

Production, Marine Larval Retention or Dispersal, and Recruitment of Amphidromous Hawaiian Gobioids: Issues and Implications

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Abstract

Freshwater habitat alteration can have detrimental effects on amphidromous Hawaiian fishes. Although much information has been collected on adult and post-larval life-stages, there is little information collected on the egg, yolk-sac, and marine larval stages. The focus of this paper is to highlight what is known and what remains to be determined about larval production, mechanisms of retention or dispersal of marine larvae, and factors governing recruitment of post-larvae to freshwater streams. We highlight areas that need further investigation, and suggest how such information would affect management of freshwater habitats and amphidromous Hawaiian fishes.

Introduction

The Hawaiian Archipelago consists of a series of remote volcanic islands in the north Pacific formed relatively recently in geological time (~5.8 million years ago), and is characterized by unique flora and fauna (Carson & Clague, 1995; Funk & Wagner, 1995; McDowell, 2003). The islands are among the most isolated of the central Pacific (Scheltema *et al.*, 1996; McDowell, 2003), and this isolation is unmistakably demonstrated in the high degree of species endemism (Fitzsimons & Nishimoto, 1990; Hourigan & Reese, 1987). Of the greater than 500 species of Hawaiian marine fishes, a little less than one third are endemic to the Hawaiian Islands, and of the 5 extant species of freshwater fishes, 4 are found only in Hawai'i (Fitzsimons & Nishimoto, 1990; Hourigan & Reese, 1987; Randall, 1998). All these indigenous freshwater fish species are amphidromous and spend most of their lives in freshwater. Three gobies, *Lentipes concolor*, *Sicyopterus stimpsoni*, *Stenogobius hawaiiensis*, and an eleotrid *Eleotris sandwicensis* are endemic, whereas a fourth goby *Awaous guamensis* is panmictic in the western Pacific Ocean (Watson, 1992). Throughout this paper we will refer to all four species of gobies and the eleotrid collectively as 'o'opu; the complete Hawaiian name for amphidromous gobioid fishes is 'o'opu wai (Pukui, 1986).

The 'o'opu have similar, but dramatic life-histories that are inextricably linked to the marine environment (Kinzie, 1988; Radtke & Kinzie, 1996). Adults spawn in streams and the eggs are tended by the male for 2-3 days until hatching; paternal care of eggs has been documented in all species except for *S. hawaiiensis* (Lindstrom, 1999). After hatching, the larvae are transported to the ocean where they reside in the plankton for several months (Radtke *et al.*, 1988). Post-larvae, or early juveniles, migrate back into freshwater *en masse* and may use freshets from flashfloods as olfactory cues (Nishimoto & Kuamo'o, 1997). How far the post-larva migrates up the stream is species-dependent. *Eleotris sandwicensis* and *S. hawaiiensis* remain near sea-level and are absent upstream of the first precipitous waterfall (Nishimoto & Kuamo'o, 1997). *Awaous guamensis*, *S. stimpsoni*, and *L. concolor* use the goby-typical fused pelvic fins as a type of suction cup, and are able to climb waterfall obstacles. *Awaous guamensis* and *S. stimpsoni* are limited to waterfalls smaller than 20 m and of ele-

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variations less than 150 m; at elevations over 300 m, *L. concolor* is the only native fish found in the streams (Fitzsimons & Nishimoto, 1990). Incredibly, *L. concolor* has been sighted at elevations as high as 1 km, in a location above a waterfall with a sheer drop of 300 m (Englund & Filbert, 1997).

Amphidromy appears to be a common life-history strategy for gobioid species that colonize many of the islands in the Indo-Pacific and Caribbean regions (Keith, 2003). Some authors suggest that the amphidromous lifestyle is an indication that Hawaiian fishes first share ancestry with other amphidromous freshwater fishes in the Indo-Pacific, and these amphidromous freshwater fishes are derived from the marine environment (McDowell, 2003). Therefore, what is known about the biology of other species of amphidromous gobies should be transferable to the Hawaiian 'o'opu, with consideration of species-specific differences and the degree of geographical isolation that is unique to the Hawaiian Islands.

