

Consequences of alternative dispersal strategies in a putatively amphidromous fish

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Abstract. Successful dispersal can enhance both individual fitness and population persistence, but the process of dispersal is often inherently risky. The interplay between the costs and benefits of dispersal are poorly documented for species with complex life histories due to the difficulty of tracking dispersing individuals. Here we investigate variability in dispersal histories of a freshwater fish, *Awaous stamineus*, across the species' entire geographic range in the Hawaiian archipelago. Like many animals endemic to tropical island streams, these gobies have an amphidromous life cycle in which a brief marine larval phase enables dispersal among isolated freshwater habitats. Using otolith microchemistry, we document three distinct marine dispersal pathways, all of which are observed on every island. Surprisingly, we also find that 62% of individuals complete their life cycle entirely within freshwater, in contrast to the assumption that amphidromy is obligate in Hawaiian stream gobies. Comparing early life history outcomes based on daily otolith growth rings, we find that individuals with marine dispersal have shorter larval durations and faster larval growth, and their growth advantage over purely freshwater counterparts continues to some degree into adult life. These individual benefits of maintaining a marine dispersal phase presumably balance against the challenge of finding and reentering an island stream from the ocean. The facultative nature of amphidromy in this species highlights the selective balance between costs and benefits of dispersal in life history evolution. Accounting for alternative dispersal strategies will be essential for conservation of the amphidromous species that often dominate tropical island streams, many of which are at risk of extinction.

Key words: amphidromy; *Awaous stamineus*; complex life cycle; connectivity; cost–benefit; dispersal strategy; fitness; growth; Hawaii; larvae; metapopulation; stream fish.

INTRODUCTION

Dispersal is ubiquitous in nature; most organisms are capable of dispersing during some part of their life history (Clobert et al. 2009). As a result, dispersal plays a profound role in ecology and evolution at the individual, population, and community levels. Dispersal contributes to individual fitness by allowing escape from poor-quality habitats, predators, and diseases, and facilitating avoidance of strong resource competition and inbreeding (Bowler and Benton 2005). Dispersal can also influence the size, stability, and persistence of populations (Hastings and Botsford 2006, Kerr et al. 2010). For example, dispersal can reduce extinction risk by enabling gene flow, which can lessen the deleterious effects of genetic drift and mutation load or inject adaptive alleles into a population (Ronce 2007).

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Dispersal can also influence the size of species ranges, and the nature of species interactions that shape community assembly and responses to environmental change (Leibold et al. 2004, Clobert et al. 2009).

The evolution of dispersal strategies reflects a balance between costs and benefits to individuals. Despite the benefits identified above, dispersal also involves significant costs, such as energy demands required for active dispersal, time allocation for dispersal rather than growth or reproduction, elevated mortality from exposure to predators and adverse environments during dispersal, and opportunity costs like the risk of settling in a poor-quality habitat when habitat quality varies in space and time (Bonte et al. 2012). These costs can have fitness consequences during emigration from natal habitat, movement between habitats, or immigration to the new habitat (McDowall 2010). Nonlethal costs incurred during dispersal can even have lifelong consequences (Bonte et al. 2012).

An individual's dispersal history, encompassing the distance and time spent dispersing as well as the environment experienced, can significantly affect its condition and fitness. Dispersal history has been linked

to larval growth rate in vertebrates and invertebrates; variation in dispersal distance and environment can produce faster or slower growth (Weiss et al. 1987, Shima and Swearer 2009). Accordingly, condition upon settlement may often reflect the environment experienced while dispersing (e.g., Hamilton et al. 2008). When dispersers arrive in good condition, they are likely to experience higher post-settlement survival (Hamilton et al. 2008) and reproductive fitness (Weiss et al. 1987).

By influencing the number and quality of incoming recruits, dispersal history can directly affect the persistence of populations. The quality of recruits can mediate realized connectivity among populations and average individual fitness in recipient populations (Shima and Swearer 2010). Furthermore, the assured replacement of local breeding stock by local recruitment (i.e., individuals that either never leave or end up returning to their natal population) can contribute strongly to the stability and persistence of local populations (Hastings and Botsford 2006, Kerr et al. 2010). Theory suggests that populations that receive both local recruits and dispersers are most likely to persist, particularly in heterogeneous landscapes (Mathias et al. 2001).

The costs and benefits incurred during dispersal are poorly documented for species with complex life histories, especially for species that undergo marine dispersal as larvae (Cowen et al. 2007). Amphidromy is an extreme case of a complex life history; adults and juveniles live in freshwater ecosystems, but larvae migrate into the ocean, potentially enabling long-distance dispersal, but also exposing larvae to marine predators, potential loss within ocean currents, and physiological costs of adaptation to the marine environment. To complete their life cycle, amphidromous larvae must locate a stream into which to recruit, and swim upstream to reach suitable habitat, which sometimes requires climbing waterfalls (McDowall 2010). The challenges associated with this life history may favor the evolution of alternative dispersal strategies, including local retention. There is growing evidence of fitness advantages for recruitment to the natal habitat in marine fishes (e.g., Shima and Swearer 2009), and a few amphidromous fishes have been able to discard the marine larval period in favor of an entirely freshwater life cycle (Michel et al. 2008).

The endemic amphidromous fishes of the Hawaiian archipelago offer exceptional opportunities to study dispersal and its consequences for individual fitness and population replenishment. Adults of these species reside in streams that are patchily distributed around the perimeter of each island, and populations are connected solely via dispersal of larvae through marine environments (McDowall 2010). Here we focus on the most common amphidromous fish in Hawaii, *Awaous stamineus*, which has heretofore been considered to be obligately amphidromous. We sampled adults and juveniles across the species' full range to test for variation in dispersal history. Using the microchemistry

of the ear-stones (otoliths) of these fishes, we asked whether marine dispersal is obligate, and whether marine dispersal pathways are uniform within and between islands across the archipelago. Based on observed differences in dispersal history among individuals, we assess the consequences of alternative dispersal strategies in terms of larval period duration, larval growth rate, and post-larval growth rate. This approach allows us to place natural variation in dispersal strategies within the context of costs and benefits for individuals and their population-level ramifications.

