samples were collected on 27 Sept. and 11 Oct. 1999 from Punaluu, Waiahole, and Manoa streams, on 25 Oct. 1999 from Manoa and Opaeula streams, on 12 April 2000 from Punaluu and Waihee streams, on 17 April 2000 from Manoa and Waiahole streams, and on 12 Dec. 1999 from Punaluu and Kaluanui streams.

ADULT FISH AND CRUSTACEAN SAMPLING

Adults were collected from four sites in Manoa Stream and one site in Palolo Stream (Manoa-Palolo watershed) to compare the composition and species abundance of the larval drift to that of adult fish and crustaceans. A Smith-Root Model 12 electrofisher was used for one-pass collections in three reaches (100–200 m long) of Manoa Stream at 350, 1,000, and 4,500 m upstream of the drift sampling site closest to the stream mouth and one reach (100 m long) of Palolo Stream at 4,500 m. Adult gobioid fish and crustaceans were identified, counted, and released. An additional snorkeling survey was conducted in upper Manoa Stream at 5,050 m upstream of the drift sampling site. In the snorkeling survey, adult fishes and crustaceans were identified and counted during a standard amount of time (3 minutes) as they entered randomly placed 0.25 m^2 quadrats along a 100 m reach. Data from adult samples were combined for analysis of species composition and abundance. These data were compared, using Pearson's correlation test, to larval species composition and abundance calculated from drift samples collected at the site below the convergence of Manoa and Palolo Streams ($n = 5$).

Results

DRIFT SAMPLES

Amphidromous larvae were collected in 65% of the drift samples from the eight streams sampled. Of these samples, 60% had crustacean larvae (>99% were *Macrobrachium)* and 29% had gobioid fish larvae (Fig. 3). Fish larvae were col-

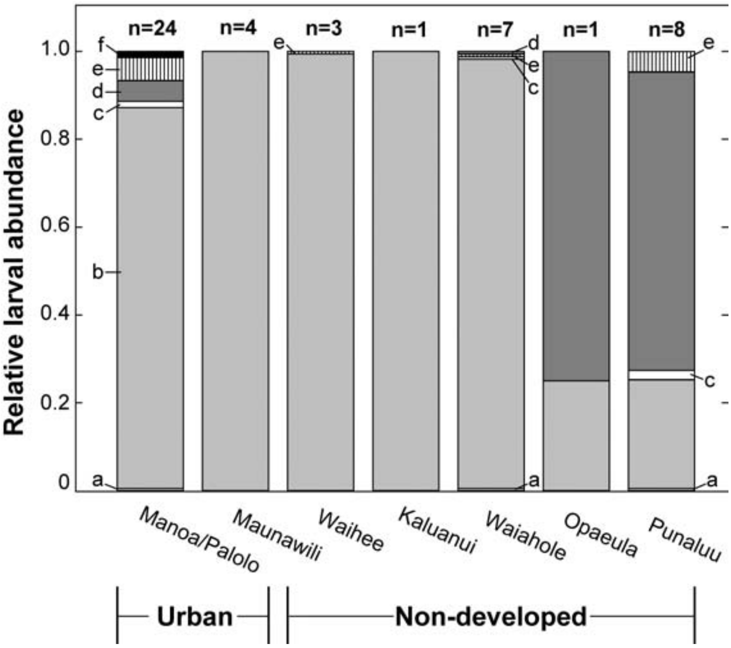

Figure 3: Relative abundance of larval (a) *Atyoida bisulcata,* (b) *Macrobrachium* sp., (c) *Awaous guamensis,* (d) *Eleotris sandwicensis,* (e) *Stenogobius hawaiiensis,* and (f) *Sicyopterous stimpsoni,* by site. Sites are arranged along the x-axis in order of decreasing urban land use. Total abundances of larval fish and crustaceans per stream are presented in Table 2.

lected most often from streams in the least altered watershed (Punaluu). No fish larvae were collected from Maunawili or Kaluanui Streams.