The Hawaiian Islands were formed by volcanic activity and have areas of high elevation (volcano peaks) that divide the islands into two distinct climates. Fresh water is predominantly restricted to small, high-gradient streams where the flow of water is dependent on orographic rainfall associated with trade winds and seasonal storms (Nishimoto & Kuamo'o, 1997). As a result, perennial streams capable of supporting populations of 'o'opu are located only on the windward sides of the islands (Fig. 1; Nishimoto & Kuamo'o, 1997), which are characterized by rain, lush vegetation, and many streams. The leeward sides are typically arid, are disproportionately populated by humans, and have been extensively developed for agriculture and tourism. Consequently, to support leeward side development, freshwater streams have undergone extensive modifications such as diversion, channelization, damming, and pollution (runoff). As a result, Hawaiian freshwater streams have declined in habitat quality and size (Brasher, 2003; Lindstrom, 1999).

Declines in suitable habitat is a problem that is much more pronounced on isolated islands like the Hawaiian Archipelago, because amphidromous species exhibit small population sizes even under pristine conditions. Mismanagement of the freshwater resource could potentially decimate populations of 'o'opu (Brasher, 2003; Radtke *et al.*, 2001).

To maintain viable populations of amphidromous gobies, effective freshwater management strategies are critical. Paradoxically, effective management of freshwater resources requires additional information on the marine larval stage. Much of the juvenile and adult life of the amphidromous 'o'opu has been studied (Keith, 2003), but there is little information available on the marine larval stage. Therefore, the focus of this paper is to review what is known about the marine larval stage, and to suggest possible mechanisms that may govern recruitment to fresh water. We will identify two main lines of scientific enquiry which we believe are critical to effective management of the 'o'opu resource. One such line is to identify mechanisms of larval retention/dispersal around the islands of Hawai'i. The second line of enquiry explores production and recruitment processes and determines whether individual freshwater streams serve as sources or sinks for 'o'opu (see McRae, this issue). The mechanisms of larval production, retention/dispersal, and recruitment to fresh waters undoubtedly are governed both by biological and physical processes. We will describe some likely mechanisms, and outline both the biological and physical processes involved. We will also highlight areas that need more information, either through carefully designed experiments, sampling regimes, or modeling.

Discussion

Larval Production

The reproductive biology of only two 'o'opu has been described (*A. guamensis* and *L. concolor*; see review by Keith, 2003). In comparison to other gobiids, amphidromous gobies are unusual; females produce many small, rather than a few larger eggs (Ha & Kinzie, 1996; Miller, 1984). As such, amphidromous gobiids are more like marine pelagic fishes that are periodic life history strategists, than typical coral reef or freshwater gobies that exhibit equilibrium-like strategies (Winemiller & Rose, 1992). A periodic strategy infers that survival of larvae is unpredictable, and environmental variations can play a dominant role in survival of a cohort.

The fecundity of *A. guamensis* is high and ranges from 56,000 to 690,000 eggs per female, with

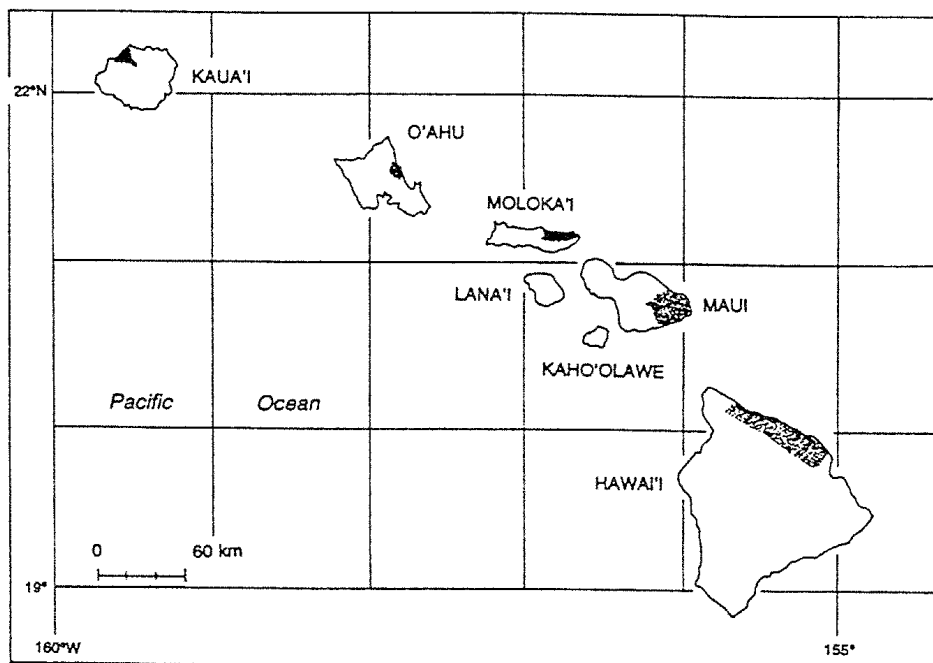


Figure 1. Main Hawaiian Islands. Stippled areas represent highest concentration of perennial streams (reprinted with permission from Nishimoto & Kuamo'o, 1997).

