The Potential for Source-Sink Population Dynamics in Hawaii's Amphidromous Fishes

MARK G. MCRAE

*Museum of Natural Science, Louisiana State University, Baton Rouge, LA 70803 U.S.A.; e-mail:
mmcrae@paws.lsu.edu*

Abstract

To ensure successful reproduction, Hawaii's amphidromous gobioid fishes (*'o'opu*) must have their
offspring successfully migrate from instream hatching sites to oceanic larval habitats. The differen-
tial ability of the five species of *'o'opu* to climb waterfalls influences how far inland each species can
invade in individual streams and determines their instream distributions. Given the short amount of
time that *'o'opu* free-embryos can persist in fresh water, a possible negative correlation exists
between the distance that an individual lives from the stream-mouth and the likelihood that the off-
spring that individual produces will successfully migrate to the ocean. Recruitment of post-larvae
originally spawned in streams that function as source habitats can sustain local populations of *'o'opu*
that live in streams that function as sink habitats. For this reason, management techniques that utilize
population density or biodiversity as indicators of habitat quality are not applicable for the manage-
ment of *'o'opu* populations. A clearer understanding of the role that the pre-marine phase is playing
in the population dynamics of *'o'opu* will allow for more responsible freshwater resource manage-
ment in Hawai'i.

Introduction

The fishes, crustaceans, and mollusks that make up Hawaii's indigenous stream-dwelling macrofau-
na are believed to be derived from marine ancestors and to have retained a pelagic marine larval
phase (Radtke & Kinzie, 1996); all nine species have amphidromous life cycles. All of the five
species of fishes are in the suborder Gobioidei and are referred to collectively as *'o'opu. Lentipes
concolor*, *Sicyopterus stimpsoni*, *Stenogobius hawaiiensis*, and *Awaous guamensis* are in the family
Gobiidae, while *Eleotris sandwicensis* is in the family Eleotridae. Amphidromy is a form of
diadromy, or a life cycle that is split between freshwater and marine environments (McDowall,
1992). Specifically, juveniles and adults live in stream or river habitats, where demersal spawning
takes place. Newly hatched free-embryos drift downstream towards their oceanic feeding sites. Once
in the ocean, the larvae become a part of the pelagic zooplankton community until they mature into
post-larvae (Radtke *et al.*, 1988). Post-larvae must then migrate back into fresh water where they
metamorphose into juveniles (Nishimoto & Kuamo'o, 1997). Due to this dependence on marine
environments, none of the indigenous species of fishes and macroinvertebrates that live in Hawaii's
streams and rivers can be considered primary or secondary freshwater organisms (McDowall, 1997;
Balon & Bruton, 1994).

Indeed, these species' life-history characteristics are much more similar to those for species
which inhabit nearshore marine environments such as coral reefs and intertidal zones (Leis, 1991;
Pfister, 1999). Similar to patch reefs and discrete tide pool habitats, each stream represents a habitat
patch (Hanski, 1991). The groups of individuals inhabiting each stream make up local populations
which are portions of the larger genetically and ecologically connected meta-population (Hanski,
1991; Chubb *et al.*, 1998). It is the marine larval phase which connects these local populations.

Stochastic phenomena in marine environments can lead to extremely high mortality rates for
ichthyoplankton through mechanisms such as starvation, predation, or advection away from suitable
larval or adult habitats (Doherty, 1991; Houde, 1989). Stochastic events have strong effects on

observed patterns in recruitment, and ultimately, adult population and community structure (Doherty & Fowler, 1994; Pfister, 1999). Organisms with amphidromous life cycles are similarly subject to high mortality rates that take place during their marine larval stage (Radtke & Kinzie, 1996). Unlike nearshore marine species, however, amphidromous species have an additional life-history stage during which they may experience high mortality rates (Bell & Brown, 1995; Iguchi & Mizuno, 1999). The time period which begins at hatching and extends until the free-embryo passes out of the mouth of the stream into the ocean represents a critical step in this complex life cycle, during which biological, hydrologic, hydrographic, geomorphometric and anthropogenic stream features may affect migratory success and survival (Iguchi & Mizuno, 1990; Bell & Brown, 1995; Lindstrom, 1998; Moriyama *et al.*, 1998; Way *et al.*, 1998; Iguchi & Mizuno, 1999; March *et al.*, 2003). The life stage during which free-embryos must migrate to the ocean can be thought of as a "pre-marine" stage (Font, 1996), and will be referred to as such throughout the remainder of this paper.