The majority of fish larvae collected were *E. sandwicensis* (88%), followed by *S. hawaiiensis* (8%), *A. guamensis* (3%) and *S. stimpsoni* (1%). *S. stimpsoni* larvae occurred in three samples from Manoa Stream. No *L. concolor* were collected during larval drift sampling. Three species of larvae *(E. sandwicensis, S. hawaiiensis,* and *A. guamensis)* were collected at most of the sampling sites where gobioid fish larvae were collected. However, at Opaeula Stream the only larvae collected were *E. sandwicensis* and at Waihee Stream only larval *S. hawaiiensis* was collected. No amphidromous larvae were collected from the sites farthest upstream in Manoa and Palolo Streams despite multiple sampling efforts. Larvae from the site nearest to the stream mouth in the Manoa-Palolo watershed accounted for >90% of the total larvae collected in that watershed.

Samples from Maunawili, Palolo, and the uppermost sites on Waiahole and Punaluu Streams contained only crustacean larvae. The majority of the larval crustaceans collected were *Macrobrachium* sp. Only eight individual atyid shrimp larvae were collected in three different samples during the study period, and seven of the eight individuals came from upstream sites on Punaluu and Waiahole Streams. More than half (55%) of the crustacean larvae collected were from Waiahole Stream; Manoa accounted for about one quarter (27%).

Table 2. Total abundances and percent of the estimated density of all larvae collected during the study by stream, and total estimated densities by site. Numbers in parentheses indicate the number of samples collected at a site.

	Total larvae collected from all sampling events						
Stream	Number of fish larvae	Number of crustacean larvae	Percent of mean larvae per m^3	Downstream sites mean larvae per m^3	(n)	Upstream sites mean larvae per m^3	(n)
Manoa-Palolo	27	180	25.3	14547	(5)	849	(14)
Palolo	4	0	<0.1	46	(3)	0	(2)
Maunawili	0	6	0.1	311	(1)	0	(3)
Waihee	1	432	7.9	25887	(1)	325	(2)
Kaluanui	0	6	0.1	311	(1)	n/a	(0)
Waiahole	10	1329	46.1	25801	(6)	437	(1)
Opaeula	18	6	<0.1	28	(1)	n/a	(0)
Punaluu	935	315	20.4	9736	(7)	575	(1)

The estimated density of larvae was highly variable among streams (Table 2). Small sample size possibly contributed to low density estimates in Opaeula and Kaluanui Streams. In all streams, the number of larvae collected was highly variable among sampling dates. The number of larvae collected in a single sample ranged from 0 to >50% of the total number of larvae collected for that stream during the study period.

SIMULTANEOUS SAMPLES

In general, when drifting larvae were collected at one site on a given night, they were collected at all sites sampled, and when few larvae were collected at one site on a given night, few larvae were collected from other sites sampled simultaneously. With the exception of Manoa and Waihee Streams, the density of larvae collected in the drift samples was similar among sites and sampling dates (Table 3) in streams sampled simultaneously. Samples from Manoa Stream (27 Sept. 1999, 17 April 2000) and Waihee Stream (12 April 2000) contained fewer larvae than those from simultaneously sampled streams (Table 3).

Table 3. Estimated density of larvae collected from streams sampled simultaneously on six separate dates. No data shown means the site was not sampled on that date.

	Number of larvae per m^3					
Stream	27 Sept. 1999	11 Oct. 1999	25 Oct. 1999	12 April 2000	17 April 2000	12 Dec. 2000
Manoa-Palolo	97	17,676	746		1,849	
Waihee				89		
Kaluanui						311
Waiahole	90,044	29,178			19,953	
Opaeula			28			
Punaluu	27,656	14,794		2,673		380

ADULT SURVEYS

The majority of adult gobies and shrimp were collected from the sampling site at the lowest altitude (350 m upstream of the mouth) in Manoa Stream, and no adult native fish were observed in either of the upper sites on Manoa (4,500 and 5,050 m upstream) or Palolo streams (4,500 m upstream). The total abundance of larval species collected in drift samples from the lowest site in the Manoa-Palolo watershed showed no correlation ($r^2 = -0.18$, $p = 0.74$) with the total abundance of adult species recorded in the surveys of Manoa and Palolo Streams (Fig. 4, presented in relative abundance). No larvae or adult fish were collected from the uppermost sampling sites. Adult *S. hawaiiensis* and *E. sandwicensis* at the lower sites were collected in greater numbers than were the larvae of those species. Few larval or adult *A. guamensis* were observed. Although *Macrobrachium* were the most numerous larvae in the Manoa-Palolo drift, few adults were collected. In addition, several separate collections of *S. stimpsoni* larvae indicated the presence of reproducing adults; however, *S. stimpsoni* were not collected or observed during the adult surveys and are considered uncommon on the island of Oahu (Hawaii Stream Assessment 1990).