a very small average egg size of 0.3 mm (Ha & Kinzie, 1996). Iteroparous females spawn once between the months of August to December (Ha & Kinzie, 1996). Less fecund, batch-spawning females of *L. concolor* produce slightly larger eggs than *A. guamensis* (0.4–0.5 mm in diameter), may spawn up to 4 times a season, and produce up to 14,000 eggs each time (Kinzie, 1993). The spawning season for *L. concolor* ranges from October to June (Kinzie, 1993). There is very little information available on the reproductive biology of the other three species of 'o'opu, but it is assumed that all five species have similar reproductive strategies (Lindstrom, 1999). Clearly, detailed reproductive studies on the remaining three species would demonstrate if such assumptions are valid. For example, because annual fecundity varies by up to 50-fold between *L. concolor* and *A. guamensis*, knowledge of whether the other 'o'opu have fecundities that fall within this range, or are more or less fecund has implications for recruitment potential and dispersal (discussed below in Passive Transport).

Eggs hatch into yolk-sac larvae, a stage that appears to be sensitive to the amount of time spent in freshwater. After hatching, yolk-sac larvae passively drift downstream to the ocean and become part of the plankton. The duration of the yolk-sac stage for some species of 'o'opu was reported as 4 days (Lindstrom, 1998), and in other amphidromous Japanese gobiids in the genus *Rhinogobius*, the yolk-sac of newly hatched larvae usually is consumed within 3–7 days (Hirashimi & Tachihara, 2000). Laboratory experiments on the yolk-sac stage suggest that as larvae mature, they become less able to tolerate freshwater (summarized in Keith, 2003). Therefore, the length of time spent in fresh water can have a direct impact on mortality rates of newly-hatched larvae and can potentially select for specific reproductive sites in streams that are at favorable distances from the ocean (Iguchi & Mizuno, 1999; Keith, 2003). We can also surmise that man-made insults to streams such as channelization, diversions, or constructions of dams (Brasher, 2003; Holmquist *et al.*, 1998), could alter the length of time that yolk-sac larvae spend in fresh water and thereby affect mortality rates and hence recruitment success (Houde, 1989).

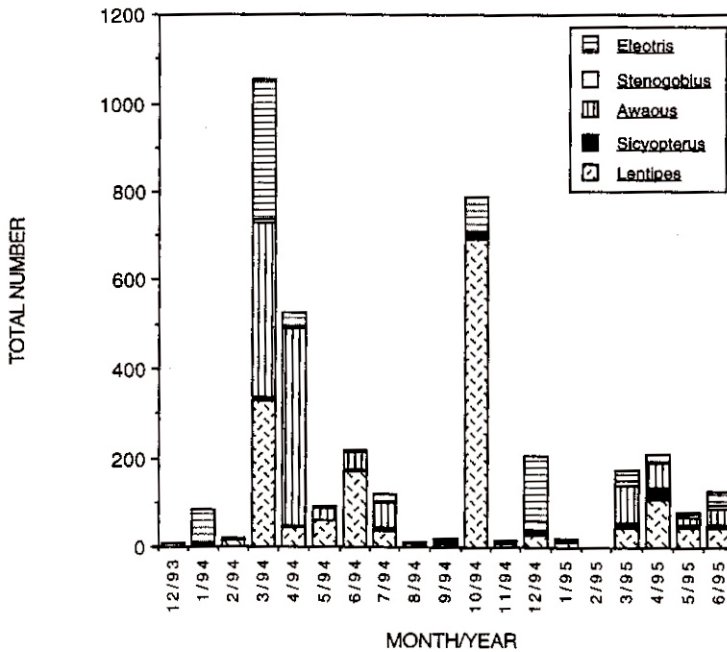


Figure 2. Monthly distribution of goby postlarvae by species trap-collected at Hakalau stream, Hawai'i, December 1993 to June 1995 (reprinted with permission from Nishimoto & Kuamo'o, 1997)

