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Behavioral Ecology of Indigenous Stream Fishes in Hawai‘i

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Abstract

Five species of amphidromous fishes comprise the indigenous vertebrate fauna of Hawaiian streams. All have a marine larval phase, and, as adults, they live in freshwater and brackish environments marked by frequent flash floods. Although these fishes are closely related and live under similar conditions in the ocean and in streams, they are remarkably diverse in their behavior and ecology. They usually occupy species-typical sections of streams ranging from near the headwaters down to the mouth or estuary; species specificity is evident also in habitat selection by adults. Two species (*Eleotris sandwicensis* and *Stenogobius hawaiiensis*) are unable to climb waterfalls. Among the climbing species, two (*Awaous guamensis* and *Lentipes concolor*) use their pelvic disk and lateral fins for climbing, and the fifth species (*Sicyopterus stimpsoni*) uses the mouth and pelvic disk as holdfasts. The pattern of instream distribution coincides with the relative development of pelvic and oral suckers used in clinging to rocks and climbing waterfalls and with each species' station-holding ability in artificial streams, but the causal factors that prompt new recruits entering from the ocean to continue moving upstream to adult habitats is incompletely understood. One species is a carnivore, one is an herbivore, and the remaining three species are omnivorous. Males of all five species engage females in distinctive courtship behaviors that precede spawning, and all but one species provide some protection for the eggs by guarding the area in which one or more nests are included. Genetic studies for all species show sharp species-level differences among species, but there are no effects of isolation and subsequent differentiation among the five major islands. The data suggest that marine larvae disperse beyond their natal streams. In contrast, analyses of naturally occurring stable isotopes in new recruits indicate that they remain close to mouths of streams while at sea. Introduced freshwater fishes are the original source of potentially harmful parasites which have infected native stream fishes. Resident fishes differ in their susceptibility to parasites. The effect of other alien introductions on aquatic animals has not been determined. Adults in fresh water and free-living embryos and larvae in the ocean have a mix of characteristics within and among species attributable to r and K selection. Although Hawaii's stream fish species are diverse in behavior and ecology, their common amphidromous life cycle provides a basis for management and conservation. Hawaii's Division of Aquatic Resources has developed four levels of stream protection and a firm policy of "no net loss of habitat" to ensure the safety and continuance of the islands' indigenous fishes.

Introduction

No primary or secondary freshwater fishes occur naturally in Hawaiian streams and estuaries (Myers, 1938). However, over 40 species of fishes are known from the islands' fresh and brackish waters (Yamamoto & Tagawa, 2000). These include a few marine species that enter estuaries and lower stream reaches, a host of freshwater fishes introduced intentionally or by accident, and a small group of indigenous fishes that occur as adults in fresh and brackish water and have an obligate marine larval period in their amphidromous life cycle (Myers, 1949; McDowall, 2003). This latter group, derived from marine ancestors, includes two families of gobioid fishes, the Gobiidae and

Eleotridae, whose species are overwhelmingly predominant in island streams throughout the high islands of the tropical Pacific (Fitzsimons *et al.*, 2002). Among these islands, a resident stream fish is very likely to be a goby or an eleotrid, and it almost certainly will have an amphidromous life cycle. Among the amphidromous fishes in Hawai‘i, the low species richness (five) and high degree of endemism (four out of five species or 80%) are in keeping with the unsurpassed isolation of the five major islands (Hawai‘i, Maui, Moloka‘i, O‘ahu, and Kaua‘i) in the archipelago that have sufficient elevation to produce the orographic rain needed to sustain perennial streams on windward slopes. Although species richness among Hawaii's amphidromous fishes is small, the degree of ecological and behavioral diversity among the five species is remarkable. Information from publications, field notes from 1984–2004, presentations from meetings, and conversations is used in this report to emphasize species similarities and differences in (1) distribution within a single stream and between streams, (2) food sources and feeding behavior, (3) reproductive behavior, (4) climbing ability, (5) genetics, (5) stable isotope analyses, (6) susceptibility to parasites, and (7) r and K selection. These fishes share an amphidromous life cycle and live under similar conditions in island streams where frequent and naturally occurring flash floods maintain ecological succession at an early stage of colonization in which the pioneering species function also as the climax species (Fitzsimons & Nishimoto, 1995). These similarities are the basis for well-established, effective procedures for conserving these animals throughout the Hawaiian high islands.

