IDENTIFYING MIGRATION FLEXIBILITY AND THE ENVIRONMENTAL FACTORS THAT INFLUENCE VARIATION IN RECRUITMENT SUCCESS IN PARTIALLY MIGRATORY HAWAIIAN FISHES

A Dissertation

by

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This dissertation meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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ABSTRACT

Behavior flexibility during the larval stage influences differential mortality, recruitment, and population dynamics; recruitment is poorly understood, yet important for understanding population persistence. The purpose of this dissertation was to examine fishes for migration flexibility and to identify factors at different spatiotemporal scales that are influential to differential survival within and across populations. I found that four underexplored native freshwater fishes of Hawaiʻi exhibited a larval migratory strategy, but many were flexible. One species (*Sicyopterus stimpsoni*) showed all individuals made a migration, and the others showed 25 – 40 % did not migrate. Next, I examined if migrant (*S. stimpsoni*) and flexible species (*Awaous stamineus*) showed lunar rhythmicity at hatching and settlement. Migrants of the flexible species showed more hatching around the full moon and settlement around the new moon, and residents showed the opposite pattern. The divergence in life-history timing appears to be a balance between ecological costs and benefits. Next, I examined the influence of variation in localized conditions on the ratio of migrant to resident contingents (*A. stamineus*) in adult populations. Residents were least represented when stream flow and nutrients were low; however, the abundance of a common invasive predator showed a negative relationship with resident abundance. Highly urbanized systems may impose such stressful conditions that resident recruitment is diminished, which underscores the importance of stream management to conserve vulnerable native species. Lastly, I examined the frequency of contingents (*A. stamineus*), larval duration, and growth rates across ENSO. The proportion of migrants was highest during La Niña, and resident proportions were highest during weak La Niña and strong El Niño; once El Niño became very strong, resident proportions decreased. Migrants had faster growth than residents across all growing stages. Migrant growth rates in the early larval stage were highest during El Niño, and pre-settlement growth was highest during La Niña. Resident growth was fastest during neutral conditions. The duration of the early fast-growing period was shortest during El Niño, and the larval duration was longer. These dissertation findings show the importance of evaluating multiple influential scales to understand life-history strategies of individuals, especially those that inhabit multiple ecotypes.

DEDICATION

This work is dedicated to my husband, Daniel, for his unwavering love, support, and encouragement throughout this process.

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INTRODUCTION

Understanding the life-history of organisms is important for understanding population-dynamics and the adaptation of species to changing conditions (Stearns 1992, Roff 1992, Stearns 2000). Life-history includes information about reproductive events, behavior, growth patterns, age at specific stages in life, and mortality (Fabian and Flatt 2012). Natural selection will shape life-histories and increase the probability of reaching sexual maturity and contributing viable offspring in the face of changing environmental conditions (Stearns 1992, Roff 1992, Stearns 2000). Life-history ecology of species will influence their responses to anthropogenic changes to the environment.

Over the past century, anthropogenic impacts have caused deleterious effects to natural systems (Smith et al. 1999). Species diversity has decreased from extinction, systems have become more homogenized from widespread invasive species introductions, and natural biogeochemical cycles have been altered by excess inputs from increased urbanization (Fisher et al. 1992; Bilotta and Brazier 2008; Di and Cameron 2002; Vitousek et al. 1997; Woodward and Hildrew 2002). Since the industrial revolution, excess greenhouse gases have caused atmospheric CO_2 to increase causing heat to become trapped within the lower atmosphere (Lacis et al. 2010). This has resulted in many large-scale changes including warming oceans and alteration to the frequency and intensity of natural climatic cycles (IPCC 2014). Localized conditions are modified and nested within larger scales of influence, and species within ecological units are affected from both bottom-up and top-down processes (Mosley 2000; Cole et al. 2002; Hollings and Gunderson 2002). Only when the effects at multiple scales of influence, including anthropogenic effects, are considered can I form a robust ecological understanding of how systems and organisms respond to variations in the environment. This full ecological understanding can be used for insight on proper management and conservation as conditions change.

Fishes have been greatly impacted by human activities and changing environments (Brasher 2003), and the processes that regulate the success or failure of larval fish to contribute to breeding populations (recruitment) is one of the least understood life-history processes (Houde 1987). Many studies have shown that physical factors like temperature, advection and transport, and nutrient availability can affect growth, behavior, and mortality (Barber and Chavez 1983; Houde 2008). In addition to physical factors, predation, starvation, and competition can influence growth and survival to recruitment (Cushing 1974, 1990; Houde 1987; Cushing 1990; Kerr and Dickie 2001; Houde 2008). Physical and biological factors can be modified locally through freshwater and nutrient input, or change may be driven by large-scale processes that shift environmental responses (Mosley 2000; Cole et al. 2002). Life-history responses to environmental stressors can be assessed with mathematical models, genetic tests, or by taking direct measurements or observations of organisms (Stearns 1992, Roff, 1992, Brommer 2000). The study of life histories of fishes was revolutionized over a century ago by the discovery that otoliths, paired calcium carbonate sensory structures in the inner ear of fish that form throughout the entire life of a fish, form concentric bands that are laid down either daily or annually and can be used to estimate growth rates and age at specific stages of the life-history (Pannella 1971; Campana 1999). The continual accretion and biological inertness of these structures make ideal for analyzing how life-history characteristics, such as behavior and growth, vary among individuals within and across populations at varying levels of influence (Campana and Jones 1992).

The purpose of this dissertation was to identify fish species with fixed and flexible life-histories and to identify how factors at different spatial and temporal scales influence the variation of responses within and among populations. The scales of influence that are assessed in this dissertation are exemplified in Figure 1. This dissertation comprises four chapters that are interrelated with an attempt to form a more robust ecological understanding of species with life-history flexibility when considering multiple scales of influence. The goal of Chapter 1 was to examine four underexplored species of endemic Hawaiian freshwater fishes to identify the occurrence of migration flexibility and to compare larval stage duration among the species. Some of the species of interest in Chapter 1 have conspecifics, confamilials, and sister taxa that exhibit flexibility and some have close relatives with no flexibility, and the flexibility of the species explored were unknown until this study. In Chapter 2, I examine two species, one with life-history flexibility and one without, to determine if the timing of hatching and metamorphosis are linked to lunar periodicity, and if so, how the timing of those events differ among migrant and resident types within and among species. In Chapter 3, I examine how varying localized conditions at the watershed-level influence recruitment success of exclusively resident types. In this chapter, I examine how stream flow variability, invasive species density, and nutrient input affect the relative proportion of residents across spatially distinct populations. In the final chapter, I examine the frequency of occurrence of migrant and resident types across ENSO phases, and how larval duration and growth rates at three important times in the life-history differ across ENSO phases for both migrant and resident types.

The findings of this dissertation show the importance of evaluating multiple scales of influence to understand the life-history strategies of individuals, which ultimately influences the adaptation and evolution of species. Without considering these multiple interactions and the synergy between scales, one can only form a partial ecological understanding of species and the systems they inhabit, which can lead to improper management and conservation. These findings can be applied directly to adaptive management strategies for the species examined; all of the species examined in this dissertation are of cultural importance, and many are of critical conservation concern. Additionally, the findings of this dissertation can be applied broadly to different taxa that have life-history flexibility for insight on the possible factors and scales of influence that affect recruitment success or failure for migratory types that experience different environments during the life-history.

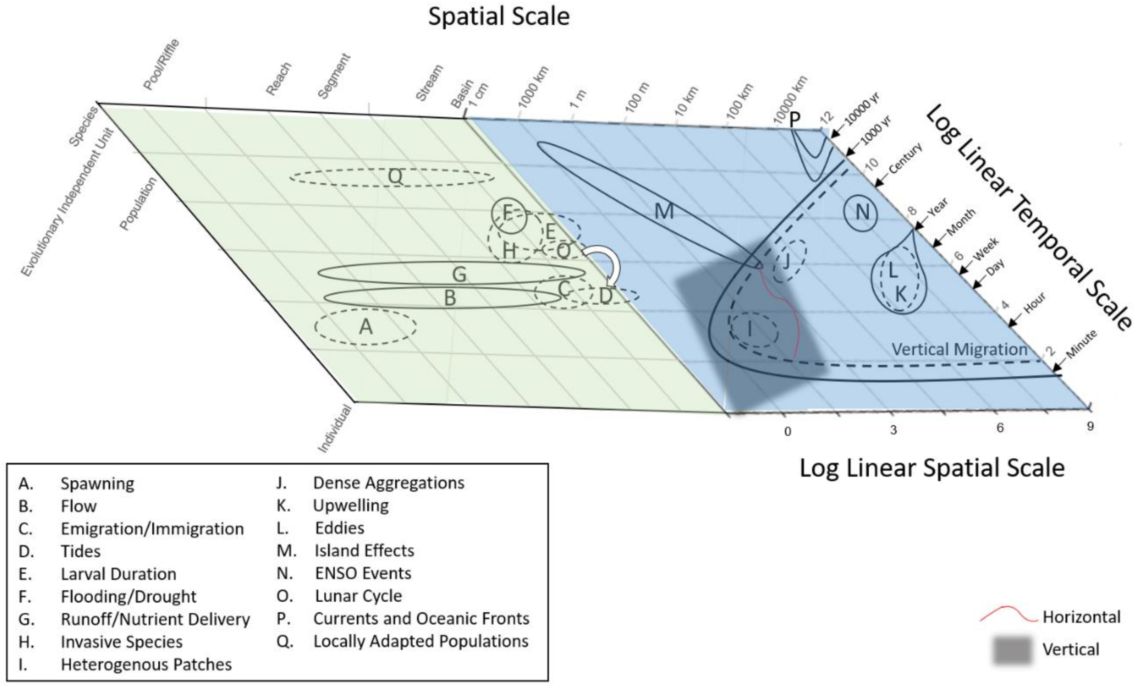

Figure 1: Stommel diagram of levels of variability in freshwater and marine environments that influence migration and recruitment dynamics of the amphidromous fishes evaluated herein (Adapted from Haury et al. 1978, Frissell et al. 1986, Gresswell 1999, Doctor 2008, Vance and Doel 2010, Torgersen et al. 2012)

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CHAPTER 1: FACULTATIVE AMPHIDROMY IS COMMON IN HAWAI‘I’S NATIVE FRESHWATER FISHES

Abstract

Amphidromy is a migratory strategy in which individuals hatch in freshwater and quickly after hatching can migrate to sea where they will spend the larval duration before returning to the freshwater at metamorphosis to rejoin juvenile and adult populations. Amphidromy is a bet-hedging migration strategy common to species living in freshwater on remote islands, and it can increase connectivity and affect population persistence. In Hawaii, for example, there are only five native extant freshwater fishes all of which are gobioids, and all are presumed to exhibit amphidromy. Some gobioid species have been shown to exhibit facultative amphidromy wherein some individuals in the populations remain in the stream the entire life. Of the Hawaii species, three have been confirmed amphidromous through otolith microchemical studies: *Awaous stamineus, Stenogobius hawaiiensis,* and *Lentipes concolor*; only *A. stamineus* has been determined to be a facultative amphidromous species while the other four species are assumed to be obligate. In this study, I examined the migratory life-history of the native freshwater fishes of Hawai‘i that have not been explored for migration flexibility. We found that all species exhibited amphidromy, and that facultative migration strategies were common among the species. Seventy-five percent of *L. concolor* (n = 8), sixty percent of *Eleotris sandwicensis* (n = 20), and seventy-three percent *of S. hawaiiensis* (n = 26) showed a migratory life-history. Only *S. stimpsoni* showed 100% of individuals (n = 55) going to sea as larvae. Additionally, larval duration (LD) of migrants varied between species. *Lentipes concolor* had the shortest average larval duration (LD) at 87 days and was followed by *E. sandwicensis* (mean LD = 102 d), then *S. hawaiiensis* (mean LD = 114 d), and *S. stimpsoni* had the longest larval duration (mean LD =

120 d). These findings provide life-history information not yet described but necessary to assist in the conservation and management of these vulnerable species, since many of the species are subject to anthropogenic pressures and stressors in both the freshwater and marine environments.

Introduction

Remote islands are known for unique flora and fauna (Wilson and McArthur 1967). Isolation from mainland sources can lead to unique species adaptations (Wilson and McArthur 1967). Once an island is first colonized, usually through long-range dispersal, exploitation of empty niches can give rise to new specialized species (Wilson and McArthur 1967). These species and systems are unique and of conservation concern since many remote islands have been heavily urbanized and impacted by human activities (Brasher 2003). Rare island biota face many challenges making it necessary to examine and understand life-history behavior and strategies.

Amphidromy is a common life-history strategy among freshwater species living on remote islands; organisms hatch in freshwater, migrate and live at sea as larvae before returning to freshwater where the life-cycle is completed (McDowall 2007a). Migrating to sea as a larva can relieve freshwater predation pressure and potentially increase the trophic position of larval individuals through access to rich marine food resources (Cushing 1975). Some migrant post-larvae have faster growth rates than their resident counterparts when they return to freshwater streams (Hogan et al. 2014), which may infer additional benefits of migrating to sea. Amphidromous fishes typically have long pelagic larval durations, and like many marine aquatic organisms, a long pelagic larval duration (PLD) can increase dispersal distance, which is important when living in remote habitats (Siegel et al. 2003). Currents in the marine environment act as a transport vessel around chain islands (Lobel and Robinson 1986). Larval movement, via currents, can facilitate connectivity among disjoined populations; adequate gene flow can help populations persist in challenging and highly dynamic environments (McIntyre et al. 2015).

An amphidromous life-history is not without risks. Species that hatch far upstream from the marine environment may face mortality from starvation or increased predation risk if the migration to the marine environment is prolonged (McDowall 2009). Additional risks occur during the return migration for stream recruitment. Physiological changes must occur for fish to be able to move between the different environments, and fish must avoid stream predators while seeking recruitment habitat and food resources that differ from that utilized in the marine environment (McDowall 2009). Migrants must cope with both the freshwater and marine environments and the pathways that join them, and then predation and physical processes in the ocean that can cause stress and mortality. This kind of triple jeopardy underscores the need to understand the life-history of migratory species and their use of these distinct environments for proper management and conservation (McIntyre et al. 2015).

Freshwater island systems are known to be dynamic environments (Oki 2004), which can pose a number of challenges to amphidromous fishes. The islands of Hawai‘i were formed from volcanic processes and are actively expanding through volcanism. Volcanic eruptions cause disturbance events to stream ecosystems and their inhabitants (McDowall 2007a). Additionally, many Hawaiian streams are ephemeral with flash flooding occurring during the wet season with near desiccation during the dry season (Oki 2004; McDowall 2007ab). Climatic processes, like El Nino Southern Oscillation and Pacific Decadal Oscillation can influence the amount and intensity of precipitation received in island streams (Ropelewski and Halpert 1987; Oki 2004). The amount of precipitation received can directly affect stream flow parameters (Oki 2004).

Urbanization of island systems has resulted in invasive species introductions, altered flow regimes from water abstraction, and altered stream water quality (Walter et al. 2012; Lisi et al. 2018). Hawaiian streams are now the home of over 60 aquatic invasive species, and these introductions have changed ecosystem function and dynamics (Walter et al. 2012; Lisi et al. 2018). Additionally, the flow in many streams has been altered for water use, channelization and removal of riparian canopy cover has increased stream temperatures, and urbanization has increased human runoff into freshwater systems (Brasher 2003, Walter et al. 2012; Lisi et al. 2018). Quality freshwater habitats are shrinking as human impacts to vulnerable ecosystems increase (Sax and Gaines 2008; Walter et al. 2012). Being amphidromous provides the potential of escaping degraded freshwater systems, through migration, and reaching higher quality freshwater streams through marine dispersal (McDowall 2007a). Migration can be evolutionarily advantageous if some progeny escape degraded habitats and recruit to better quality habitats than those in the natal environment. Understanding the life-history of threatened and endangered species is a critical step for ensuring proper management and conservation of species and ecosystems. Since amphidromous species are vulnerable in both aquatic environments, there must be management strategies for these organisms and their habitats during the critical phases of the life-history.

Life in the marine environment, even if only transient, is not easy. Marine migrants must make it to sea within the first few days of life to survive (Lindstrom 1998; Iguchi and Mizuno 1999). Physiological changes occur in the earliest days to cope with changing salinity environments (Dingle 1996). Oceanic temperatures fluctuate, especially during natural climatic events, and larvae must be able to alter physiology to tolerate and survive when conditions are extreme. Additionally, upwelling events can provide additional nutrition sources to promote growth and advancement through the larval stage (Lasker 1978, 1981). Larvae are subject to current movements and the chance of being swept too far to return to stream mouths (Hjort 1914, 1926) or may be retained in eddies and other circular water movements (Illes and Sinclair 1982; Sinclair 1988; Houde 2008). Migrants are subject to mortality from density-independent and dependent factors in the marine environment, including starvation and predation, which ultimately controls the success or failure of recruitment of migrants to freshwater populations for amphidromous species (Houde and Hoyt 1987).

For both migrant larvae in the ocean and resident larvae in streams, mortality is high and is compounded daily until the next life stage is reached (May 1974; Houde 1989); predation risk is inversely related to body size that is, as larvae increase in body size, the risk of predation decreases (Cowan and Houde 1992). If adequate nutrition is not obtained during early larval stages, larvae are not only subject to mortality caused by starvation (Cushing 1977, 1990), but prolonging the larval stage potentially increases the duration of predation exposure (Houde and Hoyt 1987; Cushing 1990). The habitat quality for early-stage larvae is critical for survival and recruitment to breeding populations.

The Hawaiian archipelago is a remote island chain in the Pacific Ocean with only five native freshwater fishes, *Eleotris sandwicensis* (Eleotridae, Vaillant and Sauvage, 1875), *Awaous stamineus* (Oxudercidae: Gobionellinae, Eydoux and Souleyet 1850), *Stenogobius hawaiiensis* (Oxudercidae: Gobionellinae, Watson, 1991), *Sicyopterus stimpsoni* (Sicydiinae, Gill, 1860), and *Lentipes concolor* (Sicydiinae, Gill, 1860); all of which are considered amphidromous. *Awaous stamineus, S. hawaiiensis*, and *L. concolor* have all been confirmed amphidromous by analysis of otolith Sr:Ca (Radtke et al. 1988, Radtke et al. 1999, Hogan et al. 2014); the other two species are assumed to be amphidromous based on the described life-histories of congeners, but that has not been confirmed, and their marine larval durations are unknown. *Awaous stamineus* has a facultative amphidromous life-history where only some individuals make marine migrations, while others stay in freshwater for their entire life-cycle, and marine migrant (called migrant hereafter) *A. stamineus* stay in the marine environment as larvae for up to six months before returning to freshwater to metamorphose into juveniles (McDowall 2007a; Hogan et al. 2014). Also known as partial migration, facultative amphidromy is considered a bet-hedging strategy where risks are balanced between two contingents, migrants and residents (Ayers 2010; Hicks 2012; Hogan et al. 2014). For the other four native species it is unknown whether they are facultative or obligate amphidromous. e;

The objectives of this study were to determine if the native Hawaiian freshwater fishes exhibit facultative or putatively obligate amphidromy and to describe the larval durations for each species to examine the duration of larval predation exposure and dispersal potential of migrants. I expected that all species would show an amphidromous life-history, but I expected, of the species examined, that the true gobies belonging to the subfamily Sicydiinae (*Lentipes concolor* and *Sicyopterus stimpsoni*) would show exclusive migration based on the previous findings of studies of congeners and confamilials (Radtke and Kinzie III 1996; Shen et al. 1998; Lord et al. 2011). Although migration flexibility has not been observed in *Eleotris* and *Stenogobius* species, I hypothesized that this would be more likely in *E. sandwicensis* and *S. hawaiiensis* based on similar findings in previous studies on confamilials (Closs et al. 2003; Tsunagawa and Arai 2008; Nordlie 2012; Kano et al. 2014; Smith and Kwak 2014).

Methods

Study Species

Of the five native Hawaiian freshwater species, all are in the sub-order Gobioidei, four of which are in the family Oxudercidae. The species included in this study are *Lentipes concolor* (Gill 1860), *Sicyopterus stimpsoni* (Gill, 1860), *Eleotris sandwicensis* (Vaillant and Sauvage 1875), and *Stenogobius hawaiiensis* (Watson 1991). *Lentipes concolor* (Gobioidei:Oxudercidae: Sicydiinae; See Kuang et al. 2018) is the rarest of the native freshwater species throughout the Hawaiian archipelago and is considered a threatened species (Kinzie III 1990). *Lentipes concolor* is known to inhabit the higher stream reaches due to its modified pelvic fins that form a sucking disc that allows it to climb waterfalls as high as 100 m (Kinzie III 1990). *Sicyopterus stimpsoni* (Gobioidei:Oxudercidae:Sicydiinae) is found in the middle reaches of streams where water quality and habitats have not been extensively altered and where there are few aquatic invasive species (Kinzie III 1990). It is known to live sympatrically with *A. stamineus* and *E. sandwicensis*; however, it is found in swifter waters than *A. stamineus* (Kinzie 1988). *Sicyopterus stimpsoni* has an extended jaw that allows it to scrape algae off rock surfaces (Kinzie III 1990). *Stenogobius hawaiiensis* (Gobioidei:Oxudercidae) occurs at the lowest stream reaches with *E. sandwicensis* in muddy substrates. It is omnivorous and has an inability to climb well or withstand fast flowing stream conditions (Schoenfuss 1997). *Eleotris sandwicensis* is a predatory piscivore belonging to the family Eleotridae (Gobioidei), and it occurs in the lowest reaches of Hawaiian streams; it lacks the fused pelvic sucker disk characteristic of the other gobioids of Hawaiʻi, as a result, its upstream movement is limited due to an inability to climb past falls or high rapids within the streams (Kinzie III 1990). *Eleotris sandwicensis* is known to depredate small fishes, including the larvae and post-larvae of the native gobioids included in this study as they recruit into streams (Kinzie III 1990).

Sample Collection and Preparation

Samples of all four species were taken opportunistically as part of two separate projects in Hawaiʻi. A total of 20 *E. sandwicensis,* 8 *L. concolor,* and 26 *S. hawaiiensis* samples were collected between March and July 2009 by snorkelers using hand nets. *E. sandwicensis* were collected from six watersheds on the island of Hawaiʻi, *L. concolor* were collected from two watersheds on Hawaiʻi, and *S. hawaiiensis* were collected from three watersheds on Hawaiʻi and two watersheds on Kauaʻi (Supplement Table 1). A total of 55 *S. stimpsoni* were collected between March and May 2011 by snorkelers using hand nets. *Sicyopterus stimpsoni* samples were collected from 15 watersheds across all five of the main Hawaiian Islands. The 2009 samples were collected live in the field and placed in 20 L buckets containing stream water and fitted with airstones. Specimens were transported back to the laboratory on each respective island, humanely euthanized with MS-222, preserved in 95% ethanol and stored at -20°C until further analysis (Clemson University approved protocols: ARC2007-090 and AUP2008-071, St. Cloud State University approved protocols: IACUC #1207 and #0113). Fish were thawed at Clemson University and sagittal otoliths were extracted following standard protocols (Bickford & Hannigan 2005). The 2011 samples of *S. stimpsoni* were collected live in the field, measured for total length (mm), humanely euthanized and kept on ice, then stored frozen at -20°C. Fish were thawed in the Hasler lab, Center for Limnology at the University of Wisconsin and sagittal otoliths were extracted. Sagittal otoliths were removed, cleaned in distilled water and allowed to dry. For fish from each project, one of the two sagittal otoliths was haphazardly selected, mounted and polished for microstructure analysis to determine age, hatching date and metamorphosis date. Otoliths were mounted sulcus side up onto glass petrographic slides and embedded in Crystalbond™ glue. To expose the daily growth rings from the edges to the primordium, otoliths were ground in the sagittal plane, using fine grit polishing pads (Buehler) and diamond lapping films (3M) ranging in grit size from 60 – 0.5 µm. The same otolith was also used for microchemical analysis to classify the individual fish as an ocean migrant versus stream resident.

Identifying Marine Migrations

Migration flexibility of *L. concolor*, *S. stimpsoni*, *E. sandwicensis,* and *S. hawaiiensis* from the wild are not well characterized but *L. concolor* and *S. stimpsoni* are assumed to be obligate migrators based on congeners and confamilials (Radtke et al. 1988; Radtke and Kinzie III 1996; Shen et al. 1998; Radtke et al. 1999; Lord et al. 2011; Mennesson et al. 2015). However, there are some Eleotrid species that show flexibility in migratory behavior (Closs et al. 2003, Smith and Kwak 2014), and sister taxa of *S. hawaiiensis* have shown migration flexibility (Tsunagawa and Arai 2008; Nordlie 2012; Hogan et al. 2014; Kano et al. 2014). To examine the ocean migration history for each fish I used laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) to quantify Sr:Ca across the otolith transect from core to edge, which represents the entirety of each fish's life span. Sr:Ca has been used extensively to investigate diadromous migrations between marine and freshwater environments because Sr:Ca concentration in the otolith is relatively high when in the marine environment (~8 $\text{mmol}\cdot\text{mol}^{-1}$) compared to otolith Sr:Ca concentration when in freshwater systems in Hawai‘i (~4-5 $\text{mmol}\cdot\text{mol}^{-1}$; Hogan et al. 2014) and the otoliths of marine migrants show a marked decline in Sr:Ca concentrations at metamorphosis/settlement indicative of the transition to freshwater from the marine environment (Hogan et al. 2017). The 2011 samples were analyzed at the Environmental Analytical Facility at University of Massachusetts – Boston (Perkin Elmer ELAN DRCII coupled to a Cetac LSX213) in March 2012, and the 2009 samples were analyzed at the Quadrupole ICP-MS Lab at University of Texas at Austin (New Wave Research UP193-FX fast excimer coupled to an Agilent 7500ce ICP-MS) in January 2018. Despite using different facilities, the protocols, including the standards used, and analyte lists were the same between the two facilities. Samples and standards were analyzed with a laser beam width of 25 µm and a scan rate of 5 $\mu m \cdot s^{-1}$. All samples were calibrated and drift corrected using calcium carbonate standards (USGS MACS-3 and NIST-612) and background corrected against the argon carrier gas from a gas blank taken before each sample analysis. Calcium (^{43}Ca) was used as an internal standard (38.8 % aragonite constant) to compensate for signal variation caused by differences in mass of ablated material. The masses of twelve isotopes were analyzed (^{42}Ca, ^{43}Ca, ^{7}Li, ^{24}Mg, ^{25}Mg, ^{55}Mn, ^{66}Zn, ^{68}Zn, ^{88}Sr, ^{137}Ba, ^{138}Ba, and ^{208}Pb), and the concentrations were calculated; relative concentrations were expressed as a ratio to ^{42}Ca. Strontium to calcium ratios were used to determine marine migrations. Even though previous studies on Hawaiian amphidromous species show a marine signature around 8 $mmol \cdot mol^{-1}$ and a freshwater signature around 4 $mmol \cdot mol^{-1}$, other otolith microchemistry studies have identified interspecific differences in Sr uptake in the otolith for sympatric species based on physiological and elemental otolith accretion rate differences (Sinclair 2005; Hamer and Jenkins 2007). Therefore, I did not set an *a priori* Sr:Ca concentration baseline for either marine or freshwater environments; rather, an individual was determined to have made a marine larval migration if there was a consistent and pronounced peak of Sr:Ca in the core region of the otolith that exceeded the otolith edge chemistry, which is representative of the freshwater environment where the individual was captured. After the initial analysis of samples by LA-ICP-MS, more than 50% of the samples for each species, including *L. concolor*, were re-polished and re-run with a new transect that bisected the core without passing through previously ablated areas. The chemical profile of the secondary run was assessed to ensure the accuracy of the categorization of the samples and that samples had not been under-polished in the lab prior to the initial run.

Determining Larval Durations

To determine LD, otoliths were imaged before microchemical analysis, and the daily growth increments (rings) were counted from the primordium to the settlement mark. The settlement mark is a relatively broad increment having high optical density (Radtke et al. 1988) that is laid down during metamorphosis from the larval form into the post-larval form, and it has been shown to correspond with the transition from the marine to the freshwater environment for migratory *A. stamineus* (Hogan et al. 2017). The 2009 samples were imaged with Nikon NIS-Elements Documentation software (v. 4.5) using a Nikon Eclipse E200-LED compound microscope (50x ocular magnification), and daily growth bands were counted from the primordium to the settlement mark. Each otolith was aged twice with two non-sequential independent reads by the same reviewer where samples were chosen at random, and any sample that exceeded 5% variation between the two reads were excluded from further analysis. For the 2011 samples, imaging and reading were done at the Hasler Lab, Center for Limnology, University of Wisconsin – Madison. Multiple images of each otolith were taken in different focal planes with a Leica digital camera mounted to a compound microscope using a 20X objective lens, and then stitched together in Photoshop© to create one image focused on the otolith increments from primordium to edge. Daily growth rings were counted using Leica Application Suite software. Otoliths were read in triplicate by a single reader; each reading was done "blind" to the sample number, with samples randomized between reads. Any otoliths that demonstrated more than 15% variation between the two closest reads were excluded from further consideration; none of the otoliths here met that criteria, so all samples were retained for analysis.

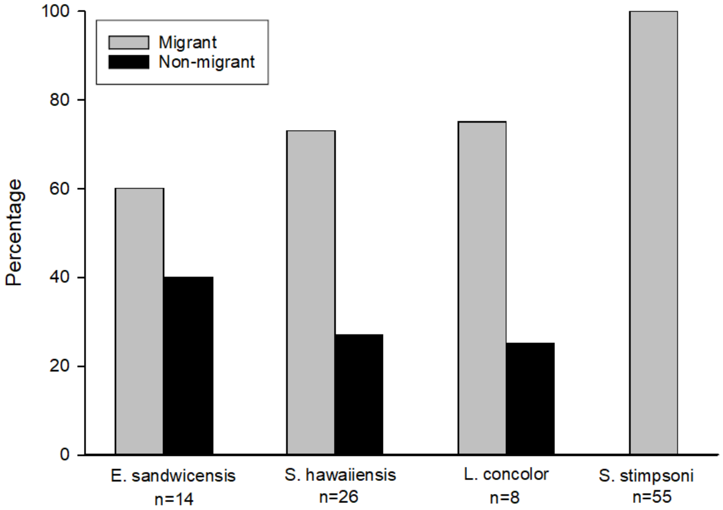

Figure 1-1: The proportion of migrant (black bars) and resident (grey bars) types for four species of native Hawaiian stream fishes

Results

Migration Patterns

The chemical profiles for *E. sandwicensis* and *S. hawaiiensis* revealed similar chemical discrimination as previous work on amphidromous Hawaiian native *A. stamineus* (Hogan et al. 2014), and a freshwater cutoff of 4 mmol·mol^{-1} was used to assign individuals as either migrant or resident; however, there was elevated chemical discrimination of Sr:Ca across the entire otolith transect for all individuals. The freshwater baseline for *L. concolor* was determined by using the outer edge chemistry of the analyzed samples, which corresponds to adult life in freshwater where the individuals were captured. The categorization of *L. concolor* samples as either migrant or resident was assessed at a freshwater cutoff of 8 mmol·mol^{-1}. Of the 8 *L. concolor* samples analyzed, 6 were categorized as migrant based on criteria outlined in the methods (Sr:Ca ~8 mmol·mol^{-1} pre-metamorphosis), and 2 were categorized as resident (Fig. 1, Supplement Table 1; chemical profiles Fig. 2). Of the 20 *E. sandwicensis* samples analyzed, 12 were categorized as migrant and 8 as resident (Fig. 1, Supplement Table 1; chemical profiles Fig. 3). Of the 26 *S. hawaiiensis* samples analyzed, 19 were categorized as migrant and 7 as resident (Fig. 1, Supplement Table 1; chemical profiles Fig. 4). Otolith microchemistry analysis of *S. stimpsoni* samples indicated that 100% of the samples (n = 55) had a migrant life-history (Fig. 1, Supplement Table 1; chemical profile Figure 5).

