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Stream and ocean hydrodynamics mediate partial migration strategies in an amphidromous Hawaiian goby

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Abstract

Partial migration strategies, in which some individuals migrate but others do not, are widely observed in populations of migratory animals. Such patterns could arise via variation in migratory behaviors made by individual animals, via genetic variation in migratory predisposition, or simply by variation in migration opportunities mediated by environmental conditions. Here we use spatiotemporal variation in partial migration across populations of an amphidromous Hawaiian goby to test whether stream or ocean conditions favor completing its life cycle entirely within freshwater streams rather than undergoing an oceanic larval migration. Across 35 watersheds, microchemical analysis of otoliths revealed that most adult *Awaous stamineus* were freshwater residents (62% of $n = 316$ in 2009, 83% of $n = 274$ in 2011), but we found considerable variation among watersheds. We then tested the hypothesis that the prevalence of freshwater residency increases with the stability of stream flows and decreases with the availability of dispersal pathways arising from ocean hydrodynamics. We found that streams with low variation of daily discharge were home to a higher incidence of freshwater residents in each survey year. The magnitude of the shift in freshwater residency between survey years was positively associated with predicted interannual variability in the success of larval settlement in streams on each island based on passive drift in ocean currents. We built on these findings by developing a theoretical model of goby life history to further evaluate whether mediation of migration outcomes by stream and ocean hydrodynamics could be sufficient to explain the range of partial migration frequency observed across populations. The model illustrates that the proportion of larvae entering the ocean and differential survival of freshwater-resident versus ocean-going larvae are plausible mechanisms for range-wide shifts in migration strategies. Thus, we propose that hydrologic variation in both ocean and stream environments contributes to spatiotemporal variation in the prevalence of migration phenotypes in *A. stamineus*. Our empirical and theoretical results suggest that the capacity for partial migration could

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enhance the persistence of metapopulations of diadromous fish when confronted with variable ocean and stream conditions.

KEYWORDS

amphidromy, bet hedging, connectivity, dispersal, partial migration

INTRODUCTION

Migration between distinct environments has proven to be a highly successful strategy (Dingle & Drake, 2007; Milner-Gulland et al., 2011), yet migratory and resident phenotypes frequently coexist within the same population. The presence of multiple migration phenotypes, also known as partial or facultative migration strategies (Chapman et al., 2012), is thought to allow populations to cope with environmental uncertainty as the cost-benefit ratio of remaining in one environment or migrating to another varies through time (Denoël et al., 2005; Werner & Gilliam, 1984). Selection can favor distributing risk by “bet hedging,” where only a fraction of the population is truly migratory, particularly under variable environmental conditions. Bet hedging can increase fitness across generations by ensuring that some proportion of individuals in a population are matched with the environment at any given time (Crean & Marshall, 2009; Schindler et al., 2015; Seger & Brockmann, 1987), thereby stabilizing populations against environmental variability such as changing climatic conditions (Bolnick et al., 2003, 2011). Despite increasing appreciation that life history diversity can exist within species, little is known about the circumstances that fuel the origin and maintenance of alternative migratory phenotypes (Luck et al., 2003).

Partial migration has arisen independently in a variety of diadromous fishes, which would ordinarily feature an obligatory migration between freshwater and marine ecosystems (Chapman et al., 2012). In the context of diadromy, partial migrations could emerge in response to environmental variation either as an inducible behavior by individuals or the passive result of fluctuations in migration opportunities or survival outcomes experienced by the population (Chapman et al., 2011; McDowall, 2009). Thus, a variety of scenarios can lead to the loss (or gain) of diadromous migrations. For instance, Dolly Varden trout (*Salvelinus malma*) are diadromous when the marine environment is accessible, but nonmigratory forms occur when barriers trap populations inland or as older fish retire from diadromy after one or two migrations because the growth benefit to marine migrations become lower than the cost

(Bond et al., 2015). In other diadromous species, the decision to forego migration can occur during a larval developmental stage with immediate and life-long consequences (Hendry et al., 2004; Hogan et al., 2014; Roberts et al., 2019). Though there is evidence of “migration genes” in diadromous species (Hecht et al., 2013; Kendall et al., 2015), it is often unclear whether partial migration represents the presence of multiple genetically fixed strategies in a population or instead are facultative outcomes of imposing phenotypic plasticity or developmental instability within a variable environment. Regardless of the degree of genetic determination of migratory phenotypes, diadromous species could be subject to strong selective filters in the freshwater environment, marine environment, or both.

Amphidromous species present outstanding opportunities to assess the conditions shaping partial migration that involves the use of two discrete environments: freshwater streams and oceans (Augsburger et al., 2017). Amphidromy is a form of diadromy whereby adults live and spawn in streams and larvae migrate to the marine environment shortly after hatching. Larvae remain in the marine environment for several weeks to months (Radtko & Kinzie, 1996) and then return to streams as postlarval juveniles (Keith, 2003; McDowall, 2009). Because amphidromy permits long distance oceanic dispersal between freshwater habitats, logic suggests (Alda et al., 2016; McDowall, 2009) that it should be the dominant life history of species inhabiting streams on oceanic islands (Thuesen et al., 2011), like the Hawaiian archipelago. However, recent work suggests otherwise. A study of the otolith microchemistry of adult *Awaous stamineus* collected across the Hawaiian archipelago revealed that 62% of individuals remained in freshwater streams for their entire lives (Hogan et al., 2014). By not migrating to the ocean as larvae, freshwater residents avoid the risk of being lost in ocean currents, while ocean migrants benefit from faster growth rates upon their return to streams (Hogan et al., 2014). A range of residency rates was also found across streams, suggesting that the fitness difference between resident and migratory strategies differs among populations.