Larval Retention or Dispersal

The marine planktonic stage of the 'o'opu is the least understood of all life-stages, and it is unknown if larvae are retained close to shore or are transported out to sea. We can think of many possible scenarios pertaining to the fate of the planktonic larvae, of which we discuss three. In the first and perhaps most likely situation, some of the planktonic larvae are not retained near shore and are passively transported out to sea, perhaps to other islands, but many remain in the 'vicinity' of their natal stream. When the 'o'opu reach competency, they are cued to settle by some type of zeitgeber and initiate active migration toward and up their natal or nearby streams (Boehlert & Munday, 1988); migration to nearby streams ensures some gene flow. It also is possible that instead of actively swimming towards the coast, post-larvae can be transported onshore passively as has been demonstrated for other systems (e.g., Norcross & Shaw; 1984; Hare & Cowen, 1996). In the second scenario, 'o'opu are transported far enough from the natal stream mouth to become entrained in ocean currents around the islands of Hawai'i. Once competency is reached, settlers locate non-natal, distant stream mouths, usually on other islands, and initiate immigration. Lastly, 'o'opu are actively retained close to the shore, either through behavioral or physical processes, and when larvae become competent to settle, they easily locate their natal or nearby stream mouths for immigration. We will discuss the evidence that supports or refutes each scenario and briefly describe how each may lead to a different freshwater management scheme.

Before we discuss the three scenarios pertaining to larval retention and dispersal, we will first discuss the larval stage duration. Long larval stage durations are generally associated with organisms that are dispersed over long distances (Bradbury & Snelgrove, 2001). However, recent studies on marine reef fish by using a variety of techniques indicate that long distance dispersal does not occur with every species of fish with teleplanic larva (Taylor & Hellberg, 2003; Jones *et al.*, 1999; Swearer *et al.*, 1999). Caribbean reef gobiids do not disperse and remain close to natal areas, a finding determined by using mitochondrial cytochrome b DNA (Taylor & Hellberg, 2003). Fluorescent tags

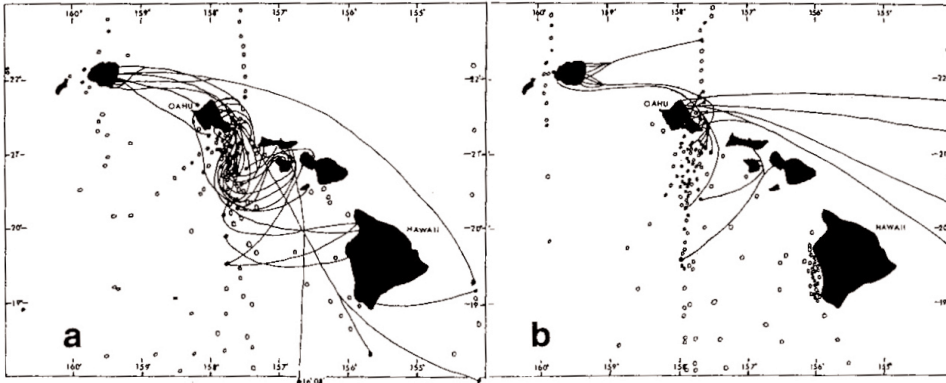


Figure 3. Drift-bottle deployments, recoveries and inferred trajectories. Open circles represent points of release but no recovery. Solid circles are sites of release with inferred trajectory to recovery location. **a:** Jan–May, **b:** Jun–Dec [from Barkley *et al.* (1964); reprinted with permission from Lobel (1989)].

applied to otoliths also showed that a larger than random sample of larvae of the damselfish *Pomacentrus amboinensis* settle back onto natal reefs (Jones *et al.*, 1999). Elemental composition analysis of the otoliths of settling larval Caribbean bluehead wrasse (*Thalassoma bifasciatum*) suggested that the larva remain close to shore (Swearer *et al.*, 1999). Therefore, the relationship between larval stage duration and dispersal is not clear, and we will discuss how long larval durations fit into each dispersal/retention scenario.