METHODS

Study species and sampling area

We studied *Awaous stamineus*, the most abundant and widespread of the amphidromous goby species endemic to the Hawaiian Islands (Keith 2003). *A. stamineus* is evolutionarily distinct from *A. guamensis*, its closest known relative, which is found in the western Pacific Ocean (Lindstrom et al. 2012). *A. stamineus* inhabit lower- and middle-elevation reaches of streams on each island (Keith 2003). Peak spawning is from August through December (Ha and Kinzie 1996); adults lay benthic eggs on the underside of rocks, eggs hatch after 48 hours and newly hatched larvae drift downstream toward the ocean within 3–4 hours, allowing little scope for growth within freshwater (Luton et al. 2005). They complete an ostensibly obligate marine phase lasting an average of 161 days (Radtke et al. 1988), during which larvae may disperse among watersheds and islands. Historically, *A. stamineus* were abundant enough to support an artisanal fishery, but population declines have led to tighter restrictions on fishing (Ha and Kinzie 1996).

We collected *Awaous stamineus* from 35 watersheds (Appendix A; Fig. A1) across the five Hawaiian islands with perennial streams (total $n = 383$ fish; stream $n = 1–23$ fish; Appendix B; Table B1). The sampled streams were representative of the diversity of habitats available to *A. stamineus* across the archipelago, and constitute ~25% of the 133 streams known to harbor *A. stamineus*.⁶ Sampling was conducted from December 2008 to November 2009. See Appendix C for detailed methods regarding sample collection and sample preparation.

Otolith structural analysis

We measured life history characteristics from the daily-ring structure of otoliths from 216 fish representing 33 of the 35 study watersheds. These characteristics included hatching and metamorphosis dates, age, larval duration, otolith size at metamorphosis, larval growth rates, and adult growth rates. The life history was divided into larval and post-larval (hereafter called “adult” for simplicity) phases based on a metamorphic

⁶ <http://hawaii.gov/dlnr/dar>

mark, a relatively broad ring having high optical density that arises during metamorphosis from the larval form into the post-larval form (Radtke et al. 1988). Age at capture and larval duration were estimated by counting otolith rings that accrue daily (Radtke et al. 1988). Otoliths were examined by three independent readers, and the mean age estimate was used when two or more readers agreed (CV < 10%). If there was not agreement, or otolith condition was too poor for reader confidence, age was not estimated. Hatching dates and metamorphosis dates were back-calculated based on the date of collection. Larval size at metamorphosis was measured as the otolith radius from the first ring to the metamorphic mark along the longest axis. We used radial measurements and ring counts to infer larval and adult growth rates based on the assumption that otolith growth is closely correlated with somatic growth (Campana and Jones 1992), but we did not directly convert otolith data into somatic length estimates. We used an exponential model to estimate compounding daily otolith growth rate (following Shima and Swearer 2009)

$$L_t = L_0 \left(e^{K(t)} \right). \quad (1)$$

where L_t is the otolith radius at time t , L_0 is the otolith radius at time zero, and we estimated K , the compounding daily growth rate parameter (a measure of the “per millimeter” rate of increase over a short time interval in units of per day). L_t for larval growth was the radius from the primordium to the metamorphic mark, and L_t for adult growth was the radius from metamorphic mark to otolith edge. For larval growth, L_0 was set at 0.01; for adult growth, L_0 was the radius from primordium to the metamorphic mark.

Otolith microchemical analysis

Otoliths from 383 individuals were analyzed with laser ablation (Cetac LSX213; Omaha, Nebraska, USA) inductively coupled plasma mass spectrometry (Perkin Elmer ELAN DRCII, Waltham, Massachusetts, USA) at the University of Massachusetts–Boston. Samples were analyzed with a laser transect starting at one edge of the otolith, bisecting the primordium, and ending at the other edge of the otolith, resulting in a palindromic signal for all samples. Eighteen isotopes were analyzed, and concentrations were calculated for the “adult” and “larval” regions of each otolith transect using GeoPro software (CETAC Technologies, Omaha, Nebraska, USA). Larval and adult chemistry was integrated from 15-second time windows in either the “core” or edge of each otolith sample. For the purposes of this study we consider the otolith “core” to be the entirety (or nearly so) of the larval period, extending well beyond the otolith primordium. Relative concentrations were expressed as a ratio against ^{46}Ca . Six isotopes were considered informative for statistical analysis based on signal:noise consider-

ations (see Appendix C for details), including ^{55}Mn , ^{85}Rb , ^{88}Sr , ^{138}Ba , ^{66}Zn , and ^{63}Cu . Finally, 15% of the total sample set were excluded from statistical analysis because more than half of their isotope ratios were outliers (>3 SD from overall mean). Limits of the blanks and measures of precision for these isotopes as well as summaries of elemental data are reported in Appendix B.

Analysis of dispersal histories

Larval chemistry data were used to ask two sequential questions about dispersal history. (1) Is amphidromy obligate in *A. stamineus*, or do some larvae remain in freshwater throughout development?; and (2) do larvae that undergo marine dispersal follow different dispersal pathways in the ocean? The Sr:Ca ratio in the larval phase was used to determine whether larvae exhibited amphidromy. Saltwater residency is indicated by elevated Sr:Ca ratios, and has been widely used to identify marine habitat use in diadromous fishes (Hale and Swearer 2008, Michel et al. 2008). Strontium peaks in the larval phase were easily identifiable and Sr:Ca declined rapidly after the metamorphic mark (Appendix A: Fig. A2). Conversely, otoliths with no evidence of marine dispersal were identified by having a low and constant Sr:Ca ratio throughout the larval and adult phases. We used principal components analysis (PCA) of adult and larval chemistry to test whether putatively freshwater (FW) larvae were similar in chemistry to the adult period, which is unquestionably spent in freshwater.