The relative abundance of migratory life histories in a watershed could reflect the prevailing conditions in the ocean. While directed movement by ocean-going larvae is

possible (Paris et al., 2013), dispersal pathways are thought to be strongly influenced by currents. Nearshore ocean currents show some predictable large-scale patterns but also vary enormously over time and at fine spatial scales. Thus, individual larvae and entire cohorts could have very different dispersal fates depending on the time and location of stream entry into the ocean (Cowen & Sponaugle, 2009). For instance, the northwestern direction of the prevailing currents along the Hawaiian archipelago (Jia et al., 2011) is expected to yield a net transport of larvae from source populations in the southeast to settlement sites in streams to the northwest (i.e., from the island of Hawai'i to the island of Kaua'i; Lobel & Robinson, 1986, Moody et al., 2019). The same directional currents presumably reduce the probability for ocean-going larvae produced in the northwest (Kaua'i) to settle in up-current watersheds. Moreover, the strength and direction of currents as well as the size of eddies on the leeward side of the islands also change seasonally and annually (Jia et al., 2011; Lindo-Atchati et al., 2020; Lobel & Robinson, 1986). Thus, spatial and temporal variation in ocean hydrodynamics is likely to play a key role in mediating the arrival rate and origins of ocean-going larvae.

Hydrodynamic conditions in streams could also mediate the balance between resident and migratory life histories in two ways. First, the likelihood that hatchlings will be able to reach the sea or that ocean-going larvae can find a stream mouth might be strongly affected by stream flow conditions. Second, the fitness of resident larvae is likely to depend upon stream flow. Stable flow regimes, as in low-gradient streams dominated by groundwater inputs or watersheds containing lakes, may create a mild stream environment for larvae that enhances survival probabilities relative to a marine migration (Augspurger et al., 2017; Hicks et al., 2017; Huey et al., 2014). More pulsed flows are thought to flush olfactory cues farther into the ocean, where ocean-going larvae may be more able to detect the presence of a stream for settlement (Nishimoto & Kuamo'o, 1997). Hawaiian streams are characteristically flashy in hydrology, but flow regimes vary widely based on geomorphology, groundwater flows, and heterogeneous precipitation on each island (Lau & Mink, 2006), which raises the possibility that partial migration reflects spatial and temporal variation in hydrological conditions within Hawaiian streams.

In this study, we examined how stream and ocean hydrodynamic variation relates to partial migration outcomes in the native Hawaiian amphidromous goby *A. stamineus*. We first characterized spatial and temporal variation in stream flow and frequency of freshwater residency to test for covariation across two separate generations by analyzing the otolith microchemistry of adult fish collected in two different periods from 35 watersheds spanning a wide range of stream flow regimes. This

enabled us to assess the hypothesis that freshwater residency decreases with stream flow variability, with the expectation that greater stream flow stability would offer safer conditions for the maturation of resident fish and a lower likelihood of larvae being flushed to the ocean. We also tested the hypothesis that the frequency of ocean-going larvae depends on stream position along the Hawaiian archipelago and the temporal variation in ocean currents at that location. We evaluated the likelihood of successful stream settlement of ocean-going larvae using the results from an empirically constrained passive transport model that utilized open-ocean and nearshore currents across the archipelago to predict dispersal outcomes in the absence of directed movement by larvae (Moody et al., 2019). Finally, we developed a theoretical model to further evaluate how differential larval mortality and emigration could yield variation in apparent rates of residency inferred from analyses of adults in streams. Our results provide evidence for the influence of both stream and ocean hydrodynamics in driving partial migration and underscore the challenge of conserving species with complex life histories when survival depends on success in multiple time-varying environments.

METHODS

Specimen collection and life history analysis

We analyzed adult *A. stamineus* from 35 watersheds across the five Hawaiian Islands, spanning the full geographic range of the species. In each watershed, we pooled fish collected from three locations in the lower and middle reaches between December 2008 and November 2009 (Hogan et al., 2014) and sampled the same reaches again between March and June 2011. Reaches were chosen based on preliminary surveys of the distribution of *A. stamineus*, which is unable to climb large waterfalls to access the upper reaches of most watersheds. Each of our two sample sets was dominated by different generational cohorts because adults live in the stream for 1–3 years following their larval period and marine dispersal averages 118 days (range 57–248 days; Hogan et al., 2014).

We characterized the proportion of *A. stamineus* in each stream that were lifelong freshwater residents, using only watersheds and years with at least $n = 4$ (median sample size $n = 10$ per watershed per year; Appendix S1: Table S1). Our state collection permits mandated minimal collections from each reach in order to avoid impacting populations of this imperiled species, and our sample size was insufficient ($n < 4$) to credibly estimate the proportion of residents in a few cases. Fish were

netted by hand by snorkelers, euthanized (Tricane MS 222) in the field, and frozen for transport. In the lab, sagittal otoliths were removed using acid-washed, Teflon-coated tools and rinsed with distilled water. Otoliths were mounted (sulcus upward) onto petrographic slides and embedded in Crystal Bond glue. Otoliths were ground and polished in the sagittal plane using fine-grit and velvet polishing pads to expose the daily growth rings from the edges to the primordium. The strontium-calcium molar ratio (Sr:Ca) microchemistry was analyzed using LA-ICP-MS (LSX213 Teledyne Cetac laser: 25- μm beam width scanning across the full diameter at 15 $\mu\text{m s}^{-1}$), coupled with a Perkin Elmer ELAN DRCII at the Environmental Analytical Facility at the University of Massachusetts. All samples were calibrated and drift corrected using two calcium carbonate standards (USGS MACS-1, ACS-3) and background corrected against the argon carrier gas in a blank sample. Calcium (^{43}Ca) was used as a reference point for the mass of ablated material. Saltwater produces Sr:Ca of ~ 0.008 , whereas freshwater residency is indicated by Sr:Ca of ~ 0.002 in both the larval and adult life stages, as detailed by Hogan et al. (2014). Thus, marine migrants were identified by elevated Sr:Ca near the center of the otolith, representing the larval life stage. Fish whose otoliths exhibiting consistently low Sr:Ca across the entire diameter (i.e., representing both larval and adult periods) were considered to be lifelong freshwater residents.

