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The Role of Behavioral Interactions of Immature Hawaiian Stream Fishes (Pisces: Gobiodei) in Population Dispersal and Distribution[1]

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Abstract—Behavioral and morphological observations on native Hawaiian freshwater fishes (Gobiodei), *Eleotris sandwicensis, Stenogobius hawaiiensis, Awaous guamensis, Lentipes concolor,* and *Sicyopterus stimpsoni* show the following diel recruitment patterns: *L. concolor* invaded streams mainly during the day with the wave surge; *S. stimpsoni* entered mostly during the day regardless of tidal conditions; *A. guamensis* were transported onshore day or night; *S. hawaiiensis* and *E. sandwicensis* entered streams by passive transport, the former by day, the latter at night.

E. sandwicensis and *S. hawaiiensis* larvae mature in the lower stream reaches while *L. concolor, S. stimpsoni,* and *A. guamensis* usually move to upstream habitats. For these latter three fishes, ontogenetic changes in behavior, including predator avoidance during recruitment and aggressive interactions between immature fishes farther upstream, act in sequence to produce the instream distribution typical of adults.

Schooling occurred in the estuary in *S. stimpsoni* and *A. guamensis* postlarvae; singles and pairs also migrated into streams. Postlarvae remained in schools through the estuary where they were vulnerable to predation by adult *E. sandwicensis* and *Kuhlia sandvicensis.* After climbing a waterfall that excluded most aquatic predators, *A. guamensis* and *S. stimpsoni* developed coloration displayed during aggressive contests. Immature *S. stimpsoni* that failed to develop bright colors lost agonistic encounters and usually fled upstream. Aggressive displays by postlarval *A. guamensis* usually displaced intruders. *L. concolor* moved quickly upstream; they did not school but exhibited agonistic behavior toward conspecifics which promoted upstream dispersal.

Introduction

Trade winds blowing across the eastern Pacific Ocean create orographic rain on the windward face of the Hawaiian volcanic high islands. Clear cold-water mountain streams that run over waterfalls and down steep-sided valleys back to the ocean are inhabited by adults and juveniles of four true gobies, *Awaous guamensis* (*'o'opu nākea*), *Sicyopterus stimpsoni* (*'o'opu nōpili*), *Lentipes concolor* (*'o'opu alamo'o*) and *Stenogobius hawaiiensis* (*'o'opu naniha*) and one eleotrid, *Eleotris*

[1]ASIH symposium on freshwater gobies

sandwicensis (*'o'opu 'akupa*). These five fishes account for the entire native freshwater fish fauna of Hawai'i. Adults show a species-typical linear distribution in Hawaiian streams; *S. hawaiiensis* and *E. sandwicensis* occupy the lower reaches below the first major waterfall, populations of *S. stimpsoni* and *A. guamensis* are greatest in the middle section of streams, and *L. concolor* is most common in the higher elevations (Fitzsimons & Nishimoto 1991, Nishimoto & Kuamo'o unpubl).

All five species are amphidromous: adults lay eggs in fresh water, and they hatch within 1–2 days (Ego 1956). Yolk-sac larvae are carried downstream in the drift into the ocean plankton where they develop for 90 to 169 days (Radtke et al. 1988, Radtke et al. 1996). Recruitment of postlarvae, called *hinana* in Hawai'i, into stream mouths occurs year round for all species, but it is most intense during the spring (Tate 1995, Nishimoto & Kuamo'o 1997). When they return to the stream mouths, postlarvae are transparent or only slightly pigmented, and they range in length from 10 to 25 mm SL depending on the species. Shortly after entering fresh water, pigmentation intensifies, and color patterns develop.

The purpose of this study of postlarval and juvenile behavior was to determine periodicity, orientation, and movement of young freshwater gobies as they entered stream mouths and then moved within the stream. Observations of the morphology and behavior of postlarvae and juveniles of the three upstream species, *L. concolor, S. stimpsoni,* and *A. guamensis* indicate that it is the immature fishes that are primarily responsible for upstream migration and the species-typical instream population distribution. Young *S. hawaiiensis* and *E. sandwicensis* remained in the lower parts of the stream below the first major waterfall.

Methods

STUDY SITES

Streams on Hawai'i and Kaua'i were study sites for the behavioral work, and specimens of fishes from these islands, as well as from Maui and O'ahu were included in morphological study (Table 1). On Kaua'i, most behavioral work was in the Wainiha River and in Hanakapi'ai Stream. Both flow through the Halele'a Forest Reserve. Wainiha arises in the wettest place on earth on the slopes and highlands of the extinct volcano, Wai'ale'ale, and along the northeastern face of the Wainiha Pali, a high tableland whose escarpment represents the eroded lip of an ancient caldera. The main river is joined by over 12 tributaries as it flows northward for two-thirds of its length then northeastward for the remainder of its 20 km run to the ocean. The estuary is over 400 m long and almost 80 m at the widest part; the stream mouth is about 20 m wide. Hanakapi'ai is a Na Pali Coast stream arising on the northeastern edge of Pu'u O Kila, a mountainous area of sheer cliffs, or pali, along the northern section of the old caldera. A single, small tributary joins the main stream along a brief six-km flow from the base of the cliffs to its terminus. Like many streams on the Na Pali Coast, this narrow stream has no estuary, but ends abruptly at the surf on a sand-and-boulder beach.

Table 1. Streams from which Hawaiian freshwater fishes were examined for mophological characteristics and behavior.

Island	Stream	Morphological data	Behavioral data
Hawai'i	Hakalau	x	x
	Honoli'i	x	x
	Kolekole	x	
	Wailoa	x	x
Maui	Hahalawe	x	x
	Iao	x	x
	Maliko	x	x
	Palikea	x	
	Piinaau	x	
Kaua'i	Awa'awapuhi	x	x
	Hanakapi'ai	x	x
	Hanapepe	x	x
	Manoa	x	
	Nu'alolo	x	x
	Wainiha	x	x
	Waimea		x
O'ahu	Moanalua	x	x

Hakalau and Honoli'i were the primary study streams for fish behavior on Hawai'i. Both arise on the northeastern flank of Mauna Kea, a dormant volcano, at about 2700 m elevation, then flow eastward for approximately 30 km through tropical rainforest and agricultural land to empty into the ocean on the Hamakua Coast. At the stream mouth, Hakalau is about 25 m wide and forms an estuary that is approximately 150 m long. Honoli'i is joined by two unnamed tributaries giving it a greater drainage area; it is about 50 m wide at the mouth, and the estuary is over 300 m long.