To confirm the inference from LA-ICP-MS (University of Massachusetts, Boston, Massachusetts, USA) that some larvae never went to sea, otoliths from eight independent samples were also analyzed with wavelength dispersive X-ray spectroscopy using an electron microprobe (EPMA). The EPMA transect paralleled the LA-ICP-MS transect on the same otolith (see Appendix C for more details), and yielded data on Sr:Ca from the otolith surface alone rather than trenching tens of micrometers deep, as in the case of LA-ICP-MS. In addition, to test whether under-polishing could be responsible for failure to detect a SW larval chemistry, we conducted a serial polishing exercise. Twenty otoliths that showed consistently low Sr:Ca during the larval phase were repeatedly polished and re-run using LA-ICP-MS up to eight times. Polishing was stopped when the metamorphic mark on each sample was no longer visible under the microscope (indicating over-polishing).

Two statistical approaches were used to assess dispersal pathways of marine larvae. First, we tested whether average microchemical signatures during marine dispersal were distinct at the island or watershed scale. Following MANOVA comparisons, we used classification success from discriminant function analysis (DFA) to quantify the strength of spatial structuring by island and watershed. A Mantel test (*vegan* package

in R v. 2.13.1) was used to test for differentiation-by-distance based on larval chemistry at the scale of islands. MANOVA and DFA analyses were performed in Statistica v.10 (StatSoft, Tulsa, Oklahoma, USA). Second, a naïve Bayesian approach was used to assess the existence of natural groupings based on chemistry of marine larvae (R v. 2.13.1 using the *cluster.optimal* function in the *bayesclust* package). This method searches for k optimal clusters in the data with no prior information about group structure (see Appendix C for detailed methods). We used the information criterion “Delta k ” (modified from Evanno et al. 2005) to identify the most parsimonious number of k groups. Frequentist statistics were used to compare the naïve groupings to a priori groupings (i.e., islands or watersheds) based on how well they explain variation in chemistry. MANOVA and DFA were used to explicitly compare the explanatory value of Bayesian vs. a priori spatial groupings for understanding chemistry patterns. We used PCA to visualize these chemical differences.

There are several hypotheses that could explain chemical differences during the marine dispersal phase, including temporal variation in ocean chemistry, larval residence in estuaries or bays, leeward vs. windward differences in ocean chemistry, and nearshore vs. offshore larval residency. To test for temporal effects, hatching and settlement dates were compared among the k Bayesian groups. To test for spatial effects (i.e., estuary or windward–leeward), the proportions of larvae from the k groups were compared between windward and leeward watersheds, or watersheds with and without estuaries. Finally, we use both otolith Cu:Ca and Sr:Ca to test for differences among the k groups. Concentrations of bioavailable copper can be enriched in coastal marine environments due to anthropogenic inputs (Stauber et al. 2005), and dissolved copper can be incorporated into otoliths from the water (Milton and Chenery 2001), though physiological regulation by the fish can also decouple environmental and otolith concentrations of copper (Miller et al. 2006). To further explore whether these elements are informative with regard to onshore vs. offshore larval habitat use, we also correlate adult (stream) and larval (marine) Cu:Ca for each Bayesian group. If marine larvae reside near the stream that they recruited to as adults, we would expect to see a correlation.

Individual condition and dispersal history

After categorizing the dispersal history of each fish (freshwater-only or one of k marine groups), we used larval duration and growth rates to assess the fitness implications of each dispersal strategy. We compared the frequency distributions of larval hatch dates, larval settlement dates, larval durations (LD), size at settlement, larval growth, and adult growth rates among dispersal groups using Kolmogorov-Smirnov (K-S) tests. First, these quantitative life history traits were compared between amphidromous and non-amphidro-

mous individuals (i.e., marine vs. freshwater larval phase). Then, the same comparisons were made among the k groups representing alternative marine larval dispersal pathways.

RESULTS

Life history characteristics

The mean age of *Awaous stamineus* in this study was 2.4 yr (range: 1.3–4.5 yr), and the mean larval duration (LD) was 118 d (range: 57–248 d). The distribution of LD was bimodal with modes around 75 d and 155 d. Most fish (>90%) hatched between November 2005 and August 2008, and metamorphosed into post-larvae between April 2006 and August 2008. There were no clear pulses in birth or settlement dates, and the oldest individual hatched in October 2002 and metamorphosed in February 2003.

*Is amphidromy obligate in *Awaous stamineus*?*

Of the 325 samples for which we could confidently profile larval chemistry, 38% showed an unambiguous, high Sr:Ca ratio that indicates an oceanic or estuarine (hereafter “SW”) larval habitat (Fig. 1; Appendix A: Fig. A2, Appendix B: Table B1; Hale and Swearer 2008). The remaining fish (62%) showed no strong Sr:Ca peak in the core, indicating probable residency in freshwater throughout the larval phase (hereafter “FW”). Independent analysis by EPMA confirmed the results of LA-ICP-MS in fish showing high ($n = 3$) or low ($n = 5$) Sr:Ca in the larval phase, indicating that these patterns are not an artifact of the depth of otolith ablation by LA-ICP-MS. Furthermore, serial polishing of a subset of putatively FW larval otoliths did not reveal any evidence of a SW larval signature despite repeated polishing and ablation, indicating that these FW signals are not an artifact of under-polishing these samples. Finally, PCA clearly indicates a chemical difference between the FW larval signatures and adult signatures. The elemental composition of otoliths can shift during ontogeny due to physiological changes rather than environmental shifts (Fowler et al. 1995). Both FW and SW larval habitats are signified by positive PC1 values, while adults in FW show negative PC1 values (Fig. 2a), indicating that the FW cores are ontogenetically larval. Taken together, these multiple lines of evidence suggest that over- or under-polishing the samples was very unlikely to falsely generate an apparently FW core signature. In contrast, FW larvae and adults did not differ significantly on PC2 or PC3. Thus, PCA reveals a combination of larval (PC1) and freshwater (PC2 and PC3) microchemical patterns that confirms that FW larvae reside purely in freshwater between hatching and metamorphosis. These patterns of concordant variation in PC1–PC3 indicate that *A. stamineus* in Hawaii are not obligately amphidromous.

The relative proportions of fish showing FW and SW dispersal histories varied among islands (33–44% SW) and watersheds (0–100% SW; Appendix B: Table B1).