Hydrodynamics and larval settlement

We quantified temporal variability in discharge as a metric of stream hydrodynamics. A decade of mean daily discharge was obtained for all available US Geological Survey stations in the Hawaiian Islands (January 2001–December 2011), and we did not attempt to estimate discharge in unmonitored watersheds. We developed daily discharge frequency exceedance curves for each monitored site and calculated high flow (5th and 10th, denoted as Q_5 and Q_{10} , respectively), median (Q_{50}), and low flow statistics (Q_{90} and Q_{95}). For example, Q_{95} can be thought of as when the discharge exceeded 95% of the time, thereby representing the lowest 5% of discharge days. We also calculated a flow variability index as the ratio of high discharge to low discharge ($Q_{10}:Q_{90}$) for each stream (Richards, 1989) and a base flow stability index ($Q_{90}:Q_{50}$) for which larger values represent more stable flows (Poff & Ward, 1989). For a third perspective, we summarized overall variation in daily discharge using the coefficient of variation (CV). Though the majority of streams in the Hawaiian Islands can be characterized as low discharge ($Q_{50} < 0.3 \text{ m}^3 \text{ s}^{-1}$) and wadeable ($< 1 \text{ m}$ deep) so that they can be sampled without a watercraft, they

exhibit a wide range of prevailing discharge. For example, the streams included in this study varied 60-fold in median discharge ($Q_{50} = 0.034 \text{ m}^3 \text{ s}^{-1}$ in Kaluanui, O‘ahu vs. $Q_{50} = 2.0 \text{ m}^3 \text{ s}^{-1}$ in Wainiha, Kaua‘i). The 2001–2011 period for our stream hydrodynamic analysis corresponded to the potential range of dates experienced by the sampled fish.

We used an ocean hydrodynamic passive transport model applied to stream mouth locations throughout the Hawaiian archipelago (Moody et al., 2019) in order to assess spatial and temporal variation in potential ocean dispersal pathways. This physical model has proven useful in predicting the position and settlement of larval reef fishes from empirical studies within the Hawaiian Islands (Wren & Kobayashi, 2016). We relied on a modified Lagrangian model (Polovina et al., 1999; Wren & Kobayashi, 2016) using the Hybrid Coordinate Ocean Model (HYCOM) mixed layer formulation (Jia et al., 2011) with 0.04° horizontal resolution. The model is eddy resolving, which is essential for simulating near-shore dispersal via eddies and local entrainment on the leeward side of each island. On each day of the simulation, 100 “larvae” were released from the mouth of each of 51 representative streams known to support populations of *A. stamineus*. The simulation began on 2 May 2009 and ended on 31 March 2014 (1594 days; Table 1), with forcing from observed weather patterns throughout that period. Each ocean-going larva was assumed to settle in the first stream mouth encountered (within 5 km, the shortest distance allowed by model resolution) after spending at least 50 days in the ocean (the minimum observed duration of the marine larval period of *A. stamineus* is 57 days; Hogan et al., 2014). Any larva that drifted for > 200 days was considered to die, thereby approximating the observed duration of larval dispersal for *A. stamineus* (mean 118 days, maximum 248 days; Hogan et al., 2014). As an index of larval settlement in a stream following a marine larval period, we calculated the proportion of all larvae that settled in each stream in each year of the simulation (Appendix S1: Table S3). The mean and CV of the annual settlement index across the 5-year simulation were used to summarize temporal variability in larval settlement for each stream (Appendix S1: Table S3). Finally, we pooled all streams on each island to summarize the average annual settlement and its temporal variability at the island scale (mean, SD, and CV; Appendix S1: Table S2).

Though our otolith analyses, stream hydrodynamic metrics, and ocean connectivity metrics have overlapping space and time domains, each was derived from independent research efforts that did not align perfectly (Appendix S1: Table S3). For instance, the set of 51 streams analyzed with

TABLE 1 Results from passive larval transport model from 2019 to 2013.

Year	Days	Streams	N migrants	N settled	N lost	Percentage settled (%)	Percentage lost (%)
2009	254	51	1,295,400	144,764	1,150,636	11	89
2010	365	51	1,861,500	160,736	1,700,764	9	91
2011	365	51	1,861,500	174,221	1,687,279	9	91
2012	366	51	1,866,600	195,217	1,671,383	10	90
2013	365	51	1,861,500	153,361	1,708,139	8	92

Note: The simulation used 51 watersheds with known populations of gobies (Moody et al., 2019). The simulation encompassed the period from 2 May 2009 to 31 March 2014. The table summarizes the annual number of larvae exported to the ocean and how many settled in a stream compared to those that were lost at sea in marine currents. A stream receives emigrating larvae if they drifted within 5 km of a stream mouth after 50 days or were lost at sea after 200 days.

the ocean hydrodynamic model included 30 of the 35 sites where we sampled fish for otolith analysis. Inclusion of the additional 21 streams in the hydrodynamic model allowed greater understanding of dispersal potential across the geographic range of *A. stamineus* (Appendix S1: Table S3) but could not be compared with otolith results. Similarly, stream discharge data were only available for a subset of the 35 watersheds where we sampled *A. stamineus*, such that only 12 watersheds had sufficient otolith samples and stream discharge data to calculate the proportion of larval residency in any given sampling year. Thus, only 11 watersheds were available for joint analysis of modeled settlement, otolith-based residency rates, and stream discharge.