On Hawai'i, most behavioral work was in Hakalau Stream. Distance and time limited collecting field data, so an intensive study was undertaken of a single stream to serve as a model with which subsequent studies could be compared. Three features make Hakalau Stream a natural laboratory for studying behavior of young stream fishes. First, a clearly defined, relatively short estuary provides an easily accessible site for work at the stream-ocean interface, as well as in the lower stream reaches. Second, a concrete low-water bridge about 200 m upstream from the rubble, pebble, and sand beach forms a waterfall across the stream that establishes a barrier restricting upstream movements of aquatic predators of immature stream fishes. The low-predator environment for upstream migrants offers opportunities for studies of behavioral changes attributable to changes in predation pressure. Finally, although much of Hakalau Stream lies in a deep steep-sided gorge, an all-weather road crosses the stream four km from the mouth and provides relatively easy access to the upstream section.

SAMPLING METHODS

Fishes examined in the morphological study were collected in a postlarval fish trap, by hook-and-line, seine, and hand net and preserved in 5% buffered formalin or in 70% buffered isopropyl alcohol. A trap modified from a "counting weir" described by Kim Bell (unpubl.) and another devised by Darrell Kuamo'o (Nishimoto & Kuamo'o 1996) were used to collect immature fishes. Postlarvae were captured at the stream-ocean interface in water depths ranging from nearly 0 m at the stream margin to 1.5 m near midstream. Collecting difficulty increased with stream depth, and it was impractical to collect fishes in water over 1.5 m deep. Smaller specimens were identified in the field often with the aid of a 10× hand lens or in the laboratory with a stereoscopic microscope; standard length was measured either from live, freshly-killed or preserved specimens.

Data on seasonality and diel periodicity of recruitment into streams by freshwater fish postlarvae were obtained by trapping at the stream mouth for a 12-hr to 24-hr period each month throughout the year from February 1993 to July 1994. The trap, designed to intercept young fishes migrating into the stream mouth, spanned 2 m of the stream width and faced the wave and tide surge. Catches were removed hourly, or more often during times of heavy recruitment.

Underwater observations were made at the mouths of Hakalau and Honoli'i streams and in Wainiha River to learn if young fishes swam into fresh water or were carried onshore by wave and tide surges or both. Variations in topography, substrate, and stream-bottom configuration as well as rate and volume of stream flow contribute to turbulence at a river mouth. Friction from water flowing along the uneven substrate in shallow areas sometimes creates reduced flow and eddies that can form countercurrents near the stream edge. As the stream becomes deeper, usually toward the middle, the current becomes stronger. The direction and relative speed of microcurrents were tracked with dye squirted into the microhabitat from a nalgene wash bottle. Because of the energetic advantage of swimming in an area of reduced current, it was expected that postlarvae bound upstream would be found in the countercurrent zone. To determine which part of the stream incoming fishes frequent when swimming into the mouth, the number and species of postlarvae moving through a transect line passing through three zones—countercurrent zone, shallow-water zone, and deep-water zone—was recorded. Fishes were identified and counted at consecutive 10-minute intervals for each zone during each observation.

Postlarvae migrate into the estuary and often continue upstream in both single-species and mixed-species schools. Information on size and composition of fish schools was recorded both from underwater and at streamside. Polarized sunglasses and binoculars reduced glare and improved visibility from shore. During streamside observations, it was not always possible to identify and count the species in schools, so they were either slowly herded into the postlarval traps or the schools were sampled by hand nets.

When postlarval fishes enter fresh water, they must run the predator gauntlet arrayed at the stream mouth. Both juvenile *Kuhlia sandvicensis,* known in Hawai'i as *aholehole,* and juvenile and adult *E. sandwicensis* (*'o'opu akupa*) are predators that patrol the estuaries and the lower reaches of Hawaiian streams below the first major waterfall. During times of heavy recruitment, fishes of each predator species were observed underwater for 10-minute periods to determine the attack rate on recruiting *hinana* (total observation time: *Eleotris,* 11 hrs; *Kuhlia,* 7 hrs). *Eleotris sandwicensis* is a benthic ambush predator that moves and feeds near the stream bottom. To find the density of *Eleotris* during recruitment periods, 2 m × 6 m plots were established in the estuaries in both Honoli'i and Hakalau streams, and the numbers over 30 mm in length were tallied. No attempt was made to find and count those fish hidden in the substrate or under rocks, sticks, or other debris. Determining the density of *K. sandvicensis* was not practical because these predators were constantly moving; both individuals and schools swam rapidly to patrol large areas of the estuary. To find the extent to which the two carnivores included young freshwater fishes in their diet, gut contents from specimens of several size-classes of both predators were examined, and the absence or presence of *hinana* in the digestive tract was noted.

Interactions of postlarvae and juveniles of Hawaiian freshwater fishes were determined by underwater observations in 10-minute periods (approximate observation times in hours: *L. concolor,* 14.5; *S. stimpsoni,* 21; *A. guamensis,* 16.5; *S. hawaiiensis,* 2; *E. sandwicensis,* 11). Records of interactions and descriptions of behavioral sequences were made under water either temporarily on a plastic slate with the notes transcribed daily or permanently on mylar sheets bound into a tablet. In Hakalau Stream and Wainiha River, the size of feeding and resting areas used by postlarvae and juveniles was estimated by sketching a map of underwater landmarks bounding the area's limits, and then measuring the distances after the observation period.

Longitudinal distribution of size classes of the five freshwater fish species in Hakalau stream was determined by a census method modified from Schill & Griffith (1984). A 5-m transect was established with a weighted line; after five to ten minutes, the line was traversed and records were made of the species and developmental classes (postlarvae, juvenile, and adult) in the field of view.

Results and Discussion

RECRUITMENT INTO STREAMS

Postlarvae of Hawaiian freshwater fishes are adapted morphologically for entering the dynamic environment of island streams through their fusiform shape and pelvic adhesive disc and behaviorally through their positive rheotropic orientation. Some streams in Hawai'i meet the ocean environment abruptly at a terminal waterfall that plunges either directly into the ocean or into a pool at the base of a rock face. Most streams, however, enter the ocean at sea level and create a short estuary. Here the opposing forces of stream outflow and onshore wave and tidal action create a high-energy environment through which returning postlarvae must pass.