The purpose of this review is to explore the existing literature on pre-marine stage amphidromous organisms, with a focus on the amphidromous fishes of the Hawaiian Islands. A description of the range of stream habitats that must be traversed by seaward migrating larvae will be followed by a description of the instream distribution patterns of the adult fishes. A review of what is currently known about the behavior, physiology, and ecology of pre-marine amphidromous fishes will then be summarized to gain insight into the potential implications that the unique aspects of this life history stage have on the population ecology and conservation of these species.

Lotic Habitats in the Hawaiian Islands

Polhemus *et al.* (1992) outlined a classification for continuous perennial stream reaches on islands in the tropical Pacific in which three main reach-type divisions were described based on gradient, physico-chemical characteristics, and faunal composition. Headwater reaches were described as being high in elevation (> 800 meters) with high gradient (> 30%), and substratum comprised mainly of bedrock. Midreach areas are generally between 50 and 800 meters in elevations, between 5% and 30% gradient, with substrata predominantly boulders, rocks and gravel. Terminal reaches were defined as "watercourses below sharp gradient that bars upstream migration of itinerant marine fishes" (Polhemus *et al.*, 1992). Elevations in terminal reaches are usually <50m and gradients <5%, with substratum consisting mainly of cobble, gravel, sand, and sediment. Mizuno & Kawanabe (1981) outlined a topographically based classification system for stream reaches in Japan which defines reach types by two topographic criteria. The first criterion is the number of riffle/pool sequences in stream segments between meander bends. Type "A" reach types have more than one riffle/pool sequence between bends, while Type "B" reaches have only one. The second criterion relates to the gradient and turbulence of riffles or cascades connecting the pools. Type "a" are waterfalls, Type "b" are turbulent, high-gradient riffles or cascades, and Type "c" are smooth, low-gradient riffles. Thus, a steep reach having two or more plunge pools separated by waterfalls in each segment between meander bends is defined as Type Aa (Fig.1), whereas a reach of moderate gradient with only one pool and turbulent riffle between bends is defined as Type Bb. Mizuno & Kawanabe's (1981) finer-scaled classification system will be used, along with the broader-scale classification of Polhemus *et al.* (1992) to describe the range of stream and reach types that amphidromous fishes inhabit in the Hawaiian Islands.

Two main stream types exist in the Hawaiian Islands, and they represent the extremes in a spectrum of stream morphologies which ranges from low discharge, high gradient streams to relatively high discharge, long streams with terminal reaches that can form estuarine habitats near the stream mouth (Nishimoto & Kuamo'o, 1991). On the geologically younger islands such as Hawai'i and Maui, short, steep, straight streams are the most common stream type (Nishimoto & Kuamo'o, 1991), with Type Aa and Ab reaches extending from the mouth of the stream up to the headwaters. In these relatively young streams, waterfalls, cascades, and plunge pools are abundant (Fig. 1), with the stream often entering the ocean as a terminal waterfall – the stream falls off the edge of a cliff

Figure 1. Midreach of Umauma Stream, Island of Hawai'i, demonstrating an example of "Aa" topography.

either into the ocean or onto a narrow rocky beach (Fig. 2). On the relatively older islands such as O'ahu and Kaua'i, larger stream systems are more common than they are on the younger islands. Long, low gradient terminal reaches exist upstream of sinuous mixohaline estuaries (Nishimoto & Kuamo'o 1991), above which can exist long midreach areas dominated by Type Bc and Type Bb reaches which grade into type Ab reaches farther inland. Type Aa reaches are encountered in these "terminal estuary streams" in upper midreach and headwater areas which can be several kilometers inland from the mouth of the stream (Fig. 3).