Our temporal coverage also did not align perfectly across data types. The ocean simulation period (2009–2014) only partly overlaps with the stream discharge period and potential hatch dates of sampled fishes (2001–2011). Despite these mismatches arising from differences in data sources, we had sufficient overlap to draw general inferences about how spatial and temporal variation in fish migration relate to stream and ocean hydrodynamics. Moreover, the cross-population comparisons emphasized in this study did not presume that our metrics of estimated hydrodynamics represented the actual conditions experienced by the sampled fish in either stream or ocean environments.

Statistical analysis

General linear models were used to test for relationships between hydrodynamic variables (stream discharge variability, simulated ocean connectivity metrics) and the proportion of *A. stamineus* that were lifelong freshwater residents across watersheds for each of our two survey years. We used the small-sample form of the Akaike information criterion (AIC_c) to compare the explanatory efficiency of alternative models in explaining variation in amphidromy across watersheds, seeking a

parsimonious balance between model fit and number of predictors (Burnham, 2004). All statistical analyses were conducted using R version 3.6.3 (R Development Core Team, 2020).

Theoretical model

To complement our empirical analyses, we developed a theoretical model of a stream goby population that calculates the expected proportion of lifelong freshwater residents based on differential larval survival in freshwater (S_f) and ocean (S_o) environments and the proportion of larvae that entered the ocean (hereafter called the amphidromy rate, α). For a given watershed, the proportion of lifelong freshwater residents (R) is the number of adults that remained in freshwater (A_f) divided by the total number of adults, including those that underwent an ocean migration as larvae (A_o). Expressing these adult numbers as the product of larval production (P), survival rates in each environment, and the amphidromy rate gives

$$R = \frac{A_f}{A_f + A_o} = \frac{P_s f (1 - \alpha)}{P_s f (1 - \alpha) + P_s o \alpha}, \tag{1}$$

Rearranging this equation separates the different biological processes (survival and amphidromy) and clarifies the importance of survival differences between larval environments:

$$R = \frac{(S_f/S_o)(1 - \alpha)}{(S_f/S_o)(1 - \alpha) + \alpha}. \tag{2}$$

This equation can also be formulated as an odds ratio (Appendix S2). To illustrate the conditions under which R can vary, we explored all possible values of relative survival between habitats (S_f/S_o) and amphidromy rate (α) both independently and jointly. To extend these

inferences, we derived general equations for calculating the change in survival or amphidromy required to permit any shift in R between generations (Appendix S2). We used these general expressions to evaluate how any given R can arise from a range of survival ratios and amphidromy rates, but we focused on values of R (60% vs. 80% residency) observed in our archipelago-wide otolith analyses.

RESULTS

The otolith microchemistry of adults collected in 2011 revealed that 83% of *A. stamineus* were lifelong freshwater residents ($N = 274$), compared to 62% in 2009 ($N = 316$; Hogan et al., 2014). Paired comparisons of our two sampling periods across watersheds indicated that this shift toward higher residency in 2011 was statistically significant (paired t -test, $df = 23$, $p < 0.001$, Appendix S1: Figure S1). The largest proportional changes between sampling periods occurred on the island of Kaua'i, where 56% of adults were freshwater residents in 2009 compared to 88% in 2011 (Appendix S1: Table S1).

The CV of daily stream discharge was most closely associated with the proportion of freshwater residence in *A. stamineus*, with a significant effect of collection year. The top model (lowest AIC_c; Appendix S1: Table S4) recovered the same regression slope on CV stream discharge in 2011 and 2009 ($\beta = -0.099$) but a different intercept for each collection year (analysis of covariance [ANCOVA], intercepts 2011 = 0.99, 2009 = 0.78; Figure 1a). The next best models included descriptors of both collection year and high flows ($\Delta AIC_c = 2.34$) or collection year alone ($\Delta AIC_c = 2.40$; Appendix S1: Table S4). The metrics median and low flows were not as strongly related to differences in freshwater residency among populations ($\Delta AIC_c > 3.5$, Appendix S1: Table S4). To evaluate whether missing samples could have biased these results, we reran the ANCOVA using only watersheds with samples in both 2009 and 2011. We again found that the CV of stream discharge coupled with a year effect resulted in the most parsimonious model (lowest AIC_c). Thus, we show the results of the ANCOVA with the full data set (Figure 1a).