Like the adults, postlarval *S. stimpsoni, L. concolor,* and *A. guamensis* have fused pelvic fins with which they can anchor to the substrate in strong currents. When entering fresh water, postlarvae most often select a route near the shoreline where the current is weak and may even be reversed (countercurrent) during wave surges (Table 2). Some travel onshore against stream outflow by orienting their torpedo-shaped bodies into the current, darting from rock to rock, and using their fused pelvic fins as an anchor. Others may reach fresh water by following passages through the rock interstices and thus avoid the brunt of the turbulence. Postlarvae of both *S. hawaiiensis* and *A. guamensis* are relatively weak swimmers, and they are transported passively (ferried) into fresh water by wave and tide forces (Table 3).

Results of 24-hour trapping showed that *L. concolor* postlarvae entered streams mainly during the day with wave and tide surges. Nishimoto & Kuamoʻo (1997) reported that postlarvae of this species entered the stream mouth on a rising tide and after dark. Several marine fishes whose larvae develop in the estuary are known to migrate onshore in two stages: first they accumulate in the nearshore area, and then they are transported into the estuary (Miller 1988). *Lentipes con-*

Table 2. Frequency of migration routes taken by Hawaiian freshwater fish recruits swimming into streams from the ocean. *L. concolor* (LC), *S. stimpsoni* (SS), *A. guamensis* (AG).

Stream		Countercurrent (stream margin)	Shallow water zone	Deep water zone
Hakalau				
	AG	52/61 = 85%	6/61 = 10%	3/61 = 5%
	LC	36/44 = 82%	8/44 = 18%	0/44
	SS	43/56 = 77%	11/56 = 20%	2/56 = 3%
Honoliʻi				
	AG	34/47 = 72%	13/47 = 28%	0/47
	LC	24/31 = 77%	7/31 = 23%	0/31
	SS	134/159 = 84%	25/159 = 16%	0/159
Wainiha				
	AG	27/49 = 55%	22/49 = 45%	0/49
	LC	4/4 = 100%	0/4	0/4
	SS	54/96 = 56%	46/96 = 48%	6/96 = 4%

Table 3. Frequency of diurnal periods and mode of onshore transport employed by Hawaiian freshwater fish recruits: *L. concolor* (LC), *S. stimpsoni* (SS), *A. guamensis* (AG), *S. hawaiiensis* (SH), *E. sandwicensis* (ES).

		Day					Night				
Ferried											
		LC	SS	AG	SH	ES	LC	SS	AG	SH	ES
	N =	928	351	124	18	8	50	25	105	0	112
	Pct.	90%	50%	49%	82%	6%	5%	4%	41%	0%	88%
Swam											
	N =	44	321	22	4	0	14	4	2	0	7
	Pct.	4%	46%	9%	18%	0%	1%	1%	1%	0%	6%

color postlarval migration peaked in the hours after sunrise during tide and wave conditions that create tidal transport (Table 3, Fig. 1). Their onshore migration pattern might be similar to that of some marine fish larvae that mature in estuaries; they mass nearshore, and then begin migrating into the estuary at first light (Miller 1988). When *L. concolor* postlarvae reach fresh water, they move directly upstream to those habitats where they mature into adults. Neither immature nor adult Hawaiian freshwater fishes are active in the streams at night. Individuals that enter streams in the morning have an advantage over those entering later in the day in that they can penetrate farther inland during their first day and distance themselves from the concentration of predators at the stream mouth.

Sicyopterus stimpsoni postlarvae, the largest among Hawaiian freshwater fishes, are strong swimmers with well-developed fins. When newly recruited, they varied in pigmentation from transparent migrants that entered mostly at night to specimens with lateral bars and dorsal saddles typical of animals that came in throughout the day (Table 3, Fig. 1). During April 1992, the outflow at the mouth of Hakalau Stream was narrowed to about 2 m by a berm formed from wave action. At low tide, *S. stimpsoni* postlarvae invaded the estuary through the narrow inlet against a strong downstream current. They successfully reached fresh water by hugging the bottom, using their sucking disc for purchase on the rocky substrate, and then, swimming in bursts, they darted from one current refugium to the next. Postlarval *S. stimpsoni* that entered the estuary were as likely to swim against the current as they were to be transported passively; additionally, only 5% came in at night and 4% of these transparent nocturnal migrants were transported passively (Table 3, Fig. 1).

Awaous guamensis postlarvae were assisted into the stream mouth by wave action and came in on tide surges day or night. Ninety per cent of those sampled in this part of the study passed into fresh water on surges, and these were about equally divided between day (49%) and night (41%). Results of a nineteen-month study on postlarvae recruitment in Hakalau Stream (Nishimoto & Kuamo'o 1997) supports the data on diel periodicity in *A. guamensis* determined in the present study. Experiments by Nishimoto & Kuamo'o (unpublished) have shown that of the three upstream species, *A. guamensis* postlarvae are the slowest climbers. Moreover, newly recruited *A. guamensis* are often found in current refugia under rocks, in slack water, and in countercurrent flows near stream edges (Table 2). These observations suggest that they may be relatively weak swimmers, and it is expected that they rely on tidal transport to move into the estuary. On the other hand, Fitzsimons (pers. comm.) has found in artificial stream studies that *A. guamensis* postlarvae are strong swimmers that can make their way upstream against a current of 71 cm/sec.

Stenogobius hawaiiensis postlarvae were rarely found in traps set at the stream mouths. In another study *S. hawaiiensis* was found to enter the stream at night on the rising tide (Kuamo'o and Nishimoto 1996); however, of the 22 *Stenogobius* postlarvae captured in this study, all were in daytime samples. Four were trapped on a falling tide that required them to swim into the estuary, whereas 18 came in with tide surges (Table 3). Most captures occurred in mid-morning