Discussion

For many decades, land use associated with habitat alteration has been considered a primary factor contributing to the decline of native fish populations in stream ecosystems (Schlosser 1991, Wang et al. 1997). Land-use change, accompanied by habitat alteration and non-native species introductions, has resulted in an increased homogenization of once unique biogeographic regions (Scott &

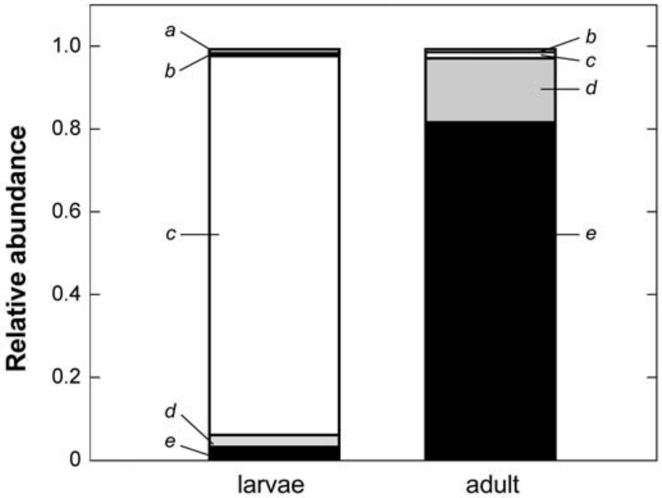

Figure 4: Relative abundance of larvae and adults of the five amphidromous species (a) *Sicyopterous stimpsoni,* (b) *Awaous guamensis* (c) *Macrobrachium* sp., (d) *Stenogobius hawaiiensis,* and (e) *Eleotris sandwicensis,* collected in the Manoa-Palolo drainage basin.

Helfman 2001). Habitat alterations associated with urbanization have resulted in lower habitat heterogeneity and increased abiotic variability, creating an environment more suitable to tolerant non-native species (Schlosser 1991, Scott & Helfman 2001, Brasher 2003). These associations have been well documented on the island of Oahu (Timbol & Maciolek 1978, Brasher et al. 2004), where native goby populations are in decline and introduced poeciliids, as well as other non-native fishes, are abundant.

One interesting result of this study in the relatively degraded (urbanized) Oahu watersheds was the scarcity of larvae compared to densities documented in less developed watersheds in Puerto Rico (March et al. 1998), Costa Rica (Pringle & Ramirez 1998), Shikoku Island, Japan (Iguchi & Mizuno 1990), and the Wainiha River on Kauai, Hawaii (Lindstrom 1998). Individual samples on Oahu contained, at most, hundreds of larvae; samples from Kauai and Costa Rica contained thousands of larvae. Tens of thousands of larvae were reported in samples from Puerto Rico. The lack of drifting fish larvae in Oahu streams was not particularly surprising as adult populations of native gobies are limited on Oahu (Timbol & Maciolek 1978). The amphidromous life cycle of the native fishes and crustaceans makes them particularly vulnerable to localized habitat alterations that may prevent downstream dispersal of larvae or upstream migration of post-larvae and can also influence the distribution of these species throughout the drainage basin (Kinzie & Ford 1982, Kinzie 1988, Resh et al. 1992, Pringle 1997, McDowall 1995, Benstead et al. 1999, Fievet et al. 2001).