Larval Stage Duration

In general, the length of the larval stage for Hawaiian amphidromous gobies is longer than other fish with teleplanic larvae in the Pacific (Radtke *et al.*, 2001) and elsewhere (e.g., Dominican gobies, Bell *et al.*, 1995). The marine larval stage lasts 119–151 d for *S. hawaiiensis*, 150–169 d for *A. guamensis*, and 63–106 d for *L. concolor* (Radtke *et al.*, 1988; Radtke *et al.*, 2001), as determined via otolith analysis. Larval stage duration of *L. concolor*, however, appears similar to the Dominican gobies; all are scydiine gobies and the marine larva stage duration may be a phylogenetic trait (Radtke *et al.*, 2001; Bell *et al.*, 1995), albeit that variations can occur in response to the influences of temperature, salinity, and prey density (Bradbury & Snelgrove, 2001).

Otolith studies of amphidromous gobies in Dominica, West Indies, demonstrate distinct seasonal cycles in age at recruitment and growth (Bell *et al.*, 1995). For two of the Hawaiian species, *A. guamensis* and *S. hawaiiensis*, otolith samples were taken from a small number of fish from one location, so determination of seasonal cycles in length of the larval duration was not possible (Radtke *et al.*, 1988). However, a much more extensive study considering geographic location, temperature, annual and seasonal cycles was done on *L. concolor* (Radtke *et al.*, 2001). Radtke *et al.* (2001) reported indications of seasonal changes in larval length; planktonic larval duration was shorter during warmer months. However, the size at settlement was also smaller during summer months and indicates that perhaps *L. concolor* do not use the marine larval stage to maximize size before recruitment. Interestingly, newly recruited *L. concolor* collected on the island of Maui consistently had shorter marine larval durations than those caught on the other islands, an observation that indicates some localized retention (Radtke *et al.*, 2001). Further research should determine whether other species of 'o'opu show similar variability in marine larval duration. Such information could provide a means by which to distinguish biology, such as species differences, from the constraints imposed by the environmental conditions (i.e., ocean currents). If all species show similar patterns, we may infer that larval duration is regulated by the physical environment.

The hypothesis that 'o'opu are retained close to natal streams may support the idea that the extended marine larval duration is not an adaptation for dispersal (Strathmann, 1985; Hohenlohe, 2004). Rather, some authors suggest that the length of the marine larval stage is dependent upon

Table 1. Drift bottles released in a quadrangle around Hawaiian Archipelago [reprinted with permission from Scheltema *et al.* (1996); summarized from Barclay *et al.* (1964)].

Time of year	# of release points*	Total # bottles released	% bottles recovered
Jan–Feb	180	1005	2.7
Mar–May	59	925	12.5
Jun–Jul	182	1840	3.5
Sep–Dec	—	200	6.0

*From March through May returns were received from 52.5% of release points. During other parts of the year returns were only received from only 9–11% of release points.

available food; less food translates into a longer duration (Strathmann, 1986). However if larval fishes remain close to shore, an area typically rich in nutrients and food resources, larval fishes should grow faster and recruit at larger sizes (Swearer *et al.*, 1999). Since three species of ‘*o’opu* have long larval durations, it is not likely that food availability regulates larval stage duration if ‘*o’opu* are retained locally. However, because the length of the larval duration for only three species of ‘*o’opu* have been estimated, and only one (*L. concolor*) in sufficient detail, we can not rule out food availability as a regulator of marine larval duration. Interestingly, one species that has not been studied in great detail is *S. stimpsoni*, a species that has a much larger size at recruitment than any of the other 4 species (Nishimoto & Kuamo‘o, 1997). Alternatively, other authors suggest that ‘*o’opu* need a long larval duration to complete development and make the necessary preparations to convert from salt water to fresh water (Radtke *et al.*, 2001). The observation that *L. concolor* has a similar marine larval duration as other sicydiine gobies located in the Caribbean indicates that the biological requirements of amphidromy, rather than physical oceanographic processes, necessitate long developmental periods (Radtke *et al.*, 2001; Bell *et al.*, 1995).

Passive Transport

Two aspects of ‘*o’opu* biology support passive transport scenarios: high fecundity and long larval duration. Passive transport scenarios assume that larval fishes act as inanimate particles that drift with prevailing currents. Larvae can be moved by wind-driven or other types of currents, but there exist no physical conditions, nor behavioral responses that act to concentrate and locally retain the larvae. As mentioned previously, ‘*o’opu* are unusually fecund for gobiid species; high fecundity increases the chance that at least a few individuals are capable of reaching suitable habitats for recruitment. ‘*O’opu* larvae are teleplanic, with larval stage durations of longer than two months which suggests a high dispersal potential (Radtke *et al.*, 2001; Bradbury & Snelgrove, 2001).