Discussion

Species distribution within and between streams

All five species of Hawaiian amphidromous fishes occur on each of the five major high islands, but all five species do not occur in every stream on these islands. Understanding the differences in the distribution of these animals between streams is simplified by understanding their distribution within individual streams.

Stream fishes in Hawai‘i are species-specific in their selection of habitats along the length of a stream (Tate, 1997). During their amphidromous life cycle, all species enter the mouths of streams when their larvae move from the ocean toward adult habitats in brackish or fresh water. Two species, *Eleotris sandwicensis* (*‘o‘opu ‘akupa*) and *Stenogobius hawaiiensis* (*‘o‘opu naniha*), remain in the estuary and lower stream reaches in areas of reduced current while the other species continue their migrations to sites farther upstream. The eleotrid lacks the fused pelvic fins which form a holdfast in gobies, and, although *S. hawaiiensis* has a pelvic disk, the structure is elongate, delicate, and better adapted for sitting on loose substrate (sand and gravel) than for adhering to rocks in swift water. The upstream extent of *E. sandwicensis* and *S. hawaiiensis* often is sharply bounded by the first waterfall or other obstruction a meter or more in height. *Awaous guamensis* (*‘o‘opu nākea*) and *Sicyopterus stimpsoni* (*‘o‘opu nōpili*) usually occur in the middle reaches of streams, but, because they differ in microhabitat selection, they seldom are close together (Kinzie, 1988). *Awaous guamensis* most often remains on or near the bottom in pools and behind boulders, and *S. stimpsoni* is common in more rapidly flowing runs and riffles and along the sides and upper surfaces of large rocks and boulders. Juveniles and adults of *Lentipes concolor* [*‘o‘opu hi‘ukole* (males) and *‘o‘opu alamo‘o* (females)] typically occur the farthest upstream well beyond the range of the other amphidromous fishes and are well known for their ability to climb high waterfalls (Englund & Filbert, 1997).

The pattern of linear instream distribution of amphidromous fish species in Hawaiian streams was mirrored precisely by each species' ability to "hold station" during experiments in artificial streams (Fitzsimons *et al.*, 1997). However, it is not known whether the distribution pattern is a simple matter of climbing ability, competition for space or food, or a reflection of "ghosts of competition past" (Connell, 1980) that occurred among the ancestors of Hawaiian stream gobies in the far western Pacific. In the latter regard, it is noteworthy that congeners and other close relatives of Hawaiian stream species living in Oceania have patterns of instream distribution that are strikingly similar to those of their Hawaiian kin (Fitzsimons *et al.*, 2002). As suggested for Micronesian stream gobies (Parham, 1995; Nelson *et al.*, 1997), the presence of predators in Hawaiian streams, primarily *E. sandwicensis* and marine-born *Kuhlia xenura* (*āholehole*) in estuaries and lower stream sections, may be a driving force that promotes upstream dispersal and species segregation. The latter hypothesis appears testable.

Topography determines which species occur in a given stream. A stream whose basin slopes gradually from the headwaters to the ocean is likely to have all five fish species. In a relatively long stream of this type, the species are likely to be separated, but, if short, there may be sites where the three upstream species (*A. guamensis, S. stimpsoni*, and *L. concolor*) occur together (Kinzie, 1988). A stream with a much steeper incline and few or no areas of reduced flow near the mouth probably will not include the two downstream species, *E. sandwicensis* and *S. hawaiiensis*. A stream ending in a waterfall that drops directly onto the beach or into the sea will not have these latter two species, and, depending on the height of the waterfall, *A. guamensis* and *S. stimpsoni* may be absent also. Streams terminating in a waterfall in excess of 30 m probably will have only *L. concolor* above the falls. Finally, a stream with a long estuary (such as Hanalei, Kahana, and Hi‘ilawe streams on Kaua‘i, O‘ahu, and Hawai‘i, respectively) will have few or no *L. concolor* near its headwaters. The relationship between stream topography and the dispersal capabilities of resident fishes is sufficiently well known that it is often possible to predict species presence and distribution in a stream merely by consulting a topographic map that includes contour intervals.