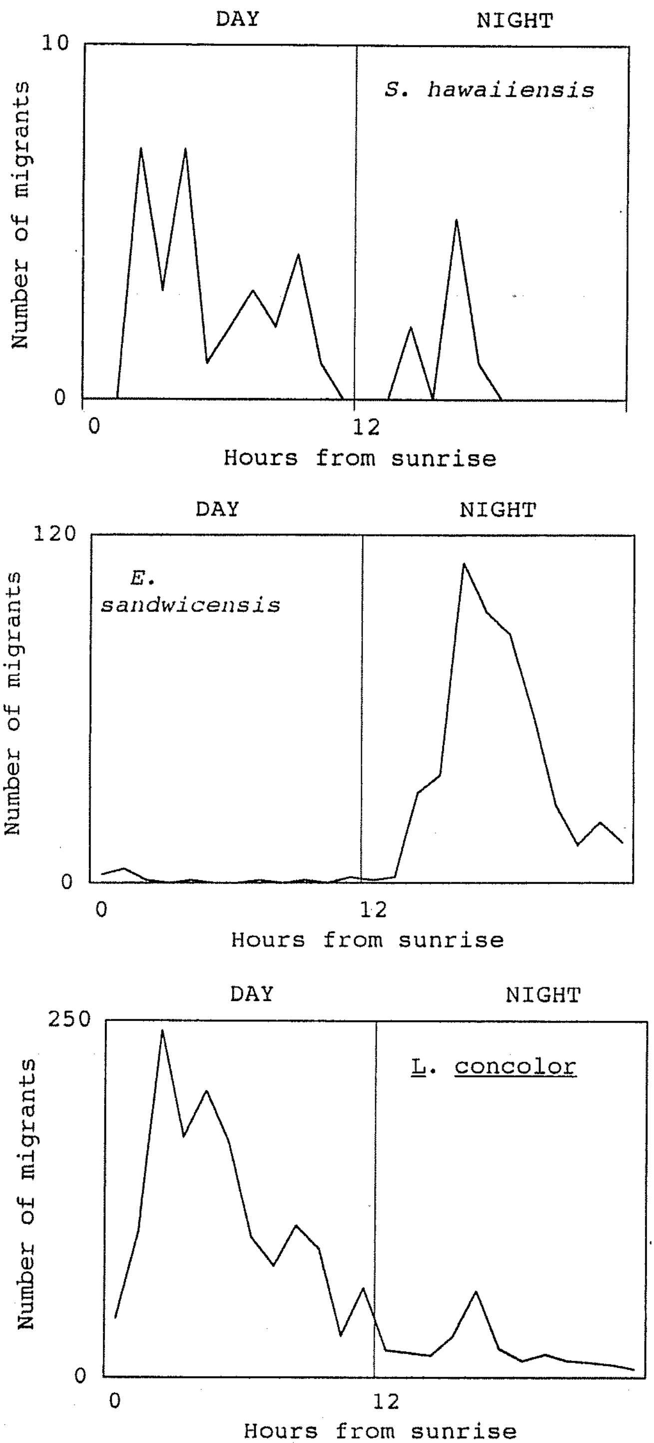
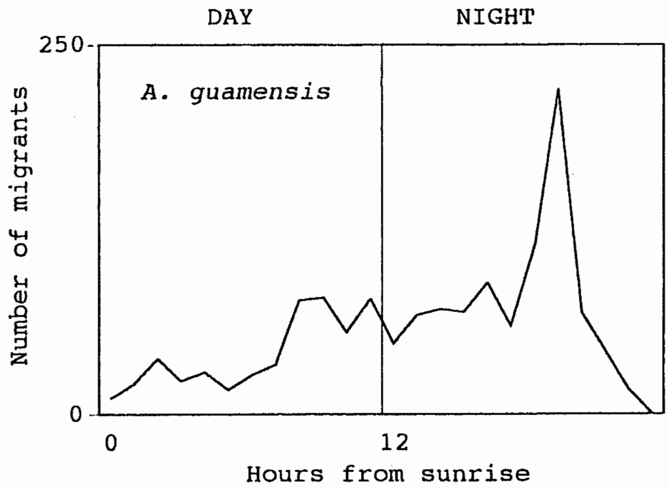


Figure 1. Diel periodicity of recruitment into fresh water by native Hawaiian stream fishes.



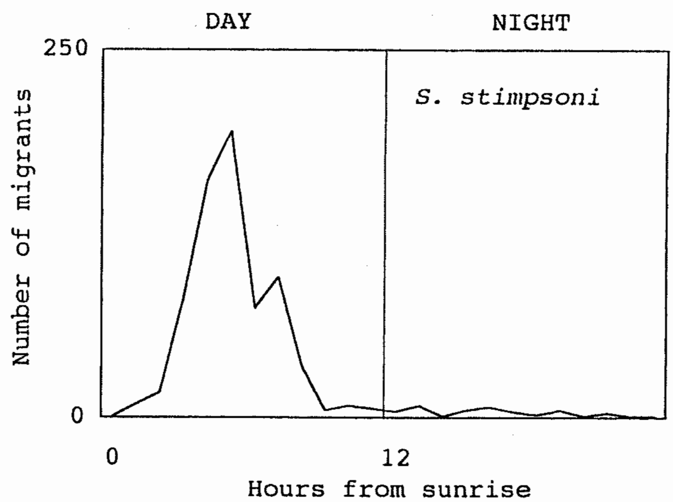


Figure 1. *Continued.*

(Fig. 1). In Honoli'i Stream during April, 1992, eight clear young *S. hawaiiensis* were uncovered under cobble-size rocks at the stream mouth, which suggests that the interstices could be another route by which this species gets into fresh water.

Inability to swim and maneuver effectively in the turbulence of the stream-ocean interface may be important in recruitment periodicity of *E. sandwicensis* postlarvae. Trap samples reveal that most postlarvae of this species were carried onshore by wave and tide surges after dark (Table 3) which agrees with the findings of Nishimoto & Kuamo'o (1997). Because they lack the pelvic-fin holdfast of true gobies, *E. sandwicensis* are unable to cling easily to the substrate, so they rely on tidal and wave action for transport into fresh water. Over 90% of young *E. sandwicensis* entered the estuary from dusk to just after sunrise; only when washed onshore by the surge were they found in daytime samples. Peak nocturnal recruiting time was early evening with a slight pulse just before dawn (Fig. 1). Observations of captive unpigmented postlarvae indicate that they are slow, tentative swimmers that hop along the bottom in short bursts. They were not found in any of the schools; when placed in an elongate plexiglass container, they always dived directly to the bottom and spent little time in open water. Because they are not adept at escaping predators by either swimming or schooling, reaching fresh water at night may provide young *Eleotris* an advantage in avoiding visually oriented predators.

SCHOOLING

Although there may be a number of reasons for schooling (shoaling) in fishes, antipredator functions and food acquisition are the primary factors that cause this behavior (Pitcher & Parrish 1993). Because newly recruited hinana must advance through a predatory enfilade created by *E. sandwicensis* and juvenile *K. sandvicensis* at the stream mouth, postlarval schooling behavior may best be explained as an antipredator adaptation. Schooling behavior occurred only in postlarvae; it was never recorded in either juveniles or adults of any of the freshwater species.

