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Migratory flexibility in native Hawai'ian amphidromous fishes

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Abstract

We assessed the prevalence of life history variation across four of the five native amphidromous Hawai'ian gobioids to determine whether some or all exhibit evidence of partial migration. Analysis of otolith Sr.: Ca concentrations affirmed that all are amphidromous and revealed evidence of partial migration in three of the four species. We found that 25% of *Lentipes concolor* ($n = 8$), 40% of *Eleotris sandwicensis* ($n = 20$) and 29% of *Stenogobius hawaiiensis* ($n = 24$) did not exhibit a migratory life-history. In contrast, all individuals of *Sicyopterus stimpsoni* ($n = 55$) included in the study went to sea as larvae. *Lentipes concolor* exhibited the shortest mean larval duration (LD) at 87 days, successively followed by *E. sandwicensis* (mean LD = 102 days), *S. hawaiiensis* (mean LD = 114 days) and *S. stimpsoni* (mean LD = 120 days). These findings offer a fresh perspective on migratory life histories that can help improve efforts to conserve and protect all of these and other at-risk amphidromous species that are subject to escalating anthropogenic pressures in both freshwater and marine environments.

KEYWORDS

amphidromy, eleotridae, larval duration, otolith Sr.: Ca, partial migration, Sicydiinae

1 | INTRODUCTION

Effective conservation and management of at-risk fishes requires an accurate understanding of habitat use (Rosenfeld & Hatfield, 2006). For migratory fishes, it is necessary to determine the habitats that species occupy during breeding and maturation (i.e., feeding and growth) as well as habitats that act as movement corridors (Hain *et al.*, 2018; McIntyre *et al.*, 2016). In part, this is because migratory fishes face the perils of triple jeopardy from unsuitable or degraded conditions in all three habitats (McIntyre *et al.*, 2016). Determining the balance of habitat occupancy is a key step towards circumscribing the nature and extent of potential threats to imperilled migratory fishes.

Increasing evidence of life-history flexibility in amphidromous gobioids (Augspurger *et al.*, 2017; Hogan *et al.*, 2014) challenges the long-standing principles underlying native fish conservation in oceanic island streams (Lisi *et al.*, 2018; McDowall, 2007a; Moody *et al.*, 2017). Most conservation efforts assume that at-risk species are obligately amphidromous, which involves hatching in freshwater and migrating to the ocean (Luton *et al.*, 2005; McDowall, 2007a), followed by a marine larval period, which may be in estuarine or pelagic marine environments, after which individuals return to freshwater and progress to habitat favourable for maturation and reproduction (Hogan *et al.*, 2017; McDowall, 2007a). Immigration from non-local sources might, therefore, help sustain or replenish populations residing in degraded catchments (Blum *et al.*, 2014). A growing number of studies indicate, however, that

amphidromous gobies exhibit ecological (*i.e.*, plastic) and evolutionary (*i.e.*, heritable) migration flexibility (Augsburger *et al.*, 2017), including partial migration bet-hedging strategies, with both ocean migrants and stream residents (Ayers, 2010; Chapman *et al.*, 2012; Hicks, 2012; Hogan *et al.*, 2014; Tabouret *et al.*, 2014). This suggests that immigration from non-local sources may not necessarily be sufficient to ensure the viability of threatened populations (Blum *et al.*, 2014).

Work on species endemic to Hawai'ian Island streams illustrates how perspectives are shifting about the incidence and nature of migratory flexibility in amphidromous gobies. All five species were once thought to be obligately amphidromous (McDowall, 2007a): *Awaous stamineus* (Eydoux and Souleyet 1850) (Oxudercidae: Gobionellinae), *Eleotris sandwicensis* Vaillant and Sauvage 1875 (Eleotridae), *Lentipes concolor* (Gill 1860) (Oxudercidae: Sicydiinae), *Sicyopterus stimpsoni* (Gill 1860) (Oxudercidae: Sicydiinae) and *Stenogobius hawaiiensis* Watson 1991 (Oxudercidae: Gobionellinae). This supposition is largely based on studies of otolith microchemistry and microstructure that affirmed field-based inferences of amphidromy and that provided estimates of larval duration for *A. stamineus*, *S. hawaiiensis* and *L. concolor* (Radtke *et al.*, 1988, 1999, 2001). It also reflects otolith-based evidence of obligate amphidromy and estimates of larval duration for congeners of *S. stimpsoni* and *E. sandwicensis*, (*e.g.*, *Sicyopterus lagocephalus* Pallas 1770 (Lord *et al.*, 2011) *Eleotris fusca* (Bloch & Schneider 1801) (Mennesson *et al.*, 2015)). More recent work indicates, however, that *A. stamineus* exhibits partial migration (Hogan *et al.*, 2014), raising the possibility that some or all of the other four species also exhibit flexible migratory strategies.