A lack of knowledge or intentional disregard of natural trends in fish distribution and the relationship between fish behavior and stream morphology has led to erroneous conclusions with implications for the conservation and management of Hawaiian stream fishes. Early stream surveyors apparently did not know that the range of adult *L. concolor* often begins well inland of the ranges of the other stream fishes. Surveys usually began at the mouth of a stream and proceeded upstream until animals were no longer observed. *Lentipes concolor* was recorded as absent in many streams where it was present farther inland. This misinformation led to a statewide classification of all streams as Lentipes Streams and Non-Lentipes Streams (Timbol *et al.*, 1980), designations which prompted a local conservationist group to sue the U.S. Fish and Wildlife Service to have *L. concolor* listed as Threatened or Endangered throughout the Hawaiian Islands. Even when advised that the basis for the listing was unfounded, the group persisted until the Hawai‘i Division of Aquatic Resources (DAR) began surveys that located populations of these fish at remote sites on all islands, including O‘ahu where the species was thought to have been extinct for many years (Higashi & Yamamoto, 1993). More recently, there have been several attempts (e.g., Kido & Smith, 1998) to standardize stream surveys in Hawai‘i by using techniques arguably effective in streams of the mainland U.S. without regard to the connection between stream morphology and fish distribution, the implications of amphidromous life cycles, and the significance of the continuous cyclic recovery of streams from the frequent flash floods.

Food and feeding

Hawaiian amphidromous fishes run the gamut from carnivory (*E. sandwicensis*) to herbivory (*S. stimpsoni*) and omnivory (*S. hawaiiensis*, *A. guamensis,* and *L. concolor*).

Eleotris sandwicensis is a carnivore that feeds opportunistically on a wide variety of animal foods, including other fishes (even their own species), crustaceans, and aquatic snails. The fish‘s large head, protrusible upper jaw, underslung lower jaw extending beyond the tip of the upper jaw (prognathony), and conic teeth are adaptive for grabbing prey and swallowing it whole. The relatively short gut of *E. sandwicensis* in comparison to other gobioid fishes in Hawaiian streams (Kido, 1996a) is consistent with its carnivorous feeding habits. The fish makes short chases after small fishes, prawns, and shrimp, but usually sits motionless on the bottom until suitable prey comes within striking distance. *Eleotris sandwicensis* congregates in large numbers near the mouths of streams at times of peak recruitment of larval *‘o‘opu* from the ocean and often feeds until the belly is distended, but the environmental or behavioral cues prompting such opportune concentrations of these predators have not been investigated. A comparative study of feeding morphology and food habits among Hawaiian stream fishes (Kido, 1996b) revealed a large amount of algae in the gut of *E. sandwicensis* from Wainiha River, Kaua‘i, but the author suggested that the plant material may have been ingested inadvertently while fish were feeding on animal material and noted that gut morphology and other features of these fish are indicative of carnivory.

Dentition, gut morphology, diet, and food selection (Kido, 1996a & b, 1997) distinguish *Sicyopterus stimpsoni* from other native freshwater fishes as an obligate herbivore. These fish feed preferentially on navicular, centric, and chain diatoms and pieces of filamentous green and blue-green algae which they scrape off rocks with brushing movements of the upper jaw armed with spatulate tricuspid teeth. Their feeding produces conspicuous scallop-edged patches or long trails on the sides and upper surfaces of rocks and boulders. Large patches prominently located on the surface of boulders near the center of the stream serve as the locus for the initiation of social behavior (territoriality and courtship) by usually large, conspicuously colored, dominant males (Fitzsimons *et al.*, 1993, 2003). While living offshore, young *S. stimpsoni* have a terminal mouth, but, upon entering fresh water, they are unable to feed (or climb) until the mouth migrates to a ventral (inferior) position. This extraordinary change in head morphology occurs within only 48 hours (Schoenfuss *et al.*, 1997).