Lentipes concolor rarely occurred in schools of *hinana* entering the estuaries. They were found in only two of the 27 schools studied in Honoli'i Stream, one of the 16 schools in Hakalau, and were absent in schools at other study sites, although some of the unidentified postlarvae could have been *L. concolor* (Table 4). In Hakalau Stream about 500 m from the stream mouth, *L. concolor* and *A. guamensis* postlarvae maintained a school in the same eddy behind a large boulder near the stream margin from 14–29 July, 1991 and from 5 June–14 July, 1993. From eight to 26 fishes made up the school, and young fishes of both species would join the group for up to ten minutes on their way upstream. The school was permanent

Table 4. Species composition of postlarval freshwater fish shoals observed in Hawaiian stream estuaries. *L. concolor* (LC), *S. stimpsoni* (SS), *A. guamensis* (AG), *S. hawaiiensis* (SH).

Stream	Date	No. of fish(es) in shoal	No. of shoals and species composition
Wailoa	7/14/93	>100	(1) all AG
Hakalau	4/14/92	>100	(1) all AG
	4/16/92	5–10	(2) all AG
		11–20	(1) all AG; (1) AG, LC
		5–10	(4) all AG; (2) SS, AG
		21–30	(1) SS, AG, unidentified
Honoli'i	4/22/92	5–10	(4) all SS; (2) SS, AG (1) SS, SH
		11–20	(7) all SS; (1) SS, LC
		21–30	(1) SS, AG; (1) SS, AG, SH
		5–10	(5) all SS; (4) SS, AG
		11–20	(1) SS, unidentified
Wainiha	2/22/93	5–10	(6) all SS
		11–20	(4) all SS; (1) SS, AG (2) SS, unidentified
	2/23/93	5–10	(5) all SS; (2) SS, AG

at that site, but the individuals comprising the school changed regularly. Schools of postlarvae have been seen occasionally in upstream habitats on Kaua'i in the Wainiha River (J. M. Fitzsimons, two sightings, July 1991, one sighting 1993), in Nu'alolo Stream (J. M. Fitzsimons, one sighting, June, 1994), and in Hakalau Stream on the Big Island (D. Kuamo'o and J. Kahiapo, multiple sightings July, 1993). However, *L. concolor* postlarvae were not identified in the schools, and observations suggest that schooling in this species is infrequent (Table 4).

Three kinds of social interactions were recorded for young *A. guamensis* as they entered fresh water and advanced through the estuary in Hakalau and Honoli'i streams. They swam in pairs, in single-species schools, and in mixed-species schools with other freshwater gobies (Table 4). Single fish often moved onshore and upstream. Most schools contained no more than about 30 fishes; however, as many as 100 *A. guamensis* postlarvae were estimated in schools in Wailoa River (14 July, 1990) and in Hakalau Stream (14 April, 1992). Single postlarvae moved upstream by swimming in short sprints, followed by resting on the bottom. Sometimes a fish darted along the bottom from one rock surface to another. Pairs of young *A. guamensis* responded to each other's movements by alternating their swimming and rest periods; they seldom moved at the same time. The tandem swimming behavior resulted in a "leapfrog" effect. Near invisibility of the postlarvae's transparent phase, cryptic coloration that developed later, and tandem swimming created pursuit-and-capture difficulties for predators of *A. guamensis* postlarvae. When moving in single-species or mixed-species schools, the individual animals stayed together as they rose into the water, moved upstream, or dived onto the bottom.

Entry of *S. stimpsoni* into fresh water occurred as single fish or small to very large schools. During the main recruitment period from February to May, large schools were evident; later in the season, singles and smaller aggregations were recorded (Table 3). *Sicyopterus stimpsoni* postlarvae reportedly migrated into estuaries in numbers so great that the stream bottom seemed to be moving (Titcomb 1972, Clara Akuna, taped interview with Wade Ishikawa). On Kaua'i, their numbers were large enough to support a legal active fishery until the 1970's. In February, 1994, a fisherman on Kaua'i reported that he recently collected over 50 lbs in a day's fishing in Lumaha'i Stream (*hinana* fishing is currently prohibited by law in Hawai'i). During the present study, extremely large schools of *postlarvae* were not seen in over 300 hours of work at the mouths of several streams. However, in February, 1991, *S. stimpsoni* postlarvae migrated into Hakalau Stream for at least three hours in a continuous swath over 1 m wide (Nishimoto & Kuamo'o, pers. comm.).

Sicyopterus stimpsoni postlarvae are more likely to be found in schools at the stream mouths than are any of the other freshwater fishes; 51 of 63 schools of postlarvae contained *S. stimpsoni,* and 31 of those were composed exclusively of this species (Table 4). In what ways may it be adaptive for these postlarvae to migrate in large schools? In addition to the antipredator and feeding advantages that might accrue to individuals, several studies have shown that schooling provides a hydrodynamic advantage and that schooling fishes expend less energy (Breder 1965, Weihs 1973, Pitcher & Parrish 1993). Migrating schools of *S. stimpsoni* postlarvae moved directly through the stream mouth in all observations, and none were observed feeding while in the schools at the stream mouths of Wainiha, Hakalau, or Honoli'i. In accounts by Nishimoto & Kuamo'o (pers. comm.), the mass of *S. stimpsoni* migrated at a relatively constant rate directly through the estuary at Hakalau and then proceeded upstream. There was no feeding, only direct swimming against the current by fish (or fishes) in the school. In these observations, schooling does not appear to be a feeding adaptation. Unlike the other gobioid postlarvae, which entered stream mouths primarily with the wave and tide surge, *S. stimpsoni* swam into the estuary as often as they were transported by surges (Table 3). Migrating onshore in schools against the downstream current may be more efficient energetically and thus adaptive for any fish in the school.

Because individual identities are obscured in a school, a fish that employs schooling behavior is less easily detected than a fish by itself. Antipredator advantages are gained by individuals in a school; extremely large schools or mass migrations from ocean to stream described for nopili may ameliorate the effect of predation through predator satiation. The large numbers of prey would overwhelm and confuse the predators during the short time of exposure to attack in the estuary. A fish in a large mass would stand a greater chance than a single fish of surviving the predator gauntlet.