Hawaiian fishes, in general, have longer larval pelagic stage durations than other marine fish in the Pacific (Victor, 1986), which may be a response to the isolation of the Hawaiian Archipelago (Radtke *et al.*, 2001). There are advantages and disadvantages to having a long larval stage. Advantages include access to a food sources that do not overlap with adult conspecifics, higher levels of competency and growth prior to settlement, and the absence of benthic predators (Doherty *et al.*, 1983; Strathmann, 1990; Radtke *et al.*, 2001). However marine fish larvae can experience higher mortality rates attributable to starvation, predation by pelagic predators, and unpredictable environmental conditions (Jackson & Strathmann, 1981), which may increase cumulative mortality if the larval stage is extended (Cushing, 1975). Dispersal may also reduce local adaptation, and makes potential settlers less able to distinguish good sites from poor, sometimes at high costs (Strathmann *et al.*, 1981). Indeed, ‘*o’opu* will recruit to any freshwater source, regardless of habitat quality (Holmquist *et al.*, 1998). Nevertheless, the selection pressure for a long larval duration must be strong for it to persevere; the result is the potential to be transported great distances. Long larval durations may be one of the mechanisms that initially brought gobies to the isolated island chain (McDowell, 2003).

If all ‘*o’opu* larvae were transported great distances, however, Pacific stocks of ‘*o’opu* would

be panmictic; endemism implies genetic isolation. Some larval transport via ocean currents between the Hawaiian Islands is a plausible scenario because there are no significant differences in the genetic composition of species on individual islands which indicates a sufficient mixing of fishes (gene flow) during the larval phase to preserve the unit stock (Zink *et al.*, 1996; Chubb *et al.*, 1998); a mixing of just 10% would ensure a genetically homogenous population (Zink *et al.*, 1996; Chubb *et al.*, 1998). Notably, of the 'o'opu studied, the nonendemic species, *A. guamensis*, has the longest stage duration (Radtke *et al.*, 1988).

Retention by Ocean Currents

Long larval stage durations of 'o'opu may be an adaptation to ensure some dispersal to maintain gene flow, but also to facilitate recruitment to the limited number of freshwater streams located in specific areas in the Hawaiian Island chain (Fig. 1). As such, larval duration may be coupled to physical oceanographic processes. Physical oceanographic processes such as prevailing currents, tides, boundary layers, and mesoscale eddies may function to retain larvae within the Hawaiian waters (Cowen *et al.*, 2000). *Awaous guamensis* spawns from August through to December (Ha & Kinzie, 1996) and has a larval period of 155 days or approximately 5 months (Radtke *et al.*, 1988); post-larval *A. guamensis* recruit from March to May, with most returning in March (Fig. 2), a pattern consistent with larval stage duration. Similarly, *L. concolor*, spawns October through May (Kinzie, 1993), and has a marine larval stage of approximately 3 months (Radtke *et al.*, 2001); *L. concolor* larval stage duration is consistent with the observed January to August recruitment pattern for the most part. However, a large pulse of recruitment occurs in October, a few months outside the hypothesized return period (Fig. 2). Reasons for this large pulse in unexplained recruits may be attributable to a lack of synchrony in space and time between studies of reproductive biology and recruitment.

A distinct seasonal pattern of currents, driven by trade winds, is observed around the Hawaiian Archipelago. Barkley *et al.* (1964) released 4000 drifters around the islands. Drifters that were released in proximity to an island tended to be recovered on the shore of nearby islands. The recovery of drifters showed distinct seasonal differences, with the highest recovery (12.5%) between the months of March and May (Table 1).

Barkley *et al.* (1964) also observed a distinct shift in ocean currents; the currents tended to flow to the northwest and parallel to Archipelago from January to May, and shift in June (with changes in the trade winds) to become more perpendicular to the Archipelago (Fig. 3; summarized by Lobel 1989). These currents, combined with other oceanographic data such as salinity and dynamic topography, demonstrate a closed gyral circulation around the Hawaiian Archipelago from March-April (summarized in Lobel, 1989). Barkley *et al.* (1964) also reported that most drifters returned to the coast between March and May (Table 1), which is coincident with the time when the majority of 'o'opu post-larvae recruit to streams (Fig. 2). The second largest recruitment of post-larvae occurs between October and December (Fig. 2), which matches the second highest return of drifters (Table 1).