Larval Durations

Almost all samples met the variation thresholds from multiple age readings and therefore were included in the age analysis. However, two *S. hawaiiensis* samples were unable to be accurately aged and were excluded from further analysis. *Lentipes concolor* had the shortest average LD where the average duration for migrants was 89 d and 82 for residents (n = 8, range: 70-106 d; SD = 11.52 d) for (Fig. 2). *Lentipes concolor* was followed by *E. sandwicensis* with an average LD of 101 d for both migrants and residents (n = 20, range: 91-117 d; SD = 7.64 d) then *S. hawaiiensis* with an average LD of 113 d for migrants and 115 d for residents (n = 24, range: 81-145 d; SD = 17.68 d) (Fig. 6). *Sicyopterus stimpsoni* had the longest average LD at 120 d (n = 55, range: 65 - 200 d; SD = 26.42 d) (Fig. 6).

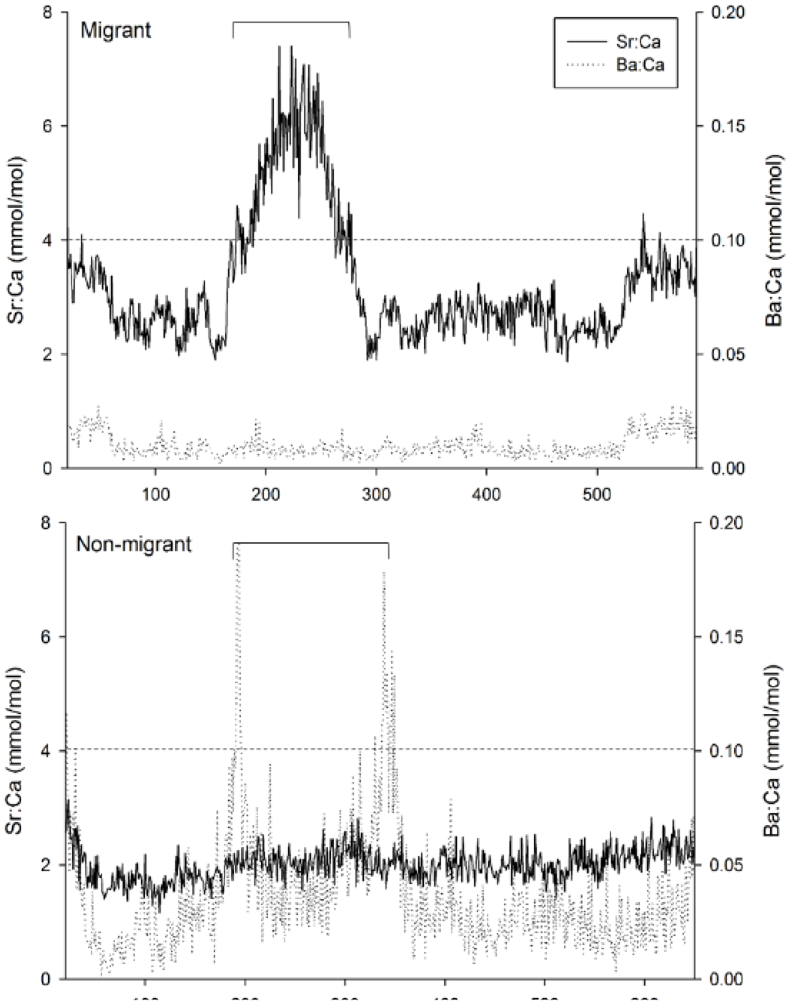

Figure 1-2: Example of L. concolor chemical profiles for migrant (top) and resident (bottom) individuals

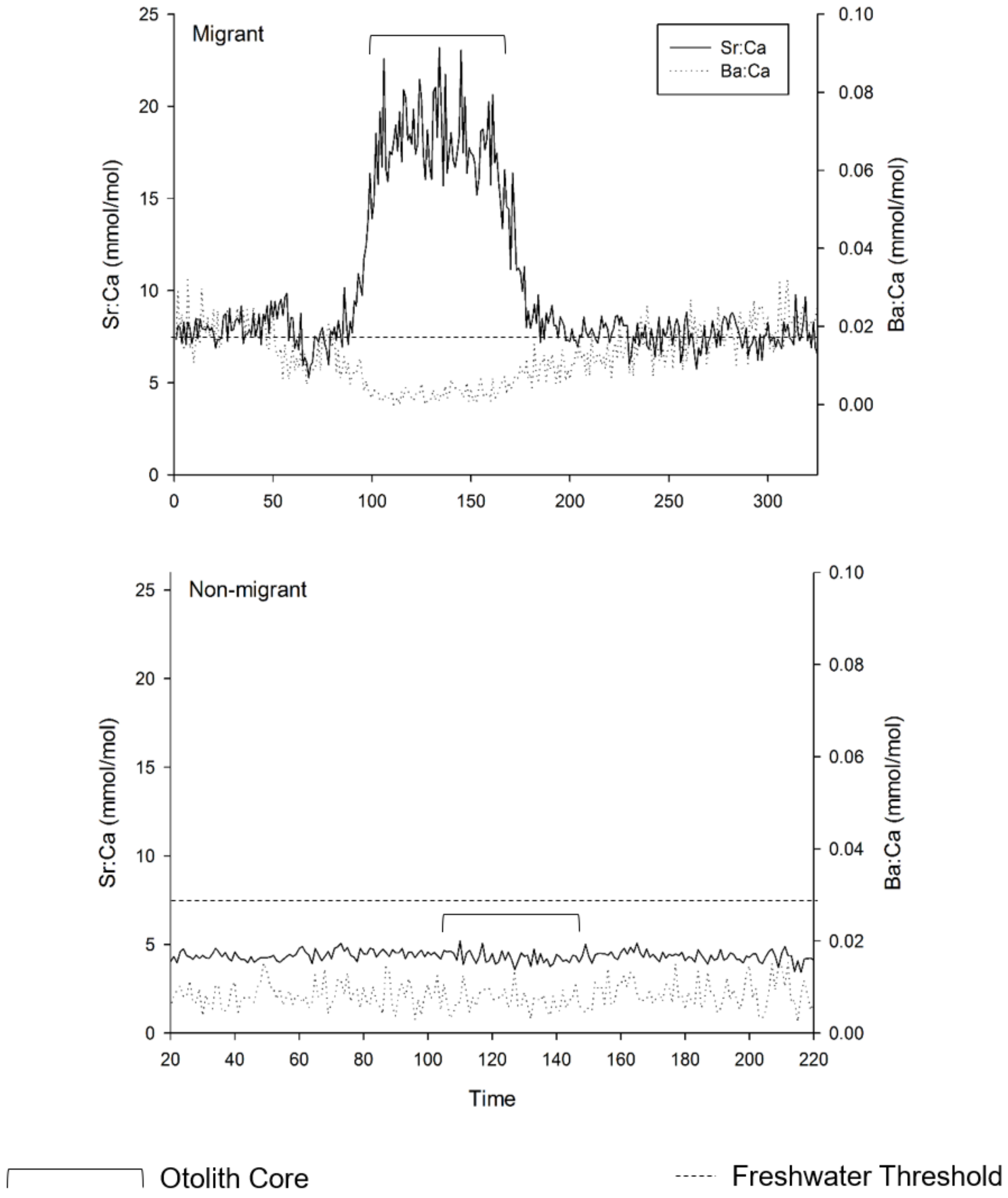

Figure 1-3: Example of E. sandwicensis chemical profiles for migrant (top) and resident (bottom) individual

Discussion

All native Hawaiian freshwater species were confirmed amphidromous, each species spending several months in the larval stage. However, all were identified as facultative migrators, except for *S. stimpsoni*, which was the only putatively obligate species identified. These results are not wholly unexpected since recent studies have shown that several amphidromous gobioid fishes are facultative (Michel et al. 2008; Smith & Kwak 2014; Hogan et al. 2014); however, the prior assumption has been that most if not all Sicydiinae gobies are obligate migrators (e.g., McDowall 2007a) incapable of surviving in freshwater as larvae (Iida et al. 2010). The fact that 80% of the species in Hawai‘i are facultative is interesting and has implications for their conservation, since some individuals remain freshwater residents while others go to sea during the larval stage.

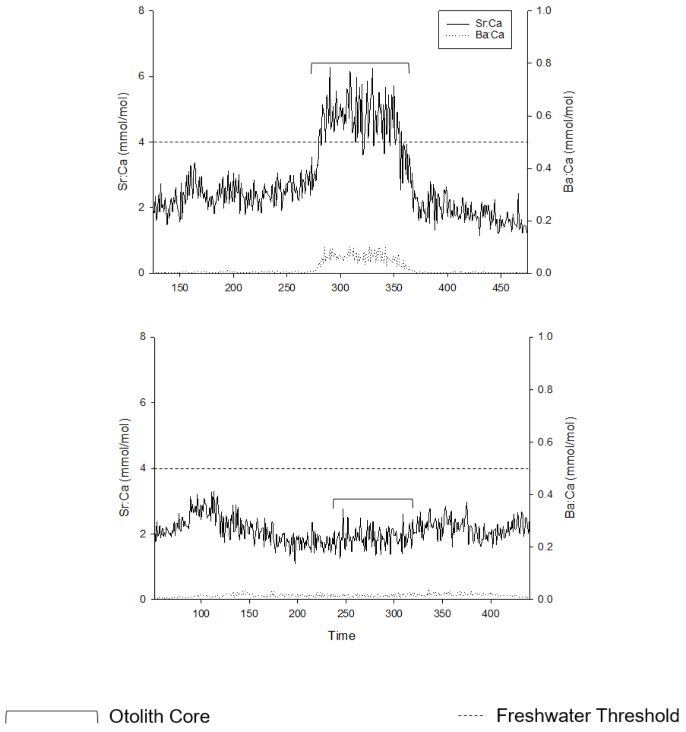

Figure 1-4: Example of S. hawaiiensis chemical profiles for migrant (top) and resident (bottom) individuals

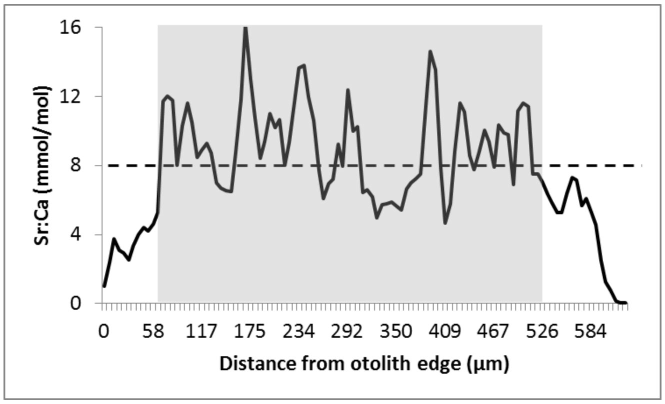

Figure 1-5: Example of S. stimpsoni chemical profile of migrant individual

Hawaiʻi is a volcanic hotspot; therefore, amphidromy allows for the colonization of newly formed streams or areas that have been disturbed from volcanic activity (McDowall 2007a). In fact, the only plausible mechanism by which these species established populations in Hawaiʻi in the first place is by marine dispersal from distant sources. Movement through the ocean to newly available habitats can increase gene flow between disconnected environments, permit colonization of new habitats, and rescue populations from extinction (Chubb et al. 1998; McDowall 2007a). The lack of strong genetic structure in neutral loci throughout the Hawaiian archipelago suggests that amphidromous movement results in widespread gene flow in these species across islands (McDowall 2007a; Moody et al. 2015).

Passive movement by larvae are subject to in-stream conditions such as flow (Huey et al. 2014). In Hawaiʻi, streams are short, with steep slopes, and largely influenced by orographic precipitation, where some streams experience periodic drought while others experience regular periods of flash flooding (Oki 2004). During times of drought, connectivity within a stream and to the marine environment can be impeded, and conversely, during flash floods, larvae can be swept down and out of the stream. An ability to physiologically cope with either the marine or freshwater environment is advantageous for survival when living in such a dynamic environment where larvae can be flushed to sea or retained in-stream.

Surprisingly, one of the two Sicydiine gobies (*L. concolor*) showed facultative amphidromy in this study, which is contrary to nearly all records in the literature for Sicydiine gobies (Augspurger et al. 2017; but see Smith and Kwak 2014 for possible evidence of resident forms of *Sicydium sp.*). Due to consistent findings of obligate amphidromy within this clade (Augspurger et al. 2017), the common belief is that sicydiine gobies depend on the marine environment to sustain gene flow between disparate populations, which is especially important for isolated island populations (McDowall 2007ab); however, our findings indicate that one of the Hawaiian Sicydiine species, *L. concolor*, may be locally adapted to have both marine and freshwater contingents due to a potential selective advantage in some Hawaiian streams (Huey et al. 2014). This could be an instance of facultative amphidromy in *L. concolor* similar to another Sicydiine goby (Smith and Kwak 2014), however, our sample size is small, and only two samples showed a purely freshwater signal.

It is possible that errors in sample preparation can lead to a false freshwater signal. When otoliths are prepared for microchemical analysis, much attention and care is given to each sample to not over- or under-polish them, particularly in the core, which is the period of life when the fish may be at sea. Incorrect polishing could result in an erroneous freshwater signal if the otolith is under-polished and the pre-settlement saltwater core has not been revealed. Alternatively, if the otolith has been over-polished, right through the core of the otolith, the saltwater core may be polished away leaving only post-larval otolith material resulting in a freshwater signal. Both of these situations could result in a low Sr:Ca concentration in the core reflective of the post-settlement freshwater part of the life-cycle and result in a fish being erroneously assigned as a resident. The chemical profile of the secondary run was assessed to ensure the accuracy of the categorization of the samples and that samples had not been under- or over-polished in the lab prior to the initial run. Additionally, *L. concolor* otolith samples were reviewed by compound microscope after the LA-ICP-MS ablation technique to ensure that the laser passed through the core and that there were no other structural defects associated with the sample (i.e., a cracked otolith) that could interfere with a proper chemical analysis. It was determined that all samples were properly prepared and analyzed, but chemical analysis on more samples is necessary for *L. concolor* to draw broad conclusions about the rate of marine larval migrations.

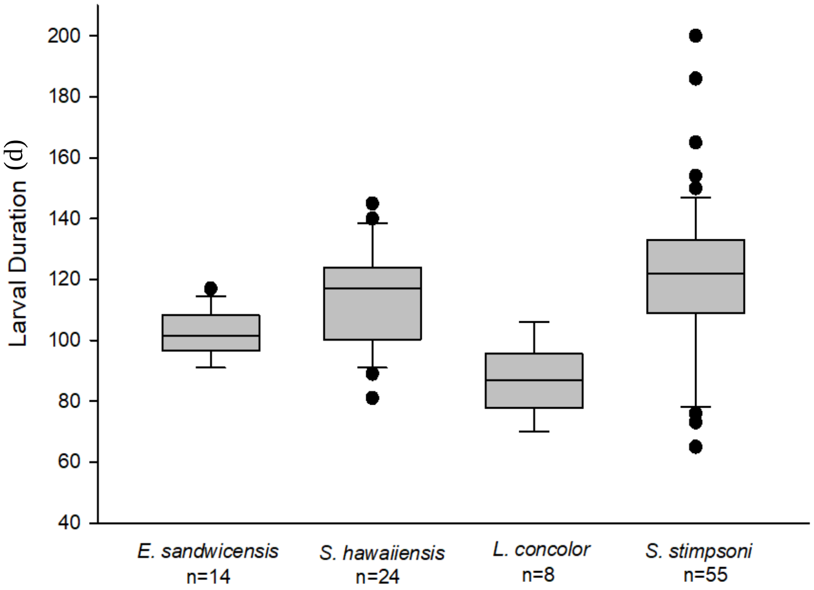

Figure 1-6: Pelagic larval duration of migrants from four native Hawaiian stream species

Many species in the family Eleotridae have shown amphidromous migration, especially those in island systems (McDowall 1995); however, it is interesting to find that *E. sandwicensis* exhibits partial migration, since this has not been demonstrated in other widespread species of the same genus (Mennesson et al. 2015; Augspurger et al. 2017). Since *E. sandwicensis* lives in the lowest reaches of the stream, closest to the mouth of the stream, and does not have morphological adaptations to adhere to rocks and other structures on the stream floor, it is not surprising that this species has evolved an ability to cope physiologically to a dynamic environment at the interface of two aquatic biomes. The ability of *E. sandwicensis* to regulate its physiology to cope with either environment may be an adaptive strategy for such dynamic stream conditions while living at the interface of the stream and the ocean. The congener *Eleotris fusca* does not show facultative amphidromy in populations across the Indo-Pacific (Mennesson et al. 2015). The facultative Hawaiian endemic *E. sandwicensis* may face selection pressures to avoid marine dispersal that the widespread *E. fuscus* does not face. Selection pressure may explain the evolution of facultative migration in *E. sandwicensis*.

Intraspecific life-history flexibility is common among taxa in the Oxudercidae (Huey et al. 2014; Hogan et al. 2014; Yamasaki et al. 2015); however, many studies are limited, and the extent to which partial migration exists among taxa is lacking (Froese and Pauly 2015). Owing to the observed plasticity within the Oxudercidae (Tsunagawa and Arai 2008; Nordlie 2012; Hogan et al. 2014; Kano et al. 2014), I expected *S. hawaiiensis* to be amphidromous with high potential for partial migration. We found that 27% of individuals were non-migratory. *Stenogobius hawaiiensis* could be locally adapted since some streams are subject to low base flows and periodic drought, which may prevent the passive movement of larvae to the marine environment (Huey et al. 2014). Like *E. sandwicensis, S. hawaiiensis* occupies habitat near the mouth of the stream and it seems plausible that they both have osmoregulatory adaptations to survive in the marine and freshwater environments, which would be advantageous in leeward side streams with extended dry periods and during times of punctuated flooding from trade wind rain and Kona storms (Lyons 1982; Chu and Chen 2005). Since this is a common strategy among Oxudercidae (excluding the Sicydiines), there appears to be a phylogenetic component to the ability toforego migration within some species (Lord et al. 2010).

Prior to this study, the LD for three of the five Hawaiian native freshwater fishes had been estimated, and only two of those with a robust sample size (*L. concolor* (Radtke et al. 2001) and *A. stamineus* (Hogan et al. 2014). Our estimation of LD for *L. concolor* aligns with previous records for this species. Radtke et al. (2001) estimated *L. concolor* average LD to be 86.2 ± 8.5 d with a range of 63-106 d, and our estimations for *L. concolor* average LD was 87 ± 11.52 d with a range of 70-106 d. Our estimation of average larval duration for *S. stimpsoni* of 120 ± 26.42 d is similar to the larval durations of cosmopolitan *S. lagocephalus* from Vanuatu and New Caledonia, which were an average of 131 ± 3.4 d (Lord et al. 2010). Our findings for the larval duration of *S. hawaiiensis* was below that previously reported by Radtke et al. (1988); they found the average larval duration to be 135 d and I found larval durations of 114 ± 17.68 d, although I had a smaller sample size with a fairly wide range. We estimated the larval duration of *E. sandwicensis* to be 102 ± 7.64 d, which overlaps with previous reports of *Eleotris* in Japan (approximately 2-4 months, Maeda et al. 2008). The extended larval durations of all species likely facilitates connectivity among populations of these species and was necessary in order for these species to originally colonize the remote Hawaiian archipelago (Radtke et al. 2001; Murphy and Cowan 2007; Alda et al. 2016). Long larval durations can prolong the duration in which larvae are exposed to high levels of predation, however, it may help extend the period of separation of resource use between different life-stages within a species (Murphy and Cowan 2007). Additionally, it is generally believed that a lack of food may result in an extension of the larval duration (Strathmann 1986); although, temperature, hydrographic variability, and other environmental factors may also be influential to the length of the larval stage (Cushing 1977;

Houde 2008). Although it has previously been considered that shortened larval durations might limit dispersal and promote the rise of endemic species (Radtke et al. 2001; Murphy and Cowan 2007), all of the extant freshwater Hawaiian species are endemic, and some have very prolonged larval durations (Hogan et al. 2014); therefore, there must be other factors controlling the rise of endemic species and the variation in larval durations among species with similar life-history strategies (Lord et al. 2010). *Lentipes concolor* had the shortest larval duration of the species examined in this study, and this could provide insight on inherent genetic differences in which the stage to metamorphosis is shorter when compared to the other species (Lord et al. 2010), or that *L. concolor* remains nearshore and avoids advective loss or transport by currents and eddies around the Hawaiian Islands (Illes and Sinclair 1982; Sinclair 1988; Houde 2008). *Lentipes concolor* is known for its ability to adhere to and climb waterfalls as high as 100 m (Kinzie III 1990); *L. concolor* morphological adaptations might allow for adherence to nearshore structures close to stream mouths to prevent an even greater extension in the marine environment at the time of metamorphosis if caught in a current or other hydrographic feature.

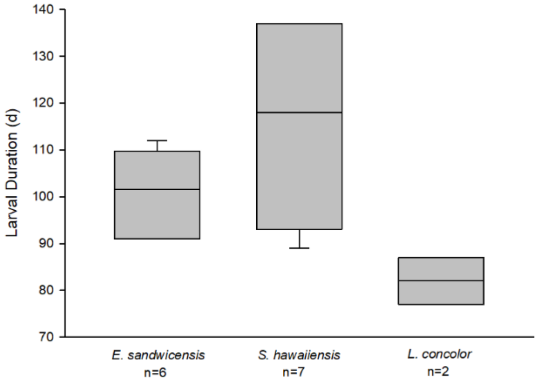

Figure 1-7: Larval duration of residents from three native Hawaiian stream species

This study underscores the importance of both the marine and freshwater environments for the survival of larvae of the native Hawaiian freshwater fishes. Having life-history flexibility can buffer populations that are at risk of high mortality rates and localized extirpation (McIntyre 2016). The ocean and Hawaiian streams are dynamic, and larvae, especially early-stage larvae, are susceptible to high mortality rates from physical processes, starvation and predation (Hjort 1914; Cushing 1977; Houde 2008). Oceans are becoming even more dynamic and unstable as changing climate progresses and natural climatic cycles become more frequent and intense (IPCC 2014), and these changing conditions can have substantial effects on recruitment success of migrant contingents. Hawaiian streams have also been subject to alteration from human activities, including water abstraction, increased land-use, and the introduction of invasive species that compete and depredate native species (Walter et al. 2012; Lisi et al. 2018). If oceans are unstable and a migratory cohort is lost, the in-stream contingents provide potential for population persistence (and vice versa) (Hogan et al. 2014). Climate change might influence the marine environment through modification of upwelling potential and increased sea surface temperatures (IPCC 2014; Chu and Chen 2005) such that pelagic larval survival is diminished due to increased metabolic needs and starvation (Lasker 1978; Houde 2008), and recruitment from the marine migrants may become more sporadic (Hjort 1914, 1926; Cushing 1975). Having a cohort of residents can buffer populations from variable marine conditions. However, the retention of larvae in streams that are also dynamic and prone to stress from human activities could result in more challenges for and increased mortality of larvae that remain in-stream (Brasher 2003; Walter et al. 2012; Lisi et al. 2018). Identifying multiple species with resident contingents has implications for management practices especially for species like the native extant Hawaiian species that are of conservation concern (Walter et al. 2012). Since the larval stage is such a critical period and since the protection of larvae in the ocean is difficult, Hawaiian stream restoration should be a top priority for the protection of these species; restoring base flows, maintaining good water quality, protecting of larval habitat, and removing invasive species that compete or depredate native larvae are critical for managing these systems to improve conditions for native larval survival (Brasher 2003; Walter et al. 2012; Lisi et al. 2018).

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CHAPTER 2: VARIABLE LUNAR RHYTHMYCITY WITHIN AND AMONG NATIVE HAWAIIAN AMPHIDROMOUS FISHES

Abstract

Many animal behaviours are associated with lunar rhythms. Lunar periodicity of spawning, migration, and recruitment are well documented for aquatic organisms. Presumably lunar timing of life-history events evolve to maximize fitness. Timing spawning or hatching with the lunar phase can be adaptive if the window of time for migration is small or if there is a benefit from coordinated movement (e.g., predator swamping). Alternative migration strategies can arise due to disruptive selection. There are many examples of alternative migratory strategies within species; for example, partial migration in which only part of the population migrates. The fitness of migrants is greater when migration is timed to lunar periods that promote movement between habitats; however, residents may not benefit from similar timing of life-history events. Here I compared the life-history timing of two species of amphidromous Hawaiian freshwater fishes that migrate to sea as larvae. One species (*Sicyopterus stimpsoni*) is assumed to be an obligate migrant and the other (*Awaous stamineus*) exhibits partial migration. We used otolith microchemistry to determine whether individuals migrated to sea or not, and I aged each individual to determine the dates of hatching and settlement relative to the lunar phase. We found a significant difference in hatching timing between *A. stamineus* migrants and residents. A higher proportion of *A. stamineus* migrants hatched at the full moon ($p < 0.001$) and settled ($p < 0.001$) at the new moon, whereas residents hatched more at the new moon ($p < 0.001$) and settled at the full moon ($p < 0.001$). The assumed obligate migrant *S. stimpsoni* tended to hatch at the new moon and metamorphose at the full moon mirroring the resident *A. stamineus*. These

convergent patterns across species suggest that the benefits of timing spawning to lunar cycles may be density dependent, such that alignment with heterospecifics is adaptive.

Introduction

Many behaviours exhibit rhythmic cycles (Gwinner 1996; Ball et al. 2001; Okamura et al 2002). Endogenous mechanisms (Harris 1963; Enright 1970) and environmental conditions (Vollestad et al. 1986; Hodgson and Quinn 2002; Tottrup et al. 2008) are known to influence the timing of rhythmic behaviours. For example, internal biological clocks can be synchronized to daily or fortnightly cyclical patterns (Enright 1970), such as photoperiod and tidal forces determined by lunar phase progression (Takemura et al. 2010).

Migration is a complex behaviour (Park et al. 1999; Elzinga et al. 2007) that exhibits lunar periodicity in a diverse range of organisms (Takemura et al. 2010). For instance, marine zooplankton, mesophotic fishes, and larval crabs undergo diel vertical migrations in response to light cycles and tidal fluctuation (Gwinner 1996; Linkowski 1996; Kronfeld-Schor et al. 2013). The onset of Coho salmon, *Oncorhynchus kisutch*, seaward migrations peaks at the new moon and gradually declines across the lunar phase (Mason 1975), while Chinook salmon show peak migration at lunar apogee when the gravitational effects of moon orbit has the smallest effect (DeVries et al. 2004).

Lunar timing of migration appears to have evolved to maximize fitness by providing a cure for coordinated behaviour and/or allowing organisms to take advantage of lunar-driven phenomena. The coordinated movement of large numbers of salmon smolt has been shown to swamp predators and reduce predation risk (Furey et al. 2016). In some reef fishes, the return migration (i.e., settlement) of larvae to reefs occur in concert with lunar phases, presumably to take advantage of incoming tides and moonlight conditions to reduce predation risk (Sponaugle and Cowan 1997). Disruptive selection can lead to the evolution of alternative migration life-histories. For example, if survival were greatest for different phenotypes on opposite ends of the lunar cycle because of the advantages of the tides or the moon illumination, then individuals migrating in the middle of the lunar cycle might be selected against.

Partial migration (PM) is an example of an alternative migratory life-history in which some individuals of a species will migrate, and others will not. It is expected that selection will act differently on migrants and residents to determine the timing of life-history events (i.e., spawning, hatching, etc.). Partial migration, which is a bet-hedging strategy, may be evolutionarily stable because it can buffer populations against the risks associated with migration, such as mortality from starvation and predation while migrating (Chapman et al. 2012a). Evidence of phenotypic differences between migratory and non-migratory individuals in partially migratory species (Jonsson and Jonnson 1993) raises the possibility that partial migratory species exhibit distinct 'rhythmic' polyphenisms associated with alternative life history strategies; however, it is not known whether migrant and resident forms of partially migratory species exhibit differences in periodicity of life-history events.

The timing of reproductive events, and the migrations associated with those events, may be different among migratory forms if there is some benefit to segregation. Different risks between migratory forms may cause variation in timing as to avoid those specific risks. For example, smaller, subordinate migratory South American Tropical Kingbird (*Tyrannus melancholicus*) are more likely to migrate than dominant counterparts, possibly to avoid intraspecific competition (Jahn et al. 2010). Similarly, faster growing anadromous brown trout are more likely to migrate, and juvenile anadromous Arctic charr, *Salvelinus alpinus*, tend to forego migration when more food is available (Jonsson and Jonsson 1993). Some plants

(*Mimulus guttatus* and *Mimulus nasutus*) and anurans (*Agalychnis* sp., *Hyla* sp., *Scinax* sp., and *Smilisca* sp.) show varying reproductive phenologies for syntopic species in response to predation pressure, and life-history events may synchronize between species to satiate predators and increase the potential of survival or progression through a life stage (Donnelly and Guyer 1994; Martin and Willis 2007). A difference in phenology, especially reproductive events, can contribute to prezygotic barriers and be a mode of isolation between species and within species between migratory types (i.e., migrant vs. resident) (Martin and Willis 2007).

Many insular aquatic organisms are amphidromous (McDowall 2007a; McDowall 2003a); they spawn in freshwater, hatchlings migrate downstream to the sea, undergo a marine phase with possible dispersal, and then migrate back to streams as juveniles to grow and reproduce (McDowall 2007b). In Hawaii there are five native fish species (all Gobioidei), some species are putatively obligate amphidromous (i.e., all larvae enter the ocean) and others are facultative amphidromous (i.e., some migrate, and others do not) (Hogan et al. 2014). Lunar periodicity of migrations is exhibited by many fishes (Lobel 1978; Taylor 1984; Sponaugle and Cowen 1994; Takemura 2004) and is well established for amphidromous gobies (Bell 2009), often exhibiting synchrony among taxa during their return migrations to freshwater streams (Shiao et al. 2015). Using lunar cycles as a reproductive cue could be adaptive for amphidromous fishes at either the onset (i.e., hatching and downstream movement) or end of migration (i.e., return to freshwater). For example, lunar cycles at hatching could synchronize larval egress with spring tides, which can promote offshore transport (Boujard and Leatherland 1992). Synchronicity of hatching with lunar phases could also help reduce predation, particularly when timed with the dark of the new moon (Lobel 1978; Boujard and Leatherland 1992).

Alignment of larval ingress and settlement with lunar or tidal phases can facilitate onshore transport, which may reduce larval predation. (Cowen and Sponaugle 1997).