The three omnivorous stream species occur in the estuary and lower stream reaches (*S.* hawaiiensis), the middle reaches (*Awaous guamensis*), and the upper sections of streams (*Lentipes concolor*). Although detailed studies are lacking, underwater observations suggest *S. hawaiiensis* are omnivores that ingest both plant and animal food by making stabbing bites at the upper surface of rocks or by swimming up into the water column to intercept items drifting downstream. *Awaous guamensis* feed on filamentous algae, diatoms, and small stream animals such as fly larvae and other benthic invertebrates (Kido, 1997). The fish usually bite off clumps of algae or take in a mouthful of sand or gravel from which algae and invertebrates are removed by comb-like gill rakers in the animal‘s “pharyngeal mill”. Once cleaned, the particles of sand and gravel are spit out or dropped from under the lower edge of the gill cover. All five gobioid species have a filtering apparatus formed by gill arches and associated bony or soft projections, but the structure is best developed in *A. guamensis*, an omnivore, and the least in *S. stimpsoni*, an herbivore (Kido, 1996a). Although typically bottom feeders, *A. guamensis* occasionally swim up from the bottom and ingest pieces of material being washed downstream. *Lentipes concolor* feed on green algae and opportunistically on stream invertebrates (Kido, 1996a). In many streams, the most common food items are the larvae of the extremely abundant chironomid flies that lay their eggs on dampened parts of rocks near the water line. These fish also frequently dart up from the bottom and intercept particles carried downstream in manner reminiscent of the sallying behavior of insectivorous birds that fly up from a perch and capture insect prey. It has not been determined to what extent the omnivorous fishes are actually digesting plant material rather than receiving nutrition from the periphyton (*aufwuchs*) attached to it. Gut morphology (length and number of loops) among the omnivores *S. hawaiiensis*, *Awaous guamensis*, and *Lentipes concolor* is intermediate between that of the carnivore (*E. sandwicensis*) and the herbivore (*S. stimpsoni*) (Kido, 1996a).

Reproductive behavior

Hawaii’s amphidromous stream fishes are egg layers. All but one species (*S. hawaiiensis*) are territorial and provide some degree of protection to egg masses by defending the larger area in which eggs are deposited. Eggs are extruded individually from the elongate urogenital papilla of females. Males fertilize the eggs shortly after they are deposited. Eggs are small (ca. 1/3 mm diameter) and encased in a gelatinous adhesive coat. The slightly buoyant eggs float up from the substrate where they have been attached, but the adhesive coat forms a stalk that anchors them and gives them the appearance of a tiny golf ball sitting on a tee. Eggs are deposited in one or more lines (*S. hawaiiensis* and small females of *E. sandwicensis, S. stimpsoni,* and *A. guamensis*) or in round and irregular patches (large females) sometimes reaching the diameter of a dinner plate (*A. guamensis*). Recently laid egg masses are white or light gray; patches of eggs where hatching has occurred are usually darker gray and have a ragged appearance. Eggs are deposited on the surface of rocks and boulders (*S. hawaiiensis* and occasionally *E. sandwicensis*), along the sides or underneath boulders (*E. sandwicensis*, *A. guamensis,* and *S. stimpsoni*), and in burrows usually located under piles of large rocks or under the downstream edge of large boulders (*L. concolor* and occasionally the other species).

All five species have an elaborate courtship ritual comprised of species-specific movements that precede pair-forming and spawning. Males approach females in or near their territories and begin a stereotypical sequence of display behavior that ends with the male leading the female to a spawning site. Pair forming is determined by female choice, but, in one species, *E. sandwicensis,* females have a mid-water display that solicits approach by males. Males of *S. hawaiiensis* initiate courtship with females, and, if the female is receptive, the male leads her to the nearest natural burrow or flat rock often near the margin of the stream where current is reduced. After a bout of spawning, the male may engage the same female in additional courtship with spawning at the same or different site. However, males usually swim along the margins of streams and pursue females encountered opportunistically. *Stenogobius hawaiiensis* differ from other stream fishes in that apparently neither the female, the eggs, nor the spawning site are defended against conspecific males.