Additionally, mesoscale eddies, that form on occasion around the islands, contain high concentrations of planktonic larvae (Lobel & Robinson, 1988). While no larval 'o'opu were reported from these eddies, these features could function in retaining larvae near the islands if 'o'opu originating in the coastal zone become advected into the eddy field. Eddies entrain and retain drifting plankton and larvae and remain near the islands for sufficient duration for some larvae to complete the pelagic phase (Lobel & Robinson, 1988). Eddies, in addition to retaining larvae, also retain larval food items. As such, local hydrographic conditions may create a stable retention mechanism that can account for Hawaiian endemism, somewhat analogous to the genetically distinct Atlantic herring stocks maintained by stable hydrographic retention areas (Iles & Sinclair, 1982).

Consistent and convergent ocean current patterns can produce an effective barrier to genetic exchange (Hohenlohe, 2004). However, the currents around Hawai'i are highly variable in direction and speed and change from year to year (Lobel & Robinson, 1986; Qui *et al.*, 1997; Radtke *et al.*, 2001). Unpredictable ocean currents may explain the lack of genetic differentiation of 'o'opu collected from different islands (Zink *et al.*, 1996; Chubb *et al.*, 1998; Radtke *et al.*, 2001).

The issue of retention is far from resolved, and indirect evidence suggests that strong localized retention is not widespread among the 'o'opu. For example, marine larvae that are retained locally based on directed swimming are more prevalent in species that are non-pelagic spawners and pro-

duce larger and more highly developed larvae (Brogan, 1994). If possible, a comparison of the distribution of organisms that have non-motile planktonic phases, such as algae, to the distribution of 'o'opu should indicate the degree to which 'o'opu can regulate their dispersal (Bradbury & Snelgrove, 2001).

Behaviorally Mediated Localized Retention

It also is possible that localized retention of 'o'opu larvae is behaviorally mediated (Boehlert & Munday, 1988; Atema *et al.*, 2002), a line of inquiry that deserves further study. Studies of some marine reef gobiid larvae suggest that larvae have the ability to actively maintain position from coastline, which thereby prevents dispersal (Leis, 1982). Indeed, the marine larvae of some species of amphidromous gobies from Dominica, West Indies, are able to maintain position at depth by choosing water masses based on salinity; actively choosing a water mass by migrating vertically can affect horizontal transportation (Boehlert & Munday, 1988; Bell & Brown, 1995). Additionally, reports that late stage marine larval fish are the strongest swimmers amongst the plankton and have the ability to swim faster than the background current, supports the hypothesis that 'o'opu can actively remain near natal stream (Stobutzki & Bellwood, 1997).

The observed behavior of larval 'o'opu in response to the physical environment also suggests they are retained close to the shore. In Hawai'i, the time between March and May is characterized by periods of heavy rainfall, and it has been hypothesized that post-larvae recruit in response to freshets that attract post-larvae to streams (Nishimoto & Kuamo'o, 1997). If attraction to freshwater is the dominant mechanism underlying migration toward shore and ultimate recruitment, we may infer that larval 'o'opu are retained nearshore and are able to detect a sudden influx of fresh water.

From a management perspective, different transport and retention scenarios have significant implications. In the unlikely scenario that larval 'o'opu are not retained by any mechanism and passively drift long distances, recruitment depends on the chance of post-larvae drifting close enough to respond to and reach an inland stream. In this case, management may need to protect spawning stock biomass in an effort to ensure the production of suitable numbers of pre-recruits. In the scenario that all 'o'opu contribute to a single larval stock that is retained around the Hawaiian Islands, some freshwater habitat may be sacrificed for human use, while other streams are maintained as 'o'opu sources (Diffendorfer, 1998). Some altered habitats (dammed, diverted) may act as 'o'opu sinks, as amphidromous gobies will recruit to any freshwater source, regardless of habitat quality (Holmquist *et al.*, 1998). Finally, if larval 'o'opu are retained much closer to natal streams, then the pattern of disrupted streams is critical. Localized retention may require management on a much finer scale (Palumbi, 1999). Prior studies on juvenile creek chubs demonstrated that the spatial distribution of source areas on a landscape, along with dispersal from those areas, can have dramatic impacts on fish populations (Schlosser, 1998). Many disrupted streams (larval sinks) adjacent to one another may cause an unrecoverable population decline.