However, the frequency of amphidromy did not differ among islands (ANOVA, $F = 0.86$, $df = 4$, $P = 0.500$), nor did any individual watershed differ significantly from the mean across all others on the same island (z tests: all $P > 0.050$). Our small sample sizes at the watershed level preclude further statistical comparisons (Appendix B: Table B1). There were no significant differences in the frequency of amphidromy between the windward and leeward sides of islands (z test, $P = 0.480$), or watersheds that have estuaries or embayments compared to those that discharge directly to the sea (z test, $P = 0.290$).

Alternative marine dispersal environments

A priori geographic groupings of SW larval chemistry revealed significant differences among islands and watersheds (MANOVA_{IS} [IS represents “islands”], $F_{6,24} = 4.2$, $P < 0.001$; MANOVA_{WA} [WA represents watersheds], $F_{6,168} = 1.8$, $P < 0.001$). However, there was no evidence of increasing chemical differentiation among islands with distance (Mantel test, $r = -0.45$, $P = 0.940$), as might be expected if larvae disperse by diffusion and the archipelago presents a directional gradient in marine chemistry. Furthermore, a priori groups were not strongly supported by discriminant function analysis (DFA). Classification accuracy was moderate for islands (60%) and poor for watersheds (37%), indicating that these geographic groups are not reliable predictors of variation in SW chemistry.

Naïve Bayesian clustering of SW larval chemistry revealed evidence of natural groups. All values of $k > 1$ (i.e., $k = 2-6$) were significantly more probable than the null hypothesis of $k = 1$ ($P < 0.010$). Likelihood values increased with the number of groups (Appendix A: Fig. A3), but the Delta k information criterion indicated that

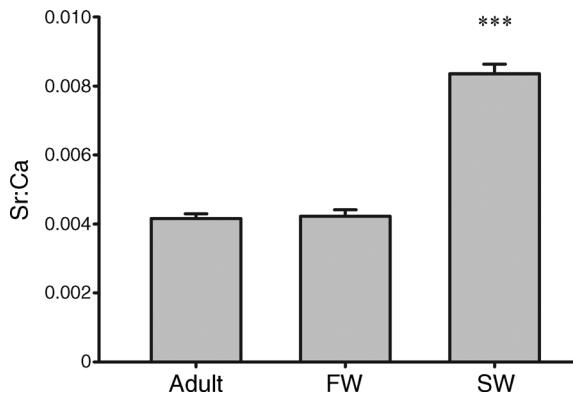


FIG. 1. Sr:Ca ratios for adults (stream) and putatively freshwater (FW) larvae and marine (SW) larvae. Values are means \pm SE.

*** $P < 0.0001$ (t test).

$k = 3$ yielded the largest change in likelihood and had the lowest variance in likelihood among model runs (Appendix A: Fig. A3). We therefore considered $k = 3$ to be the most parsimonious number of clusters, and used it for all subsequent comparisons.

The three Bayesian SW groups were highly significantly different from each other in chemistry (MANOVA_{CL} [CL represents cluster], $F_{6,18} = 16.0$, $P < 0.001$; Fig. 2). Furthermore, DFA showed high classification accuracy for all three Bayesian groups (84–96%) compared to a priori groups. The SW clusters showed gradients of both Cu and Sr concentrations across the three groups. SW1 had significantly greater concentrations of Sr and lower concentrations of Cu than other groups. SW3 had significantly greater concentrations of heavy metals (Cu, Zn) than other groups, and signif-

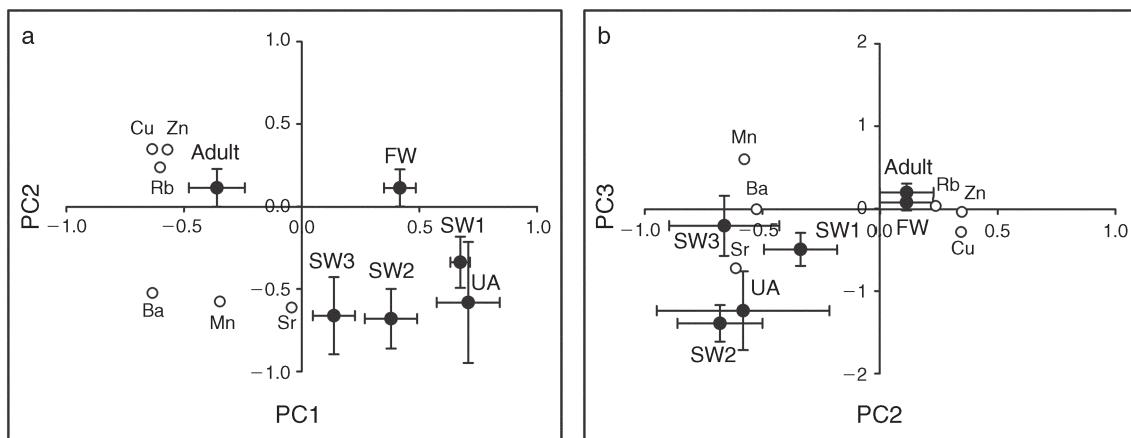


FIG. 2. Principal components analysis (PC) showing the orientation of the different chemical groupings in PC space. (a) PC1 vs. PC2; (b) PC2 vs. PC3. PC1 explains 27% of the variation in chemistry, PC2 explains 21%, and PC3 explains 16% of the variation. Solid circles are the mean PC values for each signal type, error bars are 95% confidence intervals; open circles indicate the PC loading for each of the six elements used to generate the PC plots. FW indicates freshwater larval chemistry signals; SW1, SW2, SW3 are the three marine larval clusters identified by naïve Bayesian analysis; Adult is otolith adult chemistry, representative of stream chemistry; UA are individuals that were unassigned to one of the three Bayesian clusters (for details see Appendix C).

ificantly lower concentrations of Sr than SW1, whereas SW2 had intermediate concentrations of Cu, and significantly lower Sr than SW1 (all t tests, $P < 0.001$; significant after sequential Bonferroni correction). The three SW clusters also differed significantly from FW larval and adult chemistries in the concentration of most elements (Fig. 2). Principal components (PC) analysis discriminated among the SW groups, FW larval chemistry, and adult (stream) chemistry. PC1 (27% of variance explained; Fig. 2a) predominantly separated larval and adult chemistry. PC2 (21%) and PC3 (16%) separated the SW larval groups from each other as well as from FW larval and adult microchemistry (Fig. 2b).