Awaous guamensis may be the only amphidromous fish species in Hawai‘i that has a spawning migration (Mainland in Titcomb, 1977; Yamamoto & Tagawa, 2000; Kido & Heacock, 1992). The fish are said to come downstream to sites near the mouths of streams in association with heavy rains during June or July. Streamside residents on Kaua‘i are often familiar with the movements of these fish, and taro farmers have used the expressions *‘o‘opu* rain and *‘o‘opu* flood when describing the conditions associated with the downstream migration of *A. guamensis* in the Hanalei River (Yamamoto & Tagawa, 2000). We have observed large aggregations of spawning fish in the lower section of Wainiha River after being told by a local resident that the fish moved there a week earlier in response to a moderate flash flood. An old Hawaiian proverb refers to *A. guamensis* as *Ka i‘ a ka wai nui i lawe mai ai* (“the fish borne along by the flood”; Pukui, 1983 [1323]). Although accounts are anecdotal, their frequency and similarity afford them at least a tentative “ring of truth”. The advantage of a downstream migration would be two-fold: The aggregation of adults at a common downstream spawning area would enhance the chances of an individual fish finding a receptive mate, and the newly hatched young would have a shorter distance to gain access to the sea. The latter would be of special significance in streams, such as Hanalei and Wainiha, which have long estuaries and adult fishes distributed farther inland than in most Hawaiian streams. In Japan, some amphidromous gobies (*Rhinogobius brunneus*) hatched far inland usually do not have sufficient yolk to sustain them during the long drift to the sea (Iguchi & Mizuno, 1999). The same may be true for gobies in certain Hawaiian streams.

Climbing

Hawaii’s amphidromous fishes differ in their climbing ability. Two species, *E. sandwicensis* and *S. hawaiiensis,* apparently do not climb and are limited to estuaries and the lower stream reaches below the first waterfall of a meter or more in height. However, both have morphological and behavioral adaptations that allow them to maintain position in flowing water (Fitzsimons *et al.*, 1997). The head and body of *E. sandwicensis* is slightly flattened dorsoventrally, and the head is sloped slightly downward from the nape to the tip of the snout. Water flowing over the fish tends to press it into the substrate rather than forcing it up and away from the bottom. These fish are proficient in their ability to wedge themselves between rocks and boulders while using the pelvic and pectoral fins to maneuver and to push forward or backward. By hugging the bottom and working their way upstream behind rocks and boulders, the eleotrids are capable of progressing against currents that would displace other fishes of similar size and shape attempting to swim against the flow. *Stenogobius hawaiiensis* swim off the bottom, but these fish take advantage of slack water along the margins of streams and in the shelter of large rocks and boulders.

The three upstream species, *S. stimpsoni, A. guamensis,* and *L. concolor*, can climb waterfalls and adhere to the surface of rocks and boulders in swift water with a suction disk formed by the fusion of the pelvic (ventral) fins. Even among these three species, the mode of climbing and climbing ability differ. *Awaous guamensis* and *L. concolor* rely on the pelvic disk as a holdfast when climbing, but *S. stimpsoni* uses both the pelvic disk and the mouth alternately when “inching” forward in a strong current and when climbing a cascade or waterfall (Schoenfuss *et al.*, 1997; Schoenfuss & Blob, 2003; Nishimoto & Kuamo‘o, 1997). The “powerburst climbers” (Schoenfuss & Blob, 2003), *Awaous guamensis* and *L. concolor,* push forward with the pectoral fins while detaching the pelvic disk and rapidly undulating the body from side to side. *Sicyopterus stimpsoni* and *A. guamensis* can negotiate waterfalls 10–20 m in height (Fitzsimons & Nishimoto, 1991), while adults of *L. concolor* reside in the pools above the highest waterfalls, such as Waipi‘o Valley‘s Hi‘ilawe Falls with a sheer drop of over 300 m (Englund & Filbert, 1997).

Genetics and isotope analysis

Surveys of genetic variation in Hawaiian stream fishes with protein electrophoresis (Fitzsimons *et al.*, 1990), mitochondrial DNA restriction site analysis (Zink *et al.*, 1996), and mtDNA sequencing (Chubb *et al.*, 1998) revealed no evidence of discernible geographic (island) structuring among the five species of amphidromous fishes. These data suggest that there is either a single offshore pool of larvae that recruit to each of the five major islands or that recruitment is from local offshore populations but with sufficient exchange of larvae between islands to prevent isolation and genetic differentiation.