In this study, we assessed the prevalence of life-history variation in *L. concolor*, *S. stimpsoni*, *E. sandwicensis* and *S. hawaiiensis* to determine whether migration flexibility is a common feature among gobioids in Hawai'ian streams, or if it is an idiosyncrasy of *A. stamineus*. We expected to find evidence of amphidromy in all four species. We also expected that *L. concolor* and *S. stimpsoni* would exhibit obligate amphidromy as has been observed in other Sicydiine gobies (Lord *et al.*, 2011; Radtke & Kinzie III, 1996; Shen *et al.*, 1998). Although migration flexibility has not been observed in congeners, we expected that *E. sandwicensis* and *S. hawaiiensis* were likely to exhibit flexibility based on its occurrence in confamilial species (Closs *et al.*, 2003; Kano *et al.*, 2014; Nordlie, 2012; Smith & Kwak, 2014; Tsunagawa & Arai, 2008). We also assessed the larval duration (LD) period to gain further insight into the dispersal potential of each species.

2 | MATERIALS AND METHODS

Research permits and guidance were provided by the Hawai'i Division of Aquatic Resources. The care and use of experimental animals complied with Institutional Animal Care and Use Committee animal welfare laws, guidelines and policies as approved by Clemson University (approved protocols: ARC2007-090 and AUP2008-071) and the University of Wisconsin Madison (approved protocol: L00431-O-01-11).

2.1 | Study species

All five native Hawai'ian freshwater goby species are in the sub-order Gobioidae and four are in the family Oxudercidae (Kuang *et al.*, 2018). Surveys indicate that *Lentipes concolor* (Kinzie, 1990) inhabit higher elevation stream reaches, which are achievable because modified pelvic fins allow it to climb waterfalls as high as 100 m (Englund & Filbert, 1997; Fitzsimmons & Nishimoto, 1995). Similarly, *Sicyopterus stimpsoni* is also capable of climbing waterfalls, though it is predominantly found in mid-elevation reaches of streams where water quality and habitats have not been extensively altered and where there are few aquatic invasive species (Blob *et al.*, 2008, 2010; Kinzie, 1990). It often co-occurs with *A. stamineus*, though it is typically found in swifter waters (Kinzie, 1988). In contrast, *Stenogobius hawaiiensis* occurs in estuaries and low elevation stream reaches as it lacks musculature to climb and withstand fast flowing conditions (Maie *et al.*, 2012; Schoenfuss, 1997). Likewise, *Eleotris sandwicensis* are not able to climb due to the lack of fused pelvic fins to form a pelvic sucker (Benbow *et al.*, 2004) and thus also occur in estuaries and low elevation stream reaches (Kinzie, 1990).

2.2 | Sample collection and preparation

Specimens of all four species were opportunistically collected by snorkelers using hand nets. Between March and July 2009; 20 *E. sandwicensis*, eight *L. concolor* and 24 *S. hawaiiensis* were collected on either Kaua'i or the island of Hawai'i (Table 1). A total of 55 *S. stimpsoni* were collected between March and May 2011 from 15 catchments across all five of the main Hawai'ian Islands (Table 1). All samples were collected from streams without upstream movement barriers (*e.g.*, dams) and all specimens were collected within the stream proper. Specimens obtained in 2009 were collected live in the field and placed in 20 l buckets containing stream water and fitted with air stones for transportation to a laboratory on each respective island, where they were humanely euthanised with MS-222, preserved in 95% ethanol and stored at -20°C until further analysis. Fish were then thawed at Clemson University and sagittal otoliths were extracted following standard protocols (Bickford & Hannigan, 2005). Specimens obtained in 2011 were collected live in the field, humanely euthanised and kept on ice and then stored frozen at -20°C . Fish were thawed at the University of Wisconsin and sagittal otoliths were extracted by dissection following standard protocols (Bickford & Hannigan, 2005). After removal, sagittal otoliths were cleaned in distilled water and allowed to dry. One of the two otoliths was randomly selected to be mounted and polished for microstructure analysis of age, hatching date and metamorphosis date. All otoliths were mounted sulcus side up onto glass petrographic slides and embedded in Crystalbond glue (Aremco; www.aremco.com). 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; www.buehler.co.uk) and diamond lapping film (3 M; www.3m.com) that ranged in grit size from 60–0.5 μm . The same otolith was also used for microchemical analysis of migration history.