In this study, I used migratory gobies in Hawaiian streams as a model for testing for intra- and interspecific differences in use of lunar rhythmicity as cues to coordinate important life events (i.e., hatching and metamorphosis). We took advantage of life history flexibility among Hawaiian stream gobies to test predictions about the role of periodic cues in enabling synchrony within and between species. We first drew comparisons between *Awaous stamineus*, which is facultative amphidromous (Hogan et al. 2014), and *Sicyopterus stimpsoni*, a putatively obligate amphidromous species. We expected to find lunar periodicity in hatching and metamorphosis in both species due to the advantages of egress during high tides and lower predation during new moons. We expected to find that *A. stamineus* and *S. stimpsoni* exhibit similar lunar rhythmicity due to the advantages of predator swamping. We compare migratory and non-migratory forms of *A. stamineus* to test the hypothesis that partial migratory species exhibit distinct 'rhythmic' phenologies.

Methods

Study Species

Awaous stamineus and *Sicyopterus stimpsoni* are abundant and widespread amphidromous goby species that are endemic to the Hawaiian Islands (McDowall 2003a, Lindstrom et al. 2012). These species exhibit considerable distributional overlap across the Hawaiian Islands, but *A. stamineus* inhabits lower- and middle-elevation reaches of streams, whereas *S. stimpsoni* can access higher-elevation reaches owing to its greater capacity to climb waterfalls (Kinzie 1988). The two species also prefer different microhabitats; *A. stamineus* favour low-energy areas with sand, gravel, or small rocks as substrate, whereas *S. stimpsoni* prefer faster-moving riffles with larger rock substrates (Kinzie 1988). Additionally, these species exhibit dietary differences: *A. stamineus* is omnivorous while *S. stimpsoni* is an algal scraping specialist (Kido 1997).

Both species lay adhesive eggs on rocks that are defended by males until hatching, which typically occurs within 24 hours of spawning. Migration commences with downstream larval "drift" (Fitzsimmons et al. 2007) that begins around sunset, peaks approximately one hour afterwards, and ends about four hours later (Lindstrom 1998). Though both species are known to undergo marine migrations, a majority of *A. stamineus* larvae remain in their natal stream for the entire life rather than migrating to the ocean (Hogan et al. 2014), while *Sicyopterus stimpsoni* show all individuals migrate to sea. Larval drift in both species has been observed year-round, though their spawning activities are somewhat seasonal (Lindstrom 1998); peak spawning of *A. stamineus* typically occurs from August through December (Ha & Kinzie 1996). The only previous investigation of lunar periodicity in reproduction of Hawaiian amphidromous fishes indicated greater concentrations of drifting larvae of all five species during the full moon and lesser concentrations during the new moon (Lindstrom 1998), however sample sizes were too small to allow robust statistical analysis.

Larval duration differs among amphidromous goby species and between migrant and resident forms of *A. stamineus*. *Sicyopterus stimpsoni* larval duration averages 120 d (65 - 200 d), and larval duration averages 118 d (57 - 248 d) in *A. stamineus*, although the larval duration of migratory individuals are significantly shorter (mean = 108 d) than the larval duration of non-migratory individuals (mean = 122 d; Hogan et al. 2014). Migration back to streams occurs throughout the year for both species (Kinzie 1988, Hogan et al. 2014). In *A. stamineus*, metamorphosis from larval to juvenile morphology is coincident with the return of migratory individuals to freshwater (Hogan et al. 2017), whereas metamorphosis also occurs in resident individuals in the absence of marine migrations. It is not known whether settlement and metamorphosis of either species follows a lunar period.

Sample Collection and Preparation

Samples were collected from 35 watersheds across all five main islands in two separate collection trips, one from December 2008 - November 2009 and one from March - June 2011. A total of 249 *A. stamineus* were collected from 34 of the sampled watersheds, and a total of 55 *S. stimpsoni* were collected, between March and May 2011, from 15 watersheds (see Chapter 1). Conditions in the sampled streams were representative of the diversity of habitats available to both species across the archipelago and constitute ~25% of the 133 streams known to harbour *A. stamineus* (i.e., the more widespread of the two species; http://hawaii.gov/dlnr/dar). Fish were collected by snorkelers with hand nets, and after total length was measured, fish were humanely euthanized and kept on ice (University of Wisconsin - Madison IACUC protocol #: L00431-0-01-11), then stored frozen at -20° C. Fish were thawed in the lab to extract sagittal otoliths. For each fish, one of the two sagittal otoliths was haphazardly selected, mounted and polished for microstructure analysis to determine age, hatching date and metamorphosis date. Otoliths were extracted following standard protocols (Bickford & Hannigan 2005). Sagittal otoliths were removed, cleaned in distilled water and allowed to dry. Otoliths were mounted sulcus side up onto glass petrographic slides and embedded in Crystalbond™ glue. To expose the daily growth rings from the edges to the primordium, otoliths were ground in the sagittal plane, using fine grit polishing pads (Buehler) and diamond lapping films (3M) ranging in grit size from 60 - 0.5 µm.

The same otolith was also used for microchemical analysis to classify the individual fish as an ocean migrant versus stream resident.

Analysis of developmental dates and rates

We used the existing dataset from *A. stamineus* collected by Hogan et al. (2014) for data on total age, larval duration, hatching date, and metamorphosis date of each fish. These same data were collected for *S. stimpsoni* in this study by imaging otoliths to count daily growth increments (i.e., rings). Total age corresponded to the total count of daily growth increments from the primordium to the otolith edge. Larval duration was determined by counting the rings from the primordium to the metamorphosis mark on the otoliths. The metamorphosis mark is a relatively broad increment having high optical density (Radtke et al. 1988) that is laid down during metamorphosis and corresponds precisely with the transition from marine to freshwater environments in migratory *A. stamineus* (Hogan et al. 2017). Each otolith had two independent reads and only samples that had less than 5% average percent error were included in the analysis. Hatching dates and metamorphosis dates were back calculated as follows:

$$Hatch\ Date = \ Date\ Collected - Age\ (d)\ at\ Collection$$

$$Metamorphosis\ Date = \ Hatch\ Date\ +\ Age\ (d)\ at\ metamorphosis$$

Identifying Marine Migrations

As was previously done for the 2008-2009 *A. stamineus* specimens (Hogan et al. 2014), migratory behaviour was determined for the 2011 *A. stamineus* and all *S. stimpsoni* samples using laser ablation (Cetac LSX213) inductively coupled plasma mass spectrometry (Perkin Elmer ELAN DRCII) at the Environmental Analytical Facility at University of Massachusetts -

Boston. Samples and standards were analysed with a laser beam width of 25 µm and a scan rate of 15 µm · s^{-1}. To ensure that the entire life span was sampled (i.e., both larval and post larval periods), all otoliths were analysed with a laser transect from one edge of the otolith to the other, bisecting the primordium. All samples were calibrated and drift corrected using two calcium carbonate standards (USGS MACS-1, MACS-3) and background corrected against the argon carrier gas from a gas blank taken before each sample analysis. Calcium (^{43}Ca) was used as an internal standard to compensate for signal variation caused by differences in mass of ablated material. Concentrations of 18 isotopes were calculated and analysed; relative concentrations were expressed as a ratio to ^{42}Ca. Sr:Ca ratios were used to determine marine migrations, as Sr:Ca is relatively high in the marine environment (~ 8 mmol · mol^{-1}) compared to freshwater environments in Hawaii (~ 4 mmol · mol^{-1}; Hogan et al. 2014). Prior work on Hawaiian amphidromous gobies (Hogan et al. 2017) has demonstrated that otoliths of marine migrants show a marked decline in Sr:Ca concentrations at settlement, which is indicative of the transition to freshwater from the marine environment. Evidence of a spike in Sr:Ca around 8 mmol · mol^{-1} in the pre-metamorphosis portion of the otolith indicates that the individual underwent a marine migration as a larva. If the Sr:Ca in the pre-metamorphosis portion of the otolith is low (~ 4 mmol · mol^{-1}) then the individual did not migrate as a larva.

Determining Lunar Periodicity of Hatching and Metamorphosis

Hatch and settlement dates were analysed with circular statistics (‘circular’ package RStudio) to determine if there was directionality across the lunar phase for the frequency of occurrence for the life-history events of interest. Full moon dates were obtained from the US Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil/data/docs/MoonFraction.php).

The number of days since the full moon (DFM; 0 - 29) and percent illumination were assigned to each individual based on the estimated life-history dates. The DFM was converted to angles to test with circular statistics using the following formula:

$$Angle = \frac{DFM}{29.5\ (\#\ of\ Lunar\ Cycle\ Days)} * 360$$

Rao's spacing test was used to determine if the frequency of hatch and settlement showed lunar periodicity. Rao's spacing test is robust for small sample sizes, both unimodal and multimodal distributions, and reduces the probability of committing a Type I error (Grant et al. 2009). The hypothetical null for Rao's spacing test is the distribution is uniform. The methods for Rao's spacing test were completed in accordance with that previously described in Grant et al. (2009). Although Rayleigh's test is not as powerful as Rao's spacing test, Rayleigh's can be useful in identifying when distributions are unimodal about a cyclical phase (Russell and Levitin 1995). We performed Rayleigh's test to identify if distributions were unimodal around a specific phase of the lunar cycle (Ruxton 2017) using degrees of percent illumination. A departure from the null hypothesis for Rayleigh's test indicates the data has directionality, and the assumption is that the direction is unimodal (Ruxton 2017). Hatch and settlement percent illumination was used to evaluate the frequency of occurrence from new (0% illumination) to full moon (100% illumination). The Rayleigh's test statistic was compared with the frequency of occurrence by percent illumination for the life-history events to determine agreement for the modes of occurrence about the lunar phase.

Further, I iteratively tested several specific hypotheses about migratory periodicity within and between species. First, I compared the percent illumination of the moon at hatching and metamorphosis dates for migrants of each species. Next, I tested whether the distribution of moon illumination percent of hatching dates differed between migrant and resident *A. stamineus*, and likewise for metamorphosis dates. Finally, I compared both migrant and resident *A. stamineus* percent of moon illumination at hatching dates to those of *S. stimpsoni*, and likewise for metamorphosis data. Pair-wise comparisons of all distributions were conducted using non-parametric, univariate Kolmogrov-Smirnov (KS) two-sample tests (Wilcox 2005). We used α = 0.05 as our criterion for determining significance. All two-sample tests met the statistical assumptions to perform the KS test.

Results

Migration behaviour in A. stamineus and S. stimpsoni

Of the 249 *A. stamineus* samples pooled and analysed, 76 were categorized as migrant and 173 were categorized as resident (Supplementary Table S1). Hatch dates of *A. stamineus* ranged from October 2002 to August 2010 and metamorphosis dates ranged from February 2003 to October 2010. As reported in Hogan et al. (2014), the average larval duration for *A. stamineus* was 118 d (57 - 248 d) and the average total age was 2.4 y (1.3 - 4.5 d). All 55 *S. stimpsoni* samples (Supplementary Table S2) were categorized as migrant (See Chapter 1), and the hatch dates of ranged from August 2010 to February 2011, and metamorphosis dates ranged from December 2010 to May 2011.

Species Contingent and Stage	N	Rao's spacing test (U)	Rao's p-value	Rayleigh's test (Z)	Rayleigh's p-value	Directionality
A. stamineus Migrant Hatch	76	236.84	<0.001	0.287	0.0019	Full Moon
A. stamineus Migrant Settlement	76	241.58	<0.001	0.255	0.0071	New Moon
A. stamineus Resident Hatch	173	299.65	<0.001	0.212	<0.0001	New Moon
A. stamineus Resident Metamorphosis	173	299.65	<0.001	0.156	0.016	Full Moon
S. stimpsoni Hatch	55	236.03	<0.001	0.081	0.7	New Moon
S. stimpsoni Settlement	55	255.37	<0.001	0.156	0.26	Full Moon

Table 2-1: Rao's spacing test and Rayleigh's test statistics for hatch and metamorphosis distributions of migrant and resident Awaous stamineus and migrant Sicyopterus stimpsoni

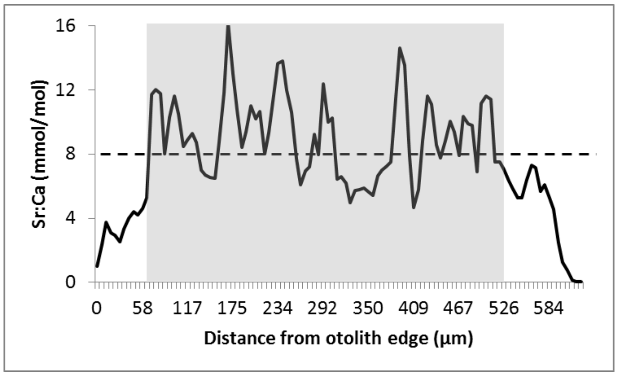

Figure 2-1: Example of a S. stimpsoni otolith chemistry transect demonstrating microchemical evidence of marine migration. Marine migration is indicated by Sr:Ca ratio at or around 8 mmol·mol^{-1} (dashed line) in the pre-metamorphosis portion of the otolith (grey box). Portions of the otolith chemistry signature outside of the grey box indicate the Sr:Ca ratio of the freshwater stream from which the fish was collected. Sr:Ca ratios are a 3-point running average to smooth analytical noise.

Lunar periodicity

All of the hatch and metamorphosis/settlement distributions deviated from the null assumption of uniformity (all Rao's *p*'s < 0.001), which indicated all distributions had directionality with regard to lunar periodicity (Table 1). Rayleigh's test indicated unimodality across all distributions except when for *S. stimpsoni* (Table 1). *Sicyopterus stimpsoni* hatch and settlement distributions show unimodal distributions with a higher frequency of occurrence around the new and full moons, respectively (Figures 2 and 3), yet Rayleigh's test was non-significant for unimodality. These results indicate that Rayleigh's test was not as sensitive as Rao's test for detecting non-uniformity in the data, therefore, Rao's test statistics and visual representation of frequency of occurrence was used for inference about the cyclicity and concentration of frequency for these distributions (Russell and Levitin 1995; Ruxton 2017).The periodicity of both hatching ($D = 0.47222$, $p < 0.0001$) and metamorphosis ($D = 0.66667$, $p < 0.0001$) differed significantly between migrant and resident *A. stamineus*;. Resident *A. stamineus* and migrant *S. stimpsoni* hatching distributions were not significantly different ($D = 0.098$, $p = 0.816$), whereas the periodicity of hatching significantly differed between migrant *A. stamineus* and *S. stimpsoni* ($D = 0.69231$, $p < 0.0001$). Distributions of metamorphosis in migrant ($D = 0.66667$, $p < 0.00001$) and resident ($D = 0.39726$, $p = 0.001$) *A. stamineus* also significantly differed from the distribution of metamorphosis in *S. stimpsoni*. Migrant forms of *A. stamineus* tended to hatch on the full moon (Figure 2) and metamorphose on the new moon (Figure 3). The opposite was found for resident forms; hatching peaked on the new moon (Figure 2) and metamorphosis peaked on the full moon (Figure 3).

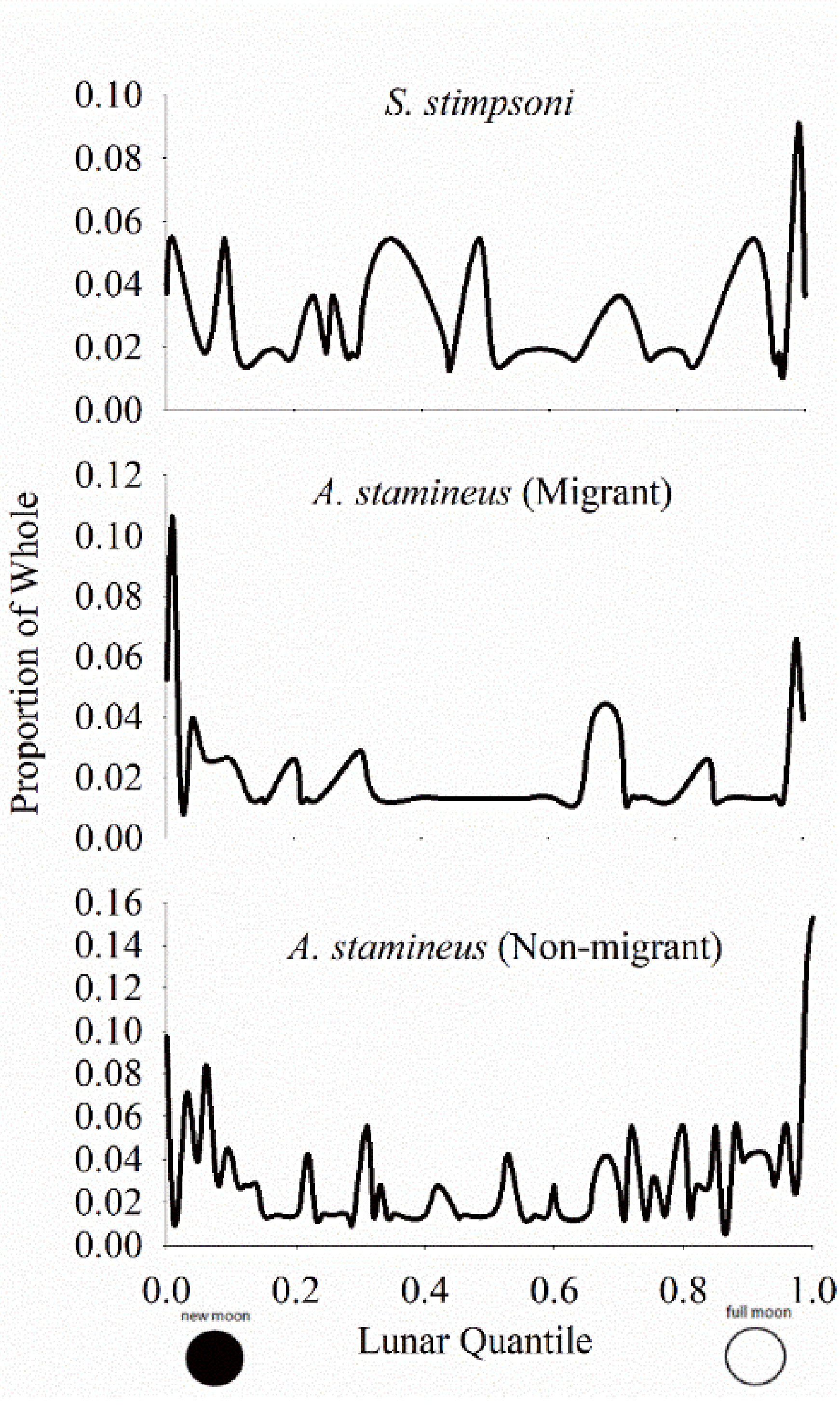

Figure 2-2: Proportionally more S. stimpsoni (n=55; p< 0.001) and A. stamineus residents hatch at the new moon than A. stamineus migrants (n=249; p= < 0.001), which proportionally hatch more frequently at the full moon.

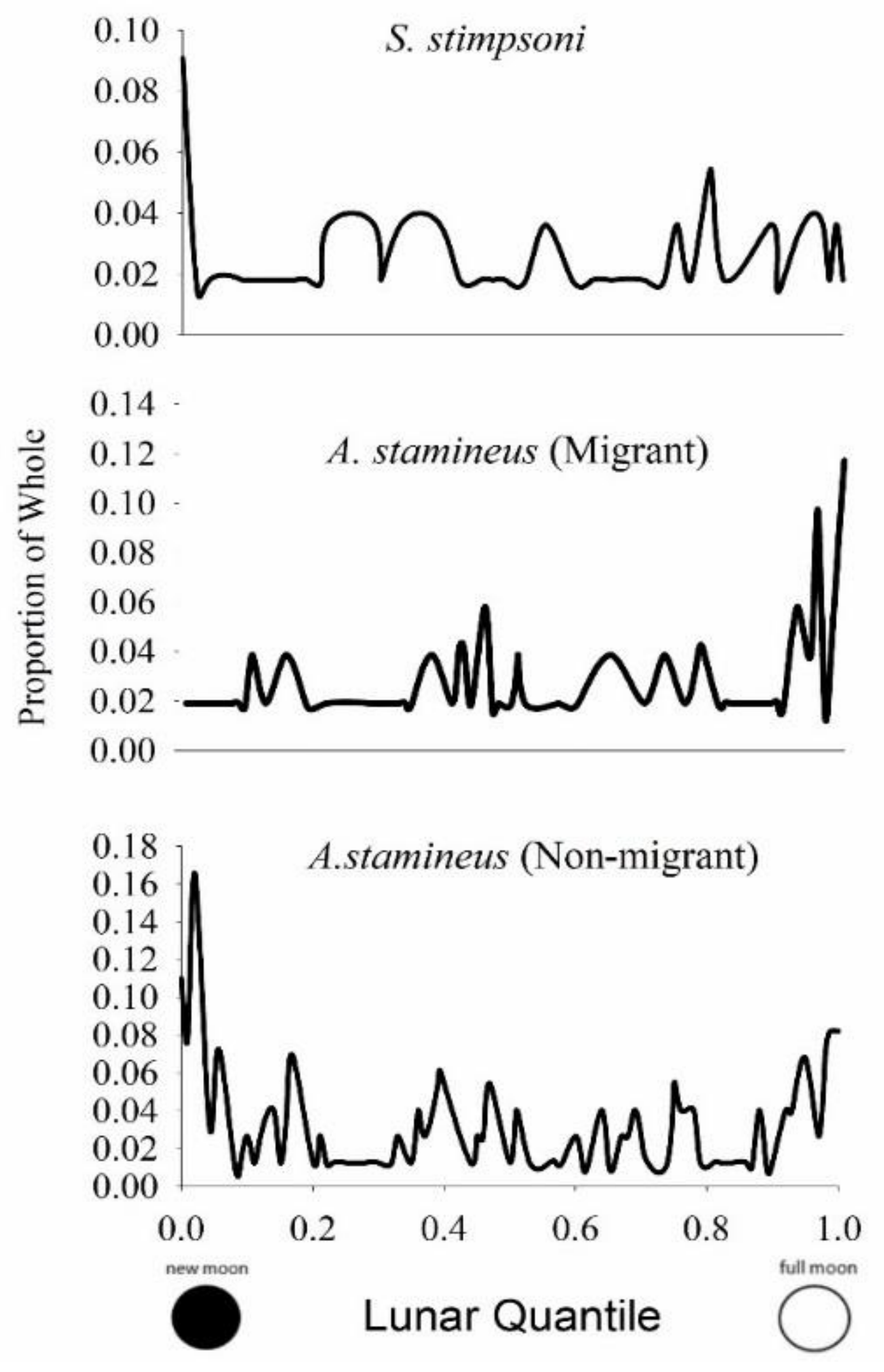

Figure 2-3: Proportionally more S. stimpsoni (n=55; p< 0.001) and A. stamineus residents metamorphosed at the full moon while more A. stamineus migrants (n=249; p< 0.001) metamorphosed at the new moon.

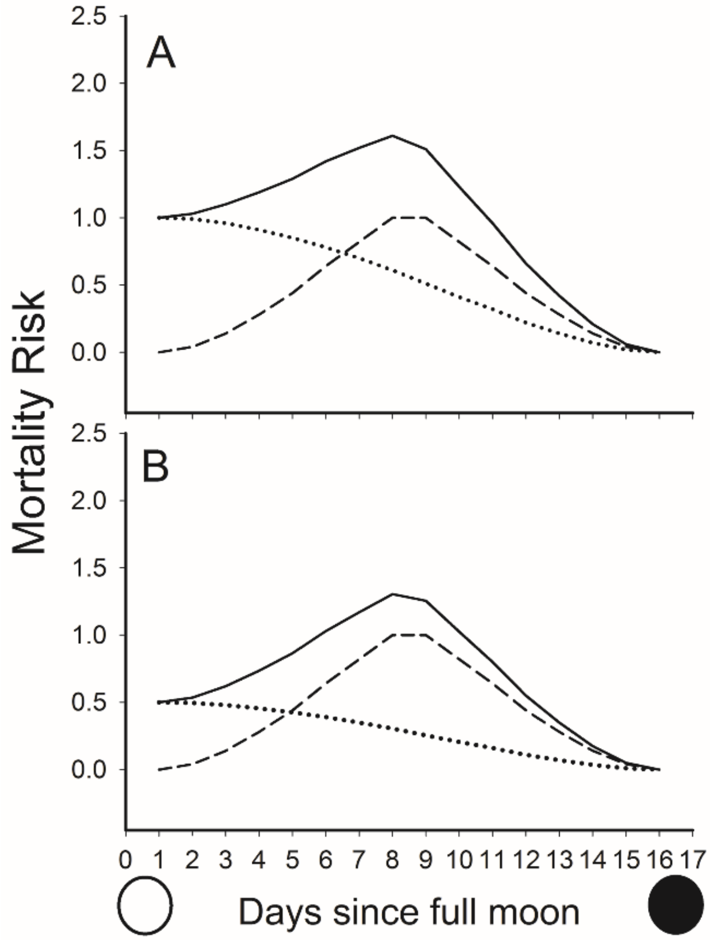

Figure 2-4: Conceptual model of mortality risks leading to divergent hatching timing in amphidromous Hawaiian fishes. A: The risks of predation (dotted line) and emigration failure (dashed line) are equal in strength; predation risk in both the marine and freshwater environment is lowest on the new moon and emigration failure is lowest on the new and full moons when tides are highest, leading to an overall risk of hatching (solid line) to be lowest at the new moon. B: The risk of predation (dotted line) is about half that of the risk of emigration failure (dashed line). This leads to a reduced overall risk (solid line) at both the new and full moon phases; this balance between predation and emigration risks could lead to divergent migration phenologies between migrant and resident individuals.

Discussion

Even though hatching and metamorphosis are occurring throughout the lunar cycle, we found support for the hypothesis that amphidromous fish native to the Hawaiian Islands exhibit lunar migratory rhythmicity where more individuals survive when these life-history events occur at at either the new or full moon, and I also found that migrant and resident forms of *A. stamineus* - a partial migratory species – have opposite phenologies. Logically, it would be expected that the pattern of hatch and metamorphosis of migratory *A. stamineus* would match that of the migratory *S. stimpsoni*, but I instead found that *S. stimpsoni* exhibited patterns of hatching and metamorphosis more similar to the resident forms of *A. stamineus*. Migrant *A. stamineus* hatched at the full moon and metamorphosed at the new moon, while resident *A. stamineus* and *S. stimpsoni* hatching peaked at the new moon and metamorphosis peaked at the full moon. These findings suggest that there are different selection pressures driving the evolution of life history phenology in migrant and resident *A. stamineus*.

Amphidromous fish encounter a range of challenges across migratory pathways that may vary with lunar phase progression. For example, upstream ingress and downstream egress cannot occur when connectivity between habitats is low. Obligate amphidromous species like *S. stimpsoni* are especially vulnerable to discontinuities that affect ocean-stream connectivity. Ocean-stream connectivity peaks around the new and full moons and thus the risk of migration failure is likely lowest during these times. Predation also can be a significant threat to individuals navigating biological 'gauntlets' during outward and return migrations (Limburg 2001, Hain 2013). Predation risk for both instream larvae and returning post-larval migrants is likely greatest at times of high lunar irradiance like during the full moon. Accordingly, the observed patterns of lunar rhythmicity exhibited by *A. stamineus* and *S. stimpsoni* are likely explained by two adaptive strategies: 1) successful migration out of the stream and 2) avoiding predation. Though differences in risk may favour a single optimal periodicity (e.g., ingress and egress might be expected to peak at the new moon), our findings suggest that phenological divergence within and among species with different migratory types may be in response to ecological tradeoffs and risks (Ydenberg et al. 2007; Chapman et al. 2011).

We observed a unimodal phenology in the migrant *S. stimpsoni* with peaks of hatching around the new moon and peaks of return-migration around the full moon. Similar migratory phenologies have been observed in other obligate diadromous species. For example, anadromous brook charr, *Salvelinus fontinalis* (Castonguay and FitzGerald 1982), river lamprey, *Lamptera fluviatilis* (Potter and Huggins 1973; Malmqvist 1980; Sjoberg 1980) and catadromous European eels, *Anguilla anguilla* (Oakamura et al. 2002), undergo migrations around the new moon. The lunar periodicity observed in *S. stimpsoni* indicates the promotion of greater survivorship associated with lunar rhythmicity may balance the risks of obligate migration as a strategy, (Ross 1983). Out-migration on the new moon corresponds to the phase of the lunar cycle when risk of predation and migration failure are expected to be lowest (Figure 4; Takemura et al. 2010; Naylor 2015). Returning on the full moon would minimize risk of migration failure, though there is likely more risk of predation. However, return-migration on the full moon would be more favourable if navigation to the stream from the marine environment requires visual cues (Kingsford et al. 2002) or if insular streamflow is influenced by the lunar phase. Inland continental streams in the United States had an increase in streamflow and precipitation in between the new and full moon phases (Cerveny et al. 2010). Island streams in Hawaii are much shorter and steeper than continental river basins, therefore, streamflow may be influenced enough by the full moon to facilitate the return of migrants.

The timing of hatching and metamorphosis of migrant *S. stimpsoni* aligned with resident *A. stamineus*, whereas, migrant *A. stamineus* hatched on the full moon and returned on the new moon. The convergent patterns of hatching and metamorphosis between *A. stamineus* residents and *S. stimpsoni* suggest that there may be benefits of synchronizing spawning to lunar cycles as a predator swamping strategy (Darling 1938; Pulliam and Caraco 1984; Ims 1990). The alignment with heterospecifics may be adaptive leading to greater fitness in both species.

We observed that migrant and resident *A. stamineus* exhibited opposite migratory phenologies. On the new moon phases, residents tended to hatch and migrants tended to return to the streams. During a full moon, residents metamorphosed into post-larvae and migrants tended to hatch and migrate to sea. Opposite migratory phenologies within *A. stamineus* must have arisen despite the benefits of predator swamping. Migrants require ocean-stream connectivity and migration failure is lowest at both extremes of the lunar cycle. However, the lowest predation risk occurs at the new moon. Therefore, hatching of migrant individuals would be favoured under full and new moon conditions, whereas resident hatching would only be favoured during the new moon, since they are not affected by ocean-stream connectivity. This dichotomy emerges in part because early stage larvae are most prone to predation (Houde and Hoyt 1987). Accordingly, hatching on the new moon would present the greatest chance of surviving to adulthood, since the darkness around the new moon would offer resident larvae a greater opportunity to “outgrow” predation risk (Houde and Hoyt 1987). Both migrants and residents are susceptible to predation, however, in-stream predation of larvae is expected to be much greater for residents since migrant individuals spend only a few hours in stream (Lindstrom 1998).

Contrasting timings may also reduce intraspecific competition, especially during life stages when mortality is relatively high and when resources are low (e.g., following metamorphosis and/or return; Ross 1983; Houde and Hoyt 1987). When applied to *A. stamineus* migrants, this logic is ostensibly counterintuitive; in-stream predation risk is expected to peak during the full moon, whereas the risk of migration failure is expected to be lowest during both phases. Thus, it would be more favourable for hatching to occur on the new moon, as is the case for *S. stimpsoni*. However, there are conditions that would favour the rise of divergent phenologies in migrants and residents. For instance, while out-migration of larvae to the ocean on the new moon should always be favoured if the risks of predation and migration failure are equal (Figure 4a), alternative 'stable states' might occur if predation risk is much less than the risk of migration failure (Figure 4b). This is particularly the case for migrant *A. stamineus* that only spend 2 - 4 hours in-stream before reaching the ocean (Lindstrom 1998).