A comparison of data from stable isotope analysis (carbon and nitrogen) of amphidromous fish recruits and fish species from marine habitats indicates that the source of nutrition for the stream species during their offshore larval period is near the mouths of streams (Hobson *et al.*, 2007). These findings support the idea that these larval fishes in the ocean remain close to freshwater plumes which function as nursery areas and suggest that amphidromous fish larvae may stay near their home island (or even natal stream?) rather than joining an offshore mass of larvae that contributes recruits to all the high islands. A finer focus with isotope analysis and genetics (such as microsatellite studies) may clarify details of the distribution, ecology, and population dynamics of amphidromous fishes during the marine period of their life cycle.

Parasites

The effects of alien species on indigenous aquatic animals are not well known. A striking exception is the investigation of parasites in native stream fishes associated with the introduction of alien fish species (Font, 1996, 1997a,b, 1998; Font & Tate, 1994). Fourteen species of helminth parasites have been found in stream fishes, but only three, a tapeworm (*Bothriocephalus acheilognathi*), leech (*Myzobdella lugubris*), and roundworm (*Camallanus cotti)*, which were introduced into the islands along with their alien fish hosts, are regarded as capable of causing disease in native fishes (Font, 2003). Hawaii's amphidromous fishes are diverse in their susceptibility to these potentially dangerous parasites. All three parasites are recorded by Font from *A. guamensis* and *E. sandwicensis*. *Lentipes concolor* has the roundworm, but not the other two parasite species. *Sicyopterus stimpsoni* often has leeches attached to the head and body but lacks both endoparasites. Finally, *Stenogobius hawaiiensis* has none of the three parasites.

r and K selection

Unbridled exponential growth is infrequent in natural populations. In the more universal logistic population growth, the rapid increase in number eventually peaks, slows, and stabilizes when the carrying capacity of the environment is reached. For this reason, population growth is more frequently represented by a sigmoid curve rather than a straight line. The equation for Logistic Population Growth is $I = rN (K - N / K)$, where I = the annual increase for the population, r = the annual growth rate, N = the population size, and K = the carrying capacity. The concepts of r and K selection originate from this equation. In a simplified definition, r selection is a form of natural selection that occurs when the environment has abundant resources that favor, among other things, a reproductive strategy of producing many offspring. Conversely, K selection is a type of selection in an environment that is at or near carrying capacity, and limited resources favor a reproductive strategy in which few offspring are produced. From that criterion alone, stream fishes in Hawai‘i are clearly r-selected. However, there are other characteristics of r- and K-selected populations that can be considered: In environments where the availability of resources exceeds demands, the lack of competition promotes selection for early reproduction, fast growth, and short life spans (= r selection of Pianka, 1970). In environments where the demand for resources is about the same as the available supply, natural selection promotes competition among species that results in the evolution of slower growth, a delay in reproduction, and longer life spans [= K selection of Pianka (1970)]. In addition, extreme r-selected species are thought to be characteristic of unstable environments and density independent interactions, while extreme K-selected species are indicative of stable environments and density dependent interactions. These and other features of r- and K-selected species that appear most relevant to fishes in general are placed in Table 1 for a discussion of Hawaiian amphidromous fishes

Table 1. Characteristics of animals that are extreme r or K strategists. Loosely based on Campbell & Reece (2002); Gould (1997); Pianka (1970); Raven & Johnson (2002); and adapted for fishes.

r	K
unstable environment	stable environment
density independent interactions	density dependent interactions
small size	large size
energy used to make each individual is low (small size at birth)	energy used to make each individual is high (large size at birth)
weak, vulnerable	robust, well-protected
high mortality	low mortality
rapid growth	slow growth
early maturation	late maturation
short life expectancy	long life expectancy
each individual reproduces only once	individuals can reproduce more than once in their lifetime
little or no care for the offspring	much care for the offspring
variable population size	stable population size

with reference to the following questions: How do Hawaiian amphidromous fishes fit into the r-K selection continuum? Are they strongly associated with one extreme or do they show a blending or mosaic of the individual attributes of r and K selection?

To begin with, it can be argued that the equation for logistic population growth cannot be applied to indigenous stream fishes in Hawai‘i because r (the annual growth rate) is based on reproduction by members of the population in essentially a closed system. Because of their amphidromous life cycle, every fish in every Hawaiian stream is a migrant and may or may not have begun life in the stream where it is observed, and there is no certainty that young animals are the offspring of adults in the same stream. The equation perhaps can be salvaged for Hawaiian stream fishes merely by changing r to R_s, the latter representing the site specific (s) annual rate of increase (R) attributable to recruitment, and rewriting it as $I = R_sN (K - N / K)$. The emphasis here is that population increases are caused by recruitment whether or not the recruits originate from the stream in question.