Instream Distributions of Hawaiian Amphidromous Gobies

The distributions of juvenile and adult amphidromous fishes in Hawaiian streams are strongly influenced by the ability of each species' postlarvae to surmount obstacles to upstream migration (Nishimoto & Kuamo'o, 1997). Three of the five species have the ability to climb the vertical rock

Figure 2. Terminal waterfall at the mouth of Manoloa Stream on the Island of Hawai‘i.

faces associated with waterfalls when they are post-larvae and juveniles by using pelvic fins which are fused to form a suction disk. *Eleotris sandwicensis* lacks fused pelvic fins while *S. hawaiiensis* has fused pelvic fins, but lacks the associated musculature necessary for climbing waterfalls (Nishimoto & Kuamo‘o, 1997). Both species, therefore, are precluded from dispersing upstream of any precipitous waterfall and are restricted in their distributions to terminal reaches and terminal estuaries. *Awaous guamensis* and *S. stimpsoni* can climb and disperse beyond moderately high waterfalls (less than ~20 m) and are found in Type Bc, Bb, and Aa midreaches up to an elevation of approximately 150 m (Fitzsimons & Nishimoto, 1990). Vertical waterfall height does not appear to be a limiting factor for *L. concolor* as they migrate upstream. *Lentipes concolor* has been sighted at elevations higher than 1 km (Fitzsimons & Nishimoto, 1990) and in stream reaches that were located above a waterfall with a more than 300 m vertical height (Englund & Filbert, 1997; personal observation).

Because the instream distributions of the five amphidromous Hawaiian gobioids are largely determined by their waterfall-climbing ability, it follows that the distribution patterns will vary with the type of stream into which they recruit (Nishimoto & Kuamo‘o, 1991). In large streams with terminal estuaries, it is common to find juveniles and adults of all five species, with *E. sandwicensis* and *S. hawaiiensis* occurring only in the terminal estuary, terminal reach, and lower midreach areas. *Awaous guamensis* and *S. stimpsoni* are common in the upper regions of the terminal reach and in midreach areas, with *L. concolor* farther upstream in the upper midreaches (Fig. 4). In these terminal estuary streams, *L. concolor* appear to migrate inland until they encounter their preferred Type Aa habitats (Kinzie, 1988) and are therefore often located farther inland than any of the other species

Figure 3. Example of a terminal estuary stream. Wailoa Stream, Waipiʻo Valley, Island of Hawaiʻi. Photo by D.G.K. Kuamoʻo.

(Nishimoto & Kuamoʻo, 1991; Kinzie, 1988; Kido *et al.*, 2002). Similar waterfall-delineated in-stream distribution patterns have been described for assemblages of amphidromous gobies in Micronesia (Parham, 1995; Nelson *et al.*, 1997).

    In terminal-waterfall streams, the two non-climbing species, *E. sandwicencis* and *S. hawaiiensis* are either absent or restricted to the short stretch of stream running across the narrow rocky beaches that are often at the base of coastal cliffs (Nishimoto & Kuamoʻo 1991; Fig. 2). The number of species that occur upstream of terminal waterfalls can range from one to three and depends on the height of the waterfall. In streams with the highest terminal falls, *L. concolor* can be the only
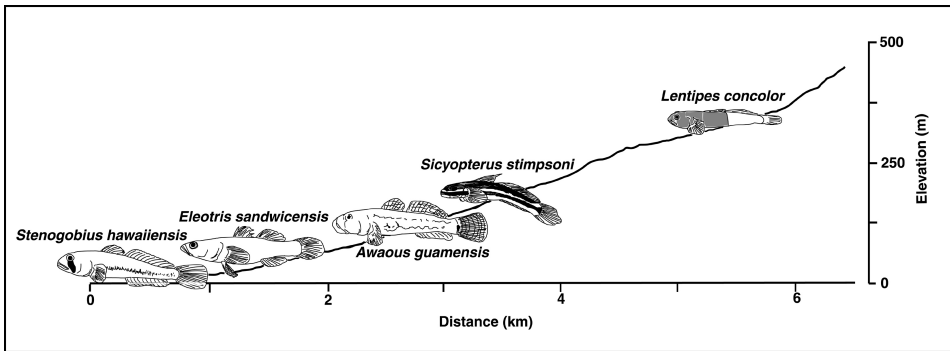
Figure 4. Elevational profile of a terminal-estuary stream on the Big Island of Hawai'i (Hakalau Stream). Adapted with permission from Nishimoto and Kuamo'o (1991).