Hatch lunar periodicity was consistently out of phase with metamorphosis (i.e., of resident *A. stamineus*) and/or return migration (i.e., of *S. stimpsoni* and migrant *A. stamineus*), but greater variability was observed in the timing of metamorphosis than the timing of hatching (Figures 2 & 3). For example, I found that *A. stamineus* migrants most frequently returned to streams on the new moon, though there was a smaller contingent that returned on the full moon (Figure 3b). Absent of other constraints, the periodicity of return migration might vary more because the risk of migration failure is low on a new and full moon, when high tides maximize ocean-stream connectivity. Flexibility might also arise due to a fixed larval duration, as has been observed with spawning and settlement in some coral reef fishes that exhibit lunar periodicity (Cowen & Sponaugle 1997), but neither *S. stimpsoni* nor *A. stamineus* have strongly constrained larval durations (Hogan et al. 2014).

Organismal phenology is often cued to external conditions that promote survival and fitness. Consistent with this, our findings suggest that migratory synchrony promotes success during a vulnerable life history stage when survival rates are low (Enright 1970). Extrinsic and endogenous factors must act in concert for migratory behaviour to unfold, where external factors trigger endogenous physiological mechanisms that elicit the expression of behaviour (Enright 1970). If endogenous mechanisms have a genetic (i.e., heritable) basis, then differential survival might result in distinct migratory phenologies (like those observed in *A. stamineus*) through adaptive evolution. Although there is little empirical evidence that migration dichotomies are genetically determined (Chapman et al. 2012a), divergent synchrony may facilitate genetic divergence between contingents that are otherwise sympatric. Further studies will be needed to determine if there are genetic differences between the two phenotypes. Genomic assays of facultative amphidromous gobies like *A. stamineus* could reveal the processes that underlie variation in migratory periodicity. These findings may provide support that partial migrants have divergent phenologies that ultimately guide evolution.

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CHAPTER 3: FACTORS THAT INFLUENCE DIFFERENTIAL SURVIVAL OF RESIDENTS OF A MIGRATORY HAWAIIAN FRESHWATER FISH ACROSS ENVIRONMENTAL AND BIOLOGICAL GRADIENTS

Abstract

Human activities have altered habitat quality and quantity of many freshwater ecosystems. Biological diversity has been simplified and many native species are imperiled from alteration in water quality, shrinking habitat, and competition and predation from introduced non-native species. To properly manage freshwater ecosystems, it is necessary to understand how humans have altered these ecosystems and the effect of those alterations on survival of native species. For partially migratory diadromous species, early life-stages may be spent in either the marine or freshwater environment. Poor habitat quality in-stream can result in population declines for these flexible species. We examined differential survival of residents of the partially migratory Hawaiian fish, *Awaous stamineus*, across gradients of human impact. Our goal was to identify if physical processes that are commonly influenced by human activities (i.e., nutrient input and flow rates) and varying densities of common aquatic invasive species were affecting the proportion of residents found in adult populations. We found that inorganic nitrate, flow variability, and soluble reactive phosphorus, likely exert the strongest effect on the survival of resident larvae; residents had reduced proportions in populations when stream flow was low and/or nutrients like phosphorus were limited. However, when non-native poeciliid predator densities were high, there was also a reduction in the proportion of residents in adult populations. Our study identified that factors that can be controlled by human activity and management affect the survival and recruitment success of fish that remain in the natal habitat for the duration of the life-cycle. These findings provide information that may be

essential to properly managing the freshwater aquatic systems in Hawaiʻi to promote the survival and persistence of native fishes that are of conservation concern.

Introduction

Historically, human activities have altered flow regimes of streams and rivers, abstracting water for industrial and residential uses, and to control floods in urban and agricultural areas (Smith et al. 1999). Dewatering has reduced base flows and promoted subsidence of stream banks (Brasher 2003). The quantity and quality of streams have decreased due to increasing land-use around riparian ecosystems, and the treatment of wastewater and other runoff has increased nutrient input into freshwater systems (Smith et al. 1999; Brasher 2003; Lisi et al. 2018). Native species diversity has decreased due to habitat alterations and the introduction of non-native species by human transplantation, which has simplified and decreased the stability and resiliency of many ecosystems (Smith et al. 1999; Lundberg and Moberg 2003). Aquatic invasive species have altered the trophic dynamics and interspecific interactions with native species in many ecosystems, which has introduced additional stress to native species that are of conservation concern (Brasher 2003; Lisi et al. 2018). To manage freshwater ecosystems properly, a better understanding on how the alteration of freshwater ecosystems has affected native species behavior and population dynamics are necessary.

The conditions experienced early in the life-history control the number of surviving individuals that recruit to adult populations (Hjort 1914, 1926; Cushing 1974; Houde 2008). Mortality rates that affect the level of recruitment may be altered by local conditions (McDowall 2007a). Habitat quality has been shown to influence the dominant recruitment type (migrant or residents) within partial migrant species (Taylor and Norris 2007), and environmental factors can influence the representation of either contingent in some diadromous fishes (Huey et al. 2014; Watanabe et al. 2014). For example, in Australia, streams with steeper gradients and higher flow rates had more migrants than slower, sluggish streams (Huey et al. 2014) presumably because high flow rates promote the migration of larvae after hatching. Large-scale climate drivers can interact with and modify local environmental conditions (Mosley 2000; Cole et al. 2002) that affect the survival and recruitment rates of contingents (Barber and Chavez 1983). Changes in rainfall and groundwater availability can alter habitat quality or quantity and are particularly influential in riverine environments (Walter et al. 2012). For example, more migrants of white perch, *Morone americana*, were found when stream flow was high, and no migrants were found during drought years (Kerr and Secor 2010). This may have been the result of increased nutrient delivery and improved environmental conditions or a larger larval cohort during high flow times (more spawning during high flow; Kerr and Secor 2010).

Nutrient delivery and additions can also affect water and habitat quality. Phosphorus is typically limited in freshwater systems, but it is important for maintaining balanced water quality and promoting primary production in lotic ecosystems (Elwood et al. 1981; Elser et al. 1990). Like orthophosphates, nitrites and nitrates occur naturally and are essential for a properly functioning ecosystem. Excess orthophosphate (reactive phosphate) and nitrate additions can alter the natural water quality of freshwater systems and lead to an overproduction of phytoplankton, plants and algae, and other biota (Fisher et al. 1992), which can cause eutrophication and decreased dissolved oxygen that can exert additional stress and mortality on organisms that reside in those habitats (Mallin et al. 2006; Bilotta and Brazier 2008). Conversely, an intermediate level of nutrient additions that don’t overstimulate primary productivity and algal growth could promote an increase in lower trophic prey items; different nutrition sources may be the result of increased primary productivity (Sagouis et al. 2015; Lisi et al. 2018). Nitrates and orthophosphates are common by-products of agricultural activities, sewage treatment, and commercial land-based practices. These nutrients, along with others, can alter water quality change nutrient inputs at the base of food webs and alter trophic interactions among species (Vitousek et al. 1997; Woodward and Hildrew 2002). These nutrients can serve as a proxy for associated human activities that influence the water quality of an ecosystem (Cole et al. 2004) since these nutrients can be delivered to freshwater aquatic systems through runoff from land-based practices such as agriculture (Fisher et al. 1992).

Although physical processes are responsible for much of early life mortality, species interactions, such as predation and competition, are also important for structuring species communities and recruitment success of larvae to adult populations (Kido 1997; Chapin III et al. 2000; Houde 2008; Chapman et al. 2011). The introduction of non-native species by humans can increase predation and competition on native species (Jenkins et al. 2010; Morrison 2016). Inter- and intraspecific competition for resources may be especially high for larva since prey sources are usually patchy and heterogeneous (Houde 2008), and larvae will experience mortality if they are unable to find or utilize food sources within the critical larval period (Hjort 1914, 1926; Cushing 1973). Additionally, nutrition sources may be available, but individuals may not be effective at capturing or digesting prey (Hjort 1914, 1926). If nutrition sources are limited and there are high rates of competition for early-stage larvae, growth may be slowed and survival to the next life-stage may be delayed (Houde and Hoyt 1987) or decreased nutritional condition may increase the susceptibility to predation and larval mortality rates (Rothschild 1986; Houde 2008). Predation rates are inversely related to body size; as individuals get larger the probability of being eaten by a predator decreases (Peterson and Wroblewski 1984; McGurk 1986). This exemplifies the importance of quality habitat with adequate nutrition sources for larvae and juveniles.

In Hawaii, streams cross extreme gradients in rainfall, streamflow, land-use, and aquatic invasive species (AIS) introductions vary within and among islands (Brasher 2003). Native fishes are exposed to a wide range of local conditions as a result (Walter et al. 2012). For example, streams on the north shore of the island of Molokaʻi are relatively pristine with little to no land-use alteration and a high abundance of native fishes (Gagne et al. 2015), while Honolulu on Oʻahu has a population of nearly 1 million people, and streams that run through the city are highly modified with altered quality and quantity of aquatic habitats (Brasher 2003). Intensifying watershed land-use in Hawaii is accompanied by physical and chemical changes to stream conditions (Lisi et al. 2018), and water extraction has reduced habitat quality and quantity; native fish abundance and diversity is considerably lower in streams that have been highly modified (Brasher 2003). Increasing urban and agricultural land-use practices have led to the nutrification of many Hawaiian streams (Lisi et al. 2018). In Hawaii, the abundance of native species varies with geomorphology and the degree of human impact to streams (Brasher 2003). However, not all native species respond the same way to urbanization and its effects (Lisi et al. 2018). All of the endemic Hawaiian freshwater fishes exhibit amphidromy (McDowall 2007b; McDowall 2003b), a life-history whereby adults live and spawn in freshwater and larvae migrate to sea for an extended period before migrating back to freshwater. Amphidromy is a distinct form of diadromy, and it can be differentiated from anadromous migrations because larvae migrate to the ocean for feeding and growth, and the juvenile and adult life-stages are spent in freshwater (McDowall 2007a). *Awaous* *stamineus (*Eydoux & Souleyet, 1850) is the most abundant native freshwater fish in Hawaii and exhibits partial migration, where there are both migrant and resident forms within adult populations (Hogan et al. 2014). Most of the native Hawaiian fishes exhibit this same flexibility. For *Awaous* the ratio of migrants to residents varies by watershed but in most adult populations, residents are the predominant form (Hogan et al. 2014). *A. stamineus* appears to be relatively insensitive to land-use alterations and it has been hypothesized that their flexible migratory life-history may be a buffer against ecosystem alteration (Lisi et al. 2018). However, it is unknown if orhow ecosystem alterations to stream flow, nutrient pollution, and AIS affect the proportions of migrants and residents in populations of this species.

The Hawaiian Archipelago crosses a natural rainfall gradient, which affects stream flow that is primarily driven by orographic precipitation (Giambelluca et al. 1986); streams on the windward side of islands receive orders of magnitude more rainfall than those on the leeward side, which are in the rain shadow of the volcanic mountains (Giambelluca 1986). The mountainous terrain produces steep, short watersheds with small watershed areas, which lead to streams that are characterized by low base flow and high flow variation (Oki 2004). Rainfall gradients among the streams are strong and can lead to streamflow gradients, which can alter community dynamics (Gagne & Blum 2016). Additionally, some streams have managed flows for flood prevention, and water may be abstracted for human use (Brasher 2003; Gopalakrishnan 2005). Newly hatched larvae may be passively displaced downstream to the marine environment (Iguchi and Mizuno 1991), and flow conditions may influence larval movement within the freshwater system and to the marine environment (Brasher 2003). Conversely, a reduction in flow or high variability in flow may impede the in- and out-migration of individuals in a stream or may cause resident fish to desiccate when during dry seasons or droughts (Brasher 2003; Lisi et al. unpublished). Subsequently, factors that impact the ability of the different contingents to recruit influence how represented either contingent group is in adult populations in-stream (Walter et al. 2012).

Hawaiian systems are naturally depauperate resulting in vacant niche spaces, and feature highly specialized native species, shorter food webs, and lower functional redundancy (D'Antonio and Dudley 1995; O'Dowd et al. 2003).This decreased ecological diversity makes these ecosystems especially vulnerable to biological invasions and, in many cases, the diversity in Hawaiian freshwater systems is highly dominated by AIS, which increases predation and competition for natives (Vitousek 1988; D'Antonio and Dudley 1995). The introduction of AIS in Hawaii are highly influenced by human densities and urban and agricultural habitat alterations (Brasher 2003; Walter et al. 2012; Moody et al. 2017; Lisi et al. 2018).

One of the most widespread and abundant AIS in Hawaii are Loricariids (e.g., armored catfishes; Walter et al. 2012). Loricariids can alter stream ecosystems by digging nests into the banks of rivers (Nico et al. 2009), which increases erosion and turbidity and alters benthic algal communities on which native fishes feed (Brasher 2003). Loricariids feed on algae similar to many of the native Hawaiian fishes, and they sequester phosphorus in bony plates on the body, which may further limit available phosphorus (Hood et al. 2005). Phosphorus limitations can affect the resource base for native species, and it can increase the risks for survival of resident larvae by potentially decreasing in-stream primary productivity and altering food web structure (Elser et al. 2001). Furthermore, since loricariids and native fishes have similar diets, loricariid density may contribute to a direct increase in interspecific competition with native fishes for food (Capps et al. 2015). Another abundant and widespread groups of AIS in Hawaii are poeciliids (e.g., guppies, mollys, swordtails), which were introduced in the early 20th century for mosquito control, and they are found on every island (Gagne et al. 2015). Poeciliids are in high abundance in many streams and are suspected to depredate the planktonic larvae of native species (Walter et al. 2012).

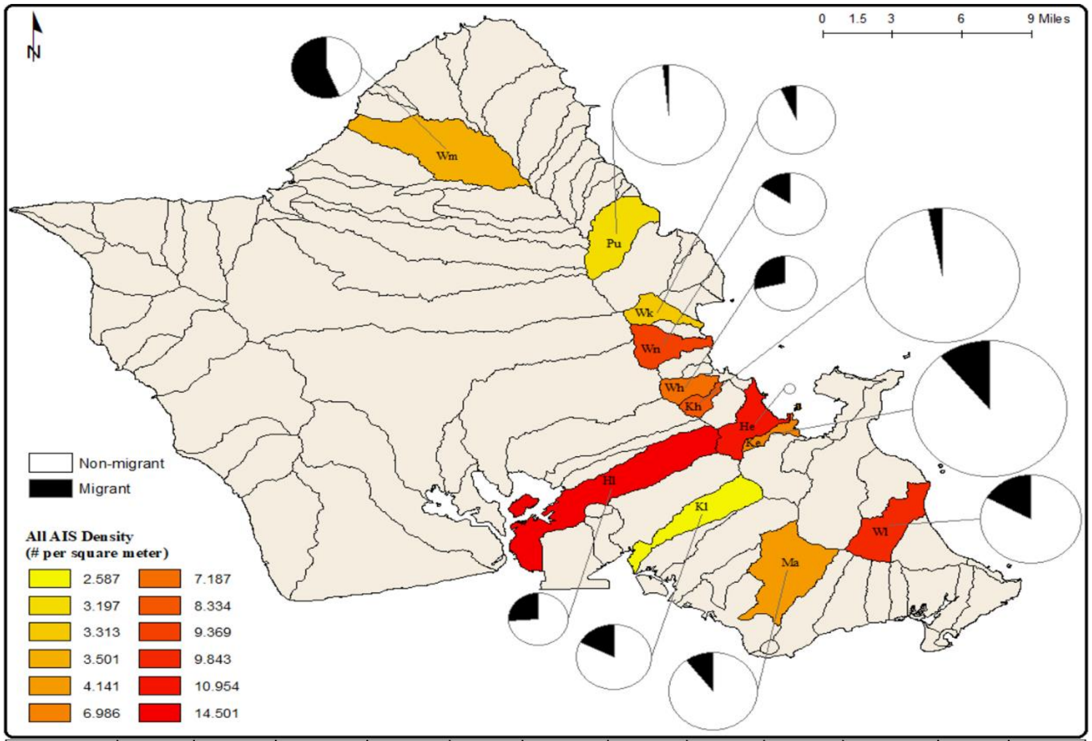
In this study, I analyzed the ratio of residents to migrants within populations of *A. stamineus* across an environmental and AIS density gradient representative of human impacts. The goal of the study was to examine how varying levels of human alteration to freshwater ecosystems influences the variation of differential survival of residents. We hypothesized that 1) when invasive species density was high there would be a lower proportion of residents due to increased competition and predation, 2) when stream flow was low and flow variation was high there would be a lower proportion of residents due to desiccation, lowered habitat quantity and quality, and reduced access to nutrition sources, and 3) pristine streams, indicated by low nutrient concentrations and low AIS densities, would have a higher proportion of residents since less stressful in-stream conditions would be more favorable for survival of resident larvae. Understanding the differential survival of residents can provide a better understanding of population and ecosystem dynamics for proper management and conservation.

Methods

Study Site and Species Collection Methods

We sampled twelve perennial streams on the island of O‘ahu for this study (Figure 1). The streams span the windward and leeward sides of the island crossing a strong rainfall gradient that leads to large differences in stream flow and variance in discharge across the watersheds.

These streams also span a wide range of human densities. Some streams run through the city of Honolulu and its suburbs, which has high human densities, while some streams run through rural areas with few people in the watershed. Human impacts on these streams include nutrient loading, stream flow alteration, water abstraction, and the introduction of AIS (Brasher 2003; Lisi et al. 2018). AIS densities are strongly influenced by human densities and land cover (Moody et al. 2017).



Watershed	Kalihi (Kl)	Punaluu (Pu)	Waikane (Wk)	Waimea (Wm)	Manoa (Ma)	Keaahala (Ke)	Waihee (Wh)	Kahaluu (Kh)	Waianu (Wn)	Waimanalo (Wl)	Heeia (He)	Halawa (Hl)
N	28	59	30	25	38	101	21	100	26	48	1	19
Non-migrants	23	58	28	11	34	90	15	97	22	40	1	14
Migrants	5	1	2	14	4	11	6	3	4	8	0	5
Poecillid Density	1.428	2.95	2.63	0.001	1.225	4.268	3.406	4.604	9.114	7.153	3.66	13.943
Loricariid Denisty	0.883	0.001	0.0331	0	0.499	2.577	3.628	3.45	0	0.065	5.83	0
*Density: #/m2												

Figure 3-1 Map of stream locations, Awaous stamineus contingent proportions, and invasive species density by stream

Density of *A. stamineus* and AIS

Monthly snorkel surveys were conducted for each stream to estimate densities of *A. stamineus* and the two most abundant AIS families; Poeciliidae, live-bearers (e.g., *Poecilia reticulata, Poecilia sphenops, Xyphophorus helleri*) and Loricariidae, armored catfishes (i.e., *Hypostomus watwata* and *Ancistrus cf. temminickii*). Surveys were completed from September 2015 to March 2017 in 100 m reaches in the middle section of each stream (i.e., not in the headwaters, and not near the mouth of the river). We used a random stratified sampling design in which random numbers were drawn to indicate the position of each of 30 1m^2 quadrats in the 100 m reach. In each quadrat, each species was identified to the lowest taxonomic level possible and enumerated. Densities are reported as #/m^2.

Stream Flow

Daily stream discharge was characterized from October 2015 - October 2016. United States Geological Survey (USGS) monitors continuous daily stream flow at eleven of the twelve study streams (Table 1). Daily discharge for USGS-based streams was downloaded with R package “dataRetrieval” (Hirsh and De Cicco, 2014). For Waianu stream, I gathered discharge records near the river mouth at main stem station Waiahole (16294100) rather than the sub-watershed scale at Waianu. In Keaʻahala, a small groundwater fed stream, water level was monitored hourly using a HOBO U20 water level data logger (Onset Computer Corp. Bourne, MA USA) and was corrected for atmospheric pressure by a logger in the adjacent riparian zone. Daily average water level measurements were used to estimate discharge based on a power function relationship between water level and direct measurements of discharge for Keaʻahala following standard methods (Hauer & Lamberti 2011). To characterize hydrographic patterns in each stream, I calculated the mean, coefficient of variation (CV), and the 95th, 90th, 50th, 10th, and 5th percentiles of discharge over the water year (m^3/sec) (Table 1).

Nutrients

We characterized average inorganic nitrogen and soluble reactive phosphorus concentrations for each stream as a proxy for anthropogenic nutrient pollution (Lisi et al. 2018). Dissolved inorganic nutrients were quantified at approximately monthly intervals from May 2015 through January 2018 in each stream. Samples were taken at or near base flows from streams using syringes, the water was filtered immediately (Whatman GFX; 0.45 µm), and then stored frozen until ready to be analyzed. Thawed samples were simultaneously run for soluble reactive phosphate (SRP, µg/L) and nitrate (NO_3, µg/L) using standard colorimetric methods on an Astoria-Pacific Autoanalyzer II (Clackamas, Oregon, USA). To represent nutrient differences among streams, I calculated the long-term mean SRP and NO_3 concentrations across the full study period.

Collection of *A. stamineus* otoliths

A. stamineus were collected by snorkelers using hand nets and were anesthetized using MS-222. Whole fish samples were stored in polypropylene vial with 95% ethanol. Sagittal otoliths were extracted using forceps and a fine-bristled paintbrush and distilled water were used to remove tissue from the calcareous structure. Otoliths were mounted on a petrographic slide using Crystalbond adhesive resin and stored until further analysis. This sampling was conducted under Animal Use Protocol AUP# 11-15 TAMUCC.

Identifying Migration Behavior

Extracted and mounted otoliths were finely polished with fine-grit diamond coated lapping paper of varying grit sizes (range 60 µm - 0.5 µm) to reveal the growth rings from the primordium to the edge. Otolith trace element chemistry was analyzed to determine migration history (migrant or resident) using Laser Ablation Inductively Coupled Plasma Mass-Spectrometry (LA-ICP-MS) at the Jackson School of Geosciences, University of Texas-Austin. A New Wave Research UP193-FX fast excimer (193 nm wavelength, 4-6 ns pulse width) laser coupled to Agilent 7500ce inductively coupled plasma mass spectrometry (ICP-MS) was used according to Seeley et al. (2015). A laser transect was set to run from the otolith edge (adult stage) to the opposite otolith edge and by bisecting the primordium to establish a palindromic chemical signature (Hogan et al. 2014). Otoliths were pre-ablated to remove any external contaminants prior to data collection (40% power, 10 Hz, 50 µm spot size, 40-50 (µm/s) scan rate, He cell flow of 300 mL/min). Ablations were operated at RF Power 1600 W with an average Ar carrier flow of 1 L/min. Samples were analyzed at 5 µm/s line traverses, using a 25 µm spot at 60% power, 10 Hz repetition rate, and He cell flow of 700 mL/min. Laser energy (fluence) during analytical sessions averaged 3.57 J/cm^2 with < 3.0% variance. Ten analytes ($^{24-25}$Mg, $^{42-43}$Ca, ^{55}Mn, ^{66}Zn, ^{68}Zn, ^{88}Sr, $^{137-138}$Ba, ^{7}Li, ^{208}Pb) were measured using a 25-millisecond integration time. Magnesium, zinc, and manganese were used to help identify areas where the laser crossed the epoxy prior to the otolith material being analyzed. Calcium was measured to identify variations in otolith calcium carbonate topography and for standardizing otolith strontium concentrations. Barium has a higher concentration in freshwater than the ocean and strontium shows the opposite pattern, and both elements can be used to verify which aquatic environment an individual experienced at a given time in the life-history. The analytical sampling period was 0.6512 seconds, which is equivalent to a reading every 7.678 μm and corresponds to 85% measurement time. Intensities of isotopes (counts) were converted to concentration (ppm) using Ioline software using ^{43}Calcium as the internal standard. Baseline gas concentrations of the analytes was determined prior to the analysis of each otolith by taking 30 second gas blank intervals that were measured while the laser was off. USGS MACS-3, a synthetic calcium carbonate standard, was used as the primary reference standard for all analytes. Recoveries (relative 1σ deviations versus GeoREM preferred values) among analytes for secondary standards (NIST612) were run as unknowns against the primary standard. Element concentrations were calculated assuming a concentration of 38.3% Ca (FEBS-1 otolith standard certificate) in the sampled outer calcium carbonate layer. Integrated Sr:Ca ratios were used to determine marine and freshwater habitat use by fish during the larval stage (pre-metamorphosis) and juvenile/adult stage (post-metamorphosis). Fish were considered migrant contingents if the Sr:Ca ratio prior to the metamorphosis mark was greater than 4 mmol/mol, and all other fish were considered residents (Hogan et al. 2014). The proportion of contingents for a stream was determined by evaluating the Sr:Ca signatures of all fish collected from a stream. Residents were assigned a value of 0, and migrant contingents were assigned a value of 1 for statistical analysis.

Population Density of *A. stamineus*

Streams vary in quality and may or may not be suitable for recruiting migrant and residents. Population density of *A. stamineus* was included in the model to assess the suitability of a stream for recruiting post-larvae. Population density was calculated by the total number of observed *A. stamineus* for a watershed divided by the number of snorkel surveys (all watersheds n = 30 except Waianu n = 33).

Analyses

Model Selection

Dredge model selection was performed using R statistical software (version 1.1.456) to identify factors that most strongly influence the proportion on residents in populations of *A. stamineus.* The best model was identified by the lowest model AIC (model fitness curve Supplemental Figure 1). The factors identified in the best model are considered to have the biggest effect on the ratio of migrant and residents within each stream. The independent variables included as main effects in the full model were loricariid density (#/m^2), poeciliid density (#/m^2), daily median stream flow (m^3/sec), stream flow variability (m^3/sec), *A. stamineus* population density for each stream (#/m^2), inorganic nitrate (µg/L), soluble reactive phosphorus (µg/L), to reduce collinearity in the model (Supplemental Figure 2) two interaction terms were included: 1) *A. stamineus* density and loricariid density, and 2) soluble reactive phosphorus concentration (µg/L) and stream flow variability (m^3/sec). Each models AIC and AUC were compared to evaluate the goodness of fit and whether it should be considered for further analysis. One watershed (He‘eia) was excluded from the analysis due to low sample size (n = 1). The total sample size for the analysis was 495 (Figure 1).

Model Analysis

The top three models identified by the dredge were analyzed by a multiple logistic regression with R statistical software (version 1.1.456) (p-value < 0.05 was considered significant). The significance of model terms, overall model significance, AIC, and AUC were compared to identify the best and final model.

Results

Study Site and Species

A total of 496 *A. stamineus* were collected from the twelve O‘ahu streams from August 2015-August 2017. The largest sample size was from Kea‘ahala (Ke, n=101) and the lowest sample size was from He‘eia (He; n=1) (Figure 1).

AIS Densities

Poeciliid density ranged from 0.001 (#/m^2) in Waimea (Wm) to 13.943 (#/m^2) in Halawa (Hl) (Figure 1). There were three streams with either zero or near zero loricariid densities (Waimea, Waianu, and Halawa: 0 #/m^2, Punalu‘u: 0.001 #/m^2), and the highest loricariid density was in Waihe‘e (Wh, 3.628 #/m^2) (Figure 1).

Stream Flow

Median daily flow ranged from 0.064 to 0.331 m^3/sec; and was lowest in Waimanalo and highest in Waimea, and flow variability (CV) ranged from 0.06 to 2.68 m^3/sec in Kea‘ahala and Halawa, respectively (Table 1).

Nutrient Concentrations

Nitrate was lowest in Waimea (9.21 µg/L) and highest in Waimanalo (314.82 µg/L) (Table 2). Soluble reactive phosphorus was lowest in Waimea (4.86 µg/L and highest in Kea‘ahala (35.37 µg/L) (Table 2).

Migration Behavior

Overall, the resident contingent (87%) was the most common among the sampled individuals. Of the streams with robust representation, Punaluʻu (Pu) had the highest proportion (98%; n = 59) of residents of all twelve streams, and Waimea had the lowest proportion (44%; n = 25) of residents (Figure 1).

Table 3-1 Flow and flow variability for 12 watersheds on Oahʻu, Hawaiʻi, including the mean, CV, 95th percentile, 90th percentile, median, 10th percentile and 5th percentile of flow

Sites	USGS site	mean Q	CV	Q95	Q90	Q50	Q10	Q5
Halawa	16226200	0.351	2.68	0.001	0.003	0.078	0.78	1.64
Heʻeia	16275000	0.108	1.99	0.052	0.055	0.068	0.18	0.2
Kahaluʻu	16283200	0.133	1.23	0.066	0.082	0.101	0.16	0.27
Kalihi	16229000	0.262	2.05	0.022	0.026	0.136	0.54	0.99
Keaʻahala	Hobo-U2	0.093	0.06	0.087	0.088	0.092	0.1	0.104
Manoa	16241600	0.599	2.11	0.118	0.121	0.289	1.08	1.79
Punaluʻu	16301050	0.881	0.77	0.513	0.543	0.72	1.16	1.71
Waiahole	16294100	1.286	0.94	0.659	0.715	1.125	1.64	2.14
Waiheʻe	16284200	0.258	1.04	0.173	0.177	0.206	0.32	0.43
Waikane	16294900	0.464	1.69	0.063	0.07	0.305	0.72	1.41
Waimanalo	16249000	0.113	1.74	0.052	0.053	0.064	0.15	0.33
Waimea	16330000	0.738	1.97	0.026	0.041	0.331	1.53	2.53

Table 3-2 Mean nutrient concentrations for 12 watersheds on O‘ahu

Watershed	Inorganic Nitrate (µg/L)	Soluble Reactive Phosphorus (µg/L)
Waimea	9.21	4.86
Punaluu	10.42	12.13
Heeia	38.2	18.71
Kalihi	38.7	9.64
Waianu	41.3	16.36
Halawa	52.49	8.88
Waihee	58.68	23.99
Waikane	60.33	12.69
Manoa	64.62	11.59
Kahaluu	89.39	21.1
Keaahala	126.43	35.37
Waimanalo	314.82	17.4

Analyses

Model Selection

There was no significant effect of loricariid density on resident proportion ($p = 0.57$, Table 3). There were fewer residents when flow variability and poeciliid density was high ($p = 0.033$ and $p = 0.0029$, respectively) (Figure 2). Also, there were fewer residents when flow variability was high and soluble reactive phosphorus was low ($p = 6.64^{-07}$, Figure 3) and at both extremes of the inorganic nitrate concentration spectrum ($p = 0.00018$, Figure 2). When loricariid density was high and *A. stamineus* population density was low, there were fewer residents ($p = 0.0065$, Figure 4). The relationship between resident proportions and SRP concentrations was complex, however, there were slightly more residents at higher concentrations ($p = 0.0028$, Figure 2). Lastly, there were more residents when loricariid and

A. stamineus population density (p = 6.64^{-07}, Figure 3) and SRP at all flow variability levels was high (p = 0.0065, Figure 2 and 4).