Simulation of ocean hydrodynamics suggested high mortality during larval dispersal: 90.5% of larvae did not passively drift within 5 km of a stream mouth during the modeled settlement period (50–200 days after hatching; Table 1). However, simulated larval settlement varied 36-fold across streams, deviating widely from equivalence (Appendix S1: Table S3). For instance, Honoli'i stream on the island of Hawai'i received a disproportionately smaller share of larval settlers (0.17%), whereas Ukumehame stream on Maui received a

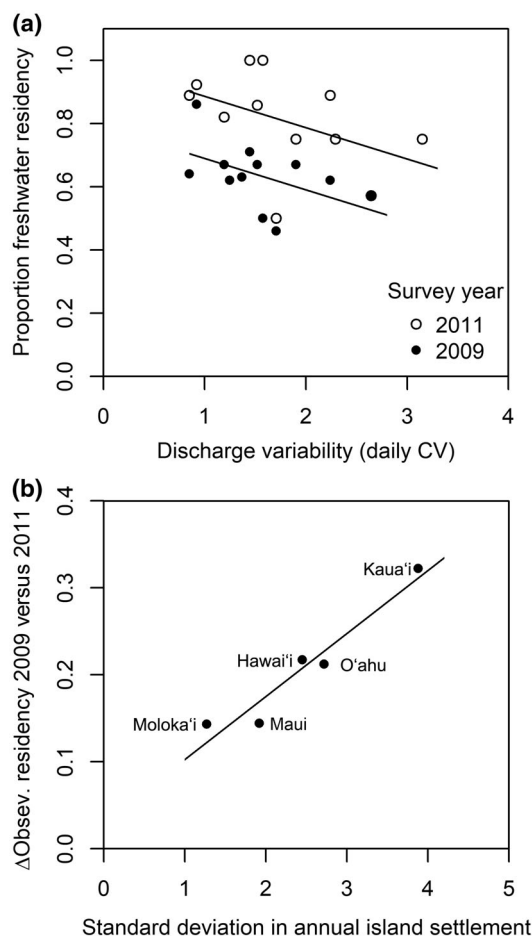


FIGURE 1 (a) Proportion of freshwater resident individuals collected from 12 streams across Hawaiian archipelago in 2009 (filled points) and 2011 (open points) as a function of stream discharge variability (daily coefficient of variation [CV] from 2001 to 2011). Regression lines are parallel in both surveys ($\beta = -0.099$), but the intercept was significantly higher in 2011 (0.99) compared to 2009 (0.78). (b) Change from 2009 to 2011 in proportion of adult *A. stamineus* identified as freshwater residents as a function of variation (SD) across 5 years (2009–2013) in proportion of ocean-going larvae reaching each island (linear regression fit line: $r^2 = 0.93$, $F_{1,3} = 39.65$). Larval settlement in each year reflects the proportion of all ocean-going larvae that successfully reached stream mouths on each island, which was inferred from the passive ocean larval dispersal simulation of larval fate from 51 representative streams.

disproportionately larger share (6.23%; Appendix S1: Table S3) relative to the other streams. Following the prevailing northwestern currents, settlement probabilities more than doubled from the island of Hawai'i to Kaua'i (island-scale geometric mean across simulation years: range from Hawai'i 0.87%, Maui: 1.43%, Moloka'i: 1.62%, O'ahu: 1.82%, Kaua'i: 2.23%).

We found a significant positive association between the observed shift in freshwater residency (2009 vs. 2011) and

the interannual variation in simulated larval settlement at the island scale (Appendix S1: Table S2; Figure 1b: island-scale settlement SD: $F_{1,3} = 39.65$, $r^2 = 0.93$, $p < 0.01$; island-scale settlement CV: $F_{1,3} = 39.65$, $r^2 = 0.58$, $p = 0.081$). Interestingly, variation in island-scale settlement was most pronounced for Kaua'i and Hawai'i at the northwest and southeast ends of the archipelago, respectively, which is also where the measured shift in freshwater residency was greatest (Figure 1b). In contrast, interannual variation in simulated settlement rates and observed changes in residency were relatively modest for the central islands of Moloka'i and Maui.

At the stream scale, simulated larval settlement and otolith-based residency data from 30 watersheds indicated no correlation (ANCOVA, $p > 0.1$). Interannual variability in simulated larval settlement (CV) was also not correlated with the magnitude of the shift in the proportion of freshwater residency between 2009 and 2011. In a joint analysis of the 11 watersheds with otolith data, stream discharge data, and simulated larval settlement, the proportion of lifelong freshwater residents was again best explained by variation in stream flow (CV) and sample year (e.g., Figure 1a; Appendix S1: Table S5). Adding metrics of simulated larval settlement did not enhance explanatory power for freshwater residency (ANCOVA, $p > 0.5$; Appendix S1: Table S5).

The structure of our theoretical model demonstrated two key factors determining the proportion of freshwater residency in a population: the ratio of freshwater to ocean larval survival and the larval amphidromy rate (Figure 2a). The proportion of lifelong freshwater residents (R) increases as larval survival in freshwater increases relative to ocean survival (Figure 2a). Alternatively, R increases with the proportion of larvae that remain in freshwater rather than going to the ocean (Figure 2b). Thus, the theoretical model suggests that changes to freshwater or ocean survival could lead to a major intergenerational shift in the proportion of resident adults, as we observed between 2009 and 2011.

Achieving any given value of R requires a different survival ratio for any given amphidromy rate, and vice versa, when the other variable is constant (Appendix S2: Figure S3a). However, if shifts in parameter values are considered multiplicatively and larval amphidromy is considered on the odds scale, then the required change in both variables is invariant (Appendix S2: Equations S1.7 and S1.9). Hence shifting from an R of 0.6 to 0.8 can occur for any larval amphidromy rate simply by increasing the survival ratio 2.67-fold (i.e., odds ratio of 0.6–0.8), regardless of the larval amphidromy rate. By extension, small shifts in both stream and marine larval survival could strongly affect R . These patterns in the theoretical model show that the spatiotemporal variation in partial