species present, and they often occur in high densities a relatively short linear distance from the mouth of the stream, presumably because they encounter preferred Type Aa stream reaches as soon as they arrive at the top of the falls (Fig. 5).

When one considers the wide range of distances and reach types that seaward migrating pre-marine amphidromous fishes must travel on their way to oceanic feeding sites, it becomes clear that there is a high potential for this pre-marine stage to play a critical role in the population dynamics of these species. This is especially true for populations of *L. concolor*, which can be found a few meters away from the ocean in small, terminal-waterfall streams, or several kilometers away from the ocean in the upper midreaches and headwaters of larger terminal-estuary streams (Nishimoto & Kuamo'o, 1991). The following section synthesizes the research that has been done on the behavior and survival of pre-marine amphidromous fishes that relates to potential survival limitations.

Pre-Marine Amphidromous Fishes

Amphidromous fishes emerge from demersally spawned eggs in a highly under-developed state and are referred to as free-embryos (Balon, 1990; Balon & Bruton, 1994). During the pre-marine stage, free-embryos are unable to feed and survive on nutrition from a yolk sac until they arrive at their oceanic feeding sites (Lindstrom, 1998; Bell & Brown, 1995). *Awaous guamensis*, *L. concolor*, and the Caribbean species *Sicydium punctatum* were all observed to die after being held in fresh water for only four days (Ego, 1956; Lindstrom, 1998; Bell & Brown, 1995). Tomihama (1972) reported that *S. stimpsoni* free-embryos died after five days in fresh water. *Rhinogobius brunneus* (Japan) free-embryos lived for seven days in fresh water (Iguchi and Mizuno, 1999), but were observed to reach an irrecoverable starvation state (ISS) after approximately six days. If it is assumed that the Hawaiian species similarly reach ISS at some point before death in fresh water, it is clear that pre-marine 'o'opu have a discrete "window of opportunity" to move from their freshwater hatching sites to their oceanic feeding sites.

Temporal patterns in seaward migration of pre-marine amphidromous fishes have been observed at both the lunar and daily scale. Lindstrom (1998) reported that spawning in captive populations of *L. concolor* peaked during the new moon, which corresponds to observed new-moon peaks in the seaward migration of *L. concolor* free-embryos captured during stationary drift-net sampling (McRae, unpublished data). Lindstrom (1998) also reported that hatching of eggs from captive *L. concolor* took place after sunset. Post-sunset hatching may explain post-sunset peaks in the daily drift patterns observed for that species in streams on the Island of Hawai'i (McRae, unpublished data). New moon and post-sunset peaks in migration possibly evolved as ways to avoid capture by visually oriented planktivores that live in lower stream reaches and estuaries. No significant seasonal pattern in seaward drift has been observed in 'o'opu free-embryos (Way *et al.*, 1998; Lindstrom, 1998).

Figure 5. Elevational profile of a terminal-waterfall stream (Manoloa Stream) on the Big Island of Hawai'i. Adapted with permission from Nishimoto & Kuamo'o (1991).