There were no significant differences among islands in the proportion of fishes from each of the three Bayesian SW larval groups (pairwise z tests, all $P > 0.150$). Sample sizes at the watershed level were too small to allow for any statistical comparisons within islands. There were no significant differences between the windward vs. leeward sides of islands (z tests, all $P > 0.200$), or based on the presence of estuarine habitats (z tests, all $P > 0.250$). However, larvae in the SW3 group, which featured the highest copper concentrations, exhibited a significant correlation between copper in the marine larval phase and the stream-dwelling adult phase ($r^2 = 0.43$, $P = 0.001$; Fig. 3), suggesting nearshore residency of SW3 larvae. There was little evidence of such a correlation in the other two clusters of marine larvae (SW1, $r^2 = 0.03$, $P = 0.380$; SW2, $r^2 = 0.08$, $P = 0.070$).

Individual quality and dispersal history

There was no difference in the average age of fish with different larval dispersal strategies (mean, SW = 881 d; FW = 890 d; $t = -0.19$, $P = 0.560$). Hatching and metamorphosis dates did not differ significantly between fishes with SW and FW larval chemistries (K-S_{Hatch}: $d_{\max} = 13$, $k = 67$, $n = 162$, $P = 0.050$; K-S_{Settle}: $d_{\max} = 8$, $k = 67$, $n = 162$, $P > 0.050$; Fig. 4), nor among the three SW groups (all $P \geq 0.050$). However, fishes of SW and FW larval histories did differ in the means and frequency distributions of other individual traits. Fishes that went to sea as larvae had significantly shorter larval durations ([LD], K-S_{LD}, $P < 0.001$; means, SW = 108 d, FW = 122 d; $t = -2.31$, $P = 0.020$), tended to metamorphose at a smaller size ([SS], K-S_{SS}, $P < 0.001$; means, SW = 2.39 mm, FW = 2.49 mm; $t = -1.87$, $P = 0.060$), and exhibited significantly faster larval growth rates ([LG], K-S_{LG}, $P < 0.001$; means, SW = $0.053 \text{ mm}\cdot\text{mm}^{-1}\cdot\text{d}^{-1}$, FW = $0.044 \text{ mm}\cdot\text{mm}^{-1}\cdot\text{d}^{-1}$; $t = 2.67$, $P < 0.010$). Also, fish that went to sea as larvae tended to have faster adult (post-metamorphosis) growth rates (K-S_{PMM_{growth}}, $P < 0.001$; Fig. 4) although the means were not different (mean, SW = $0.0025 \text{ mm}\cdot\text{mm}^{-1}\cdot\text{d}^{-1}$, FW = $0.0023 \text{ mm}\cdot\text{mm}^{-1}\cdot\text{d}^{-1}$; $t = 1.17$, $P = 0.240$). There were no significant differences in any life history traits among Bayesian groups of fish with

different SW dispersal histories, but our sample sizes were small.

DISCUSSION

Our microchemical analyses of otoliths from an endemic stream goby reveal multiple dispersal histories among larvae recruiting to watersheds across the Hawaiian archipelago. The most striking result is that amphidromy is not obligate in *A. stamineus*; to the contrary, a majority of larvae remain in their natal stream throughout their lives. Those larvae that did go to sea showed three distinct marine chemistries, providing evidence of variation in dispersal even within an amphidromous life history. In connecting this diversity of dispersal pathways with longer-term life history traits, we find that marine-dispersing larvae experienced faster growth and development rates than counterparts that remained in freshwater. The ubiquity of both freshwater and marine strategies across the species range suggests an intriguing balance between the costs and benefits of alternative dispersal strategies in *A. stamineus*.

Until now, *A. stamineus* and most other putatively amphidromous gobies were thought to have an obligate marine larval period (McDowall 2010). Hatchlings of amphidromous goby species experience high mortality if exposed to freshwater for extended periods (Iida et al. 2010), providing indirect evidence that individuals must complete a marine dispersal phase to survive. However, direct evidence of facultative amphidromy has been shown in other species of gobioid fishes, suggesting that obligate amphidromy cannot be assumed, even for species in the same taxonomic family (e.g., Michel et al. 2008).

Several mechanisms could explain the origin and maintenance of amphidromous and non-amphidromous phenotypes in *A. stamineus* and other species. Loss of amphidromy can arise when populations become isolated from the ocean by physical barriers or distance, followed by subsequent genetic differentiation (Michel et al. 2008). Trapping within streams does not appear to be the mechanism giving rise to loss of amphidromy in Hawaiian *A. stamineus*, as there is no evidence of genetic isolation anywhere in the archipelago (Chubb et al. 1998, Lindstrom et al. 2012), and both marine-dispersing and freshwater-resident phenotypes are ubiquitous across the species' range. Given that the Hawaiian archipelago must have been colonized by individuals with a marine phase, one might infer that evolution of non-amphidromy must have arisen within the archipelago. However, non-amphidromy also could be ancestral to the Hawaiian populations, perhaps as a recessive trait carried via marine dispersal from founding populations located in Guam or elsewhere in the Indo-Pacific (Lindstrom et al. 2012). This could be addressed with a phylogenetic analysis of facultative amphidromy within *Awaous* and related genera to examine the evolutionary history of this trait. However, a genetic basis for phenotypic variation is not certain. Possibly the