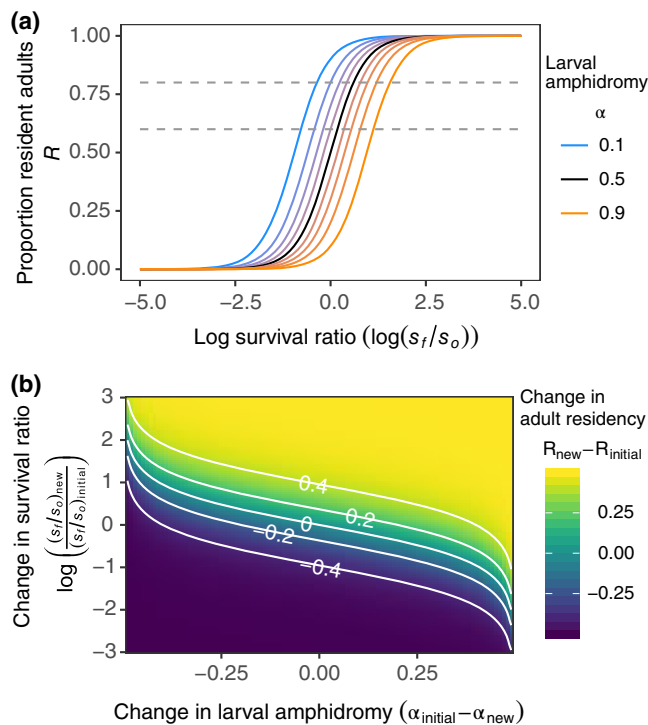


FIGURE 2 (a) Proportion of adult gobies that are lifelong freshwater residents R as a function of the larval survival ratio in freshwater streams versus ocean ($\log(s_f/s_o)$) and the larval amphidromy rate (α). Dashed lines at $R = 0.6$ and 0.8 reflect the observed proportion of freshwater resident adults in 2009 and 2011, respectively. (b) Change in proportion of freshwater resident adults as larval survival ratio (y-axis) and larval amphidromy rate (x-axis) vary. The proportion of resident adults increases both when larval survival increases disproportionately in freshwater and when the rate of larval amphidromy declines. The baseline conditions are $\alpha = 0.5$ and $(s_f/s_o) = 1$.

migration in *A. stamineus* could arise from many different combinations of amphidromy rate, stream larval survival, and marine larval survival (Appendix S2: Figure S3b).

DISCUSSION

Our quantification of amphidromy in two successive generations across the entire range of *A. stamineus* revealed that partial migration could vary widely in both time and space and that this variation was likely associated with both stream and ocean hydrodynamics. In comparison to our 2009 survey (Hogan et al., 2014), we documented a noteworthy 21% increase in the number *A. stamineus* that were lifelong freshwater residents in 2011. The proportion of freshwater residents increased between generations in almost all of our 35 study streams, despite uncertainty from limited sample sizes (Appendix S1:

Figure S1). Stream flow variability was the best predictor of the proportion of residents in both years; the more stable the stream discharge, the more likely that gobies were freshwater residents (Figure 1a). However, the increase in freshwater residency between survey years was consistent across a wide gradient of stream discharge, suggesting the influence of an archipelago-wide environmental variable. Our multiyear simulations of ocean hydrodynamics suggested that island-scale temporal variability in the simulated settlement of ocean-going larvae was positively associated with the magnitude of observed intergenerational shift in freshwater residency (Figure 1b). Our theoretical model highlights the potential for dual hydrodynamic filters to mediate partial migration patterns (Figure 2), offering further insight into the spatial and temporal variation in amphidromy that we document across the Hawaiian archipelago.

Environmental controls on partial migration

Our findings suggested that variability in stream and ocean hydrodynamics contributed to observed patterns of partial migration in *A. stamineus*. Streams with more variable flows harbor a lower proportion of freshwater residents, which could be the result of several underlying mechanisms. As illustrated in our theoretical model, a key element could be differential larval survival in the ocean versus stream environment (Figure 1a). Simply put, flashier flows may result in more stressful physical conditions in streams, from stranding larvae or adults during dry months to burying them during frequent flooding (Fitzsimons & Nishimoto, 1995). Additionally, pulsed flows may be more likely to flush newly emerged larvae to the ocean (Iguchil & Mizuno, 1991). Pulsed stream flows may also attract more ocean-going migrants by pushing a ribbon of low-density freshwater further offshore (Nishimoto & Kuamo'o, 1997). Determining the mechanisms by which stream hydrodynamics affect partial migration is an important frontier for enhancing understanding of diadromous life histories.

Other studies indicated that *A. stamineus* were not the only amphidromous species in which stream flow variability and landscape factors engender partial migrations (Augspurger et al., 2017). Huey et al. (2014), for example, found that the prevalence of ocean-going larvae in Australian *Awaous acritosus* increased with catchment steepness and attributed the pattern to flashier discharge in high-gradient stream channels. The reverse hydrodynamic pattern exists with stream geomorphology across the Hawaiian Islands: Flow stability often increases with watershed slope because of greater rainfall at higher elevations

and because erosional down-cutting of the streambed bed is more likely to intersect the water table before reaching a terminal cascade (Takasaki & Mink, 1985). Hicks et al. (2017, 2021) also found that amphidromous galaxiids exhibited partial migration depending on catchment hydrology in a system where lakes create opportunities for lifelong residence in freshwater. These examples provide evidence for the expression of different (Augspurger et al., 2017) migration strategies within amphidromous species due to the interactions between climate and landscape features.

Our simulation of ocean dispersal illustrated the perils inherent in an amphidromous migration strategy. Based on the assumption that migrating larvae passively drift in the ocean, our estimates indicate that more than 90% of larvae perish simply because prevailing currents prevent them from returning to the coast (Table 1). Predation or starvation during ocean dispersal would be expected to further reduce the proportion of larvae that survive long enough to recruit to a stream. Thus, the interannual variation in larval survival predicted from ocean hydrodynamics could easily drive the balance between resident and migrant larvae recruiting to populations in each stream. Our theoretical model underscores the potential for such spatial and temporal differences in the survival of ocean-going larvae to range-wide variation in which migration strategy dominates populations (Figure 2).