It has been hypothesized that pre-marine amphidromous fishes can experience high mortality rates during their downstream journey towards the ocean. *Sicydium punctatum* free-embryos captured in streams on the island of Dominica, W.I. were generally <24 hours old (Bell & Brown, 1995). Bell & Brown (1995) also estimated that mortality rates for newly hatched *S. punctatum* were as high as 50% hour[-1]. Moriyama *et al.* (1998) concluded that in normal or low river flow conditions, most *R. brunneus* free-embyos hatched at high gradient upstream reaches likely starved to death before reaching the sea.

Adults of the amphidromous species *A. guamensis* in Hawai'i (Ego, 1956; Harrison *et al.*, 1991; Kido & Heacock, 1991) and *Plecoglossus altivelis* in Japan (Iguchi *et al.*, 1998) migrate to spawning sites in lowland stream reaches near to stream mouths presumably as a strategy that reduces the distance and time required for free-embryos to reach the ocean. However, for species such as *L. concolor*, which often inhabit stream reaches that are upstream of major waterfalls, such downstream migrations have not been observed. For these species, the distance that free-embryos are required to migrate downstream roughly estimates total drifting time (Iguchi & Mizuno, 1999) and as a result likely has a strong effect on the overall fitness of individuals in local populations. The following section describes features of Hawaiian streams that may lengthen total drifting time and contribute to increased risk of mortality for pre-marine amphidromous gobies.

Instream Obstacles to Seaward Migration

Stream features that exist between hatching sites and the ocean can potentially increase the amount of time that *'o'opu* free-embryos spend in-transit on their way to their oceanic feeding sites and consequently can decrease their chances for survival. Low water velocity habitats in midreach, terminal reach, and terminal estuaries can retain the passively migrating free-embryos in freshwater habitats. Terminal reaches and estuaries also often have high densities of introduced freshwater and itinerant marine zooplanktivorous fishes (McRae, 2001) that likely prey upon drifting *'o'opu*.

Low water velocity habitats, such as plunge pools, side pools, and backwater eddies are abundant in the Aa and Ab reaches that are common in the headwaters and upper midreaches of Hawaiian

streams. On the geologically young islands of the Hawaiian Archipelago, waterfalls are abundant throughout the midreaches of perennial streams. Their associated plunge pools can be very deep and wide in spite of the relatively low discharge of these watersheds (Fig. 1). Each of these plunge pools, during all but the most intense freshets, represents a naturally semi-impounded habitat, inside which water velocities can be practically imperceptible. These midreach low-water-velocity habitats are likely significant obstacles to pre-marine gobies as they migrate to sea (Moriyama *et al.*, 1998). Plunge-pools can also contain large populations of introduced poeciliid fishes (e.g., guppies, *Poecilia reticulata* and swordtails, *Xiphophorus helleri*) that may prey upon the free-embryonic gobies that are entrained in these low-water-velocity habitats.

Similarly, long terminal stream reaches and terminal estuaries not only increase the amount of time that pre-marine *‘o‘opu* spend in transit to the ocean, but they also are often home to large populations of native and introduced zooplanktivorous freshwater and marine fishes (McRae, 2001). The endemic āholehole, *Kuhlia xenura*, feed actively on food items drifting downstream and are common in terminal stream reaches in Hawai‘i. Their adaptation for nocturnal activity patterns potentially allow them to feed during the post-sunset peak in seaward migration of pre-marine gobies. Introduced mosquitofish, *Gambusia affinis*, are well known larvivores and zooplanktivores (Arthington, 1991; Komak & Crossland, 2000) that likely feed very heavily on any free-embryonic amphidromous organisms that end up in the slack-water habitats they prefer (McRae, 2001). Shortfin mollies, *Poecilia mexicana*, swordtails, and tilapia, *Oreochromis mossambicus* are common introduced fishes in Hawaii's terminal streams and estuaries (Devick, 1991; McRae, 2001) that are known to be at least opportunistically zooplanktivorous.