TABLE 1 Sampling sites and the percentage of contingents (ocean migrant and stream resident) for *Sicyopterus stimpsoni*, *Stenogobius hawaiiensis*, *Lentipes concolor*, and *Eleotris sandwicensis*; reach is the relative sampling location within a stream segment where high is the highest altitude and furthest distance from the ocean, mid is the middle of the stream segment and low is the lowest altitude and closest to the ocean

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

2.3 | Identifying marine migrations

To determine whether an individual underwent a larval marine phase, laser-ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) was used to quantify Sr:Ca and Ba:Ca across a core-to-edge transect of each mounted otolith, which is representative of a full life span. This approach has been extensively used to investigate diadromous migration between marine and freshwater environments because Sr:Ca is relatively high in the ocean (c. 8 mmol mol⁻¹) compared with freshwater conditions (c. 4–5 mmol mol⁻¹) and the opposite relationship exists for Ba:Ca in the ocean and freshwater (Hogan *et al.*, 2014). All otoliths showed a clear metamorphosis mark (Radtko *et al.* 1988), regardless of their migratory life history, that indicates the transition from larval to post-larval forms (Hogan *et al.* 2017).

Otoliths of marine migrants also typically exhibit a marked decline in Sr:Ca (and an increase of Ba:Ca) at metamorphosis–settlement, which is indicative of the transition to freshwater from the marine environment (Hogan *et al.*, 2017). It can be difficult to distinguish marine and estuarine waters using Sr:Ca (Walther & Nims, 2015) so here we refer to the marine environment as one being predominantly salt water (estuarine or marine). However, it should be noted that Hawaiian streams do not empty into large estuaries as is common in larger islands or continents. Specimens obtained in 2009 were analysed at the Quadrupole ICP-MS Lab at University of Texas at Austin (New Wave Research UP193-FX fast excimer (Electro Scientific Industries; www.esi.com) coupled to an Agilent 7500ce ICP-MS (www.agilent.com)) in January 2018. Specimens obtained in 2011 were analysed at the Environmental Analytical Facility at University of Massachusetts,

Boston (Perkin Elmer ELAN DRCII (www.perkinelmer.com) coupled to a Cetac LSX213 (Teledyne Cetac; www.teledynecetac.com) in March 2012. The same protocols, standards and analyte lists were used to collect data from all specimens. Samples and standards were analysed with a laser-beam width of 25 μm and a scan rate of 5 $\mu\text{m s}^{-1}$. All samples were calibrated and drift corrected using calcium carbonate standards (USGS MACS-3 and NIST-612; www.usgs.gov/centers/gggsc) 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 the mass of ablated material. The masses of 12 isotopes were analysed (^{42}Ca , ^7Li , ^{24}Mg , ^{25}Mg , ^{55}Mn , ^{66}Zn , ^{68}Zn , ^{88}Sr , ^{137}Ba , ^{138}Ba and ^{208}Pb) and the concentrations were calculated, with relative concentrations expressed as a ratio to ^{42}Ca . After the completion of initial LA-ICP-MS analyses, more than 50% of the samples for each species were re-polished and re-run with a new transect that bisected the core without passing through previously ablated areas. The chemical profiles of secondary runs were assessed to ensure that the samples had not been under-polished prior to the initial run.

Analyses of otolith Sr:Ca patterns can potentially lead to erroneous inferences about the occurrence and prevalence of migration flexibility. Mistakes in sample preparation and analysis can lead to false identification of freshwater residency (Hogan *et al.*, 2014; Hogan *et al.*, 2017). Thus, it is important to identify and control possible sources of error when characterising migratory flexibility. For example, attention and care must be taken to not over or under-polish otoliths for microchemical analysis, particularly in the core area of an otolith, which corresponds to the life stage when an amphidromous goby might be at sea. Incorrect polishing could result in an erroneous freshwater signal. If the otolith is under-polished, the pre-settlement marine core may not have been revealed and if the otolith has been over-polished (*i.e.*, through the core of the otolith), the marine core may have been removed, leaving only post-larval otolith material, which would produce a false pattern of lifelong freshwater residency. An individual fish might consequently be erroneously categorised as a stream resident instead of an ocean migrant. Understanding this risk, we took measures to control for both over and under-polishing. First, we ensured that the otolith primordium (*i.e.*, the origin point of the otolith) was always visible when polishing samples prior to laser ablation. Accordingly, if the primordium was polished away, we considered the sample to be over-polished. To control for under-polishing, we re-polished otoliths (while still retaining the primordium) that exhibited a freshwater signature in the core. Conducting a second LA-ICP-MS run on the re-polished otoliths enabled us to compare and confirm categorisations based on independently derived chemical profiles. Additionally, all otoliths were reviewed under a compound microscope after LA-ICP-MS ablation to ensure that the laser passed through the core and that there were no other structural defects associated with the sample (*e.g.*, a cracked otolith) that could interfere with chemical analyses. Though lengthy, taking steps like these should be widely adopted and considered to be a standard quality-assurance-quality-control treatment when reporting Sr:Ca of resident

forms of migratory fishes to ensure that analytical error is minimised. We also explored a Mn-based confirmation method of the primordium, but averaging material from a small primordium using a much larger three-dimensional laser spot made that approach infeasible-unreliable.