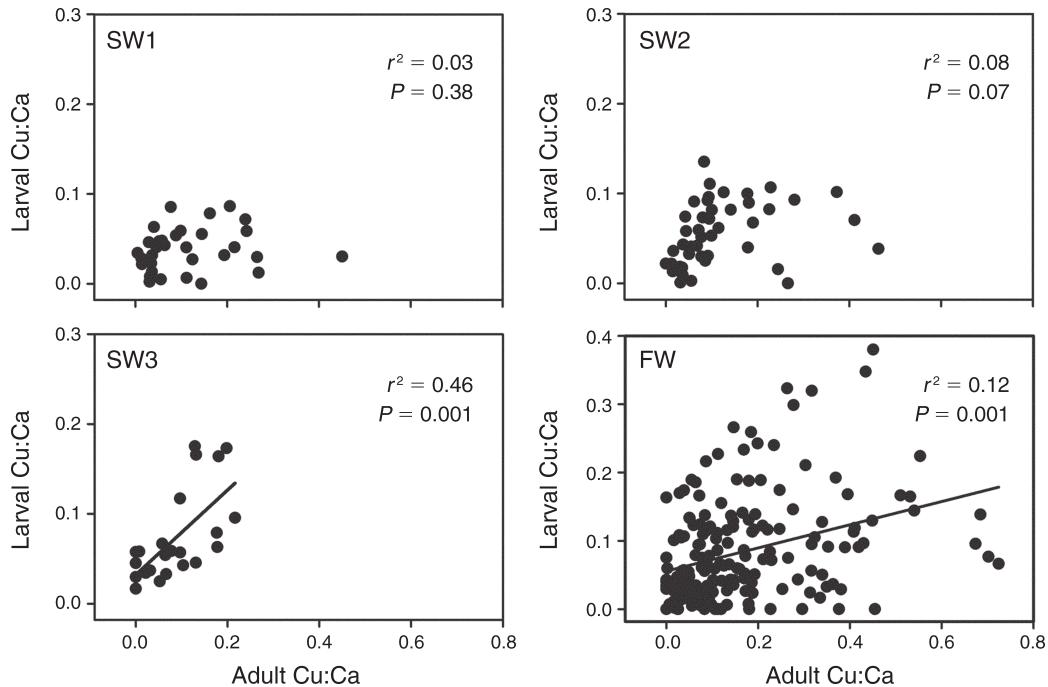


FIG. 3. Correlations between adult and larval Cu:Ca concentrations for the four larval types; FW (freshwater), SW1, SW2, SW3 (saltwater).

polymorphism represents a plastic phenotype dependent on environmental or individual conditions (Bonte and De la Pena 2009). This hypothesis could be addressed by identifying conditions that may promote larval retention in streams, such as unpredictable stream flow. Preliminary evaluation of environmental variation among our sampling sites does not suggest any obvious environmental correlates, but more direct tests would be needed to determine whether amphidromy is fixed or plastic at the individual level. Additional comparative studies are also warranted to determine whether facultative amphidromy is exhibited in other amphidromous fauna in Hawaii and elsewhere (Michel et al. 2008).

We found evidence that at least three different marine environments are occupied by fish that went to sea as larvae. The marine dispersal histories identified by Bayesian clustering were distributed across most of our sampled populations, indicating that each marine environment is present across the species' range (Appendix B: Table B1). One potential explanation for the observed differences in marine chemistry experienced by *A. stamineus* larvae is use of nearshore vs. offshore waters by ocean-going larvae. This mechanism has been identified as an explanation for otolith chemical variation among larval cohorts of at least one marine fish species (Hamilton et al. 2008). Metals such as copper (Cu) are linked with anthropogenic sources in the marine environment (Stauber et al. 2005); hence high concentrations of these metals in otoliths may indicate near-shore residency of larvae. The three marine clusters

all differed significantly from each other in concentrations of Cu and Sr. SW3 had high Cu and low Sr, SW1 had low Cu but high Sr, and SW2 had high Sr and intermediate Cu. Furthermore, we found that stream and marine Cu:Ca were correlated for fishes experiencing the SW3 environment (Fig. 3), suggesting that the SW3 larvae may have resided near the stream they recruited to.

The degree to which Cu in otoliths reflects environmental concentrations is unclear (Milton and Cheney 2001), particularly given that not all Cu in the environment is bioavailable for uptake. Though much of the copper in aquatic environments may be bound to organic ligands and hence not freely available, bioavailable forms of Cu can nonetheless reflect overall spatial variability in the environment (Stauber et al. 2005). Cu serves as a trace nutrient when scarce but becomes toxic at high concentrations, and blood concentrations are regulated to some degree by the fish's metabolic system. However, experiments show that otolith Cu concentrations are related to those of the water if present in high enough concentrations (Milton and Cheney 2001). We found that larval otolith Cu was correlated with adult otolith Cu in both the SW3 and FW larval groups (Fig. 3). This indicates that the otoliths may be picking up an environmental signal associated with copper discharge from streams. Thus, it is plausible that the three Bayesian groups of marine-dispersing larvae represent differences in the distance of dispersal and duration spent inshore vs. offshore. Under this scenario, we