Conclusions

Population Ecology

The term "metapopulation" has been defined as a system of local populations connected by dispersing individuals (Hanski, 1991). The local populations of amphidromous fishes that live in individual streams throughout the Hawaiian Islands likely represent portions of a larger, interconnected metapopulation (Kinzie, 1993; Font, 1996). Linked closely with this concept is the idea that habitat-specific demographic rates of local populations can have significant impacts on the growth and regulation of the overall metapopulation (Pulliam, 1988). "Sink" habitats are habitat patches (e.g., individual streams) where within-habitat reproduction is insufficient to balance local mortality. Local populations in sink habitats can nonetheless persist through the input of continual immigration from more-productive "source" habitats. Source habitats are, in general, net exporters of individuals, while sinks are net importers of individuals (Pulliam, 1988).

Large streams with terminal estuaries may be playing a critical role as source habitats for metapopulations of non-climbing *‘o‘opu* (*S. hawaiiensis* and *E. sandwicensis*) throughout the Hawaiian Islands. The low gradient, low water velocity habitats that are preferred by nonclimbing *‘o‘opu* are abundant in the long, sinuous terminal reaches of these streams, and these habitats are located close to stream mouths, where free-embryos can have easy access to marine larval habitats. The large, high discharge systems produce large freshwater plumes that extend into the nearshore marine environment and likely act as strong olfactory navigational cues for post-larvae of all five species to recruit into these streams (Nishimoto & Kuamo‘o, 1997). Individuals of the three climbing *‘o‘opu* (*A. guamensis*, *S. stimpsoni*, and *L. concolor*) disperse upstream until they encounter the large amounts of suitable adult habitat that exists in the inland mid and headwater reaches. These relatively large stream systems may represent ecological sinks for the three species of climbing goby that recruit into these habitat patches because a large proportion of their offspring may starve to death and/or be eaten before reaching the ocean. This may be especially true for *L. concolor* because of their tendency to occur farther inland in streams of this type than any other species of *‘o‘opu* (Fig. 4). It is possible that the turbulent flow characteristics of these inland, high gradient reaches, together with the length, low-gradient, and high predator densities of terminal reaches and estuaries may retain *L. concolor* free-embryos at instream sites longer than their three to four day

migratory "window-of-opportunity" (Lindstrom, 1998). Large inland populations of *L. concolor* and *S. stimpsoni* (Nishimoto & Kuamoʻo, 1991; Kido *et al.*, 2002) are possibly sustained by recruitment of post-larvae originally spawned in smaller streams by relatively small, near-shore adult populations.

Conversely, the smaller terminal waterfall streams are probably important ecological sources for the three waterfall climbing species. This is especially likely for *L. concolor* which can be found in very high population densities a very short distance from the ocean in these streams (Fig. 5). Thus, the majority of the free-embryos that are produced in terminal waterfall streams are likely successful in migrating downstream to their oceanic larval habitats. These small, high gradient systems, however, are almost assuredly ecological dead ends, or sinks, for individuals of the two non-climbing amphidromous fishes that may recruit into them.

There are many streams throughout the Hawaiian Islands that are intermediate in length, gradient, and reach-type diversity and are not categorized adequately by either the terminal-waterfall or terminal-estuary stream descriptions. The distribution of *L. concolor* and/or *S. stimpsoni* in these watersheds can often start a few to a few hundred meters above the stream mouth and extend for several kilometers inland. If individual fitness is defined by the contribution made to future generations (Smith, 1995), then there could be a negative correlation between fitness and distance from the stream mouth for individuals of the waterfall-climbing species of *ʻoʻopu* in Hawaiian streams.

Conservation

Most fishes that live in continental streams and rivers are primary freshwater fishes that complete their entire life cycles within individual streams. As such, the fitness or health of individual populations in continental streams can be correlated with population size. Similarly, in these "closed" systems, it can be argued that population size is an indicator of habitat quality. These relationships between population size and population fitness or habitat quality have led to the development of management techniques that allow a comparison of the relative health (or biological integrity) of individual habitats (Karr & Chu, 1999). Specific management plans can then be developed for individual habitats based on these assessments.