We referred to Sr:Ca and Ba:Ca across each core-to-edge transect in order to determine whether an individual had a migratory (*i.e.*, marine) or non-migratory (*i.e.*, natal freshwater residential) life history. While previous studies of Hawai'ian amphidromous species have found that marine signatures register at c. 8 mmol mol^{-1} and freshwater signatures register at c. 4–5 mmol mol^{-1} Sr:Ca, other studies have identified differences in Sr uptake among co-occurring species that reflect variation in physiological and elemental otolith accretion rates (Hamer & Jenkins, 2007; Sinclair, 2005). Therefore, we did not set an *a priori* Sr:Ca or Ba:Ca baseline for either marine or freshwater environments; rather, an individual was determined to have had a marine larval phase if there was a consistent and pronounced peak of Sr:Ca in the core region of the otolith that exceeded the Sr:Ca at the otolith edge, which corresponds to the freshwater environment where the individual was captured. Nonetheless, we found that Sr:Ca values at the outer otolith edge for *E. sandwicensis*, *S. hawaiiensis* and *S. stimpsoni* were c. 4 mmol mol^{-1} , which is similar to values that have been obtained for *A. stamineus* (Hogan *et al.*, 2014). Accordingly, a freshwater cut-off of 4 mmol mol^{-1} Sr:Ca and increased Ba:Ca signature was used to determine whether an individual was an ocean migrant or stream resident, respectively. The freshwater baseline for *L. concolor* was notably higher, at c. 8 mmol mol^{-1} . We therefore used 8 mmol mol^{-1} Sr:Ca as a cut-off to classify each *L. concolor* individual as either an ocean migrant or stream resident.

2.4 | Determining larval duration

To determine LD, otoliths were imaged before microchemical analysis and the daily growth increments (*i.e.*, bands) were counted from the primordium to the settlement mark. The settlement mark is a relatively broad increment that exhibits high optical density (Radtko *et al.*, 1988) that is laid down during metamorphosis from the larval form into the post-larval form. It also corresponds with the transition from the marine to the freshwater environment for migratory *A. stamineus* (Hogan *et al.*, 2017). Specimens from 2009 were imaged with a Nikon digital sight DS-fi2 camera and Nikon NIS-elements documentation software using a Nikon Eclipse E200-LED compound microscope ($\times 50$ ocular magnification; www.microscope.healthcare.nikon.com) to count daily growth bands. Each otolith was examined twice by non-sequential independent reads completed by the same reviewer, with samples chosen at random. Any sample that exceeded 5% average per cent error (APE) between the two reads were excluded from further analyses. For the 2011 specimens, multiple images of each otolith were taken in different focal planes with a Leica digital camera mounted to a compound microscope using a $\times 20$ objective lens. The images were then aligned using Adobe Photoshop (www.adobe.com) to create one image of the otolith increments from primordium to