Although juveniles and adults of amphidromous species in Hawai‘i live in an unstable environment because of recurring flash floods, it might be argued that their free-living embryos and larvae in the ocean live in a relatively more stable environment. If this assumption is correct, these fishes are r-selected in fresh water and K-selected in marine environments (Table 1). The situation in terms of r and K selection in the two environments is reversed when considering that density independent interactions, a feature of r-selected populations, are likely among the thousands of young fishes washed out of streams into the ocean, while the highly social adults are concentrated in finite sections of streams where interactions are density dependent, a feature of K-selected populations. Small size (r) characterizes the newly hatched free-living embryos (ca. 1.5 mm total length); adults are appreciably larger (K) even in comparison to the adults of most species of marine gobies and eleotrids. The energy used to make each individual, i.e., relative size at birth, is clearly low, an r-selected feature. Although the terms are subjective, amphidromous fishes offshore could be described as weak and vulnerable (r). In contrast, adults in streams, particularly the three upstream species, are much larger, robust, and mostly free from predators (K). Mortality rates are unknown for amphidromous fishes, but it is likely that there is higher mortality (r) among recently hatched fishes and lower mortality (K) among adult fishes once they are established in species-specific stream habitats. Evaluating growth as rapid or slow among amphidromous fishes is tentative because age-and-growth studies are lacking. Depending on the species, newly hatched embryos can increase in total length as much as 16 times (e.g., 1.5 mm TL for embryos vs almost 24 mm for recruiting *S. stimpsoni*; Nishimoto & Kuamoʻo, 1997). Casual underwater observations suggest that males and females have indeterminant growth, but a change in size associated with the transition from juvenile to adult or with growth among adults is much less dramatic among stream-living fishes (K) than among conspecific young fishes in the ocean (r). Stream fishes mature late (K) when the lengthy larval period is added. Although there is no published information on age at maturity, the small size of spawning fishes observed underwater indicates they become reproductively competent in a short time (r), i.e., less than a year, after recruiting into streams. If *L. concolor* is typical of other stream fishes in Hawaiʻi, life expectancy would be considered long (K) in comparison to other similar sized fishes (Nishimoto & Fitzsimons, 1986). Stream gobies and eleotrids reproduce more than once in their lifetime (K); none die after spawning as do many species of anadromous fishes that also leave the marine environment and reproduce in fresh water. All but one species (*S. hawaiiensis*) are territorial at spawning sites and provide some amount of protection for the eggs (K). Population sizes are unknown for larval amphidromous fishes, but the potential for tracking changes in population size for adults in streams may be possible soon by using the freshwater database being developed by the Hawaiʻi Division of Aquatic Resources. In an island stream, population size reflects the balance between mortality and recruitment, but not reproduction, unless it can be demonstrated that recruitment involves significant homing to a natal stream. Recall that the equation proposed above for logistic population growth in Hawaiian streams substitutes recruitment for natural reproduction.

When the results of this discussion are tallied, larval fishes during the marine period of their life cycles appear to be mostly r-selected, while adults established in species-typical stream habitats are mostly K-selected.

Although this discussion is largely moot and academic, there are two possible conclusions that may have some practical merit. First, an amphidromous life cycle involving life in both fresh water and the sea makes it difficult, if not impossible, to apply to Hawaiian streams many analytical techniques basic to understanding the biology of streams and rivers on continents. Clearly, the biology of island amphidromous fishes is "strongly influenced by both these hydrologic systems" (Kinzie, 1988). Secondly, this discussion has proceeded mostly from educated guesses rather than hard data, and, instead of providing valuable reference material, it shows that even the most rudimentary baseline studies for Hawaiian stream fishes are either deficient or absent. The inevitable statement "more studies are needed" applies here.