PREDATION

Young gobies may be an important food resource in the estuary and in the nearshore marine food web. Kinzie & Ford (1982) discussed the postlarvae's susceptibility to predation, and they speculated on the potential effects of predation on goby populations. When *hinana* enter the estuary, they are faced with the benthic predators, *E. sandwicensis* and *Polydactylus sexfilis* (called *moi* in Hawai'i), as well as a host of *K. sandvicensis* foraging in mid-water. From observations underwater and from shore, *E. sandwicensis* was discovered to ambush postlarvae as they passed upstream along the bottom. That this species is an important predator on young fishes in Hawaiian streams has been recognized in several studies (Kido 1996a, Kinzie 1990, Kinzie & Ford 1982). The predator's cryptic mottled pattern hides it from the young gobies, and its tactic of lying still under sticks and debris and burying itself in the substrate conceals it as well; often only the upper part of the body or the snout and eyes are exposed. They often broke cover and made a short dash to capture a postlarval fish; at other times they lay still on the bottom and engulfed any postlarva that came too near. *Kuhlia* cruised the estuary singly and in schools and attacked postlarvae in the open water, although they also were seen to pick off young fishes that rested or moved along the bottom.

Surveys of *E. sandwicensis* density at the mouth of Honoli'i and Hakalau streams during *hinana* recruitment in April, 1992, showed that the akupa density ranged from $0.58/m^2$ to $1.5/m^2$ (Table 5). These predators moved to the shallow waters into the path of the migrating *hinana* during the day and attacked as their prey moved upstream. In 11 hours of watching *E. sandwicensis* feed on young gobioids, 19 successful attacks in 26 attempts were noted. Single fishes rather than

Table 5. Densities of the benthic freshwater predator, *E. sandwicensis,* in 2-m × 6-m plots in Honoli'i and Hakalau Streams.

Stream	Date	Time	No. fish	Density (fish/m^2)
Honoli'i	4/9/92	10:00 hrs	18	1.50
		12:00	11	0.91
		14:00	13	1.08
		16:00	9	0.75
	4/18/92	10:00	8	0.67
		11:00	12	1.00
Hakalau	4/16/92	12:00	9	0.75
		13:00	9	0.75
		14:00	7	0.58
		15:00	11	0.91
mean = 0.89/m^2				
Std. dev. = 0.26				

those in schools were taken; a successful attack was not seen on a *hinana* that was either in a school or one of a pair.

Kuhlia sandvicensis juveniles ranging from 25 mm to over 100 mm in length were recorded foraging in the Hakalau Stream estuary during all tide and wave conditions. Groups were seen in a number of microhabitats including the open water zone at all depths, cutbank and shaded areas, eddies both near the shoreline and downstream of boulders and other obstacles, and in the surge zone during a rising tide when strong wave action and turbulence characterized the stream-mouth environment. In seven hours of underwater observation, nine successful attacks on postlarvae in 33 attempts were recorded. Gut content data show that over one third of the *Kuhlia* examined had been preying on postlarval fishes (Table 6). They are swift and agile hunters and appear to be equally effective in capturing *hinana* in a variety of microhabitats. Because the sampling period was limited for collecting predation data, information about predation at other times and in other streams was not obtained.

Table 6. Predation frequency on postlarval freshwater fishes by *E. sandwicensis* and *K. sandvicensis* determined by gut examination.

Size classes	Frequency of hinana remains in gut	
Std. length in mm	*E. sandwicensis*	*K. sandvicensis*
26–35	2/11 = 18%	2/9 = 22%
36–45	7/17 = 41%	1/5 = 20%
46–55	10/21 = 47%	6/17 = 35%
56–65	5/13 = 38%	7/16 = 44%
66–75	3/7 = 43%	2/4 = 50%
76–85	1/3 = 33%	0/1 = 0%
86–95	0/1 = 0%	0/0 = 0%
Total	28/73 = 38%	18/53 = 34%

The most profound effect of predation on stream fish populations may be the displacement of the young fishes to upstream habitats. Although predation reduces the numbers of young gobies migrating inland, the direct impact of reduced numbers of recruits on adult populations in upstream habitats is unknown. However, the most important result of predation on postlarval fishes in the estuary and nearshore area may be the escape response by *hinana* to avoid being eaten—behaviors such as schooling, tandem swimming, and alternately using the open water and the stream bottom as upstream conduits. The escape route is upstream away from the concentration of predators at the stream mouth and estuary.

There may be some spatial partitioning of the postlarval fish resource between the two principle predators in the estuary, with *E. sandwicensis* feeding mainly on the bottom and *K. sandvicensis* foraging in mid-water. Two specimens of moi taken from the mouth of Waimea River on Kaua'i contained remains of *hinana* (*E. sandwicensis* and other unidentified immature gobies) in their stomachs; over 20 *Polydactylus* taken from nearshore areas on the Big Island also fed on *hinana,* but the analysis is incomplete (R. T. Nishimoto pers. comm.). Ecotones such as the stream-ocean interface are known to be highly productive areas and active zones of trophic energy transfer (Odum 1959). Secondary productivity represented by the immature freshwater fishes as they pass through this zone has important management implications for nearshore marine fisheries, and the role of hinana in the food web needs further investigation.

UPSTREAM MOVEMENT

Adult Hawaiian freshwater fishes show species-specific longitudinal distribution in streams (Fitzsimons & Nishimoto 1991), and the results of this study provide evidence that it is the young fishes that migrate to the habitats they occupy as adults. Of the three species that live in higher elevations in Hakalau Stream (*L. concolor, S. stimpsoni,* and *A. guamensis*), only *L. concolor* advanced directly from the ocean to the habitats upstream, while the others took more time in their migration. Postlarval *E. sandwicensis* and *S. hawaiiensis* were not found above the first major waterfall in any stream; the role of postlarvae in the distribution of adults of these two species within lower stream reaches was not determined.