Though the oceanic dispersal model and otolith analyses both indicated that some watersheds were better positioned to receive ocean-going larvae than others, we found that the observed proportion of freshwater residents was not correlated with stream-scale average or variation in larval settlement rates. This mismatch could reflect the simplifying assumptions of the model (Moody et al., 2019), such as equal input of larvae to the ocean from every stream, no postsettlement filters upon survival of recruiting postlarvae in streams (Hain et al., 2019), and no variation among streams in their capacity to attract marine larvae as they approach the shore. However, the stream-level mismatch could also be unrelated to passive oceanic dispersal but instead reflect differences in the survival of resident larvae or the efficiency of delivering hatchling larvae to the coast.

Our oceanic dispersal model also made key simplifying assumptions with respect to larval behavior, which we treated as completely passive rather than including vertical migration, olfactory cuing, or active swimming. Similarly to reef fish larvae (Paris et al., 2013), larval gobies may exhibit behaviors (Nishimoto & Kuamo'o, 1997) that result in some fish remaining in the coastal zone close to their natal site (Hughes et al., 2014; Kaemingk et al., 2019; Sorensen & Hobson, 2005). Such behaviors may reduce the mortality of marine larvae and facilitate their re-entry

into the stream environment. Further, the capacity to actively orient to and swim toward freshwater plumes or other olfactory cues in the marine environment, as documented in some larval fishes (Acou et al., 2009; Hale et al., 2008), could enhance the likelihood of marine larvae successfully recruiting to streams and might also reduce dispersal distances. At present, the behavioral capabilities of *A. stamineus* and other Hawaiian gobies are unknown, and our otolith microchemistry analyses reveal nothing about the nature of the marine environment experienced during marine larval migration.

In light of these limitations, it is remarkable that the observed increase in freshwater residency between generations was positively associated with interannual variation in simulated larval settlement at the island scale (Figure 1b). We were surprised to find that temporal fluctuations in simulated larval settlement peaked at both ends of the archipelago, rather than showing a simple directional trend. Perhaps nearshore currents and eddies are less variable in the center of island archipelagoes. In any case, our oceanic dispersal model indicated that spatiotemporal variation in ocean currents could mediate the recruitment of goby larvae to Hawaiian streams, even without accounting for larval behavior. In combination with differences among streams as hospitable environments for resident larvae, the variability of marine dispersal success indicated by our model suggests that dispersal polymorphisms may be essential for avoiding local extirpations and even archipelago-wide extinction in the long run.

Our theoretical model indicates that the ~20% increase in the proportion of resident adults observed between 2009 and 2011 could plausibly arise by multiple pathways. The magnitudes of either increased survival of freshwater resident larvae (S_f) or decreased prevalence of amphidromy (α) required to raise the net proportion of resident adults (R) from 0.6 to 0.8 are quite reasonable, even if only one or the other were to shift (Appendix S2: Figure S3). For example, an increase in freshwater larval survival from 8% to 15.5% coupled with a reduction of marine larval survival from 11% to 8% (well within interannual variability in larval settlement predicted by our passive ocean dispersal model; Table S1) would yield a 2.67-fold increase in the survival ratio. This would increase R from 60% to 80% even in the absence of any change in larval amphidromy (Appendix S2: Equations S1.6, S1.9). Although we have no way of estimating freshwater larval survival or larval amphidromy rates, it is very plausible that S_f , S_o , and α could each vary enough among years to result in the change in R that we documented. If these variables were to shift in concert, the required change in each one would be even smaller.

Integrating the results of our empirical surveys, marine dispersal model, and theoretical model, we

inferred that either stream or ocean hydrodynamic variability could be sufficient to create considerable spatio-temporal variation in partial migration. However, we believe that the wide range of observed freshwater residency rates most likely arises from the joint effects of variation in both the freshwater and marine environments. Most diadromous fishes (e.g., salmon, eels, sardines) are likely to encounter such dual hydrodynamic challenges, so our analyses of *A. stamineus* in Hawai'i may have much broader relevance.

Reconsidering obligate amphidromy in Hawaiian freshwater fishes

Surveys of otolith microchemistry indicate that lifelong freshwater residency is a successful life history strategy for *A. stamineus*. The fact that 60%–80% of otoliths lacked a chemical signature of an marine migration represents a dramatic departure from the long-standing assumption of obligate amphidromy in most animals inhabiting streams on tropical oceanic islands (McDowall, 2009; Radtke & Kinzie, 1996). Our results are supported by a growing number of studies of other tropical gobies that have also found evidence of facultative amphidromy (Augspurger et al., 2017). For instance, a high proportion of *A. acritosus* (63%) were found to be freshwater residents along the northeast coast of Australia (Huey et al., 2014). A small proportion of freshwater residents were also found in three of four goby species on Puerto Rico, including *Awaous banana* (6.7% nonamphidromous, Smith & Kwak, 2014). Consistent with work done on congeners (Mennesson et al., 2015), comparative studies of other Hawaiian gobioid species suggest that all but one (*Sicyopterus stimpsoni*) are facultatively amphidromous (Heim-Ballew et al., 2020). More expansive analyses are warranted to confirm these findings and to determine whether similar factors govern the balance of migratory life histories in other lineages.