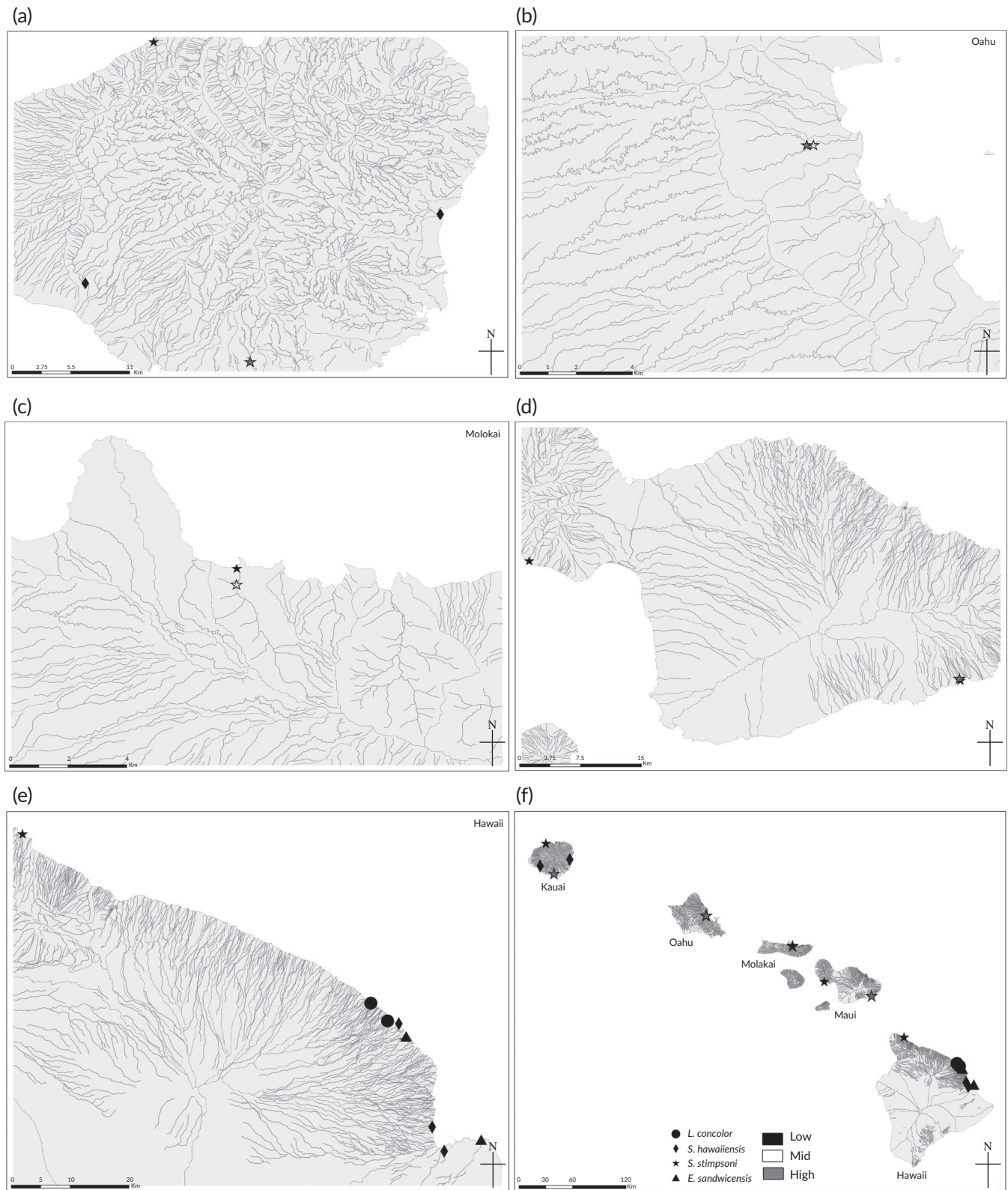


FIGURE 1 Map of Hawaiian islands and river network with gobysampling locations across (a) Kau'ui, (b) Oahu, (c) Molokai, (d) Maui, (e) Hawai'i, (f) the Hawai'ian Archipelago: ●, *Lentipes concolor*; ◆, *Stenogobius hawaiiensis*; ★, *Sicyopterus stimpsoni*; ▲, *Eleotris sandwicensis*. ■ Low, □ Mid, ■ High

edge. Daily growth bands were then 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

randomised between reads. Otoliths that demonstrated more than 5% APE between the two closest reads were excluded from further consideration.