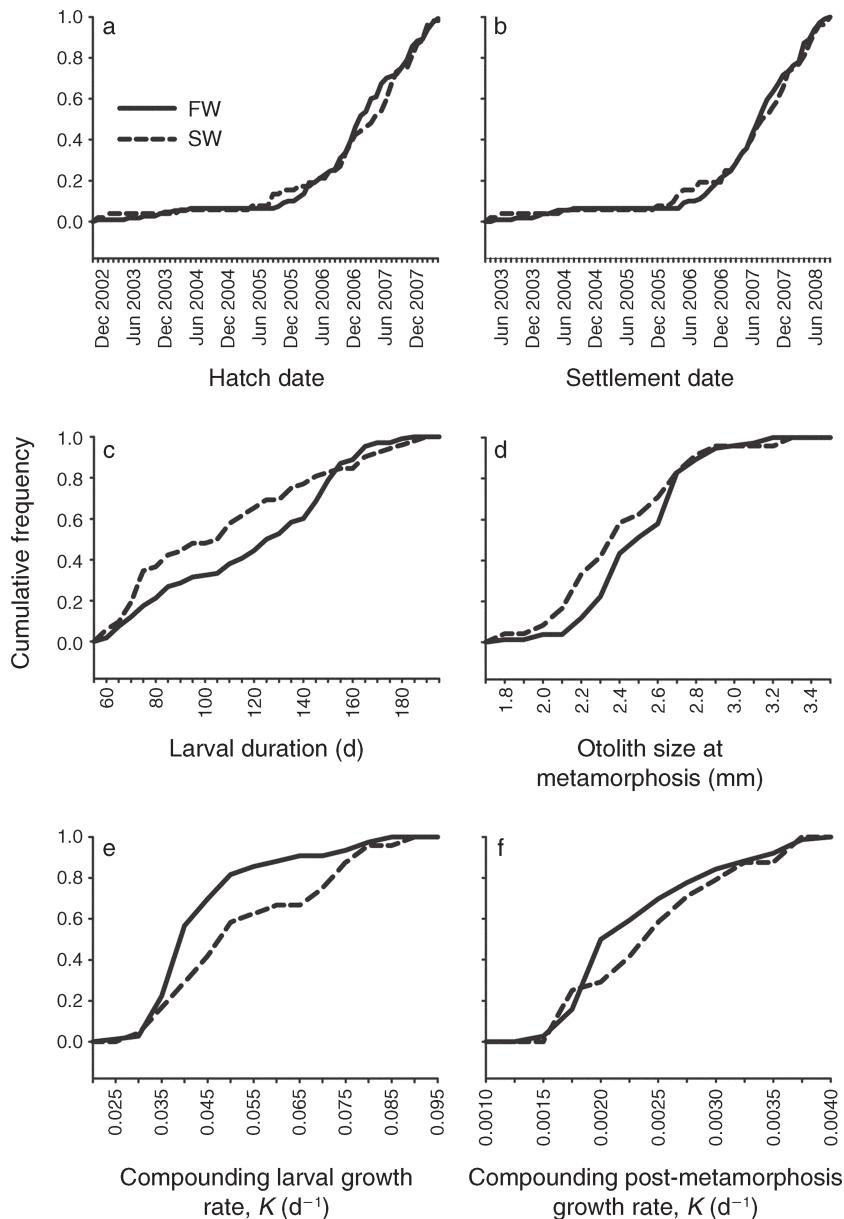


FIG. 4. Cumulative frequency curves illustrating the differences between amphidromous (dashed line) and non-amphidromous (solid line) larvae in the distributions of (a) hatch dates, (b) settlement dates, (c) larval durations, (d) otolith radius size at metamorphosis, (e) compounding daily larval growth rate, and (f) compounding daily post-metamorphosis growth rate. Compounding growth rates were estimated from the von Bertalanffy growth equation (see *Methods*). Distributions of hatch and metamorphosis dates are not significantly different (K-S tests: $P > 0.05$). All other distributions do differ significantly (K-S tests: $P < 0.001$). There were no differences found in any trait among the three SW clusters.

would interpret SW3 larvae as having been retained near shore, perhaps even spending some period of time in a low-salinity estuarine environment before settling to the stream habitat. A stable isotope study suggests that estuarine residency by larvae is at least possible for Hawaiian amphidromous gobies, showing that recently settled post-larvae had isotope signatures of estuaries or streams rather than oceanic environments (Sorenson and Hobson 2005). SW1 larvae are interpreted as

residing primarily offshore and perhaps transported long distances, and SW2 larvae as spending time both inshore and offshore.

Several other hypotheses could also explain chemical differences among the marine environments experienced by *A. stamineus* larvae, although our data offer no support for these alternatives. First, temporal changes in marine chemistry can create distinct chemical groupings if larvae are at sea at different times or seasons

(Gillanders 2002). We found that *A. stamineus* larvae hatched over a protracted period of time with no distinct seasonal patterns, and no statistical difference in the distribution of hatching or settlement dates among the three marine clusters. Distinct spatial variation within the islands could be generated by the stark climatic differences between the windward and leeward sides of islands (Appendix A: Fig. A1). Windward and leeward sides differ in river discharge, driven by orographic precipitation (Giambelluca et al. 1986), as well as ocean circulation patterns (Toonen et al. 2011; Appendix A: Fig. A1). Either factor could create distinctive chemical environments and aid in retaining larvae on one side of the islands, yet we found no difference in the proportions of the three marine clusters between leeward and windward watersheds. This is not surprising, as there is not a major barrier to dispersal between windward and leeward habitats for marine taxa in the Hawaiian Islands (Toonen et al. 2011; Appendix A: Fig. A1). Estuaries or embayments in watersheds could also create spatial structure; both have high water retention, which could retain outgoing larval fishes and influence their otolith chemistry (Shima and Swearer 2009). Nonetheless, we found no evidence that fishes recruiting to watersheds with estuaries or embayments were exposed to distinct chemical environments. Thus, our otolith chemistry data do not allow confident resolution of the causal basis for SW groups, but they are most consistent with the idea that larvae vary in whether they stay inshore or disperse more widely offshore.

Amphidromy has clear potential costs associated with the marine larval phase, including risk of predation, physiological costs of adjusting to the marine environment, energy costs of locomotion in the pelagic zone, and the challenge of finding the way back to extremely patchy stream habitats (McDowall 2010). These costs could be mitigated by reducing the length of the marine dispersal period, or by reducing the distance of dispersal from the natal habitat either by taking advantage of currents or by active natal homing (McDowall 2010). Avoidance of a marine phase altogether is the most extreme form of limiting dispersal costs, and appears to be a favorable strategy for *A. stamineus*. Furthermore, given our findings of differences in otolith chemistry among ocean-going larvae, we surmise that active near-shore retention may be a mechanism used by some marine larvae to reduce dispersal distance. This raises the question of why amphidromy is retained at all following colonization of productive tropical island streams (Bonte and De la Pena 2009).