From an evolutionary standpoint, the facultative loss of transitions between freshwater and marine environments represents a profound change, but whether this life history variation represents phenotypic plasticity, adaptive evolution, or phylogenetic history in Hawai'i is unresolved. Diadromy is not entirely lost in any of the populations that we surveyed, and we cannot resolve whether partial migration reflects a genetically encoded polymorphism or phenotypic plasticity (Bonte & De La Peña, 2009). The available surveys of mitochondrial haplotype variation suggest no geographic structure among islands or watersheds (Alda et al., 2016; Chubb et al., 1998), so alleles for either fixed residency or full plasticity could spread easily in *A. stamineus*. Invasive

predatory fishes are common in most Hawaiian streams (Hain et al., 2019; Moody et al., 2017), and they could impose strong selection against freshwater residency. However, the resident strategy could yield high fitness in streams where the lack of predators creates a safe environment for all life stages. The heterogeneity of in-stream selective pressures could easily favor plasticity in migration strategy in *A. stamineus*, particularly given that high gene flow among populations would limit local adaptation. Though *A. stamineus* is undoubtedly derived from ancestors with a long enough marine larval period to allow colonization of the oceanic islands of the Hawaiian archipelago (Alda et al., 2016; Lindstrom et al., 2012), we must also recognize that partial migration has been documented in multiple species of *Awaous* (Hogan et al., 2014; Huey et al., 2014; Smith & Kwak, 2014). Thus, the possibility that facultative amphidromy is an ancestral trait in *A. stamineus* must be considered when interpreting the current ecological context for partial migration. Given that our findings offer strong support for conditional environmental filtering of which migration strategy life histories “work” based on ocean and stream conditions, perhaps future work could couple genomic, phenotypic, and environmental surveys to resolve the roles of genetic control versus phenotypic plasticity in governing partial migration.

If freshwater residency is the dominant strategy for *A. stamineus*, why does the species retain amphidromy at all? As migrant and resident strategies are represented in most populations, it is possible that they differ in other ways. For instance, we have found that migrants and residents differ in breeding phenology relative to lunar phases (J. D. Hogan et al., unpublished). Such temporal separation of breeding could stabilize the coexistence of migrant and resident strategies by reducing gene flow, but it might also have consequences for intraspecific competition for stream resources or differential exposure to flashy stream hydrology. Thus, the persistence of amphidromy via partial migration could involve bet hedging in many dimensions beyond the environment experienced by larvae.

Persistence of amphidromous fishes facing environmental change

Given the uncertainties of dual hydrodynamic variation, we suggest that partial migration provides an effective bet-hedging strategy that ensures persistence. When fluctuating ocean conditions might doom an entire cohort of ocean-going larvae across the archipelago, it would be beneficial for some larvae to remain in streams. When

streams can regularly flood or dry out, it would be beneficial for some larvae to go to sea. Given the uncertainty of survival in both environments, partial migration is likely to enhance the persistence of each local population as well as the species-level metapopulation. Indeed, it is possible that the flexible migration strategy documented herein may help to explain the broader distribution and greater abundance of *A. stamineus* across the Hawaiian archipelago relative to other endemic stream gobies (Lisi et al., 2018; Moody et al., 2017).

Though partial migration has the potential to enhance population resilience, it is becoming increasingly evident that conservation efforts are necessary to sustain the endemic species inhabiting Hawaiian streams. Widespread urbanization, water abstraction, climate change, and invasive species are depressing several other gobies across the Hawaiian archipelago (Moody et al., 2017, 2021; Walter et al., 2012). Moreover, since all of these species are at least partially amphidromous, each may be sensitive to variation in both stream flows and ocean currents in the fashion documented herein. For instance, periodic climate fluctuations (e.g., El Niño-La Niña oscillations) could shift larval mortality at sea (Moody et al., 2019) and alter precipitation patterns that drive variation in stream flows. Such large-scale climatic forcing could affect recruitment across the entire range of these species, creating particular challenges for obligately amphidromous species. Our theoretical modeling framework could be expanded to evaluate the implications of environmental fluctuations for individual populations or entire metapopulations as a function of their migration strategy.

Recognizing partial migration in *A. stamineus* may complicate efforts to conserve and protect the endemic fauna of Hawaiian streams, in part because it requires that plans address a range of migration strategies. For obligate amphidromous Hawaiian species that lack the insurance afforded by partial migrations, management strategies must continue to stress stream–ocean connectivity. Yet for species with partial migrations, preserving connectivity to enable consistent population rescue via marine dispersal may be less valuable than improving stream habitat quality because both the growth and reproductive phases of the life cycle can occur in streams. Thus, prioritization of management approaches and watersheds should be informed by surveys of life history variation within species (Heim-Ballew et al., 2020), and interventions to improve stream habitat quality should account for whether focal species are lifelong residents or not (Moody et al., 2021). Preserving diversity in ecosystems requires considering a well-balanced combination of options, including broad precautionary measures

intended to counter the unpredictability of natural environments (Schindler & Hilborn, 2015). In light of the profound life history variation represented by partial migrations of *A. stamineus*, investing in diverse conservation measures would be a sensible precaution, hedging our bets, just as the fish do.

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CONFLICT OF INTEREST


The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Previously published data on dispersal life histories from Hogan et al. (2014) are available on Figshare <https://doi.org/10.6084/m9.figshare.c.3307041.v1>. Ocean hydrodynamic model output from Moody et al. (2019) and code are available through Open Science Framework at <https://doi.org/10.17605/OSF.IO/M5SBH>. Additional summary tables of both data sets are provided in Appendix S1. Proof of the theoretical model appears in Appendix S2, and R code (Holt, 2022) for all figures is available on Zenodo at <https://doi.org/10.5281/zenodo.6575262>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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