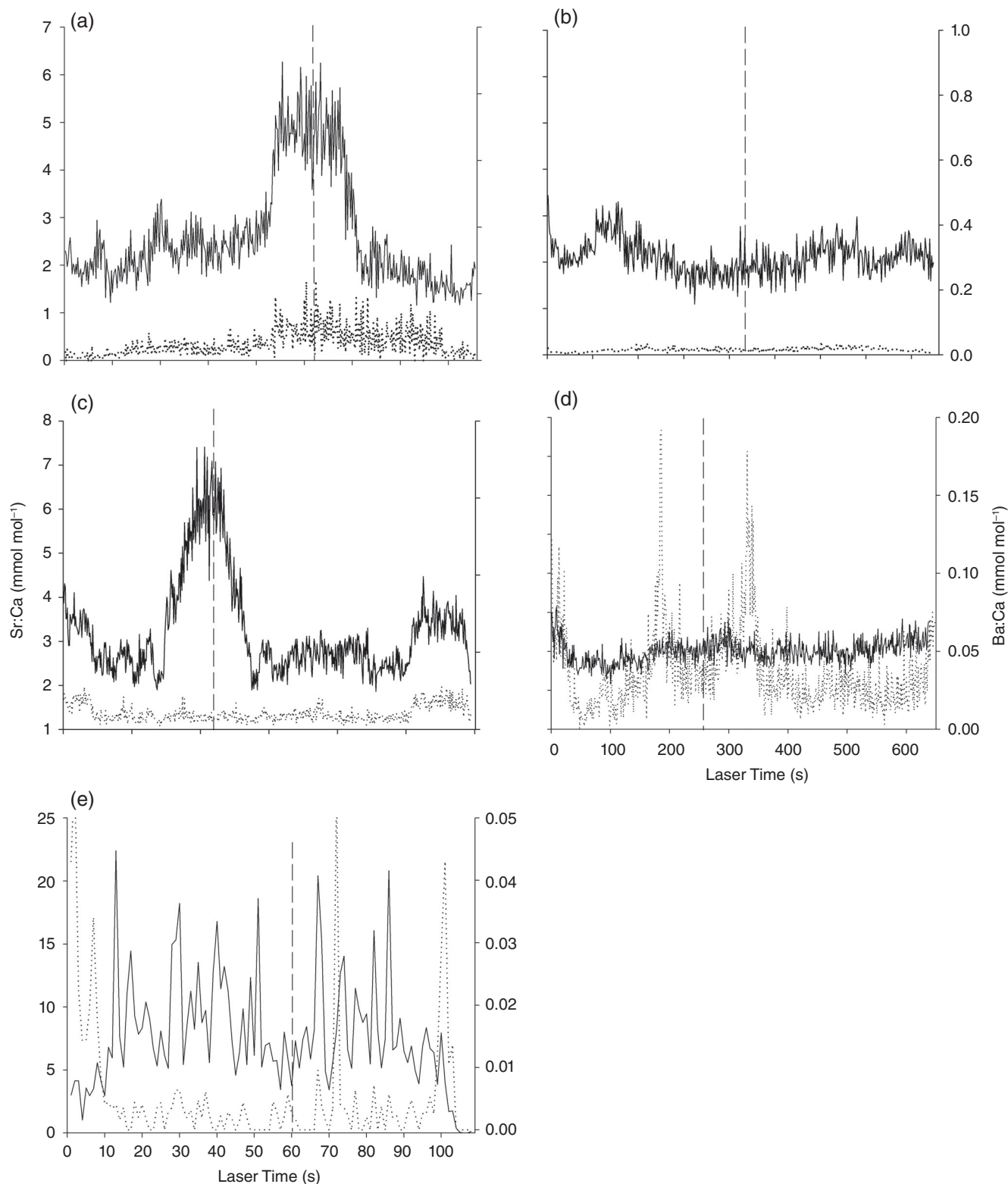


FIGURE 2 Representative Sr:Ca (—) and Ba:Ca (.....) otolith profiles for: (a) migrant and (b) resident *Stenogobius hawaiiensis*, in Hawai'i Honoli'i–Maili Stream; (c) migrant and (d) resident *Eleotris sandwicensis* in Hawai'i Hakalau stream and (e) *Sicyopterus stimpsoni*. †, position of otolith primordium. ---- Primordium, — Sr:Ca, and Ba:Ca