The scarcity of potential spawners (and hence drifting larvae) combined with high uncertainty as to the temporal pattern of spawning and drift events (March et al. 1998, Lindstrom 1998) made sampling particularly difficult and could have contributed to the variability in larval density and composition observed among streams during this study. Some studies have indicated a seasonal (Ego 1956, Resh et al. 1990, 1992, Ha & Kinzie 1996, McDowall 1995) or lunar (Erdman 1986) periodicity for tropical insular freshwater gobies and crustaceans. Many species appear to have multiple periods of reproduction throughout the year (Manacop 1953, Couret 1976, Kinzie & Ford 1982, Kinzie 1990, 1993, Bell & Brown 1995, Lindstrom 1998). In certain locations, some species appear to spawn seasonally while others reproduce throughout the year (Resh et al. 1992). Because we were unable to predict when spawning events would occur, it is possible that we did not sample during drift events. This likely occurred at Opaeula, Kaluanui, and Maunawili Streams, which were sampled during a period when few larvae were collected in drift samples from simultaneously sampled streams.

One additional factor possibly affecting larval densities was a prolonged drought that spanned the sampling period. Stream discharge for 1999 and 2000 was about half of the mean annual discharge for the past 30–50 years (calculated from U.S. Geological Survey streamflow-gaging station records). Lindstrom (1998) hypothesized that constraints on adult gobies during periods of low stream productivity may limit their reproductive output. Drought may also exacerbate the effects of human caused habitat alterations such as water diversions.

The comparison among adult population surveys and larval drift samples from Manoa Stream indicates that drift sampling, although potentially useful in indicating the overall reproductive output of a stream, may not accurately predict the abundance of adult shrimp and gobies. Very few larvae of the native atyid shrimp *(A. bisulcata)* were collected in drift samples, although adults were abundant in several of the streams sampled (Brasher et al. 2004).

The results do indicate that drift sampling can be used to examine the faunal composition of streams if sampling is repeated in the stream over time, especially when conducted in conjunction with surveys of adult populations. Similar to the findings of Pringle and Ramirez (1998), drift sampling provided information on the presence of a species *(S. stimpsoni)* in Manoa Stream that was not observed during adult surveys.

Because larval drift is a function of the adult assemblages in streams, and adult assemblages are associated with environmental conditions in the streams (Brasher 2003), land use (particularly urban) can ultimately be expected to impact larval drift. Habitat conditions such as water temperature, water quality, substrate type, depth, velocity, and extent of riparian vegetation have been shown to be affected by urbanization (Pringle 1997, Wang et al. 1997, Brasher et al. 2004). Because amphidromous species in Hawaii do not necessarily return to the stream where they were born (Fitzsimons et al. 1990), habitat modification in one stream could potentially determine recruitment (and subsequent reproduction) in a different stream.

Of the study streams, Punaluu Stream had the least urbanized watershed and is relatively unmodified in its upper reaches, although the lower reaches are fairly degraded. Streams that are highly urbanized throughout the watershed, such as Manoa Stream, tend to be channelized with little riparian vegetation, higher water temperature, and reduced boulder habitat (Brasher et al. 2004), all of which likely impact adult populations. The relatively unmodified habitat available in upper Punaluu Stream is more likely to sustain larger adult populations of native macrofauna. This may explain the greater abundances of drifting fish larvae collected there, despite degraded conditions in the lower reaches.

Some factors associated with habitat alteration on Oahu are decreased habitat heterogeneity and increased water temperatures in channelized areas, and dewatered stream segments (Brasher et al. 2004). Streams on Oahu nonetheless support large populations of non-native fish and crustaceans that tend to be better adapted for these type of habitats. Successful recruitment to and migration up streams is required for the completion of an amphidromous life cycle of the native species. Streams with high percentages of urban land use and greater degrees of alteration in the lower stream reaches are less likely to support substantial adult populations of native species (Brown 2000, Fitzpatrick et al. 2004), and therefore likely contain fewer adult native fishes and fewer drifting larvae.

The direct association between habitat alteration and larval densities will require additional investigation because this study focused specifically on species presence/absence in larval drift from a range of land-use types and watershed sizes on the island of Oahu, and because of the high variability in drift events. Additional studies may shed light on both timing of drift and variability in life history strategies among amphidromous species. However, drift sampling was shown to provide information on the presence of an uncommon taxa missed during adult surveys. To most effectively document the status of native amphidromous fauna in Hawaii's streams and in tropical streams throughout the world, in conjunction with other more traditional sampling methods (such as surveys of adult populations) and/or monitoring of postlarval recruitment back into the streams, drift sampling can be a valuable monitoring technique.

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