Conservation

None of the five species of Hawaiian amphidromous fishes is currently threatened or endangered (Devick *et al.*, 1995). Because of the earthʻs rotation, trade winds continue to flow up the northeast sides of the high islands to cooler elevations where they produce the orographic rainfall that maintains forests, the perennial streams that run through them, and the animals that live in the clear, cold water. The larvae of amphidromous fishes, limpets, shrimp, and prawns continue to recruit from the ocean into brackish and fresh waters where they complete their life cycles. Periodic flash floods continue to clean out streams, and recruits from the ocean periodically "top off" populations of aquatic animals. This perpetual natural recycling maintains the dynamic conditions in Hawaiian streams that guarantee the persistence of a unique assemblage of organisms. These animals persist as living links to the evolutionary origins of both aquatic and terrestrial life on these islands, and they were vital to survival of the Polynesians who first colonized Hawaiʻi. The situation seems at once idyllic, perpetual, and maybe even unassailable. But there are catches.

In Hawaiʻi, freshwater organisms are confined to relatively small streams where they are easily vulnerable to human influences. Any material taken from a stream or dumped into it is likely to have an immediate effect. Any activity that blocks access to or from the sea shuts down the life cycles of the principal stream animals and eventually results in the loss of those species from the stream. Fresh water is usually abundant on each of the major islands. However, it is not limitless, and it seldom occurs naturally on the leeward sides of islands. The disparity in the distribution of rainfall on the islands in combination with human needs and wants – and these are not necessarily synonymous – automatically makes water a potentially scarce resource.

Until the late 1980s, the prevailing attitude was that water flowing into the sea was wasted (Devick, 1995). Indiscriminate diversion of water for agriculture (mainly sugar cane), development (often in arid areas), and other activities led to a wide-spread diminution of flow or a complete dewatering of many streams. The result was a loss of aquatic communities, a decline in taro production, and a reduction of productivity in the ocean near the coast where streams once emptied. Conditions began improving in 1987 with the establishment of a State Water Code and the formation of the Commission on Water Resource Management (Devick, 1995; Devick *et al.*, 1992); these two actions gave the State, rather than individual landowners, authority over the use of streams.

Hawai‘i has been faulted for not joining other western states in the designation of minimum flow requirements to protect its stream animals. Critics do not understand the variable nature of flow in Hawaii’s streams, know little or nothing of amphidromy, and have not experienced in their own states the flash floods that occur frequently in Hawai‘i. In lieu of setting meaningless minimum flow requirements for all Hawaiian streams, William S. Devick, Administrator of the Division of Aquatic Resources, established a policy of “no net loss of habitat” in stream-use decisions (Devick, 1995). This approach has been successful, and, in retrospect, it is infinitely more logical and amenable to implementation than mainland procedures because the focus is on the requirements of stream animals rather than on a range of numbers describing the amount of water that flows over a section of stream during a certain period of time.

During Devick‘s service as DAR Administrator, he established four levels of stream protection (Devick *et al.*, 1992) that go well beyond conservation measures developed for streams in other states. Conservation zoning places designated streams into discrete Conservation Districts (1) which extend protection to entire stream corridors and incorporate all perennial streams. Interim Instream Flow Standards (2) for individual streams are based on existing flows, and activities affecting the stream beds, i.e., animal habitats, are closely regulated. The program of Stream Ecosystem Protection (3) halts further development of selected streams and their corridors while retaining existing uses. The development of a Natural Areas Reserve System (NARS) (4) preserves and restores designated areas that represent important freshwater ecosystems.

The Endangered Species Act is viewed sometimes as the first and sometimes as the last defense against the extinction of a species. A correlative idea is that protection of one species provides protection for all the other organisms in the area. This notion seems applicable to Hawaiian stream fishes because of their amphidromous life cycles, but, as emphasized throughout this paper, the five species of fishes are different in where they live in a stream and what they do for a living. A focused effort for restoring and protecting one species may or may not provide assistance to others. Instead, actions that provide protection of habitat by preserving entire ecosystems are preferable to a limited concentration on single species (Devick *et al.*, 1995). An ideal tactic is to maintain aquatic ecosystems so that invoking the Endangered Species Act never becomes necessary. The five species of fishes discussed in this paper possess remarkable diversity in their behavior and ecology, but the key to their protection lies with their common amphidromous life cycle. For an unaltered stream that flows briskly into the ocean along an open coast, the best protection may be to do nothing at all. Simply leave the stream unaltered. The animals themselves will take it from there.

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