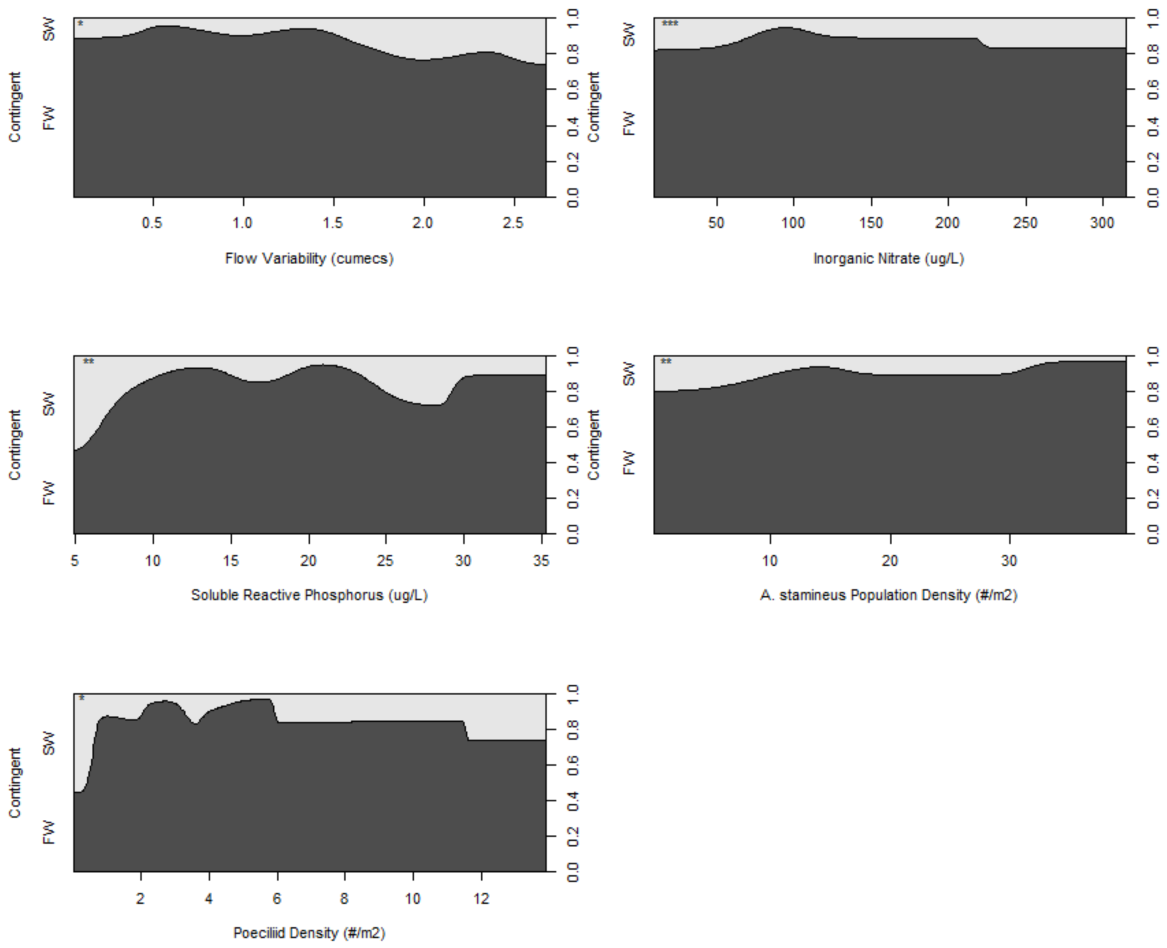


Figure 3-2 Main effects plots for significant variables

Significance indicated: '.' p-value <0.1, '' p-value <0.05, '**' p-value<0.01, '***' p-value<0.001*

Discussion

Several factors have been indicated as threats to the populations of native Hawaiian freshwater fishes including water quality and quantity, and invasive species (Brasher 2003; Lisi et al. 2018). In-stream conditions are expected to have a greater effect on the survival of the early life-stages of resident individuals of this partially migratory species. We aimed to test how the quality and quantity of stream water, and the densities of invasive species affect the population dynamics of the native fish *Awaous stamineus*; particularly how the proportion of residents in populations of *A. stamineus* change in response to these factors. We found that variability in stream flow, densities of invasive poeciliids, loads of key nutrients nitrogen and phosphorus, as well as population density of *A. stamineus* all had significant direct effects on the proportion of residents in those populations. Overall, the proportion of residents was greatest when phosphorus concentrations were high and *A. stamineus* population densities were high. Surprisingly, the densities of invasive loricariid catfishes were also correlated with high phosphorus concentrations and indirectly related to greater resident proportions. Conversely, resident proportions were lowest in streams with high variability in flow and greater densities of the invasive poeciliid predators. Streams with intermediate nitrogen concentrations tended to have greater proportions of residents.

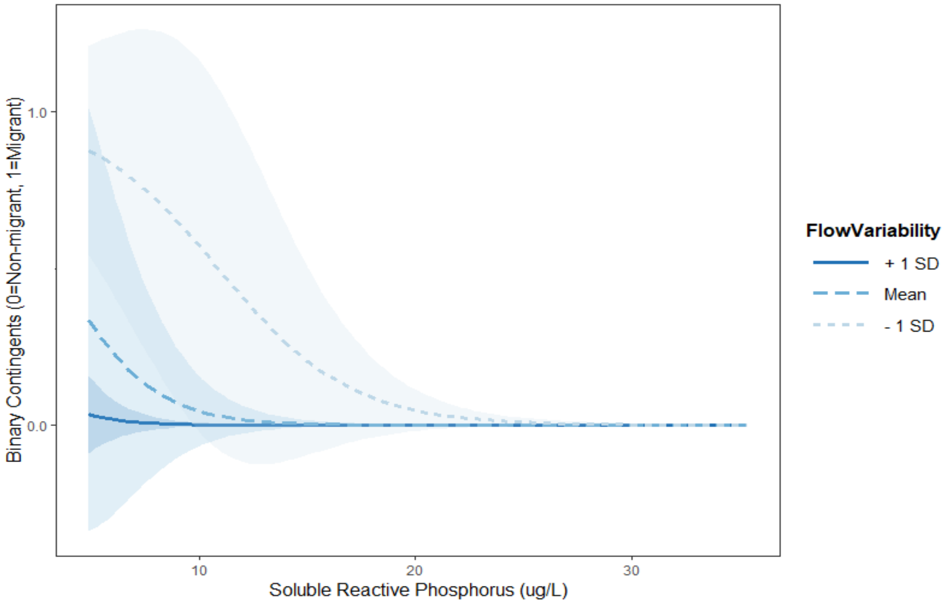


Figure 3-3 Interaction plot between flow variability and soluble reactive phosphorus

Table 3-3 Logistic regression output for best selected model explaining variation in resident proportions among 12 study watersheds

Significance indicated: ‘.’ p-value <0.1, ‘’ p-value <0.05, ‘**’ p-value<0.01, ‘***’ p-value<0.001*

Coefficients	Estimate	Std. Error	Z value	p-value	Relative Contribution (%)	Significance
Intercept	10.248697	3.446396	2.974	0.002942	-	**
Flow Variability	-2.634966	1.185061	-2.223	0.026183	2.896115	*
Poeciliid Density	0.128751	0.060225	2.138	0.032532	3.147698	*
Loricariid Density	0.295555	0.516758	0.572	0.567361	0	ns
Phosphorus	-0.242487	0.081197	-2.986	0.002823	0.381879	**
Nitrate	0.014077	0.003763	3.741	0.000183	10.67714	***
As Population Density	-0.829836	0.270559	-3.067	0.002161	26.46525	**
Flow Variability* Phosphorus	-0.186752	0.037565	-4.971	6.64e-07	40.76633	***
Loricariid Density * As Population Density	0.215804	0.079351	2.720	0.006536	15.66559	**

Our findings suggest that populations of loricariids and *A. stamineus* may be better supported in systems that are more enriched with phosphorus and other nutrients that may co-occur from land-based human activities.

There was no direct significant effect of loricariid density on the proportion of residents; however, the interaction between the *A. stamineus* population density and loricariid density had a significant effect on the proportion of residents in adult populations. Phosphorus is typically a limiting nutrient in freshwater systems (Elser et al. 2007), and low levels of phosphorus may indicate a system is nutrient limited and may not support high densities of residents. Since loricariids sequester phosphorus (Hood et al. 2005), one would expect that high loricariid density would result in decreased phosphorus concentration, however, I saw the opposite in our study; there was high positive collinearity between loricariid density and phosphorus, and there were more residents when both loricariid density and the *A. stamineus* population density was high. (Supplemental Figure 2). Finding excess phosphorus in the study systems with high densities of loricariids indicates that phosphorus must be entering the system faster than it can be sequestered by the catfish (Carlson and Simpson 1996). Phosphorus may be entering streams from effluent and may be accompanied by many other nutrients associated with land-based activities (Ellison and Brett 2006). Nutrients like phosphorus and nitrate may act as a proxy for other terrestrial runoff that can either decrease water quality or stimulate food web production (Ellison and Brett 2006). Additionally, the high and positive correlation between loricariid density and phosphorus (0.69) may indicate that loricariids are disturbing stream banks enough to cause phosphorus to be transported from sediment to the water column; river bank erosion is a primary and natural means of phosphorus entering rivers and streams (Ellison and Brett 2006). Nitrate was positively correlated with phosphorus (0.36), which may indicate the two nutrients, and likely many others, are transported to streams by similar means. Nitrate also had a significant effect on the proportion of residents; there were more residents at intermediate nitrate levels.

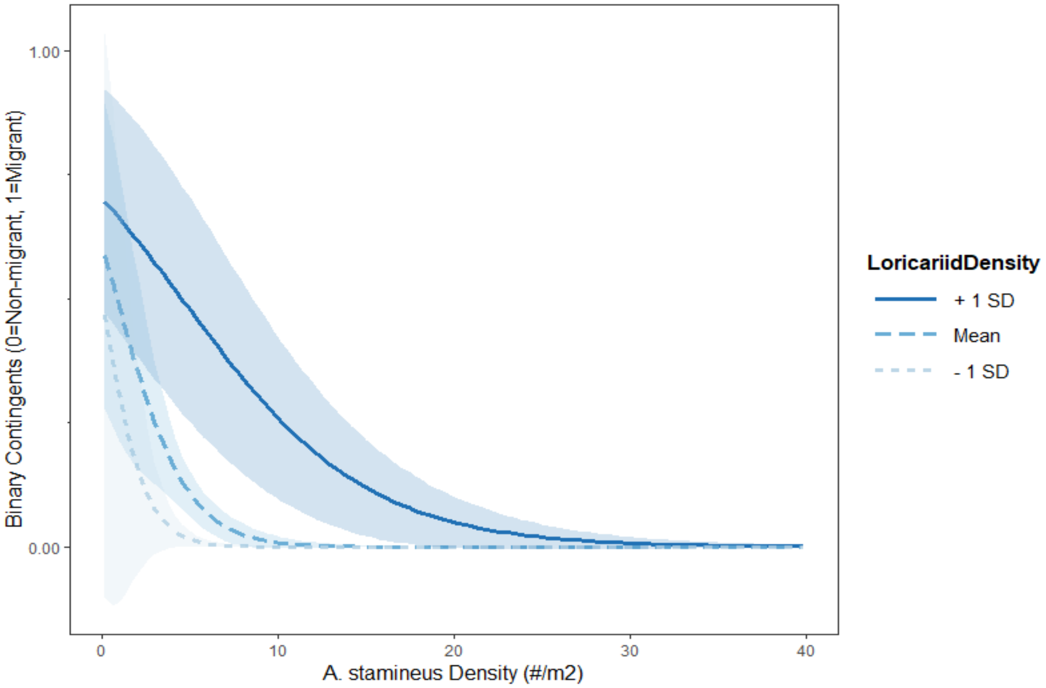


Figure 3-4 Interaction plot between loricariid density and Awaous stamineus population density

In our study, there were more residents when flow variability was low indicating stable flows likely improve in-stream conditions thereby resulting in more surviving resident larvae. Increased water movement has been shown to increase the feeding potential of larvae (Rothschild and Osborn 1988; Sundby and Fossum 1990; MacKenzie et al. 1994), and stable base flows may increase the encounters larvae have with their prey. There was a clear relationship between SRP and flow variability (Supplemental Figure 3), where the concentration of SRP decreased with increasing flow variability. Increased water movement may increase nutrient transport throughout the stream, which may promote primary and secondary producers that act as nutrition sources for larvae (Ellison and Brett 2006). If a stream tends to “dry up” for periods of time (high variability) then the transport or movement of phosphorus within a stream may be limited or reduced (Ellison and Brett 2006). Stable base flows may facilitate the physical movement of larvae and interaction with prey sources may increase, and stable base flows may increase nutrient delivery, which promotes the production of nutrition sources; more residents may survive the larval stage when they have increased access to more abundant prey (Houde 2008). Interestingly, I found that there were more residents regardless of flow variability levels when phosphorus concentrations were intermediate to high indicating that some phosphorus enrichment may increase the productivity of a system.

Our findings showed that the proportion of residents decreased with increasing abundance of poeciliid predators and when stream flow rates were little to none. Poeciliids are known to depredate resident larvae, and high densities of poeciliids could exert high levels of mortality directly on larval residents (Walter et al. 2012). Migrant larvae would also be subject to mortality by poeciliids, but only in the first few hours before they flush out to sea (Lindstrom 1998) and so their abundance will be much less affected by in-stream predation. The flushing of larvae to sea is promoted by greater stream flows and steeper stream slopes (Huey et al. 2014), which decreases the number of resident larvae that are able to recruit to adult populations. In our study, I found that there were fewer residents when flow variability was high. All streams experience punctuated periods of flooding that are of similar magnitude and duration. Flow variability is driven more by periods of intermediate to low flow rates with some streams nearly going dry for periods of time and others maintain good base flows year-round (https://waterdata.usgs.gov/nwis/rt, Table 1); that is, high flow variability is characterized by periods of major flooding accompanied by periods of really low base flow, and low flow variability is characterized by periods of major flooding accompanied by periods of intermediate to high base flows. In this study, flow variability may contribute to the starvation and loss of resident larvae. The overall proportion of residents was lower when flow variability was high, indicating that dry events may increase larval mortality of residents. Habitat may be lost from the drying up of streams, which may result in desiccation. Additionally, streams with high flow variability may have reduced nutrient transport, which may increase stress, starvation, and larval mortality of residents from limited nutrition sources and/or limited access to those sources. Additionally, drying tends to cause water to pool, concentrating high densities of in-stream residents including predatory poeciliids; this may increase predation rate on non-migratory larvae. Dewatering of streams and other water abstraction processes could clearly have implications on lowering the abundance of non-native migrants within these systems.

The interaction between physical and biological processes ultimately contribute to mortality and recruitment success (Houde 2008), and “quality” habitats generally support higher densities of natives with higher proportions of non-migrants. Our results suggest that the multiple points of anthropogenic activities affect the mortality of pre-recruit residents. That is, certain AIS may negatively impact larvae, too high or too low nutrient concentration may increase larval mortality, and the disruption of normal base flows can decrease stream habitat and nutrient delivery, which may cause larvae to desiccate or have limited interaction with prey during a critical period of the larval stage. The resident type appears to be the most dominant recruitment type for these populations (Hogan et al. 2014, This Chapter); this may be due to the high and variable rates of mortality for ocean-going migrants (Heim-Ballew Chapter 4). Thus, the dynamics of these stream populations will be strongly impacted by factors that lead to decreases in resident recruitment. These findings indicate that restoration and proper management of streams should be a top priority for the conservation of Hawaiian freshwater fishes since native fishes are susceptible to larval losses when faced with stressors and pressures that come directly from human activities. In these systems, it will be important to stabilize base flows whenever possible and ensure that essential nutrients are balanced within streams, avoiding excesses of nitrogen. Additionally, the introduction of invasive species in these systems must be prohibited, and there should be proper management on those that already inhabit these freshwater systems and exert additional pressure on native fishes. A holistic management approach will be necessary to restore degraded systems; both unnatural physical and biological additions to freshwater ecosystems must be mitigated and managed in concert to restore systems to more natural-like conditions in order to promote long term persistence of these species. There are many island systems under similar anthropogenic pressures as Hawaii with threatened native species. It will be important to assess the responses of species with similar life-history strategies that vary spatially to better understand if the responses I saw in this study are consistent to provide insight on the potential for broad-scale management for sensitive species.

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CHAPTER 4: CLIMATIC VARIATION INFLUENCES RECRUITMENT SUCCESS AND GROWTH OF DIFFERENT LIFE-HISTORIES IN A FACULTATIVELY MIGRATORY HAWAIIAN FISH

Abstract

Climate cycles modify environments throughout the world through atmospheric teleconnections. The El Niño Southern Oscillation (ENSO) is known to influence sea surface temperature and air pressure, and the freshwater budget at many locations. Many studies have examined the responses of freshwater and marine species to El Niño and La Niña; however, few studies have evaluated the responses of multiple life-history strategies within the same species to ENSO. In this study, I determined the proportion of migrants and residents within populations of a migratory freshwater fish, *Awaous stamineus*, and how those proportions changed across the Multivariate El Niño Index to identify relative recruitment success. I estimated growth rate at three important life-history stages to identify how growth responds to ENSO. Lastly, I examined if the duration of the larval stage differs between life-histories across ENSO episodes. Overall there were more residents across all populations; however, there was an increased proportion of migrants during La Niña and very strong El Niño episodes, and an increased proportion of residents during moderate to strong El Niño episodes. Growth rates of migrant individuals were higher than that of residents in general. Early larval growth rates of migrants was elevated during El Niño periods likely corresponding to an increase in sea surface temperature and metabolic activity. During La Niña periods, migrant individuals tended to grow faster just before settlement; this may be a result of increased coastal upwelling during La Niña driving greater primary production, that make prey sources more abundant for late-larval stage individuals. Resident growth rates were

fastest in the early larval stage during neutral episodes, which may indicate that freshwater habitats are optimal for larval growth during moderate conditions. Immediately before metamorphosis, resident growth rates were lowest during El Niño episodes, indicating that this is a stressful condition for in-stream larvae. For both life-histories, La Niña led to a prolonged period of early-fast larval growth, which resulted in shorter larval durations during La Niña. These results indicate that the differential survival of contingents is dependent on success and survival during the larval stage, which is affected by the influence of ENSO on marine and freshwater habitats. La Niña conditions may provide ideal ocean conditions for marine migrant larvae to survive and recruit. As El Niño progresses, ocean conditions become harsher for marine larvae and reduced stream flow due to reduced rainfall can retain more larvae in-stream. In extreme El Niño conditions, severe drought can cause resident larvae to be exposed to crowding, thermal stress, and increased predation. Since residents are the dominant recruits to these populations, it will be important to restore and conserve freshwater habitats to ensure the health of these populations.

Introduction

Variation in climate can influence the dynamics of fish populations through a variety of pathways at a multitude of spatial and temporal scales (Otterson et al. 2010). Broad-scale changes in the ocean and atmosphere influence climatic conditions around the world, known as teleconnections (Gillson 2011), and these changes can influence ecosystems and species over a large geographic span (Gillson 2011). The El Niño Southern Oscillation (ENSO) is a natural oceanic-atmospheric process, originating in the equatorial Pacific (Trenberth 1997), that occurs cyclically every 2-6 years (Chu and Chen 2005), and it influences global climate variability between seasons and years (Wolter and Timlin 2011; Chiew et al. 1998). During the warm phase (El Niño), sea level pressure decreases from decreased atmospheric pressure, easterly trade winds slacken, oceanic temperatures increase, and upwelling decreases, and during the cool phase (La Niña) sea level pressure increases, easterly trade winds intensify, oceanic temperatures are below average, and coastal upwelling increases (Oki 2004). These large-scale teleconnections have strong influences on fish populations in both marine and freshwater ecosystems (Ottersen et al. 2010).

Ecological processes, such as migration, recruitment, growth, mortality, and dispersal are influenced by physical dynamics (Ottersen et al. 2010, Houde 2008; see Table 1). For example, temperature can affect physiology, metabolic activity, behavior, and growth of larvae (Houde 2008), and nutrient availability that promotes primary production is linked to feeding opportunities for larval fish (Lasker 1978, 1981). Starvation, and predation risk are important for recruitment success to adult populations (Cushing 1974, 1990; Houde 1987; Cushing 1990; Kerr and Dickie 2001; Houde 2008). Prey of larval fish often form aggregations that are heterogeneously distributed throughout the water column, and unless larvae encounter and effectively capture prey, they are subject to high rates of mortality during critical periods of the larval stage during which the likelihood of survival decreases (Hjort 1914, 1926; Cushing 1973; Houde 2008). The interplay between physical and biological processes influence larval mortality and recruitment to breeding populations (Nishimoto et al. 1997; Hamilton et al. 2008; Grorud-Colvert and Sponaugle 2011) and since both factors are influenced by climate, it is important to understand how populations respond to variations in climate.

Different systems will respond differently to changing climate, localized conditions may affect the survival and recruitment rates of larvae due to their differential exposures. Newly hatched larvae may be passively displaced downstream to the marine environment (Iguchi and Mizuno 1991), and flow conditions may influence larval movement within the freshwater system (Brasher 2003). Conversely, a reduction in flow or high flow variability may impede the movement of individuals within a stream or coastal environment; freshwater fishes may desiccate when base flows are low or non-existent (Brasher 2003). Marine larvae must manage salinity and temperature changes, find adequate food resources, while subjected to advective processes (Iguchi and Mizuno 1999; Ottersen et al. 2010). Subsequently, the factors that impact the ability of larvae to recruit, whether in freshwater or the ocean, influence adult population size and composition (McDowall 2007b; Walter et al. 2012). Previous studies have evaluated how freshwater and marine species respond to variation in climate, particularly, ENSO; however, there are few studies that have evaluated the responses of different life histories to ENSO within a species with life-history flexibility. The goal of this study is to evaluate migration and growth responses across the ENSO cycle to identify if responses differed between migrants and residents of a partially migratory species with individuals that live in either freshwater or marine environments during the larval stage and rejoin as juveniles in stream populations.

Change in climate, like those caused by ENSO, can have a substantial effect on freshwater ecosystems and population dynamics of species (Walter et al. 2012). It is well documented that ENSO is related to precipitation patterns around the world (Rasmusson and Wallace 1983), especially in the tropics and southern hemisphere (Ropelewski and Halpert 1986). El Niño and La Niña modify localized precipitation patterns (Mosley 2000; Cole et al.

2002); some regions of the world receive monsoon-like rains (Kripalani and Kulkarni 1997), while others have a decreased freshwater budget (Ropelewski and Halpert 1986). In the southern hemisphere, El Niño increases precipitation and La Niña is associated with drought (Garcia et al. 2001). In the tropics, early stages of El Niño increase precipitation to freshwater systems, however, as El Niño progresses drought sets in during the winter and can last up to a year after the event (Oki 2004). Typically, La Niña episodes result in an overall increase in freshwater input to freshwater ecosystems (Oki 2004).

Changes to stream flow can influence the fish that inhabit those streams (Walter et al. 2012; Lisi et al. 2018). Localized changes in rainfall can alter habitat quality or quantity for organisms in riverine environments (Gillson 2011; Walter et al. 2012). During times when freshwater input is increased, and stream flow is high, there is an increase in riverine habitat and food (Goulding 1980; Rypel 2009). There is a strong relationship with rainfall and terrestrial primary production (Murphy 1975) but rainfall increases aquatic volume and provides more refugia for prey, so more energy is required to find prey (Rypel 2009). Conversely, drought can influence spawning, feeding, growth, and other population dynamics (Matthews 1998; Ficke 2007). A decrease in stream water volume associated with drought causes increased predation from crowding (Rypel 2009). Desiccation leads to increased temperature, thermal oscillations, evapotranspiration, and oxygen depletion from decreased stream flow and leaf litter decay (Jacobs 1992; Mol et al. 2000), which causes increased mortality of freshwater fishes from biological stress and decreased prey abundance (Mol et al. 1993b; Mol et al. 2000). Shrinking of riverine habitat can limit access to spawning grounds; a decrease in reproductive success and even failure of reproduction during El Niño drought has been reported for freshwater fishes in South America (Mol et al. 2000). A previous study indicates the growth of freshwater fishes is highest during warm and dry ENSO episodes, and growth is lowest during cold wet ENSO episodes (Rypel 2009). Freshwater fish must have adequate in-stream connectivity to find optimal thermal strata, prey sources, refugia, and spawning grounds, and drought can limit movement between habitats (Matthews 1998; Ficke 2007).

Characteristics of the ocean change in response to ENSO phases, primarily through changes in sea surface temperature and wind stress (Chu and Chen 2005); however, freshwater processes at the interface of the coastal nearshore are influential to marine fishes (Garcia et al. 2001). Increased freshwater inflow during La Niña events can cause plumes of chlorophyll a in nearshore coastal environments, which spark primary production and bottom-up processes (Signorini et al. 1999). If larvae are able to remain in nearshore environments during periods of high productivity growth, survival, and therefore recruitment of marine larvae may increase (Day et al. 1989; Kennish 1990; Santos and Bianchini 1996). During El Niño, decreased coastal upwelling and an increase in sea-surface temperature causes a more stratified water column with pronounced thermoclines (Liu et al. 1995; Xie et al. 2001; Chavez et al. 2002; Chu and Chen 2005). If marine larvae are transported away from coastal zones, these larvae may be constrained to warm upper strata and may experience temperature and salinity stress (Sanchez-Velaso et al. 2000). During El Niño, marine prey regimes shift with less diverse phyto- and zooplankton communities, and there is a reduction prey abundance due to decreased upwelling.

Changes in prey abundance and diversity can influence larval mortality if appropriate prey availability is misaligned with critical periods for larval feeding (Barber and Chavez 1983; Ottersen et al. 2010). A reduction in prey (Barber and Chavez 1983) can result in fish prolonging the larval stage to reach the metabolic thresholds required for metamorphosis (Houde 1987; McCormick and Molony 1992; Sponaugle and Cowen 1997), and/or increased mortality of larvae. The risk of predation is inversely related to body size (Peterson and Wroblewski 1984; McGurk 1986; Cowan et al. 1996), so if growth is slowed and the larval stage is prolonged, so is the period of high predation pressure, which can reduce recruitment success (Houde 2008). Reduced recruitment of marine species during El Niño is associated with decreased prey availability caused by reduced primary production (Lu et al. 1998). However, previous studies indicate warmer waters cause shorter incubation periods, increased growth rates, shorter larval duration, and higher swimming abilities earlier in the larval stage (Pearce and Hutchins 2009), which may be advantageous to larvae if there is adequate access to appropriate food resources (McLeod et al. 2013). Additionally, change in currents during El Niño may cause greater advection than during normal conditions, which can increase the chances of loss mortality (Barber and Chavez 1983). For species that can migrate between marine and freshwater environments, the effects of ENSO on both systems is important for the growth and recruitment of individuals to populations. For species that exhibit distinct migratory life-histories, such as partially migratory species, the differential effects of ENSO on marine and freshwater ecosystems can differentially affect the growth and recruitment of migrants and residents.

The Hawaiian system offers a unique opportunity to examine recruitment dynamics in response to large-scale climatic drivers of individuals within a species that encounter different early life environments. There are five extant Hawaiian freshwater fishes, and all are endemic and exhibit amphidromy (McDowall 2007b; McDowall 2003). Adults spawn in freshwater and larvae can be displaced downstream to the sea where they will spend the larval stage and will return to the stream at the time of metamorphosis (Hogan et al. 2014). Most of the Hawaiian fishes exhibit partial migration with migrant and resident contingents in each population. This system provides an opportunity to examine how ENSO differentially impacts the growth and recruitment of different life-history variants within a species.

One Hawaiian freshwater species, *Awaous stamineus* (Eydoux & Souleyet, 1850), exhibits partial migration (Hogan et al. 2014), a common bet-hedging strategy (Chapman 2011) that buffers the risks associated with migrating or remaining resident (Chapman et al. 2012). The representation of migrant and resident forms across Hawaiian populations varies (Hogan et al. 2014), and the factors that influence this differential representation has largely been unexplored. For species with life-history flexibility, recruitment success is dependent on localized conditions in the larval habitat (McDowall 2007a). For example, residents of diadromous fish species are controlled by the conditions in the natal habitat while migrants experience risks through the migratory corridor and in the immigration habitat (McIntyre et al. 2016). These conditions can be vastly different, especially for species that move between two distinct aquatic biomes (i.e., freshwater streams to the ocean), and as such, these contingencies will be represented differently in adult populations based on larval mortality and recruitment success (Houde 1987; McDowall 2007b). Habitat quality and the abiotic environment are large contributors to the survival of migratory contingents (migrants or residents) (Taylor and Norris 2007; Huey et al. 2014; Watanabe et al. 2014). A modification of larval habitat can lead to differential representation of contingents within populations (Walter et al. 2012). In similar systems, streams with higher stream flow have shown a higher representation of migrants (Huey et al. 2014; Kerr and Secor 2010), and those streams subject to drought or dry conditions had fewer migrants (Kerr and Secor 2010). In Hawaiʻi, the representation of native freshwater fishes is in part driven by stream flow variability, where there are more residents in adult populations when stream flow is stable and high and there are more migrants during drier conditions.

Our first goal of this study was to examine the differential representation of the two contingent types (migrant and resident) in populations across the Hawaiian archipelago with respect to the phases of ENSO. Since flexible species experience different larval habitats under different conditions, I next examined if there were differences in growth between the two contingents with respect to ENSO phases during three important stages of the life-history; the early-larval stage, the pre-settlement stage, and early post-settlement. The early larval stage has been shown to be a period of fast growth that varies in duration (hereafter referred to as early fast growth stage or EFG) (Hogan et al. 2017), and this period corresponds to a critical period when larvae must find appropriate prey resources to avoid starvation (Hjort 1914, 1926; Cushing 1973; Houde 2008). Metamorphosis is a stressful period in the life-history when many morphological and physiological changes occur, often accompanied by a change in habitat, and organisms are sensitive to changes in environmental conditions (Barton 2002). Larval mortality tends to be high immediately post-settlement (Hixon & Beets 1993) and growth is known to stabilize (Houde 1987); partially migratory species reunite in the same environment. Lastly, I examined if the duration of the early fast-growing (EFG) period and larval duration were different between the contingent types across the ENSO phases. I expected there to be more migrants during La Niña, because migrant larvae may be better able to cue to stream mouths from additional discharge at the time of recruitment, and because intensified upwelling increases prey abundance and trophic interactions in the ocean.