Adults of all species of Hawaiian upstream gobies are able to cling to vertical surfaces, and, on occasion, they may climb short waterfalls (one sighting each for *L. concolor* in Manoloa Stream, Hawai'i: male flushed upstream by observer, and in Makaleha Stream, Kaua'i: several males and females videotaped while moving up 1 m waterfall created by reopening an irrigation weir). However, only a few adults have been observed on waterfalls whereas hundreds of migrating young have been collected or videotaped while climbing waterfalls ranging in height from less than 1 m (Hanapepe River, Kaua'i) to over 20 m (Awa'awapuhi Stream, Kaua'i; Hakalau Stream, Hawai'i). Adult *L. concolor* (especially males) are strongly site specific, and some individual males are known to stay in the same place for over four years (Nishimoto & Fitzsimons 1986, Fitzsimons & Nishimoto 1990). Adult *A. guamensis* may remain for several months in the same stretch of stream between small waterfalls (observations in Nu'alolo Stream, Kaua'i, October, 1992; February, June, and October, 1993; and February and June, 1994—J. M. Fitzsimons, pers. comm.) unless migrating downstream during the spawning season (Ego 1956). Observations in this study suggest that antipredator behavior by postlarvae in the estuary results in escape upstream. Above the first major waterfall, which acts as a barrier to the young gobies' main predators, schooling and escape behavior is supplanted by agonistic interactions as young fishes compete for food and space. Predation and competition act in sequence to drive upstream migration.

Sicyopterus stimpsoni.—Two morphological varieties of *S. stimpsoni* postlarvae and juveniles that represent two behavioral types were found in Hakalau Stream on Hawai'i, and in Awa'awapuhi Stream and Wainiha River on Kaua'i. In Hakalau Stream, some *S. stimpsoni* that entered fresh water developed signaling colors used in establishing and defending a feeding area (Table 7). Other recruits did not develop the striking pigmentation displayed in agonistic encounters, and they continued to move upstream when they were displaced by more colorful and aggressive conspecifics. Aggression by the postlarval and juvenile dark, pigmented morphs and their success in resource defense results in the movement upstream of the less colorful form and drives the instream distribution of *S. stimpsoni.*

In Hakalau Stream, postlarvae, juvenile, and adult nopili grazed singly and in groups on rock surfaces that appeared to be bare of macrophytes. Bare patches were not only the major feeding areas used by this species, but they were also used as display sites during courtship (Fitzsimons & Nishimoto 1993). Microscopic examination of scrapings from the bare patches revealed pennate diatoms, including

Table 7. Size of feeding areas defended by size classes of juvenile *A. guamensis* and *S. stimpsoni.*

	A. guamensis		*S. stimpsoni*	
Size class in mm (SL)	Obs. time in min.	Area in cm^2	Obs. time in min.	Area in cm^2
25–29	30	600	17	200
	14	700	10	500
	20	800	16	800
	30	800		
	26	1050		
	30	1250		
30–35	30	600	10	150
	12	900	20	370
	20	850	10	400
	20	450		
36–40			11	250
			20	250
			18	280
			30	320
			65	550
	Mean =	815		380
	Std. dev. =	212		175
	Range =	600–1250		150–800

representatives of the genera *Navicula, Nitzschia,* and *Pinnularia.* Filamentous algae of the genera *Ulothrix, Spirogyra, Oscillatoria,* and *Cladophora* were also identified from rock scrapings. Stomach contents of 20 *S. stimpsoni* revealed that diatoms and filamentous algae of the above genera constituted much of their ingested material (Tate unpubl.). Kido (1996b) reported that *S. stimpsoni* from Kaua'i streams included the same plant foods in their diet. Feeding-patch resources maintained by grazing are sometimes shared and sometimes contested by immature individuals. When a patch was shared, spacing was maintained by agonistic signals—usually a flick of the dorsal fin displaying the shiny red and black bands spanning the membranes. Drab morphs were routinely forced from the feeding patch by darker, more showy aggressors or by adults (Table 8). In almost all contests, the displaced drab intruder relocated to an adjacent unoccupied rock or moved upstream. Some young showy *S. stimpsoni* defended areas on feeding rocks and challenged intruders of all species, except large adults. Collections either on the face of waterfalls or immediately upstream suggest that it is the drab morph that continues upstream migration. In seven hours of trapping atop the 25-m terminal waterfall on Awa'awapuhi Stream on Kaua'i, all 14 *S. stimpsoni* migrants captured were drab morphs from 25–31 mm SL. The plunge pool at the base of the falls and the 25 m stream that ran through the boulder beach to the surf was packed with aggressive showy morphs. All 11 specimens climbing a waterfall on Hakalau Stream 2.3 km inland were drab. In Wainiha River on Kaua'i approximately 4 km from the mouth, all 22 immature individuals climbing at the base of a concrete diversion weir were drab.

That some *S. stimpsoni* enter fresh water as transparent postlarvae while others are already well pigmented (Nishimoto & Kuamo'o 1996, this study) offers some evidence that two morphological types enter streams from the ocean. Those with the full complement of signaling colors and pigment patterns are better equipped to defend spaces on feeding rocks, while those whose colors are yet to develop lose aggressive encounters and are forced upstream. When they reach a site in the stream where a low density of aggressors causes fewer encounters, they cease migrating, settle, and begin developing pigmentation. Aggression plays a critical role in distribution when adults and well-pigmented juveniles displace young that have poorly developed signaling colors.

Table 8. Aggressive encounters (contests) of two *S. stimpsoni* juvenile morphological types with each other and with adults in Hakalau Stream.

	Number of contests won			
Contest	Showy	Drab	Adult	Draw
Showy vs Drab	116	0		17
Drab vs Drab		8		5
Showy vs Showy	16			13
Adult vs Showy	0		56	0
Adult vs Drab		0	39	0

Lentipes concolor.—Postlarval *L. concolor* did not remain in the short estuary at Hakalau Stream; they swam directly upstream at a rate of about 90 m/hr to the low-water bridge, climbed it, then rested and fed. The low-water bridge restricts the upstream movement of both species of aquatic predators, aholehole and akupa, and creates a "safety zone" for the young gobies above the waterfall obstacle. Almost all *L. concolor* below the low-water bridge were transparent postlarvae of about 14 mm SL. A comparison of mean standard length measured to the nearest millimeter at the observation station 200-m above the barrier ($n = 22$, $x = 14.5$, std. dev. $= 0.77$) with that below it ($n = 20$, $x = 14.2$, std. dev. $= 0.64$), was not significantly different (t-test; $P < 0.05$); pigmentation of specimens from both sites was about the same. Similarity in size and degree of pigmentation of young fish above the barrier and in the estuary indicate *L. concolor* hinana spent little time—no more than a day—in the "predator zone" below the barrier. Agonistic interactions of *L. concolor* postlarvae in the lower reaches of Hakalau Stream above the low-water bridge result in upstream displacement of the young fish. Unlike *A. guamensis* (see below), young *L. concolor* did not develop signaling pigmentation in their dorsal fins, and, in the lower stream reaches, they defended their feeding areas by charging similar-sized intruders of any fish species (Table 9). In the upper reaches of Hakalau Stream where *L. concolor* is the only fish present, aggression of young fishes toward each other was reduced, and no agonistic encounters between adults and immature *L. concolor* were recorded (Table 9). Reduced aggression in the upstream habitats removes the impetus for further migration. Frequencies of postlarvae, juveniles, and adults of *L. concolor* along the length of Hakalau stream support the hypothesis that immature fish are responsible for distribution of adults. Frequency of postlarvae varies inversely with their distance from the stream mouth and older classes vary directly, which indicates that immature fish are not settling in the lower reaches but are moving upstream (Fig. 2).