Larval Recruitment

After spending several months as ichthyoplankton, post-larval 'o'opu recruit *en masse* to perennial streams located on the windward sides of the Hawaiian Islands. There exist much circumstantial evidence and anecdotes on recruitment, but not much has been published. One study by Nishimoto & Kuamo'o (1997) documented recruitment to one stream on the island of Hawai'i. In this study, all five species of 'o'opu recruited to the stream during third quarter lunar phase, generally after a flash flooding episode, but with distinct seasonality (Fig. 2). Recruits of *L. concolor* were most abundant, followed by *A. guamensis* and *E. sandwicensis*. In comparison, very few *S. stimpsoni* and *S. hawaiiensis* entered the stream (Nishimoto & Kuamo'o, 1997). Each species began upstream migration at different times of the day, both sicydiine gobiids, *L. concolor* and *S. stimpsoni*, recruited just after sunrise. *S. hawaiiensis* and *E. sandwicensis* predominantly began upstream migration as the tide rose just after dark whereas *A. guamensis* recruited throughout the day, but showed a distinct pulse just after dark at high tide (Nishimoto & Kuamo'o, 1997).

The recruitment pattern of 'o'opu suggests that both physical and biological processes are involved (Nishimoto & Kuamo'o, 1997). Although the recruitment study was conducted on only one stream, and on only one island, there is enough evidence to suggest that physical processes such as

diurnal cycles, moon phases, tides, flash floods, and season play a role in shaping patterns of recruitment of 'o'opu. Variations in such physical processes have been shown to create patterns in recruitment for different species of wrasses (*Labridae*) from Barbados (Sponaugle & Cowen, 1997).

Indirect evidence also suggests that biological processes are involved in recruitment. Such evidence manifests in species differences, such as size at recruitment and time of recruitment. Also, post-larval *A. guamensis* school and migrate upstream together; such behavior suggests that predation may affect recruitment processes (Tate, 1997). Other biological processes that may affect recruitment, such as density dependence, remain to be determined.

The issue of recruitment is complicated by the lack of information on the mechanisms of marine larval retention/dispersal. If the marine larvae are dispersed far from natal streams, the recruitment processes are decoupled from local spawning which makes the population more or less open (Caley *et al.*, 1996). However, if marine larvae remain close to natal streams, the recruitment processes can be directly related to local spawning events, and the local population can be considered more or less closed. In reality, the populations probably do not fully resemble either endpoint, each of which requires a different population modeling approach to inform the management process. We can construct population models of 'o'opu if we know whether the local population is open or closed, or somewhere in between. If the local population is closed, or semi-closed, stage-based matrix projections models can be constructed for each stream. To construct such models, we need estimates of demographic traits, such as fecundities, abundances, and growth and mortality rates for each life stage (Caswell, 2001). If the local population is open, a number of different population modeling approaches have been developed for settling marine sessile invertebrates with long larval durations (e.g., Alexander & Roughgarden, 1996). Individual-based modeling to determine population dynamics is another modeling approach with higher predictive potential because transport, food-availability, behavior, and predator/prey interactions can be incorporated. However, individual-based modeling is a data-intensive approach, and there may not be enough information available at the present time (Hinckley *et al.*, 1996; Grimm, 1999; Werner *et al.* 2001).

Future Studies

The processes regulating production, marine larval retention or dispersal and recruitment are not well understood for amphidromous Hawaiian fishes. We can construct population models to assist management of 'o'opu, but such models require critical demographic information such as timing and rates of reproduction for each species. Mortality rates and duration of the yolk-sac larva stage are also types of demographic information that are critical to model development. As discussed in detail in this paper, it is obvious that much information is needed on the marine larval phase of the amphidromous gobies, and we have mentioned a few examples where a little data would go a long way. For example, valuable information would include the length of the larval period for every species and whether growth and recruitment patterns vary seasonally. Because larval 'o'opu can be identified through molecular markers (Lindstrom, 1999), quantification of abundance at location is possible. Therefore, deploying extensive ichthyoplankton surveys year round in areas close to the river mouths and amongst the cyclonic eddies and gyres off the coast may assist in determining the mechanisms behind dispersal or retention. Models can then be developed to predict the abundance of recruits from a source population by considering mesoscale features of ocean currents that interact with coastal habitat structure (e.g., Possingham & Roughgarden, 1990; Alexander & Roughgarden, 1996). Synthesis of all this information should provide the State of Hawai'i with an effective management tool and answer some fundamental questions in marine larval ecology.

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