Increased prey abundance during La Niña should lead to increased growth rates, and since larval growth would not be limited by food availability, I expected marine migrant EFG to be longest during La Niña. A prolonged period of early fast growth would help progress larvae through the larval stage faster resulting in a shorter larval duration. Conversely, I expected migrant growth rates to be higher during El Niño from increased metabolic activity from increased sea surface temperature. Decreased prey abundance would result in a shorter EFG duration, and a decrease in wind stress associated with El Niño would further limit larvae from interacting with prey; therefore, lack of access to prey would shorten the fast-growing period because of prey limitations. I expected the larval duration of migrants would be longer during El Niño because of a decrease in appropriate prey, a decrease in prey interaction from decreased wind stress and micro-movements, and the need to prolong the larval stage to reach the biological requirements for transitioning through metamorphosis. I expected migrant growth rates to be higher than residents, since migrants can access a wider variety of prey species in the ocean than in streams, and because ocean temperatures are warmer around Hawaiʻi than stream temperatures (Hogan et al. 2014). I expected there to be fewer residents during El Niño due to a decreased freshwater budget that limits in-stream connectivity and the ability to interact with prey and desiccation may occur. I expected resident growth rates would be highest during Neutral conditions because of heightened stress during both El Niño and La Niña. For the same reasons, I expected resident EFG to be shortest during El Niño; a shortened EFG would lead to a prolonged larval duration. Conversely, La Niña might cause fewer overall residents since increased precipitation associated with La Niña could increase stream flow and larvae would be more likely flushed to sea rather than retained in-stream. Resident larval duration is expected to be shortest during moderate La Niña with moderate levels of freshwater input; this would allow for increased nutrient delivery, which would spark primary production making food more available and accessible. Under these conditions, residents would grow faster and move through the larval stage quicker.

Methods

Study Site and Species Collection and Preparation Methods

Awaous stamineus were collected as part of two separate projects in Hawaiʻi, Project Part 1 during 2009 and 2011, and Hawaiʻi Project Part 2 from 2015 to 2017. Fish were hand-netted out of streams and humanely euthanized before sagittal otoliths were extracted and prepared in the laboratory. After preparation, otoliths were imaged, and microstructure was analyzed to estimate hatch and settlement dates and growth rates during three stages of the life-history (described below). Each otolith was subject to two independent reads and only those with measurements with less than 5% variation were included for analysis. Detailed methods for Hawaiʻi Project Part 1 can be found in Chapter 2 and Hawaiʻi Project Part 2 in Chapter 3.

Hatch Date Estimation

Imaged otoliths were used to count the daily growth increments from the edge of the otolith to the primordium to estimate the age of the fish in days. Back-calculation was performed with the date of capture less the total number of days to estimate hatch date. Once an individual was assigned as migrant or resident and a hatch date was estimated, a corresponding ENSO index value was assigned. The ENSO index value assigned to each individual was based on historical Multivariate El Niño Index (MEI) values (http://www.noaa.esrl.noaa.gov/psd/people/klaus.wolter/MEI/), which is a seasonally adjusted principal component index on a bi-monthly sliding scale that utilizes six major atmospheric and oceanic components (sea-level pressure, zonal and meridional components of the surface wind, sea surface temperature, surface air temperature, and sky cloudiness fraction) to accurately detect the signal and intensity of the oceanic-atmospheric phenomenon of ENSO (Wolter and Timlin 1993; Wolter and Timlin 2011). The MEI index is considered the most superior of the indices used to identify an ENSO event and its intensity (Wolter and Timlin 2011; Mazzarella et al. 2012). Since the MEI is on a bi-monthly sliding scale, a hatch date with monthly days between 1 and 15 were assigned to the MEI value when a month was first reported, and a hatch date with monthly days between 16 and 31 were assigned to the MEI value when a month was reported second (Supplemental Table 3). A La Niña event is indicated when an MEI value is at or below -0.5, an El Niño event is indicated with an MEI value is at or above 0.5, and Neutral conditions are at MEI values in between a La Niña and El Niño categorization (http://www.noaa.esrl.noaa.gov/psd/MEI/). The intensity of an ENSO event can be identified by the distance of an observed MEI value from the starting value for an ENSO phase event. For example, El Niño can be broken down into weak (0.5 to 0.9), moderate (1.0 to 1.4), strong (1.5 to 2.0), and very strong (>2.0). The intensity of La Niña has similar categories, only intensity is described by decreasing MEI values from -0.5 (http://www.noaa.esrl.noaa.gov/psd/MEI/). Since individuals were collected from two different projects that spanned two discontinuous timeframes, each dataset was analyzed separately. Additionally, the samples from the second project were collected over a span of time when El Niño dominated and La Niña events were underrepresented. By evaluating both datasets separately, the effects of "normal ENSO episodes" (Project 1 timeframe) and the most intense ENSO on record (Project 2 timeframe) (http://www.noaa.esrl.noaa.gov/psd/MEI/) on the differential representation of the two contingents can be assessed. The effect of MEI (fixed explanatory factor) on migration rate (binary response factor of migrant or resident) was analyzed with a binomial GLM with individual as a random block factor (RStudio). Significance was determined at alpha = 0.05.

Identifying Migration Behavior

Otolith Microchemistry Methods

After microstructure analysis, all otoliths were analyzed using Laser Ablation Inductively Coupled Plasma Mass-Spectrometry (LA-ICP-MS) to identify if individuals made marine migrations during the larval stage. Individuals were assigned as a migrant if otolith core chemistry exceeded the freshwater edge chemistry and was sustained across the larval period using previous microchemical research on this species as a baseline (Hogan et al. 2014, 2017). Detailed methods for Hawaiʻi Project Part 1 can be found in Chapter 2 and Hawaiʻi Project Part 2 in Chapter 3.

Growth Rate Estimation

If a strong relationship exists between otolith size and the body size of a fish, it can be inferred that otolith growth is related to somatic growth (Campana 1999). To determine this relationship, imaged otoliths were used to measure the otolith radius from the primordium to the edge of the otolith, and this was used as the response factor in a simple linear regression with body size at capture as an explanatory factor. Similarly, otolith radius was used as the response factor to examine the relationship with age. The adjusted R^2 was used to determine the strength of the relationship and whether the otolith grows in parallel with somatic growth.

Otolith relationship analyses were done in RStudio using alpha 0.05 as the threshold for significance.

Growth rates were determined for three distinct life-history phases of both migrant and resident contingents: larval early fast-growing period (EFG), pre-settlement (migrant contingents)/pre-metamorphosis (resident contingents) (S), post-settlement (migrant contingents)/post metamorphosis (resident contingents) (PS). The EFG growth rates were estimated using a diminishing growth curve of larval stage growth rates. The EFG was considered the time in the early larval stage in which growth rates exceeded larval stage mean growth rate (Hogan et al. 2017) (Supplemental Figure 2). The EFG growth rate was the quotient of the distance of the EFG period on the otolith and the corresponding number of days. The pre-settlement/pre-metamorphosis period was considered the 30 days prior to settlement/metamorphosis. Pre-settlement growth rate was the quotient of the distance of the pre-settlement/metamorphosis period and the corresponding number of days (30). The post-settlement period was considered the 30 days after settlement/metamorphosis. The post-settlement growth rate was the quotient of the distance of the post-settlement period and the corresponding number of days (30).

First, I compared the growth rates between the two contingent types (migrant and resident) to determine if they differed. This analysis was completed using a binomial GLM with migratory type as the response factor, growth rate as a fixed factor, and individual as a random block factor in RStudio. The AIC of a null model without the random block factor was compared to the AIC of the full model with the random block factor (Mazerolle 2017, RStudio) and the variance contribution of the random block factor was considered to determine if the random block factor should be included in subsequent model analysis. A minimization of AIC was used to determine which model, null without block factor and full with block factor, was superior. If growth rates differed between the two contingencies, the growth rates of each were analyzed separately with respect to growing stages (i.e., EFG, S, PS) and climatic phase (El Niño: ≥ 0.5; La Niña: < -0.5; Neutral: -0.4 – 0.4 MEI). This analysis type was completed for all pairwise comparisons for each contingent. Additionally, the growth rates for a contingent type within a distinct growing stage across the three climatic phases were analyzed to identify if there were any differences in growth rates within a single growing stage between climatic events (i.e. Resident El Niño EFG). All pairwise comparisons were completed with one-way ANOVA with Tukey HSD post-hoc with Westfall adjustment for balanced data and Shaffer adjustment for unbalanced data in RStudio. Significance was determined at alpha less than 0.05.

EFG Duration Estimation

The duration of the EFG was determined using the previously described larval stage diminishing growth curve (Supplemental Figure 2). The EFG was the number of days in which early larval stage growth rate exceeded the mean (Hogan et al. 2017). The duration of the EFG (response factor) was compared between the contingents (explanatory factor) and across the three climatic phases (explanatory factor) using ANOVA and Tukey HSD post-hoc with Westfall adjustment for balanced data and Shaffer adjustment for unbalanced data in RStudio. Significance was determined at alpha less than 0.05.

Larval Duration Estimation

To estimate the duration of the larval stage (LD), the daily growth bands were counted from the primordium to the settlement mark. The duration of the larval stage (response factor) was compared between the contingents (explanatory factor) and across the three climatic phases (explanatory factor) using ANOVA and Tukey HSD post-hoc with Westfall adjustment for balanced data and Shaffer adjustment for unbalanced data in RStudio. Significance was determined at alpha less than 0.05.

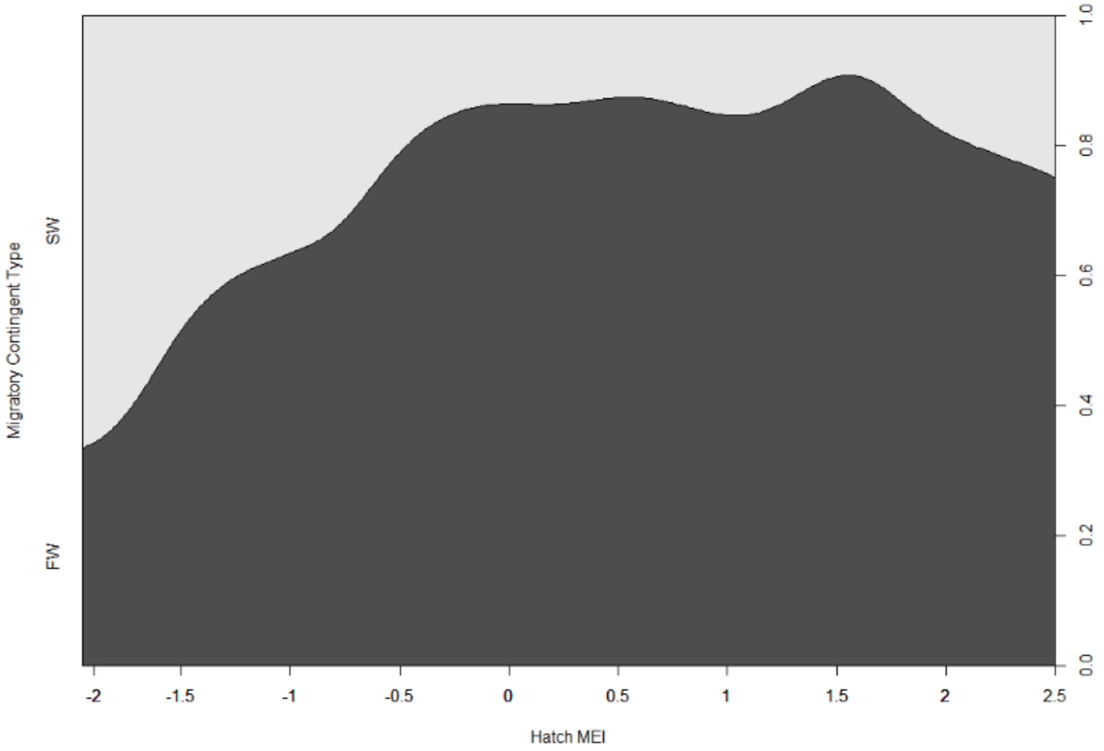

Figure 4-1 Proportion of Awaous stamineus migrant and resident types across the Multivariate El Niño Index (MEI) values for hatch dates

Results

Larval Hatching and ENSO Index

Hatch dates of fish from Project Part 1 ranged from October 10, 2002 to August 28, 2010 (hatch dates, n=250), which crossed strong La Niña (-1.5 – -1.9 MEI) and strong El Niño (1.5 – 1.9 MEI) events. When individuals hatched during La Niña, there were less resident contingents in adult stream populations, and when individuals hatched during El Niño there were more resident contingents ($p < 0.001$) (Fig. 1, Table 2).

Hatch dates of fish from Project Part 2 ranged from August 5, 2014 to November 6, 2017 (hatch dates, n=496), which crossed weak La Niña (-0.5 – -0.9 MEI) and very strong El Niño (≥ 2.0 MEI) events. During weak La Niña to strong El Niño, resident contingents nearly dominated the adult stream populations; however, during very strong El Niño events, there were fewer resident contingents ($p < 0.001$) (Fig. 1, Table 2).

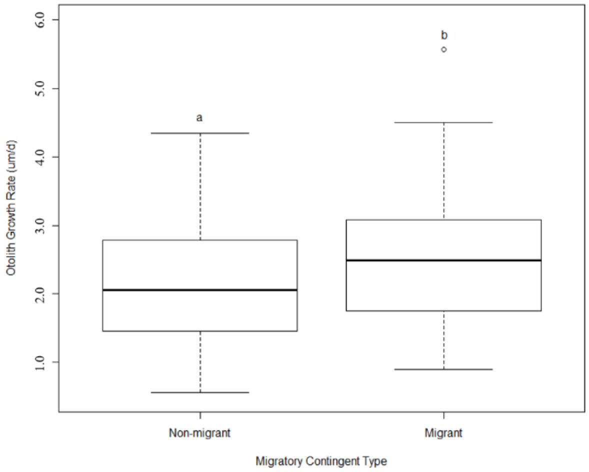

Figure 4-2 Otolith growth rates for resident and migrant contingents of Awaous stamineus; similar letters indicate no significant difference at alpha = 0.05

Growth Rate and Migratory Type

I found tightly coupled relationships between otolith size and age (Resident: $p < 2^{-16}$, $R^2 = 0.8247$; Migrant: $p = 4.58^{-13}$, $R^2 = 0.9273$) and body length (Resident: $p = 1.52^{-08}$, $R^2 = 0.4013$; Migrant: $p = 2.82^{-08}$, $R^2 = 0.7827$) (Supplemental Figures 3 and 4 and Supplemental Tables 1 and 2, respectively) making it possible to make inferences about somatic growth using otolith growth rates.

Table 4-1 Dominant Mechanisms of Larval Mortality; FW=Residents, SW=Marine Migrants

Mechanism	**Control**	**Hypothesis**	**Type Affected**
Predation	Predation rates inversely related to size; slow growing and smaller fish vulnerable to predation for a longer duration	Stage Duration (Houde 1987 and Cushing 1990); Size-Spectrum Theory (Kerr and Dickie 2001)	FW and SW
Prey and Nutritional Deficiencies	Ability to find and effectively capture nutrition sources	Match-Mismatch (Cushing 1974, 1990); Critical Period (Hjort 1914, 1926); Micro-turbulence (Rothschild and Osborn 1988)	FW and SW
Temperature	Physiology, Metabolic Activity, Behavior, and Growth (Houde 2008)		FW and SW
Physical Processes	Advective loss, retention, and transport of larvae by hydrographic variability (Houde 2008); water quality disturbances (more extreme in shallow waters) can enhance mortality or influence movement (Breitburg 1992)	Triangle of Migration (Harden-Jones 1968; Cushing 1975); Abberant Drift (Hjort 1914, 1923); Stable Ocean (Lasker 1978, 1981); Retention Hypothesis (Illes and Sinclair 1982 and Sinclair 1988); Optimum Environmental Window (Cury and Roy 1989 and Roy et al. 1992)	FW
	Advective loss, retention, and transport of larvae by circulation and frontal features and hydrographic variability (Houde 2008); Upwelling temporarily stratifies the water where larvae aggregate for increased feeding opportunities; Recruitment levels are dome shaped with moderate stress promoting foraging success and controlling losses.	Triangle of Migration (Harden-Jones 1968; Cushing 1975); Abberant Drift (Hjort 1914, 1923); Stable Ocean (Lasker 1978, 1981); Retention Hypothesis (Illes and Sinclair 1982 and Sinclair 1988); Optimum Environmental Window (Cury and Roy 1989 and Roy et al. 1992)	SW

Migrant growth rates were generally significantly higher than that of residents (Fig. 2, Table 3). Settlement and post-settlement growth rates of migrants were significantly higher than that of residents during La Niña ($p < 0.01$, Fig. 3, Table 3) and El Niño episodes ($p \leq 0.05$, Fig. 3, Table 3). Additionally, EFG growth rates were higher for migrants during El

Niño (p ≤ 0.05, Fig. 3, Table 3). During Neutral conditions, there were no significant differences in growth rates between the two contingent types (p > 0.1, Fig. 3, Table 3).

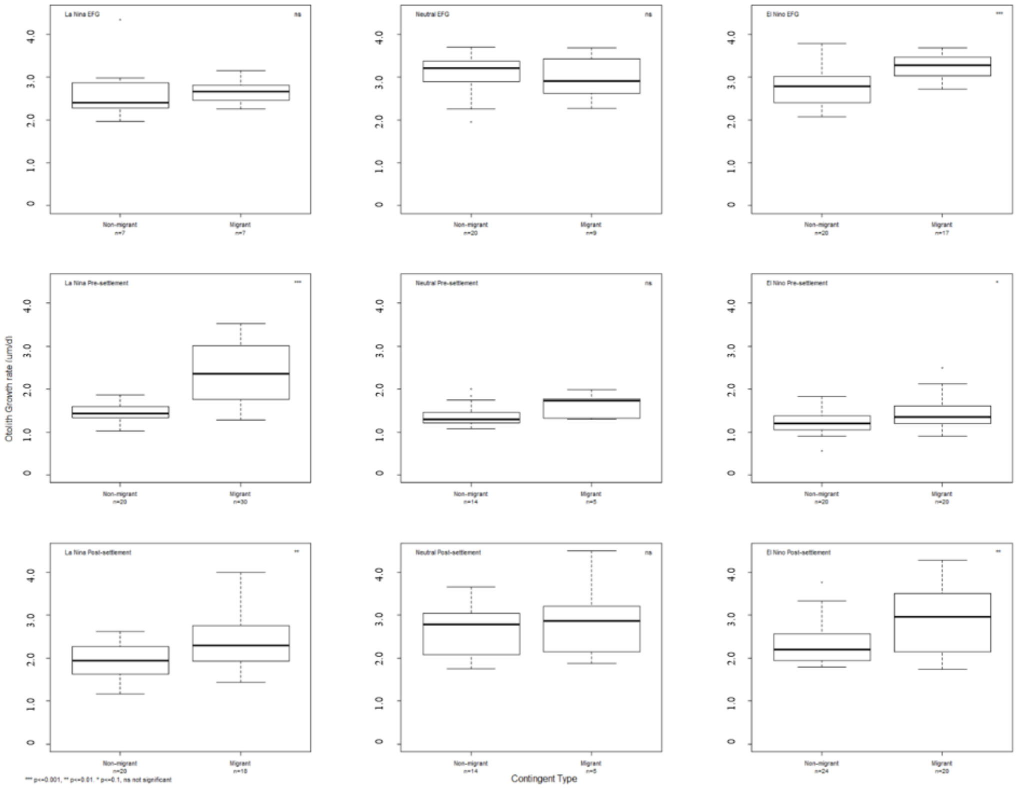

*Figure 4-3 Otolith growth rates for resident and migrant contingents of Awaous stamineus by ENSO phase and growing stage; ‘*** p < 0.001’, ‘**p ≤ 0.01’, ‘* p ≤ 0.1’, ns = not significant’*

Growth Rate and Life-history Stage and Climate Phase

For migrant and resident fish, the EFG period was the period of fastest growth during the life-span (Fig 4 & 5; Table 4). This was followed invariably, by a period of very slow growth in the late larval period just prior to settlement (S) (Fig 4 & 5; Table 4). Growth then increased again post-settlement but never typically reached the rate of EFG growth (Figure 4 & 5; Table 4). These patterns generally held true regardless of ENSO phase; however, migrant fish that hatched during La Niña climate periods had no significant difference in growth rate across the life-history stages (Fig 5; Table 4). Growth rates of residents during the EFG was fastest during Neutral conditions, the slowest growth rates pre-settlement was during El Niño, and growth rates were slowest post-settlement during La Niña (Figure 6; Table 5). Growth rates of migrants during the EFG were fastest during El Niño, highest in La Niña pre-settlement, and there was no significant difference in growth rates between climate phases post-settlement (Figure 6; Table 5).

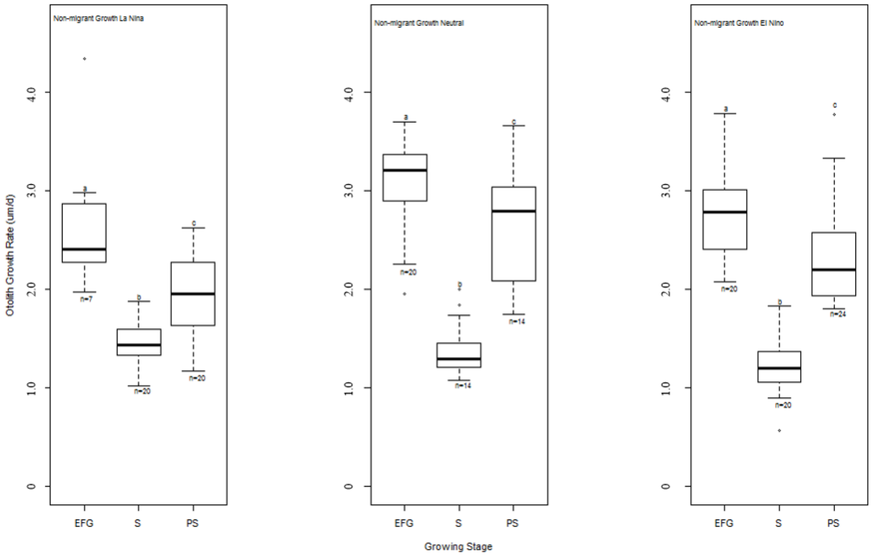

Figure 4-4 Resident growth rates of Awaous stamineus across growing stages within ENSO phases; similar letters indicate no significant difference at alpha = 0.05

Early fast-growth and Larval Stage Duration

The EFG duration did not significantly differ between the contingent types for the EFG (Fig 7; Table 6), but resident larval duration significantly longer than migrants (Fig 8; Table 7). Regardless, the pattern of larval duration across ENSO phases between the contingents was the same; larval duration was shortest during La Niña (Fig 9; Table 7). Resident larval duration was longer than Neutral conditions, but there was no difference in migrant larval duration between El Niño and Neutral conditions (Fig 9; Table 7).

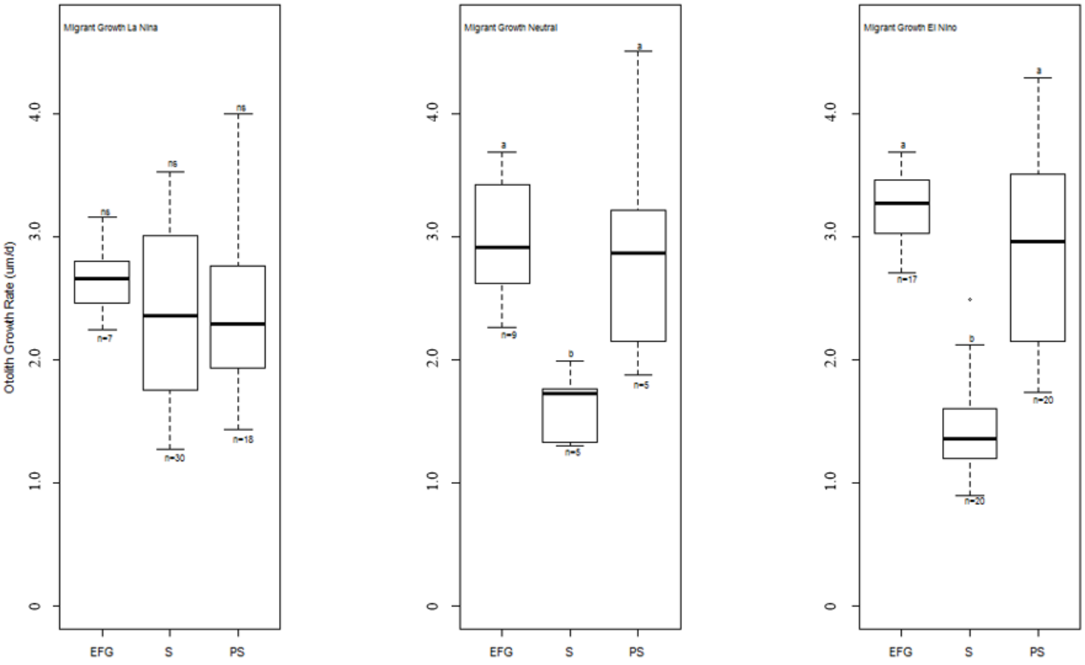

Figure 4-5 Migrant growth rates of Awaous stamineus across growing stages within ENSO phases; similar letters indicate no significant difference at alpha = 0.05

Table 4-2 Logistic regression on contingent representation frequency across MEI hatch date range

Project 1 Hatch and ENSO Index (n=250)					
Fixed Effects	Estimate	Std. Error	z value	p-value	significance
Intercept	-0.8205	0.1406	-5.834	5.41E-09	***
Hatch MEI	-0.4767	0.1518	-3.141	0.00168	**
Correlation of Fixed Effects: 0.103					
Random Effects	Variance	Std. Deviation			
Individual	5.58E-13	7.47E-07			
Project 2 Hatch and ENSO Index (n=489)					
Fixed Effects	Estimate	Std. Error	z value	p-value	significance
Intercept	-3.494	0.3979	-8.782	< 2E-16	***
Hatch MEI	0.9691	0.1995	4.857	1.19E-06	**
Correlation of Fixed Effects: -0.936					
Random Effects	Variance	Std. Deviation			
Individual	0	0			

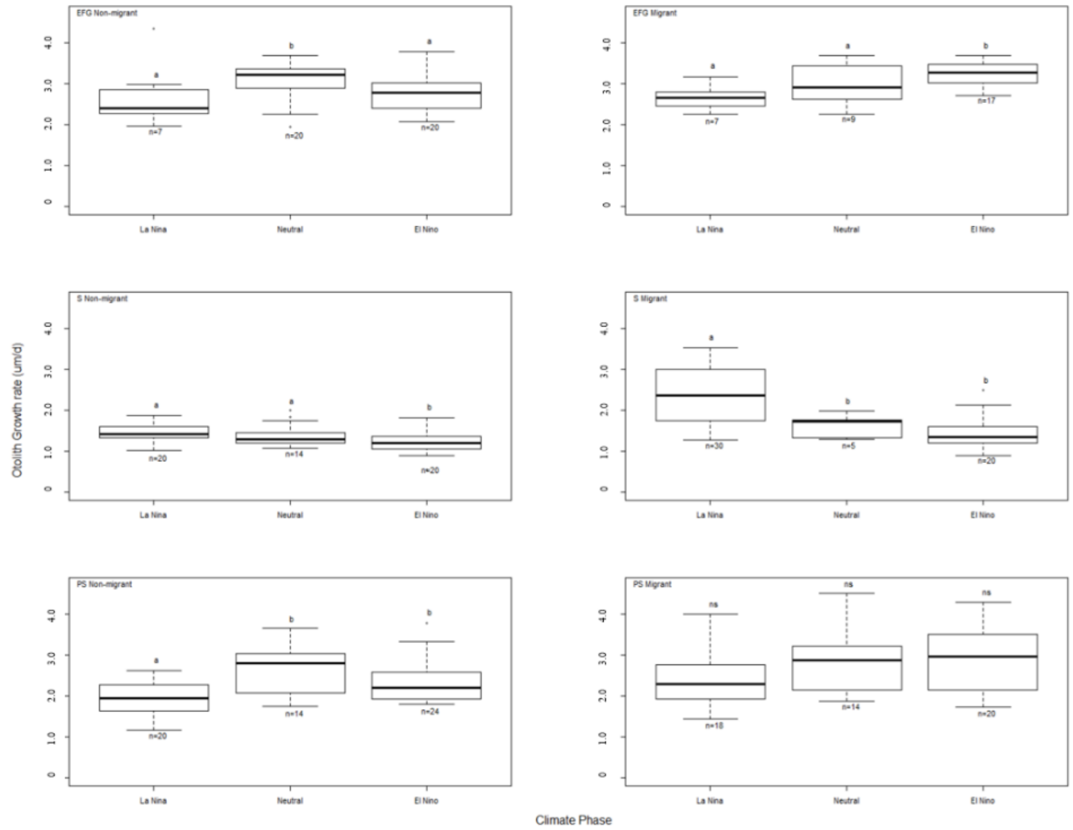

Figure 4-6 Resident and migrant growth rates of Awaous stamineus within a growing stage across ENSO phases; similar letters indicate no significant difference at alpha = 0.05

Discussion

Large-scale climate fluctuations can influence the survival of the early life-stages of fishes. Climate can differentially affect individuals with different life-history strategies resulting in changes in population dynamics. Here I found ENSO differentially influenced the growth rates and recruitment of migrant and resident individuals of a partially migratory fish species. Recruitment of migrants was most favored during La Niña and least favored during El Niño. Migrant EFG and resident post-settlement growth rates were highest during El Niño, and migrant and resident pre-settlement growth rates were higher during La Niña. For both migrants and residents, a longer EFG growing period associated with La Niña resulted in a shorter overall larval duration. I demonstrate that climate forces such as ENSO can modulate the relative success of different life-histories within populations.

Table 4-3 ANOVA on growth rates between contingents

Growth Rate between Contingent Types				
Fixed Effects	DF	F-value	p-value	significance
Intercept	205	2168.23	<0.0001	***
Migratory Contingent Type	83	11.6127	0.001	**
Random Effects	Variance	Std. Deviation		
Individual	0	0		

In the populations of *A. stamineus* I found that there were always a greater proportion of residents than migrants in the populations regardless of the climate regime. However, a greater proportion of migrant individuals were found in adult populations that hatched during La Niña compared to El Niño. The increased proportion of migrants during these climate periods could be a result of recruitment success of migrants from favorable ocean conditions or recruitment failure of residents from suboptimal in-stream conditions. Migrants may have increased recruitment success from increased prey abundance due to intensified upwelling and increased prey interactions due to increased microturbulence in the ocean (Guillen et al. 1969; Lasker 1978, 1981; Walsh et al. 1980; Lobel and Robinson 1988; Chavez et al. 2002). During La Niña, Hawaiʻi receives greater rainfall on average thus greater stream discharge (Giambelluca et al. 1986; Oki 2004; Tim and Diaz 2009). This could lead to greater cues for return-migrating marine larvae, making it easier to find a suitable stream habitat (Delacroix and Champeau 1992; Nishimoto et al. 1997; Smith and Smith 1998; Murphy and Cowan 2007). Meanwhile, the resident counterpart encounters a very different larval environment in-stream. Streams in Hawaiʻi are largely affected by the freshwater input to them (Oki 2004). During La Niña, freshwater systems are highly modified by an increase in freshwater budget, which directly influences the amount of larval habitat for residents. Since early-stage larvae are highly underdeveloped, they are susceptible to environmental forces; the downstream migration is assumed to be largely passive and driven by stream flow (Barber and Chavez 1983; Cushing 1990; Kerr and Dickie 2001; McDowall 2007; Houde 2008). Large pulses of rain into these systems may flush larvae out to sea, leading to lower retention of larvae in-stream (Garcia et al. 2001; Huey et al. 2014). I observed a lower proportion of resident *A. stamineus* during La Niña, which may suggest that residents may have a higher level of recruitment failure than migrants from the changes that occur to freshwater systems, or that a greater proportion of hatching larvae are flushed to sea and forced to migrate in the ocean. Drought associated with early-stage La Niña may cause overcrowding, increased predation, and increased stress from thermal oscillations and low dissolved oxygen in streams (Jacobs 1992; Harper and Mavuti 1996; Mol et al. 2000), which may increase larval mortality that results in lowered recruitment.