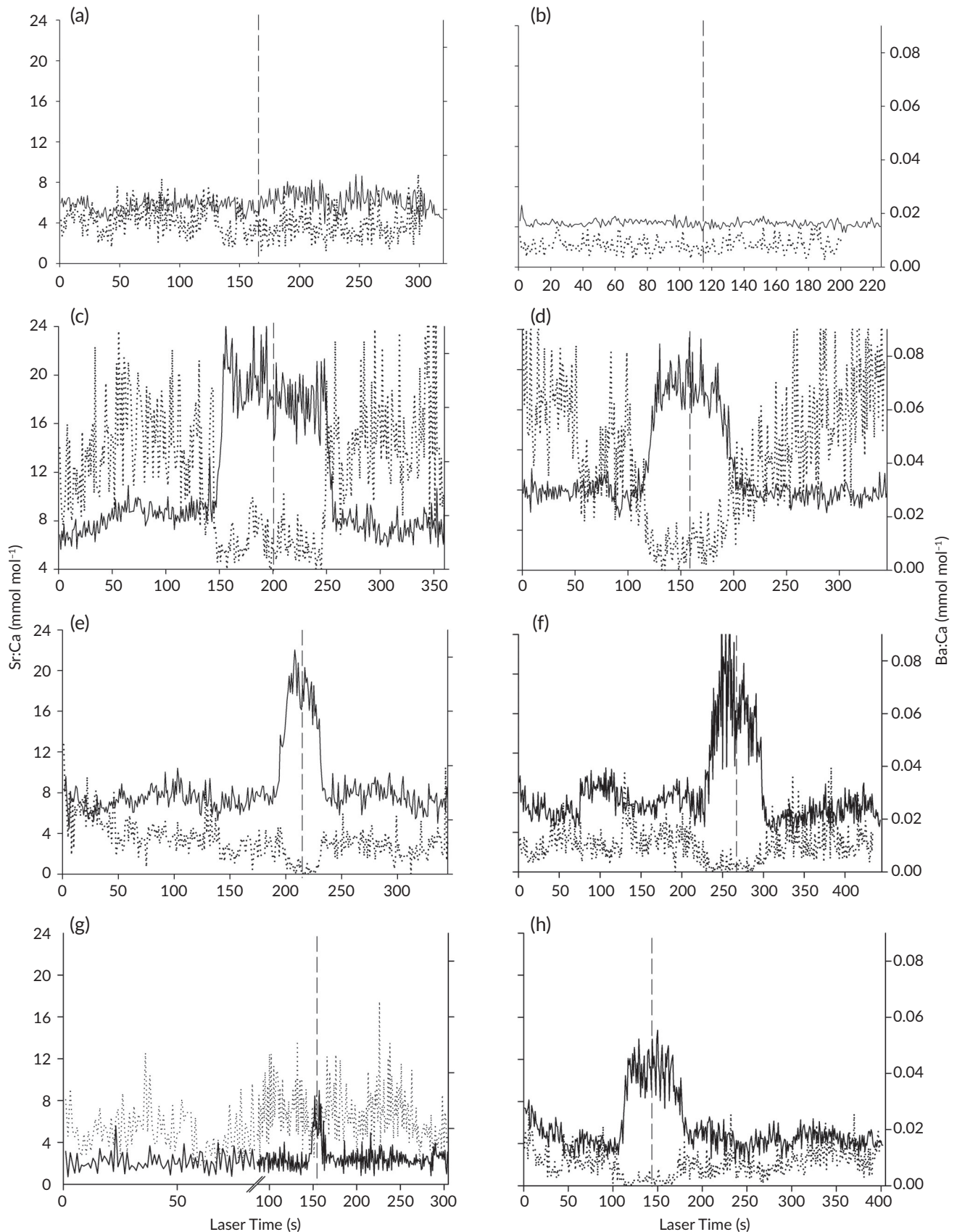


FIGURE 3 Otolith Sr:Ca (—) and Ba:Ca (.....) profiles for all *Lentipes concolor* samples examined in this study ($n = 8$). (a) Migrant and (b) resident individuals from Hawai'i Manoloa Stream deemed not to have migrated to the open ocean due to the lack of Sr:Ca peak at the primordium (|) and the overall lower Sr:Ca values across the entire sample with respect to other samples with visible Sr:Ca peaks at the otolith core. (c), (e) Migrant and (d), (f), (h) resident individuals from Hawai'i Manoloa Stream; (g) migrant individual from Hawai'i Nanue Stream (broken x-axis excludes 2 s of laser time data due to irregularity in otolith). ---- Primordium, — Sr:Ca, and Ba:Ca

3 | RESULTS

3.1 | Marine migration

We found evidence of partial migration in all but one of the study species. Of the eight *L. concolor* specimens analysed, six were categorised as ocean migrants based on the Sr:Ca freshwater cut-off of 8 mmol mol^{-1} and the other two specimens were categorised as stream residents (Figures 1 and 2 and Table 1). Of the 20 *E. sandwicensis* samples analysed, 12 were categorised as ocean migrants and eight were categorised as stream residents (Figures 1 and 3 and Table 1). Of the 26 *S. hawaiiensis* samples analysed, 19 were categorised as ocean migrants and seven were categorised as stream residents (Figures 1 and 3 and Table 1). Analysis of *S. stimpsoni* specimens indicated that all individuals ($n = 55$) were ocean migrants (Figures 1 and 3 and Table 1).

3.2 | Larval duration

All but two specimens met the error threshold (APE <5%) from multiple readings. We were unable to accurately age 2 *S. hawaiiensis* specimens; consequently, both were excluded from further consideration. We found that *L. concolor* exhibited the shortest average LD, which was 89 days for ocean migrants and 82 days for stream residents ($n = 8$, range, 70–106 days, SD = 11.52 days; Figure 2). In comparison, *E. sandwicensis* exhibited an average LD of 101 days for both ocean migrants and stream residents ($n = 20$, range 91–117 days, SD = 7.64 days), whereas *S. hawaiiensis* exhibited an average LD of 113 days for ocean migrants and 115 days for stream residents ($n = 24$, range 81–145 days, SD = 17.68 days; Figure 3). Notably, *Sicyopterus stimpsoni* exhibited the longest average LD at 120 days ($n = 55$, range 65–200 days, SD = 26.42 days; Figure 3).

4 | DISCUSSION

4.1 | Migration chronology

As expected, our findings affirmed that all native Hawai'ian stream gobies exhibit an amphidromous life history, but our results also indicate that all but one exhibit migratory flexibility. Analysis of otolith microchemistry showed that at least one individual of *E. sandwicensis*, *L. concolor* and *S. hawaiiensis* exhibited signatures of lifelong freshwater residency. In contrast, we found that all 55 individuals of *S. stimpsoni* exhibited a signature of marine residency during the larval stage, indicating that the species is obligately amphidromous. These results are not wholly unexpected considering that recent studies have shown that *A. stamineus* and several other amphidromous gobioid fishes exhibit migratory flexibility (Augsburger *et al.*, 2017; Hogan *et al.*, 2014; Michel *et al.*, 2008; Smith & Kwak, 2014). Evidence of migratory flexibility in *L. concolor* ($n = 2$ of 8 individuals) is notable considering the long-standing supposition that all Sicydiine gobies are obligately amphidromous (Iida *et al.*, 2010; McDowall,

2007a). Accordingly, our results indicate that adopting fresh perspectives on migratory flexibility in amphidromous gobies can help improve efforts to conserve and protect at-risk species that are subject to escalating anthropogenic pressures in freshwater and marine environments.