In *A. stamineus*, it appears that marine larval dispersal has benefits that balance against its costs, leading to a persistent polymorphism via unknown processes of frequency dependence. We found that dispersal through the marine environment was associated with enhanced larval condition, which likely translates into increased lifetime fitness. Fishes that went to sea as larvae grew significantly faster during the larval period, spent

significantly less time as larvae, and tended to metamorphose into post-larvae at a smaller size compared to fishes that stayed in the streams as larvae. Larval growth advantages have been demonstrated to continue for a short period following metamorphosis (Sponaugle et al. 2006), but our results suggest that differential growth may continue for years. We found that fish that went to sea as larvae tended to have faster adult growth rates than non-amphidromous fish (although mean growth rate was not significantly different), despite living in the same stream environment together for most of their lives. The distinctions we found between FW and SW life histories are not wholesale differences in range of values of these traits, but rather significant shifts in the frequency distribution. Each of these traits has been shown to be related to larval survivorship (Searcy and Sponaugle 2001), early post-metamorphosis condition (Hamilton et al. 2008), early post-metamorphosis survivorship (Sponaugle et al. 2006), adult survival (Goater 1994), longevity and reproductive success (Taylor et al. 1998) in such disparate taxon as fishes, amphibians, and insects. These traits also have been previously linked to dispersal histories in fishes (Shima and Swearer 2009) and insects (Weiss et al. 1987).

The evidence for long-lasting benefits of a marine larval existence suggests the possibility of an influence on lifetime fitness through reproductive advantages. We found that the mean ages at sampling were not different between adult fish that experienced freshwater vs. marine larval periods. Assuming a comparable minimum size at sexual maturity, the faster-growing amphidromous fishes would then begin reproducing earlier, which could impart a fitness advantage for fast-growing, amphidromous individuals. The possible fitness advantage from faster growth of marine larvae would presumably select for marine dispersal, balancing against the benefits of larval retention discussed earlier. This balance could serve as an evolutionary mechanism for the maintenance of a dispersal bet-hedging strategy (e.g., Krug 2009). Specifically, remaining in a stream as a larva would reduce mortality (i.e., predation, becoming lost at sea) and energetic costs (e.g., physiological acclimatization, locomotion) associated with marine dispersal, yet lead to a slower larval growth rate, delayed metamorphosis, and perhaps diminished adult growth rate. As a result, the amphidromous life history strategy is not lost over evolutionary time scales because it confers certain individual benefits beyond the potential to colonize new habitats. Our analysis highlights the opportunities to use measures of individual history and performance to assess the selective costs and benefits at play in generating and maintaining intraspecific variation in dispersal.

The dispersal polymorphism described here could have far-reaching consequences for the ecology and evolution of populations. Dispersal among subpopulations can promote demographic and genetic stability of subpopulations and the metapopulation (Holland and

Hastings 2008, Walter et al. 2009, Kerr et al. 2010). Amphidromy undoubtedly facilitates dispersal of *A. stamineus* among watersheds. Long-distance dispersal, connecting populations among islands or even disparate archipelagos, seems likely in *A. stamineus* because the average larval duration is 118 days, and genetic studies indicate that between-island differentiation is minimal (Chubb et al. 1998, Lindstrom et al. 2012). While we found that only ~40% of fish disperse out to sea, this appears to be enough to prevent large-scale population differentiation (Chubb et al. 1998, Lindstrom et al. 2012). Furthermore, long-distance dispersal is expected to reduce adaptation to local environments (e.g., Bradbury et al. 2008), but can replenish disturbed and declining populations (Walter et al. 2012).

While dispersal can contribute to persistence of local populations and of meta-populations, local retention of some larvae can also promote long-term persistence of meta-populations (Hastings and Botsford 2006) through the replacement of local breeding stock (Botsford et al. 2009). In the case of *A. stamineus* across Hawaii, most larvae appear to stay within their natal stream throughout development, but the proportions of locally recruiting larvae varied widely among streams. The rates of local recruitment (through non-amphidromy and possibly also nearshore retention of SW3 marine larvae) we observed are comparable to the highest estimates of self-recruitment for marine species with dispersive larvae (Almany et al. 2007, Hogan et al. 2012). Most previous studies quantifying local retention were conducted at small scales relative to the range of larval dispersal distances (Hogan et al. 2012). Our study is among the first to examine rates of self-recruitment and potential dispersal for populations across an entire species' range, providing a comprehensive perspective on how processes that determine connectivity and population replenishment within a species can be spatially variable (Appendix B: Table B1). Our findings illustrate the importance of sampling both intensively and broadly to achieve robust estimates of dispersal for a meta-population or species.

Variation in dispersal strategies could have profound consequences for the conservation of amphidromous species. Oceanic island streams are severely threatened by habitat alteration, invasive species, water abstraction, and drying due to climate change (Brasher 2003, Walter et al. 2012). Successful conservation actions rely on an adequate understanding of the biology of the focal species, especially when management efforts can be politically contentious. For species with obligate amphidromy, preserving ocean-stream connectivity by eliminating barriers to upstream migration (e.g., dams and dewatering of streambeds) would likely provide enormous benefits (Walter et al. 2012). In this scenario, all streams would become open to immigration, and declining populations could rely on rescue from distant sources. However, in-stream habitat quality would be expected to play a much larger role in population

persistence under conditions of facultative amphidromy where local recruitment is common. Such populations would likely benefit most from improving habitat structure, restoring natural flow regimes, and removing invasive species (Brasher 2003, Walter et al. 2012).

We do not know whether the observed patterns of variation in self-recruitment and dispersal are temporally stable. Stream conditions in the Hawaiian archipelago and other oceanic islands are highly variable within and between years, potentially creating a temporally dynamic balance of self-recruitment and dispersal. In some years, marine dispersal may be favored, while in others non-amphidromy may win the day. Further comparisons will be necessary to determine the full range of life history flexibility in *A. stamineus* and other amphidromous species that occupy temporally variable and spatially patchy environments. In any case, the impressive variation in dispersal strategies revealed by our analysis of a single amphidromous species suggest that fertile ground for understanding controls on the ecology and evolution of dispersal strategies.

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SUPPLEMENTAL MATERIAL

Appendix A

Figures showing Hawaii map, example LA-ICP-MS transects, and results of the Delta K information criterion (*Ecological Archives* E095-213-A1).

Appendix B

Data collection summary statistics, LA-ICP-MS quality control data, and univariate statistics for element : calcium ratios from otolith samples (*Ecological Archives* E095-213-A2).

Appendix C

Detailed methodology: otolith preparation, microchemical analysis, and Bayesian analysis. (*Ecological Archives* E095-213-A3).