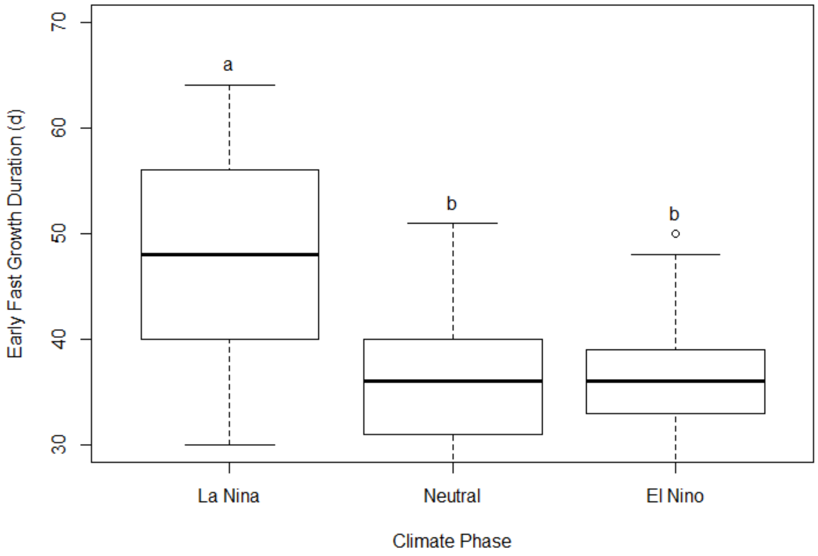

Figure 4-7 Early fast-growth (EFG) duration across ENSO phases of pooled Awaous stamineus ($p > 0.05$ between contingents); similar letters indicate no significant difference at alpha = 0.05

As ENSO shifted from strong La Niña to Neutral conditions and into Strong El Niño periods, the proportions of migrants went down considerably from approximately 40% (strong La Niña) to <10% (strong El Niño). As El Niño intensifies so does its influence on the environment. In freshwater systems there may be more intense periods of flooding with prolonged drought periods (Oki 2004). In neutral and early El Niño episodes, this may simply result in less larval flushing after hatching and stable nutrient delivery to enhance productivity in streams (Murphy 1975), retaining a greater percentage of larvae in-stream. Additionally, conditions in the marine environment become harsher for marine migrant larvae. Poor recruitment of fishes during El Niño is tied to high mortality of yolk-sac larvae (Fielder et al. 1986), and lower availability of appropriate food resources due to decreased upwelling (Walsh et al. 1980; Lu et al. 1998).

However, as El Niño progressed, and became very strong, migrants again became more prevalent, increasing to ~25% of the population. In these extreme conditions, the prolonged drought and severe drying of the streams can reduce suitable larval habitat and create in-stream conditions that increase the mortality of resident larvae (Matthew 1998; Mol et al. 2000; Ficke 2007). Conditions in the marine environment do not become more favorable for migrant larval survival, they are still subject to decreased access to prey and increased food requirements due to metabolic activity from an elevated sea surface temperature (Lu et al. 1998; Garcia et al. 2001).

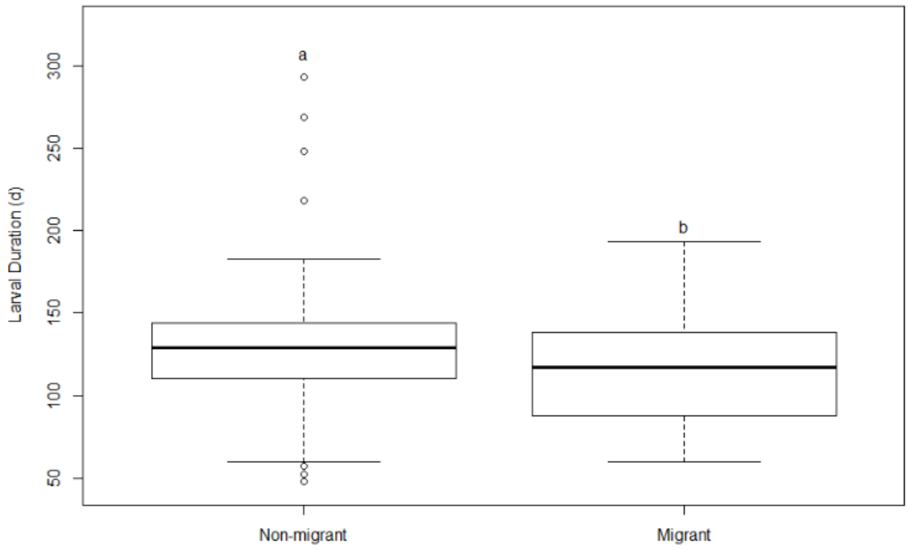

Figure 4-8 Larval duration differences between of Awaous stamineus resident and resident contingents; similar letters indicate no significant difference at alpha = 0.05

Table 4-4 ANOVA on growth rates of migrants and residents and comparisons between growing stages

La Niña Growth					
Resident	Contrast	Estimate	Std. Error	t value	p value
	S - EFG	-12.515	1.864	-6.713	< 0.0001
	PS - EFG	-7.935	1.864	-4.256	0.000107
	PS - S	4.579	1.342	3.411	0.001
Migrant	S - EFG	-2.7643	2.6849	-1.03	0.924
	PS - EFG	-2.2597	2.8491	-0.793	0.924
	PS - S	0.5047	1.907	0.265	0.924
Neutral Growth					
Resident	Contrast	Estimate	Std. Error	t value	p value
	S - EFG	-17.044	1.576	-10.817	<0.001
	PS - EFG	-4.213	1.576	-2.674	0.0104
	PS - S	12.83	1.709	7.507	<0.001
Migrant	S - EFG	-13.3042	3.5939	-3.702	0.00525
	PS - EFG	-0.2834	3.5939	-0.079	0.93813
	PS - S	13.0209	4.0751	3.195	0.00563
El Niño Growth					
Resident	Contrast	Estimate	Std. Error	t value	p value
	S - EFG	-15.256	1.365	-11.178	<0.0001
	PS - EFG	-3.883	1.307	-2.972	0.00423
	PS - S	11.373	1.307	8.703	<0.0001
Migrant	S - EFG	-17.982	2.1	-8.563	<0.0001
	PS - EFG	-2.88	2.1	-1.375	0.175
	PS - S	-15.094	2.013	-7.499	<0.0001

The increase in the proportion of migrants as El Niño becomes extreme may reflect more on the relative success of migrant and resident larvae than an improvement of marine conditions for larval survival.

Previous studies on *A. stamineus* showed faster growth rates for marine migrants than residents, both in the larval stage as well as post-settlement as in-stream adults (Hogan et al. 2014). I found that growth responses to changes in climate due to ENSO also differed between migrants and residents. Overall, migrant growth rates were significantly higher than residents as previously observed. During El Niño, migrants had faster growth rates when compared to residents across all growing stages. Early-stage migrant larvae face many stresses within the first few days of life; the migration from freshwater must occur, then they must find appropriate food resources within a critical period or they will starve (Hjort 1914, 1926; Cushing 1973; Iguchi and Mizuno 1999; Houde 2008). Marine larvae may be more susceptible to the physical changes in the ocean by El Niño; therefore, finding enough of the right prey sources is necessary in this early growing period to reduce heightened vulnerability (Barber and Chavez 1983). It is well documented that as temperature increases so does metabolic activity until a threshold is reached and then mortality results (Johansen and Jones 2011; Neuheimer et al. 2011). During El Niño, sea surface temperature increases, and the surface westerlies intensify, which weakens the trade winds (Oki 2004). The increase in temperature due to El Niño likely causes larvae to have increased metabolic activity, which is reflected in the otolith (Neuheimer et al. 2011). However, increases in metabolic activity (increased growth rates) may not equate to an improvement in body condition (Neuheimer et al. 2011; Auer et al. 2015). For increased metabolism to translate into increased condition, food availability (quality, quantity, and frequency of encounter) must also increase (Auer et al. 2015).

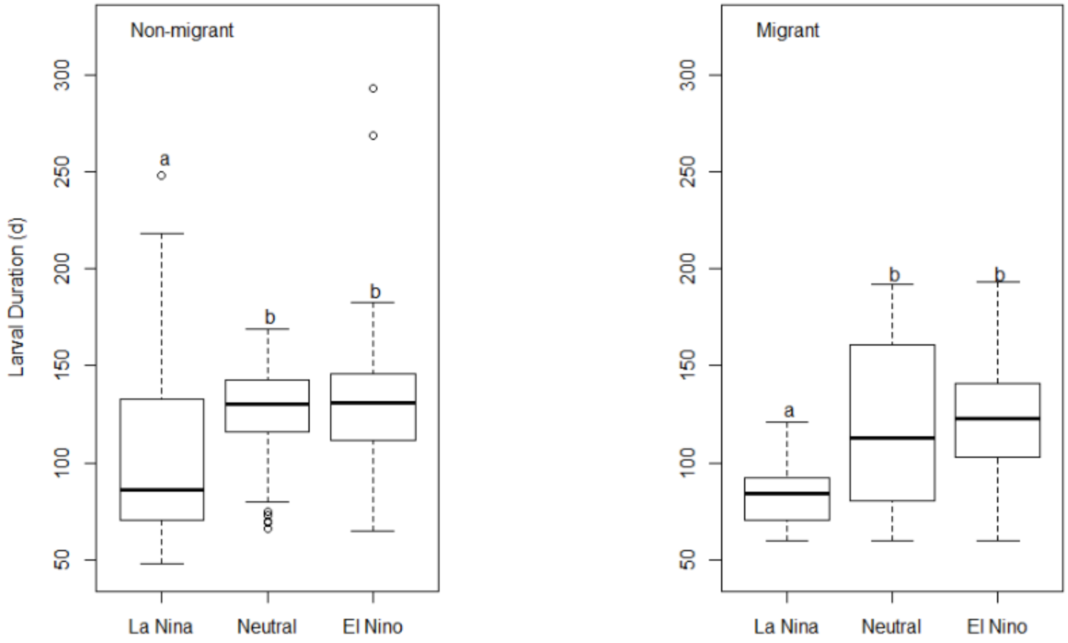

Figure 4-9 Awaous stamineus resident and migrant larval durations across ENSO phases; similar letters indicate no significant difference at alpha = 0.05

The changes that El Niño brings causes changes in the community composition of plankton food resources that fish larvae feed upon (Barber and Chavez 1983; Ottersen et al. 2010); primary production in the ocean decreases during El Niño making prey for larval fishes more scarce (Lu et al. 1998). Additionally, regime shifts occur for phyto- and zooplankton, so the abundance of regular prey species decreases during El Niño (Barber and Chavez 1983). The observed increase in metabolic activity of marine migrants during El Niño coupled with a likely decrease in the abundance and quality of food may increase mortality for migratory larvae. During El Niño, both migrant and residents had a shorter early fast-growing period, and the larval duration was longer. This may indicate that food resources early in larval life are limited during El Niño for both migrants and residents. Some species can prolong the larval duration if their condition is poor and they have not met the metabolic threshold for

Table 4-5 ANOVA on early fast growing period by contingent with climate phase comparisons

Early Fast Growth (EFG)					
Resident	Contrast	Estimate	Std. Error	t value	p value
	La Niña - El Niño	-0.5008	2.1662	-0.231	0.8182
	Neutral - El Niño	3.3354	1.5599	2.138	0.0917
	Neutral - La Niña	3.8362	2.1662	1.771	0.0917
Migrant	La Niña - El Niño	-5.88	1.566	-3.756	0.0019
	Neutral - El Niño	-2.934	1.437	-2.042	0.0501
	Neutral - La Niña	2.946	1.757	1.677	0.1039
Pre-settlement Growth (S)					
Resident	Contrast	Estimate	Std. Error	t value	p value
	La Niña - El Niño	2.2408	0.8239	2.72	0.0236
	Neutral - El Niño	1.5481	0.9079	1.705	0.0942
	Neutral - La Niña	-0.6927	0.9079	-0.763	0.449
Migrant	La Niña - El Niño	9.338	1.52	6.144	<0.001
	Neutral - El Niño	1.744	2.632	0.663	0.5105
	Neutral - La Niña	-7.593	2.543	-2.986	0.0043
Post-settlement Growth (PS)					
Resident	Contrast	Estimate	Std. Error	t value	p value
	La Niña - El Niño	-4.553	1.545	-2.946	0.00471
	Neutral - El Niño	3.005	1.716	1.751	0.08554
	Neutral - La Niña	7.558	1.778	4.25	<0.001
Migrant	La Niña - El Niño	-5.2522	2.8941	-1.815	0.173
	Neutral - El Niño	-0.3295	4.454	-0.074	0.941
	Neutral - La Niña	4.9228	4.5032	1.093	0.281

Table 4-6 ANOVA on early fast growth (EFG) duration and comparison between migrants and residents

Early Fast Growth Duration					
	Sum Sq	**Mean Sq**	**f value**	**p value**	
Climate Phase	1366.8	683.41	14.3709	5.09E-06	
Contingent Type	8.6	8.58	0.1804	0.6722	
Climate Phase	**Contrast**	**Estimate**	**Std. Error**	**t value**	**p value**
	Neutral - La Niña	-11.02	2.2643	-4.867	1.58E-05
	El Niño - La Niña	-10.6098	2.1648	-4.901	1.58E-05
	El Niño - Neutral	0.4102	1.7266	0.238	0.813

metamorphosis to occur (Houde 1987; McCormick and Molony 1992; Sponaugle and Cowen 1997). Drought in streams and decreased production and increased temperature in the ocean associated with El Niño may cause an increase in metabolic activity from an increase in thermal conditions, but food resources are low in both environments; it may take a larva longer to reach the metabolic state to begin metamorphosis (Houde 1987; McCormick and Molony 1992; Sponaugle and Cowen 1997). In addition to an overall decrease in prey, a decrease in wind stress associated with El Niño would further limit larvae from interacting with prey (Rothschild and Osborn 1988), which may result in a shorter EFG period and a longer larval duration; therefore, prey limitations would shorten the fast-growing period and prolong the larval stage. During La Niña, migrants had faster growth rates when compared to resident's right before and immediately after settlement. Late-stage larvae are better developed and better able to alter physiology to maintain optimum homeostasis (Pous et al. 2010), and they can swim more efficiently. Since fish are ectotherms, late-stage larvae are better developed to make behavioral and physiological changes to find water masses that align with internal optimal conditions

Table 4-7 ANOVA on larval duration and comparison between migrants and residents

Larval Stage Duration				
Response	**Sum Sq**	**Mean Sq**	**F value**	**p value**
Contingent Type	7800	7800.1	9.8422	0.001774
Contrasts	**Estimate**	**Std Error**	**t value**	**p value**
SW - FW = 0	-8.446	2.692	-3.137	1.77E-03
Resident	**Sum Sq**	**Mean Sq**	**F value**	**p value**
Climate Phase	21237	10618.3	13.904	1.26E-06
Contrasts	**Estimate**	**Std Error**	**t value**	**p value**
Neutral - La Nina = 0	27.3973	4.2127	6.504	1.46E-10
El Nino - La Nina = 0	28.1987	3.9011	7.228	3.71E-12
El Nino - Neutral = 0	0.8014	2.3976	0.334	7.38E-01
Migrant	**Sum Sq**	**Mean Sq**	**F value**	**p value**
Climate Phase	23071	11540.4	12.594	9.80E-06
Contrasts	**Estimate**	**Std Error**	**t value**	**p value**
Neutral - La Nina = 0	34.9	8.998	3.879	0.000164
El Nino - La Nina = 0	38.174	7.65	4.99	5.56E-06
El Nino - Neutral = 0	3.274	6.559	0.499	0.618494

(Hunter 1981; Lasker 1981; Cowan and Sponaugle 1997; Houde 1997; Leis 2004; Ficke 2007). In Hawai‘i, upwelling can occur from strong surface winds and shallow thermoclines, which allow more mixing and a less stratified boundary (Xie and Phillanders 1994; Xie et al. 2001; Chavez et al. 2002). The waves around the Hawaiian Islands are primarily driven by the trade winds, and they can cause waves that bring nutrient dense cold waters from the ocean depths to the surface (Liu et al. 1995; Chavez et al. 2002). During La Niña, natural upwelling increases and is further intensified by the strong trade winds (Liu et al. 1995). This increases surface nutrient concentrations and primary production, which can enhance growth of marine larvae by bottom-up processes (Roels et al. 1978; Liu et al. 1995; Chavez et al. 2002). If food sources are more available during this time and that is coupled with increased growth, this might explain why migrant larval duration was shorter during La Niña.

Life in-stream for resident larvae also changes drastically across the ENSO cycle, which can affect their growth. I observed a greater proportion of residents in adult populations that hatched during weak La Niña and the early stages of El Niño, and growth rates were highest during Neutral conditions. This may imply that residents have an ‘optimal environmental window’ during which higher growth rates are promoted (Cury and Roy 1989; Roy et al. 1992). Late-stage La Niña and early-stage El Niño episodes bring about higher than average rainfall in Hawaiʻi ((Ropelewski and Halpert 1986; Chu and Chen 2005); as El Niño progresses, drought sets in throughout the winter and spring seasons and up to a year after the El Niño episode began (Chu 1995; Oki 2004; Chu and Chen 2005). La Niña brings greater average rainfall to Hawaiʻi with the highest amounts usually occurring in January and February after the start of the La Niña episode (Chu and Chen 2005). Streams of oceanic high islands are typically prone to dynamic changes over short timescales (Cooper et al. 1998; Poff et al. 1997); the in-stream environment for non-migratory fish larvae can change rapidly and dramatically (Collier and Quinn 2003). Neutral or moderate conditions may be best for resident larvae growth and recruitment since moderate levels of freshwater may increase nutrient delivery and interaction with prey (Rothschild and Osbourn 1988; Kerr and Secor 2010). Fish larvae are more prone to being flushed out of the stream during flooding or may find it more difficult to feed during periods of high flow. In fact, Maie et al. (2009) showed that *A. stamineus* were adapted to feed at slower stream flows than other native Hawaiian freshwater species. Therefore, drought during early La Niña and greater stream flows during late-stage and strong La Niña episodes could reduce feeding efficiency and growth and the ability to retain larvae within streams. During drought periods brought on by late-stage El Niño episodes, larval habitat and that of their prey can be reduced; in extreme cases streams may dry completely (Closs et al. 2003; Kerr and Secor 2010; Huey et al. 2014). Small pool habitats can cause crowding, increased predation, increased temperature, decreased dissolved oxygen, increased ammonia and nitrate (Welcomme 1979; Jacobs 1992; Harper and Mavuti 1996; Ficke 2007; Rypel 2009), which may decrease survival of larvae and reduce recruitment.

Our findings suggest that climate forces modulate the relative success of different life-histories within this species. The ratio of migrants to residents of *A. stamineus* is driven by the life-history that has better growth and survival given the particular climate conditions. ENSO acts as a mechanism that, in part, controls the relative success of both strategies, leading to differential recruitment of the alternative life-histories to the breeding population. This finding has broad implications for the ecology and evolution of these populations. Across all ENSO periods, recruitment is primarily coming from resident larvae, and the proportion remains stable across most El Niño conditions, resulting in nearly total recruitment failure from the oceanic migrants during strong El Niño episodes. This suggests that in-stream conditions suitable for the survival of resident larvae plays an outsized role in the replenishment of these populations. Conditions that reduces in-stream survival will likely reduce the entire population. Only when El Niño intensified to very strong conditions did non-migrant proportion decrease, likely from prolonged drought in freshwater habitats. It has been shown that the amount and variability of stream flow, the abundance of nutrients, and the abundance of invasive species can reduce the survival of resident larvae of *A. stamineus* in Hawai‘i. Managers should focus on reducing stressful conditions imposed by human activities to promote the survival of resident larvae, and this should have an outsized effect on the overall population health. In addition, the severe reduction in surviving migrant individuals during strong El Niño episodes indicates that gene flow and connectivity among streams is heavily reduced during these periods. Reduced connectivity of dispersing larvae can reduce the “rescue effect” of metapopulations (Gotelli 1991) and may result in genetic isolation of these populations for periods of time (Richards 2000).

My findings also have implications for population dynamics under future climate scenarios. El Niño is projected to become more frequent and more intense in the future (IPCC 2014); this will only exacerbate the reductions in connectivity and gene flow and make populations more reliant on recruitment from residents. In addition, the overall climate in Hawai‘i has tended toward lower rainfall. Regional climate models predict that precipitation will decrease by 5 to 10% during the wet seasons, and that dry season precipitation will only increase marginally (~5%) (Timm & Diaz 2009). Additionally, annual precipitation has decline by 15% over the last 20 years and is expected to continue on this trajectory (Chu & Chen 2005, Diaz et al. 2005); and surface stream flows have been declining (Oki 2004). A reduction in rainfall will put greater stress on resident larvae. Effective water management coupled with invasive species control will be critical to maintain recruitment of *A. stamineus* and promote persistence of its populations into the future.

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SUMMARY

Biological systems are interconnected at multiple scales that are nested within each other from large and slow to small and fast cycles (Gotts 2007), and these various scales must be considered to form the most robust ecological understanding of a species or system (Gunderson and Holling 2002). Understanding the life-history or the changes by organisms across the life-cycle is important for understanding population-dynamics and the adaptation of species to changing conditions (Stearns 1992; Roff 1992; Stearns 2000). Life-history includes information about reproductive events, behavior, growth patterns, age at specific stages in life, and mortality (Fabian and Flatt 2012), and the ultimate goal is to optimize the probability of reaching sexual maturity and contributing viable offspring in the face of changing environmental conditions (Stearns 1992; Roff 1992; Stearns 2000). In this study, I identified fish species with fixed and flexible life-histories to further explore how factors at different spatial and temporal scales influence the variation of responses within and among populations. My results indicate the importance of understanding the strategies within species and evaluating factors at different temporal and spatial scales to identify how behaviors and strategies differ between individuals and how that contributes to varying population dynamics.

Before this research only two of the five native Hawaiian freshwater species had been thoroughly evaluated for amphidromy, and the other three species were putatively amphidromous based on the life-history of closely related species; other than *Awaous stamineus*, the identification of partial migration had not been robustly examined. I found that three of the four underexplored species exhibited amphidromy and partial migration. The findings for *Lentipes concolor* are counter to previous knowledge that indicated all sicydiine gobies have a fixed migratory strategy (Radtke and Kinzie III 1996; Shen et al. 1998; Lord et al. 2011). Having migratory flexibility can buffer populations where individuals are exposed to high predation rates or that may be locally extirpated from dynamic conditions (drying up or destruction from natural events) (McIntyre 2016). Hawaiian streams and the ocean are dynamic, and larvae, especially early-stage larvae, are susceptible to high larval losses from the physical environment and from predation and starvation. The dynamic stream environments may have promoted the adaptation of physiological mechanisms to cope with both the marine and freshwater environments in case larvae are flushed to sea or retained in-stream due to reduced flow and lack of connectivity to the ocean (Lyons 1982; Chu and Chen 2005; Huey et al. 2014). All species showed an extended larval duration, which is linked to gene flow and connectivity between populations or finding and colonizing new habitats; extended larval durations were necessary for the original colonization between island systems (like the Hawaiian archipelago) that are separated by long distances (Radtke et al. 2001; Murphy and Cowan 2007; Alda et al. 2016). Additionally, all but *Stenogobius hawaiiensis* and *Eleotris sandwicensis* have morphological adaptations that may influence the ability to remain close to shore and decrease the potential for advection or transport away from freshwater habitats, which may affect larval duration variation between species (Kinzie III 1990). For example, *Lentipes concolor* is known to scale waterfalls and cliffs that exceed 100 m (Kinzie III 1990), and in our study *L. concolor* had the shortest larval duration; in-depth studies are needed to identify if *L. concolor* adheres to nearshore structures close to stream mouths allowing for quicker settlement back into streams once developmentally ready for emigration and metamorphosis, which may result in a shorter larval duration, comparatively. Our findings indicate that endemism must be controlled by factors other than limited dispersal and shortened larval durations, like remoteness, since all of the Hawaiian native freshwater fishes are endemic with prolonged larval durations (Radtke et al. 2001; Murphy and Cowan 2007; Lord et al. 2010; Hogan et al. 2014). This study underscores the importance of both the marine and freshwater environments for the survival of larvae of native Hawaiian freshwater fishes. Since the larval stage is such a critical period, and since the protection of larvae in the ocean is difficult, Hawaiian stream restoration should be a top priority for the protection of species with larval residents; restoring base flows, maintaining good water quality, protecting of larval habitat, and removing invasive species that compete or depredate native larvae are critical for managing these systems to improve conditions for native larval survival (Brasher 2003; Walter et al. 2012; Lisi et al. 2018).

Although hatching and settlement occurred throughout the lunar cycle, more migrant *A. stamineus* survived when hatch was around the full moon and more survived when settlement was around the new moon, and resident *A. stamineus* and migrant *Sicyopterus stimpsoni* showed an opposite but similar pattern. Although I expected the pattern of hatch and metamorphosis of migratory *A. stamineus* to match that of migratory *S. stimpsoni*, our opposite findings support the idea that divergent life-history and synchrony provide advantages (Closs et al. 2013) that promote survival during a critical time when individuals are vulnerable, and survival is low (Enright 1970). Our findings suggest that life-history timing is balanced between risks of migration failure and predation risk; that is, the timing of hatch or settlement is aligned with when the greater of the two risks is minimized (Ross 1983), and this timing may differ between groups with a similar migratory strategy (Ydenberg et al. 2007; Chapman et al. 2011). These findings may provide support that species with flexible migration behaviours have divergent phenologies that may ultimately guide evolution; however, further genetic studies are necessary to determine if *A. stamineus* migratory types are genetically different. Genomic assays may reveal the processes that underlie variation in migratory periodicity.

We found that multiple sources of human impact contribute to the loss of resident larvae in streams. Introduced species may depredate native larvae while others may influence or may have synergistic effects on water quality that influence the quality of habitat for resident larvae. Base flows may be impacted by human water usage, and low to no flow resulted in fewer residents either through desiccation or lack of interaction with prey. Since residents dominated most of the stream populations of *A. stamineus*, population dynamics are largely influenced by the mortality and survival of residents. Therefore, the restoration and proper management of streams should be a high priority since native fish are susceptible to larval losses when faced with stressors and pressures that come directly from human activities. Each stream and the native populations therein should be considered and managed independently of other streams since the conditions are very different across the biological and environmental gradients. Unnatural physical and biological additions to freshwater ecosystems must be mitigated and managed in concert to restore systems to more natural-like conditions to assist with population recovery of native fishes that are threatened or of conservation concern.

Modifications in the larval habitat, even by natural processes, can have a significant effect on growth and mortality, which ultimately results in recruitment success to breeding populations. The stressors and intensity of those stressors during an ENSO phase differs between freshwater and marine environments. Since El Niño is projected to become more frequent and more intense in the future (IPCC 2014), species that utilize multiple aquatic environments may be affected differently; that is, if changing conditions expose residents to more stressors, migrants may dominate adult populations and vice versa. During a particular phase, the marine environment may have more intense stressors on migrants than those experienced in streams and vice versa. Recruitment failure may be caused by larval loss from stressful abiotic conditions and/or limited access to prey sources. Differential survival of *A. stamineus* contingents may explain the variation in representation of contingents across ENSO phases. The environment that pushes individuals past biological thresholds without meeting biological requirements for growth and progression through the larval stage will result in a greater proportion of larval loss making the other contingent more represented in adult populations. Alternatively, in quality habitats where resident recruitment is high, this may lead to less ecological space for migrants to occupy and survive, which would result in a decreased representation of migrants. Conversely, in streams of poor quality and a reduction of resident recruitment, more migrants would be able to colonize and recruit to breeding populations leading to an increased representation of migrant types. Growth rate responses may be directly influenced by changes in temperature with a mismatch in food resource availability. For example, increased temperature may increase metabolic activity, but if the proper food resources are not available or accessible, an individual may have a prolonged larval duration since it would take a longer time to progress to metamorphosis. It is difficult to protect migrant larvae at sea; therefore, the restoration of stream habitats must be prioritized so that in-stream stressors on contingents are minimized when large-scale changes occur.

The findings of this dissertation show the importance of evaluating multiple scales of influence to understand the life-history strategies of individuals, which ultimately influences the adaptation and evolution of species. Without considering these multiple interactions and influences at different scales, one can only form a partial ecological understanding of species and the systems they inhabit, which can lead to improper management. Potential underlying genetic variability and modifications in the larval habitat within and among species can have significant effects on individual responses and ultimately the success of individuals to recruit to breeding populations; additive effects between anthropogenic impacts and natural variation may negatively impact larval survival. We found that both larval habitats are important for determining recruitment success and the makeup of adult populations, and the progressing alteration to both habitats from human use and influence may have negative impacts on species with contingents that utilize both habitats. These findings can be applied directly for adaptive management strategies for the species examined; all examined in this dissertation are of cultural importance, and many are of critical conservation concern. Protecting migrant larvae at sea is difficult since the habitat is on such a large scale; however, for residents, reducing instream pressures (i.e., maintain stable base flow, limit excess nutrient input, and manage invasive species) should be a priority so a proportion of the populations are buffered and the stressors to overcome by vulnerable larvae are minimized.

The findings of this dissertation are an example of how to evaluate species that have life-history flexibility with populations that cross biological and environmental gradients that vary across scales. To ensure proper management of other species, studies should be designed to include multiple scales that influence system and biological dynamics. Furthermore, systems that vary in space and time that host distinct populations should be evaluated independently rather than as a homogenized unit, since each population is subject to *in situ* conditions and responses over time. An ecosystem-based management approach should be adopted for systems with discrete populations to identify the factors that elicit different biological responses. Management and conservation of species becomes more complex when a species exhibits life-history flexibility where some contingents experience different conditions than other contingents. In this case, influential factors at multiple spatial and temporal scales, within a system, for each contingent must be managed independently as the factors of influence can be different and result in different biological responses between contingents of a population or species. Although this dissertation focused on fishes, the findings can be applied broadly to different taxa that have life-history flexibility. Many vertebrate species show partial migration (Jonsson and Jonsson 1993; Donnelly and Guyer 1994; Martin and Willis 2007; Jahn et al. 2010) where contingents migrate and rejoin, but during part of the life, those contingents are separate, and their experiences are different. Whether marine or freshwater aquatic, terrestrial, or a combination of both, it will be important that future studies are designed with a panarchical approach to form a robust understanding of the timing of life-history events and to identify the spatiotemporal factors that influence individual behavior. Managers and conservationists must consider these findings and use adaptive ecosystem-based management techniques so that populations and species are robustly understood and properly managed in the face of changing environmental conditions.