The unique aspects of the life-history strategies and population ecology of the indigenous fishes that live in Hawaii's streams and rivers necessitate unique approaches in the management of these species. The profound differences in the biological characteristics and ecological requirements that exist between adult fishes and free-embryos result in no direct correlation between adult local population density and the ability of the individuals in that local population to successfully reproduce. A similar lack of a relationship exists between local population density and habitat quality. If a habitat is defined as an area in which a local population can successfully live and reproduce, then for Hawaiian amphidromous fishes, population size or density alone does not necessarily correspond to habitat quality. Habitat quality in individual streams must be assessed with regard to whether the habitat patch is a net exporter (source) or net importer (sink) of individuals. Such definitions of habitat quality depend on many variables including distance of reproducing individuals from the ocean, overall stream gradient between hatching sites and the ocean, water velocity-depth relationships between hatching sites and the ocean, overall densities and distributions of predators downstream from hatching sites, *as well as* the local population density of adult *ʻoʻopu* that occupy that stream. When such variables are acknowledged as being critical measures of habitat quality in a stream, it becomes clear that densities of adult fishes in lower-quality, sink habitats may actually be greater at times than in the high-quality source habitats (Van Horne, 1983; Pulliam, 1988). If amphidromous fishes in Hawaiʻi exist in open populations, then the scale at which habitat quality assessments should be made increases beyond the level of individual streams (Caley *et al*., 1996).

Patterns in the instream distributions of adult amphidromous fishes in Hawaiian streams are species-specific (Nishimoto & Kuamoʻo, 1991). Stream characteristics that define high-quality source habitats for one species (e.g. terminal waterfall streams for *L. concolor*) can define low-quality sink habitats for another species (e.g., terminal waterfall streams for *E. sandwicensis*). The overall biodiversity of native amphidromous fishes in a single habitat patch (stream) is not, therefore, necessarily correlated to habitat quality. A stream that contains the entire compliment of Hawaii's amphidromous fishes may only be a source for those species that live nearest to the mouth of the stream. For those species that live relatively far inland in these streams, recruitment into the habitat could far exceed

successful seaward migration. Conversely, a stream could only have one species of fish present, and yet such a stream could "export" far more individuals of that one species than it "imports".

Most anthropogenic perturbations in streams take place in lowland, nearshore reaches that lie between hatching sites and the ocean. Such habitat alterations could negatively impact the species of 'o'opu that inhabit the affected reaches (e.g., *S. hawaiiensis* and *E. sandwicensis*), as well as species that may live farther upstream (e.g., *L. concolor* and *S. stimpsoni*). Channelization or water extraction can alter stream morphologies and flow characteristics which could decrease the chances of successful seaward migration of 'o'opu free-embryos. The high densities of introduced larvivorous fishes that are commonly found in lowland terminal reaches could also result in significant increases in the mortality of pre-marine 'o'opu. Human disturbances in lowland areas can also eliminate near-ocean, high quality adult habitats for *L. concolor* and *S. stimpsoni* while allowing upstream, inland populations to persist in undisturbed adult habitats in the same watershed. The high population densities of these species that exist in the inland reaches of such streams could actually be utilizing the lowest quality habitats present in that watershed because they might only rarely, if ever, have their offspring successfully migrate to sea.

While a handful of landmark studies have focused on the pre-marine stage in the life cycle of Hawaii's amphidromous fishes (Ego, 1956; Lindstrom, 1998) detailed descriptions of the biology, behavior, and ecology of the pre-marine stages of all 'o'opu species are needed. What are the spatial and temporal patterns in seaward migration for all five species? Are some streams or stream reaches functioning as source habitats and others as sink habitats? Are introduced predators consuming significant numbers of larval 'o'opu? What is the appropriate scale at which to assess habitat quality for amphidromous fishes in Hawai'i? These, and related questions need to be addressed so that resource managers in Hawai'i will be equipped to make responsible decisions regarding stream protection and restoration.

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