Awaous guamensis.—Postlarvae of *A. guamensis* enter fresh water at lengths ranging from 14–17 mm SL; many may spend four or more weeks in the estuary. A survey of the parasitic helminths of *A. guamensis* from the estuary at Hakalau Stream revealed adults of the freshwater nematode *Camallanus cotti* in the gut of postlarvae 17–20 mm SL (Font & Tate 1994). Stumpp (1975) reported that it takes about four weeks for the worms to reach maturity, so it appears that some of the young *A. guamensis* remain in the lower stream for at least a month during migration.

Table 9. Agonistic responses of three size classes of *L. concolor* to encounters with conspecifics and other gobioid species in Hakalau Stream (14 hours of observation).

Encounter	Interaction (agonistic responses/encounters)
Adults & Juveniles	0/51
Juveniles & Juveniles	10/26
Postlarvae (*L. concolor*) & Postlarvae (all species)	38/44

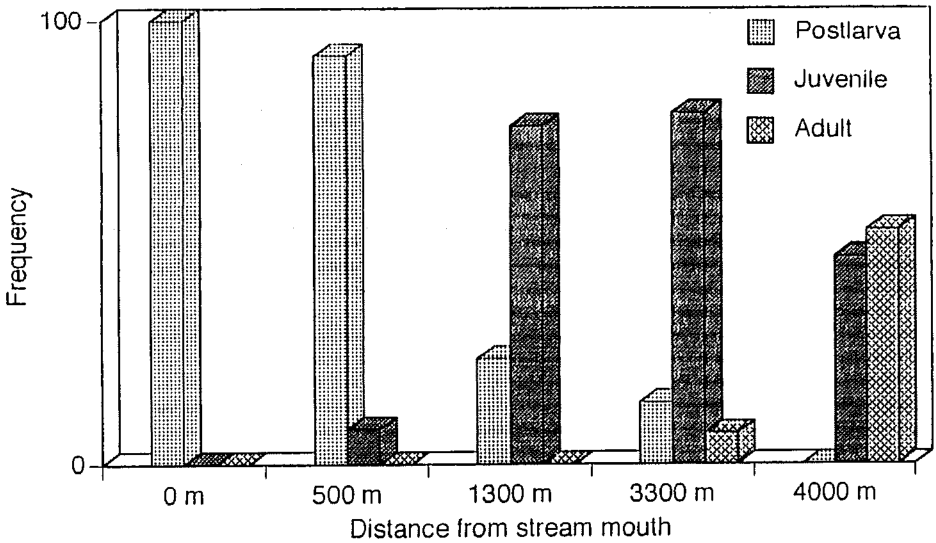


Figure 2. Longitudinal distribution of developmental classes of *Lentipes* in Hakalau Stream.

Schooling by *A. guamensis* postlarvae (Table 4) offers protection from predators and typifies behavior of immature *A. guamensis* below the low-water bridge in Hakalau Stream. Above the barrier, most young fish darkened and developed a well-defined red-bordered black spot in the spiny dorsal fin. Also, a decided behavioral change occurred; schooling was rare, and individual fish established tem-

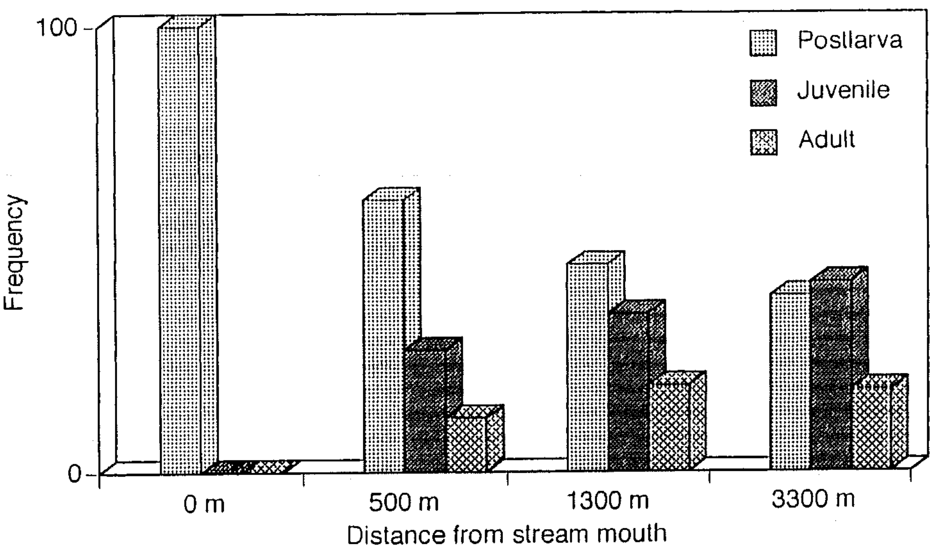


Figure 3. Longitudinal distribution of developmental classes of *Awaous* in Hakalau Stream.

porary feeding and resting areas (Table 7), which they defended by orienting laterally to an intruder and raising the dorsal black-and-red "flag". Most similar-sized intruders were ejected by this aggressive display. Intruders leaving the contested area fled either upstream or into shallow areas along the stream margins. The net result of predation in the estuary and competition in the lower stream was upstream movement by immature *A. guamensis.* Census data from the recruiting season at Hakalau Stream revealed that the frequency of postlarvae varies inversely with distance from the stream mouth and that frequency of juveniles vary directly. These data indicate that immature fish are not settling in the lower reaches but are moving upstream (Fig. 3). Migration of adults downstream during spawning in the fall (Ego 1956) may redistribute the population of adults of *A. guamensis* and open habitats in the upper stream for the younger fish not involved in spawning.

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