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LIST OF APPENDICES

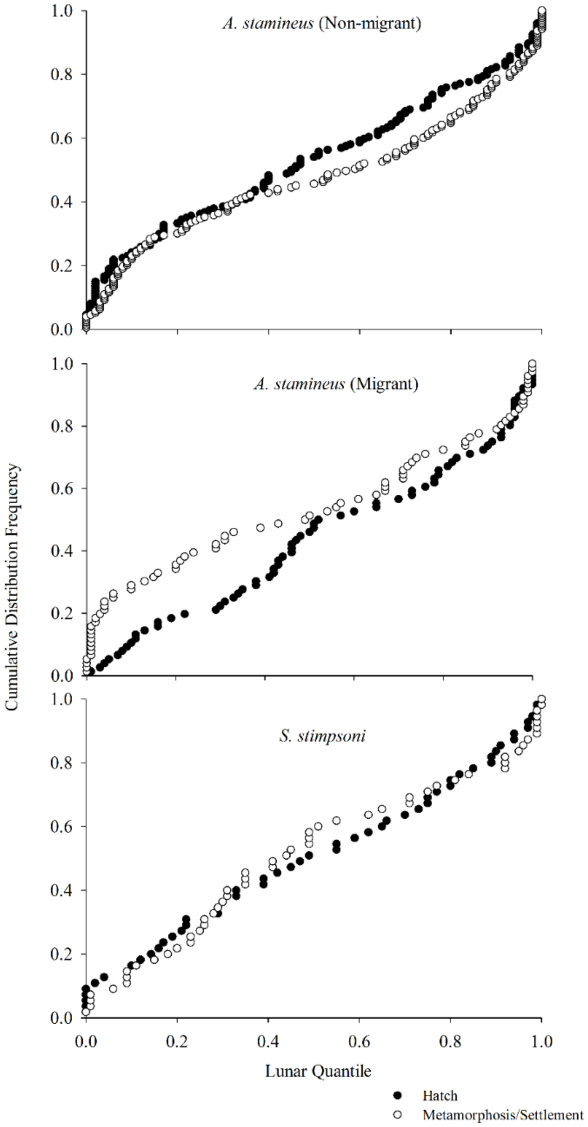
APPENDIX PAGE

Appendix 1: Chapter 1 Supplementary Information

Species	Island	Watershed	n	Migrant (%)	Resident (%)
Sicyopterus stimpsoni	Hawaii				
		Waipio	3	100	0
		Niulii	7	100	0
		Hakalau	3	100	0
	Kauai				
		Wainiha	2	100	0
		Hanakapiai	3	100	0
		Lawai	4	100	0
	Maui				
		Piinaau	4	100	0
		Alelele	9	100	0
		Ukumehame	3	100	0
	Molokai				
		Wailau	3	100	0
		Pelekunu	2	100	0
		Halawa	1	100	0
		Waikolu	5	100	0
	Oahu				
		Waiahole	5	100	0
		Kaluanui	1	100	0
Stenogobius hawaiiensis	Hawaii				
		Hakalau	8	25	75
		Honolii	3	33	67
		Waiakea Pond	5	0	100
	Kauai				
		Waimea	6	17	83
		Wailua	4	0	100
Lentipes concolor	Hawaii				
		Manoloa	7	71	29
		Nanue	1	0	100
Eleotris sandwicensis	Hawaii				
		Hakalau	9	22	78
		Honolii	1	0	100
		Maili	1	0	100
		Richardson's Beach	5	20	80
		Waiakea Pond	4	50	50

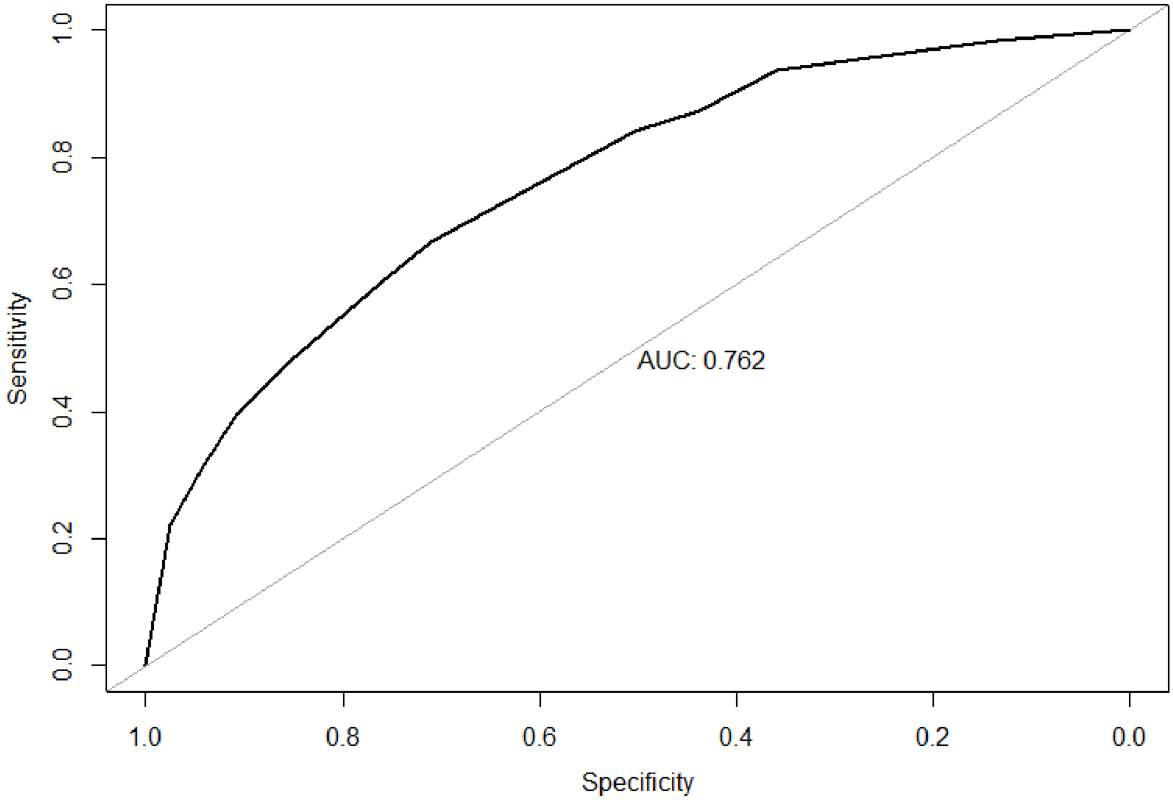
Supplementary Table 1-1 Sampling sites and the proportion of contingents within each species

Appendix 2: Chapter 2 Supplementary Information

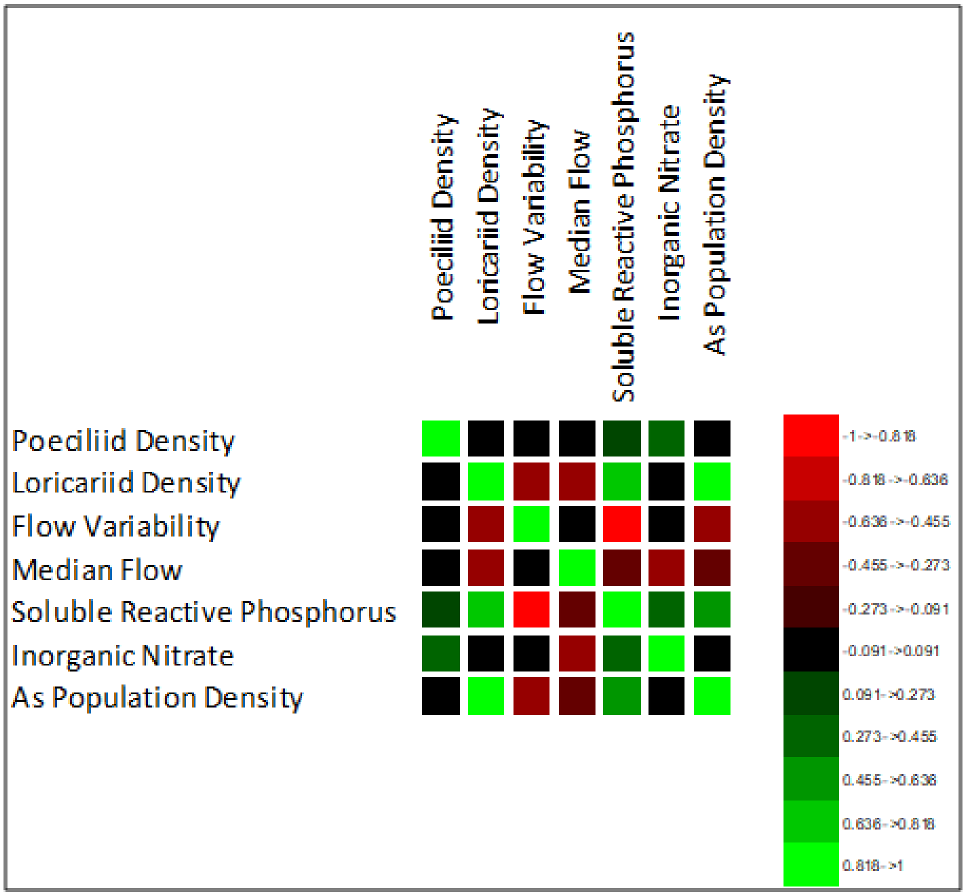


Supplementary Figure 2-2 Life-history Distribution Frequency Comparisons between Facultative Migrant *Awaous stamineus* (resident open-circles, migrant closed-circles) and Migrant *Sicyopterus stimpsoni* (x symbols)

Appendix 3: Chapter 3 Supplementary Information

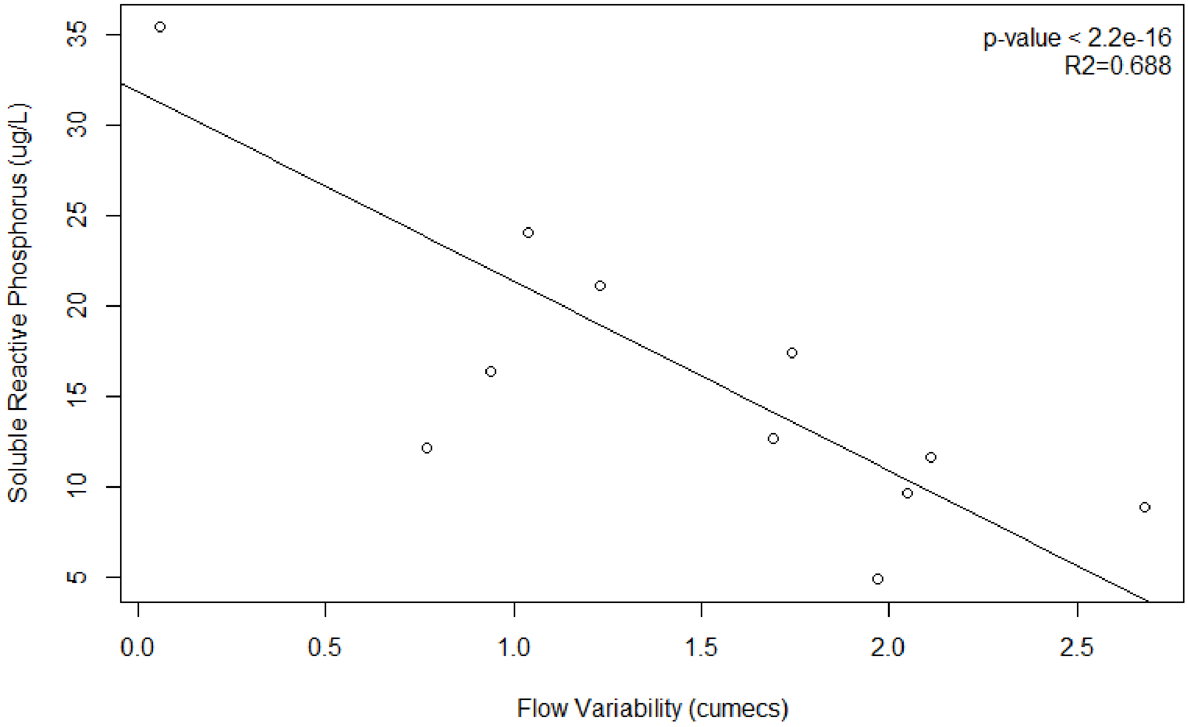


Supplemental Figure 3-1 ROC curve for model fitness for the best model identified by statistical dredge

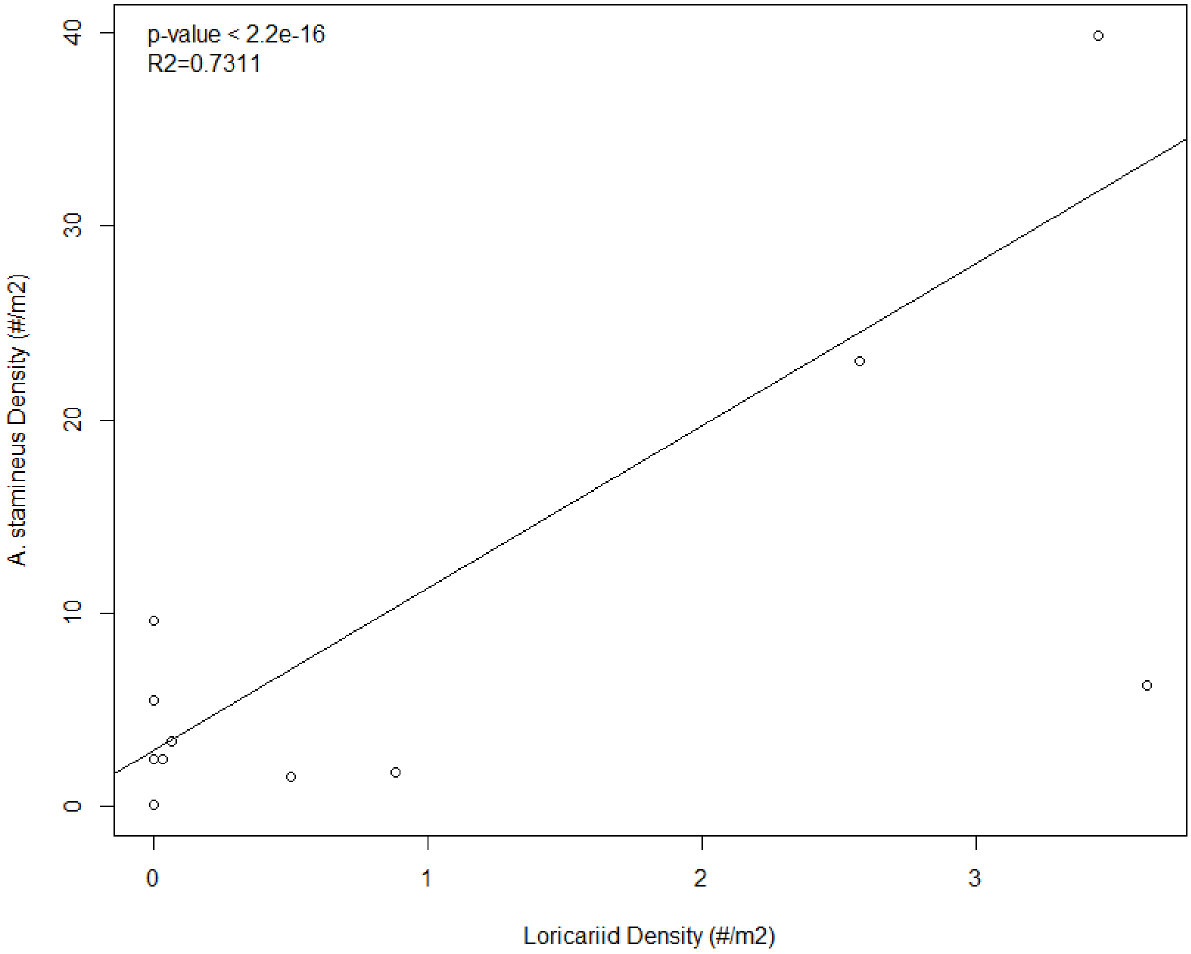


Supplemental Figure 3-2 Correlation diagnostics of model covariates;

As population Density = *A. stamineus* population density

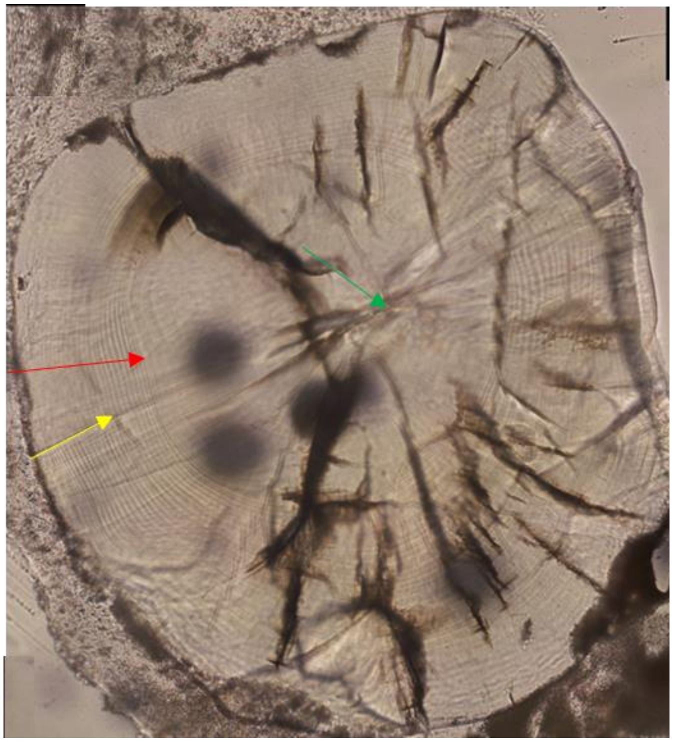


Supplemental Figure 3-3 Relationship between flow variability (cumecs) and soluble reactive phosphorus (SRP) (µg/L); as flow variability increases (drier conditions) SRP concentration decreases.

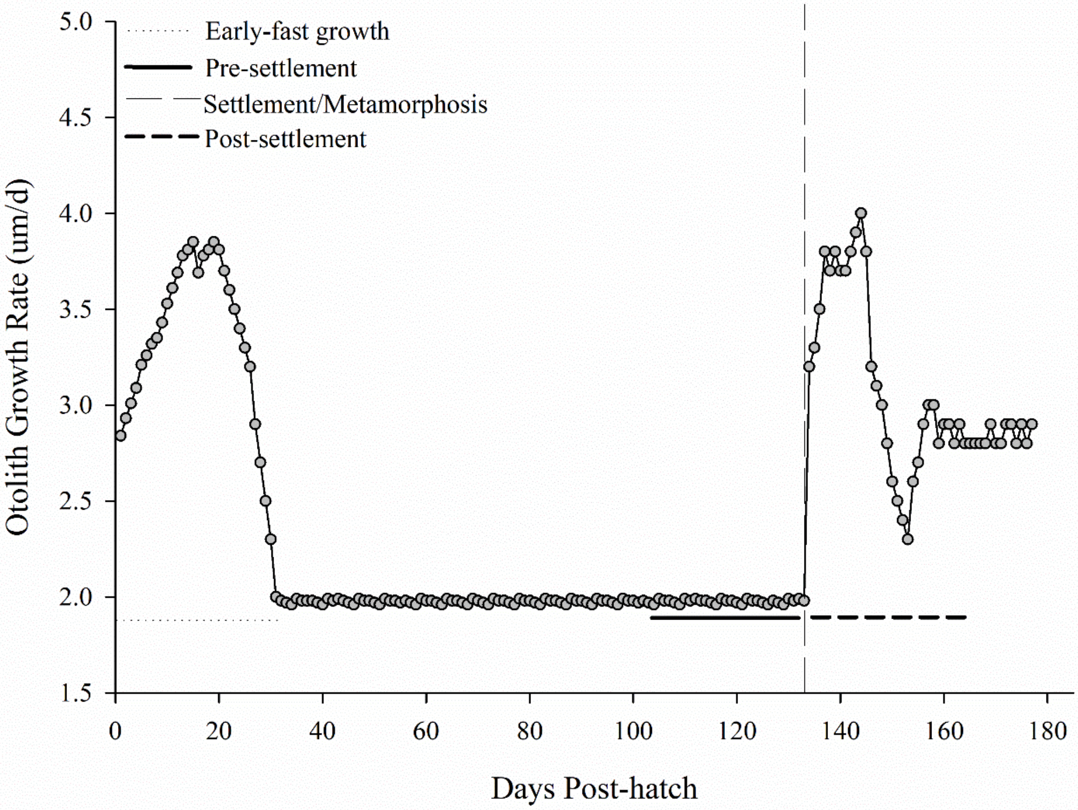


Supplemental Figure 3-4 Relationship between *A. stamineus* population density (#/m^2) and loricariid density (#/m^2); as loricariid density increases so does the population density of *A. stamineus*

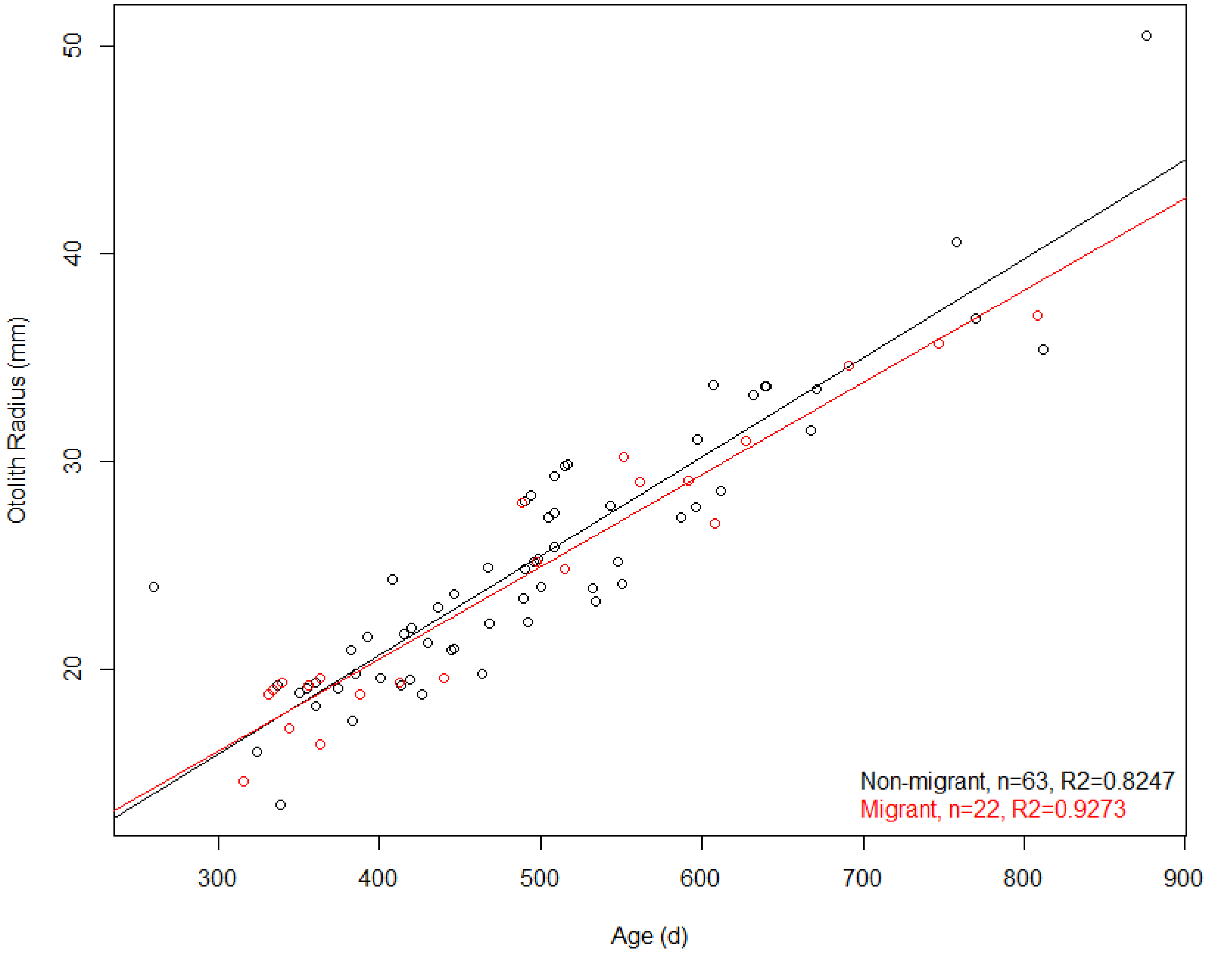
Appendix 4: Chapter 4 Supplementary Information



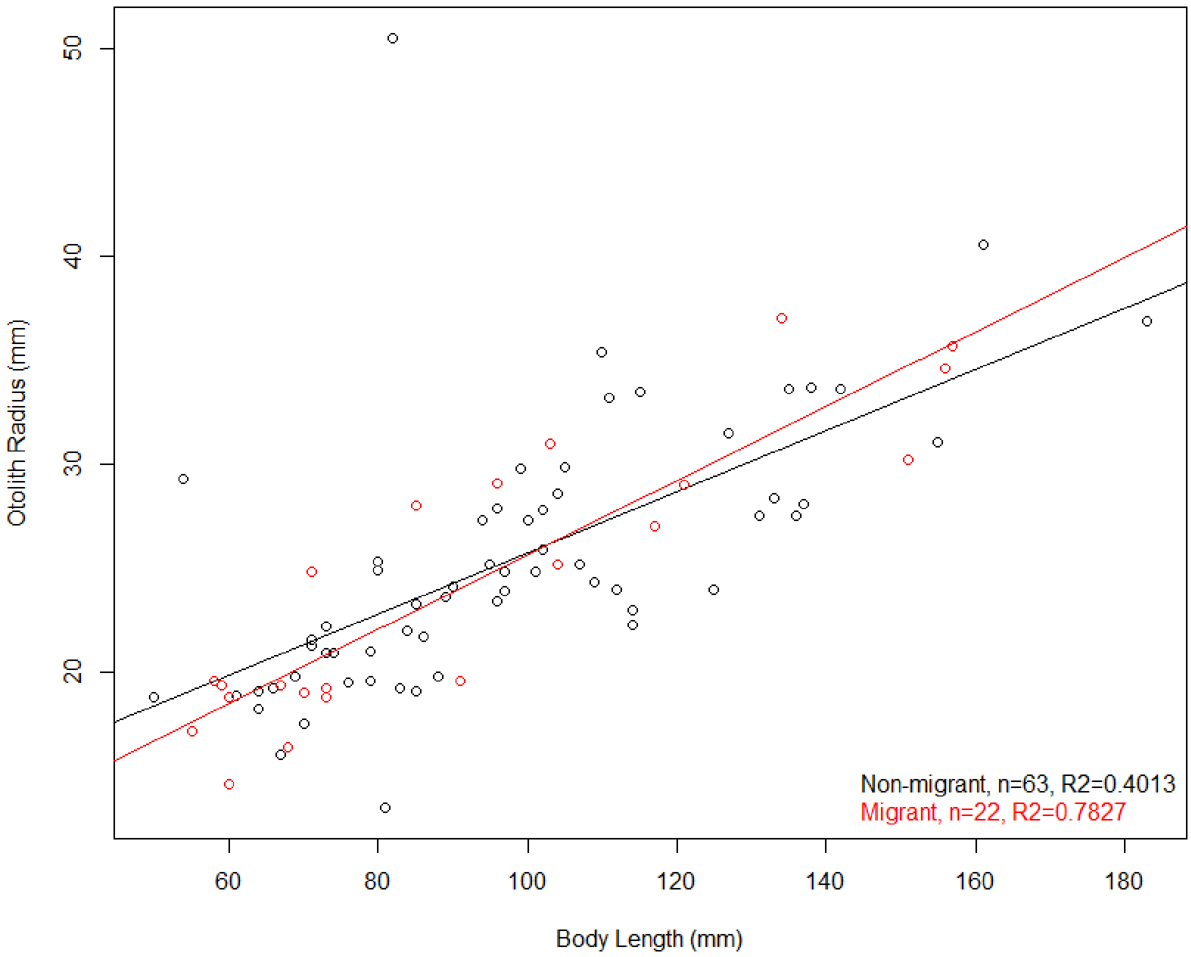
Supplemental Figure 4-1 Imaged *A. stamineus* otolith; the green arrow indicates the primoridum and time of hatch, the red arrow indicates the metamorphosis/settlement mark, and the yellow band indicates one of the daily growth bands used to estimate the age of a fish.



Supplemental Figure 4-2 Diminishing growth curve of *A. stamineus* across the larval stage and growing stages that were analyzed; lengths of horizontal lines represent the duration of the early-fast growth, pre-settlement, and post-settlement growing stages used for analysis (Adapted from Hogan et al. 2017).



Supplemental Figure 4-3 Relationship between otolith radius size (mm) and age (d) of *Awaous stamineus* migrants (red; $p = 4.58^{-13}$, $R^2 = 0.9273$) and residents (black; $p < 2^{-16}$, $R^2 = 0.8247$)



Supplemental Figure 4-4 Relationship between otolith radius size (mm) and body length (mm) of *Awaous stamineus* migrants (red; $p = 2.82^{-08}$, $R^2 = 0.7827$) and residents (black; $p < 1.52^{-08}$, $R^2 = 0.4013$)

Supplemental Table 4-1 Otolith and radius linear regression for migrant and resident *Awaous stamineus*

Otolith Radius and Total Age Relationship					
Non-migrant	n=63				
Coefficients	Estimate	Std. Error	t value	p-value	significance
Intercept	1.625082	1.424351	1.141	2.58E-01	***
Age	0.047689	0.002787	17.108	<2E-16	***
R2: 0.8247					
Migrant	n=22				
Intercept	2.730651	1.368446	1.995	0.0598	.
Age	0.044375	0.002705	16.402	4.58E-13	***
R2: 0.9273					

Supplemental Table 4-2 Radius and body size linear regression for migrant and resident *Awaous stamineus*

Otolith Radius and Body Relationship					
Non-migrant	n=63				
Coefficients	Estimate	Std. Error	t value	p-value	significance
Intercept	11.00398	2.27859	4.829	9.58E-06	***
Body Length	0.14731	0.02258	6.523	1.52E-08	***
R2: 0.4013					
Migrant	n=22				
Intercept	7.80241	1.99551	3.91	0.000868	***
Body Length	0.17839	0.02038	8.755	2.82E-08	***
R2: 0.7827					

Supplemental Table 4-3 Sample MEI table and selection process

Sample MEI Value Table

	2003	2004
DECJAN	1.214	0.332
JANFEB	0.944	0.37
FEBMAR	0.83	-0.036
MARAPR	0.413	0.358
APRMAY	0.214	0.558
MAYJUN	0.107	0.315
JUNJUL	0.177	0.571
JULAUG	0.309	0.617
AUGSEP	0.492	0.591
SEPOCT	0.534	0.524
OCTNOV	0.584	0.818
NOVDEC	0.362	0.684

The Multivariate El Nino Index (MEI) is a bi-monthly sliding scale that indicates an ENSO event and its intensity. Each individual was assigned an MEI value based on its estimated hatch date. Since the MEI is bi-monthly, individuals with hatch dates with monthly days between 1 and 15 would be assigned the value for when the month was first reported, and individuals with hatch dates between 16 and 31 were assigned the value for when the month was reported second. For example, an individual with a hatch date of February 7, 2003 would be assigned the MEI value of 0.944 since this is the first time a February value was reported in 2003; an individual with a hatch date of Dec 22, 2003 would be assigned the value of 0.332 since this was the second time a value was reported for December 2003.