Marine migration has long been considered a defining dimension of the ecology and evolutionary biology of native Hawai'ian amphidromous gobies (Alda *et al.*, 2016; McDowall, 2007a; Moody *et al.*, 2015, 2019). Amphidromy allows for the colonisation of newly formed streams or recolonisation of areas that have been disturbed by volcanic or human activity (McDowall, 2007a). Indeed, it is the only plausible mechanism (*i.e.*, marine dispersal from distant sources) allowing for initial colonisation and establishment of resident populations in Hawai'i (Alda *et al.*, 2016; McDowall, 2007a). Similarly, oceanic dispersal can promote non-local immigration and promote gene flow between disjunct environments, which can sustain or rescue imperilled populations (Berrebi *et al.*, 2005; Blum *et al.*, 2014; Chubb *et al.*, 1998; Cook *et al.*, 2009; McDowall, 2007a). This inference is largely based on evidence of little to no neutral genetic structure in native gobies throughout the Hawai'ian Archipelago, suggesting that marine larval dispersal results in widespread population connectivity among streams and across islands (Alda *et al.*, 2016; Chubb *et al.*, 1998; McDowall, 2007a; Moody *et al.*, 2015). Archipelago-wide stream surveys (Blum *et al.*, 2014) as well as morphometric and simulation studies (Moody *et al.*, 2015; Moody *et al.*, 2019) indicate, however, that larval dispersal is more constrained, perhaps scaling to all catchments (Blum *et al.*, 2014) or to one or a handful of proximate catchments (Moody *et al.*, 2015; Moody *et al.*, 2019) on an island. Evidence of partial migration in all but one species also indicates that obligate marine larval dispersal is not as prevalent as has been previously supposed.

Flexibility in freshwater or marine habitat use can be advantageous for obligate and facultative amphidromous species in oceanic island streams. In Hawai'i and other oceanic high islands, streams are short, with steep slopes and are largely influenced by orographic precipitation. Consequently, streams can be subject to periodic drought and regular periods of flash flooding (Oki, 2004). Because passive downstream movement of larvae (*i.e.*, within a given catchment) is largely driven by surface flow and associated in-stream conditions (Huey *et al.*, 2014), ocean-stream connectivity can be impeded during times of drought and conversely, larvae can be unpredictably swept down and out of a stream during flash floods. Thus, an ability to physiologically cope with unanticipated exposure to marine or freshwater conditions can be advantageous and potentially adaptive, for survival in such spatially and temporally dynamic conditions.

One of the two Sicydiine gobies in this study, *L. concolor* appears to exhibit migratory flexibility. We found that two of the eight specimens analysed did not exhibit an elevated (*i.e.*, marine) Sr:Ca signal in the pre-metamorphosis portion of the otolith. This finding runs contrary to nearly all earlier work indicating that Sicydiine gobies exhibit obligate amphidromy (Augsburger *et al.*, 2017). It is also inconsistent with evidence that there is a phylogenetic component to the ability to forego a marine migration (Augsburger *et al.*, 2017; Lord *et al.*, 2010).

Additionally, it does not align with the widely held perspective that members of the clade depend on the marine environment for larval development (Iida *et al.*, 2010). It also does not align with the premise that marine larval dispersal is essential for sustaining gene flow between disparate populations that can be particularly vulnerable to spatiotemporal variability in ocean-stream connectivity due to a predilection for occupying high elevation and headwater reaches (Chubb *et al.*, 1998; McDowall, 2007a,b). Our findings are consistent, however, with evidence that species of *Sicydium* Gill 1860 are facultatively amphidromous (Smith & Kwak, 2014). This reinforces the possibility that *L. concolor* exhibit plastic or adaptive migratory flexibility that allows for both marine and freshwater contingents. Previous genetic studies indicate a lack of genetic structure in these Hawai'ian freshwater species across the archipelago (McDowall, 2007a; Moody *et al.*, 2015), which may indicate the presence of two life-history types may be triggered by external conditions (Enright, 1970). Species having both residents and marine migrants could be the result of increased mortality from a long migratory corridor (McDowall, 2009) or a bet-hedging strategy due to dynamic larval environments (McIntyre *et al.*, 2016). Accordingly, further work is warranted to confirm our findings and to determine the prevalence and viability of freshwater residency in *L. concolor*.

Migratory flexibility has been demonstrated in two amphidromous eleotrids (Closs *et al.*, 2003; Michel *et al.*, 2008; Smith & Kwak, 2014), often associated with land-locked populations; although it has not been demonstrated in widespread species in the genus *Eleotris* Poey 1860 inhabiting insular streams (Frotté *et al.*, 2020; Mennesson *et al.*, 2015). Members of Oxudercid sub-clades including *Awaous* Valenciennes 1837 and *Rhinogobius* Gill 1859 also show migratory flexibility (Hogan *et al.*, 2014; Huey *et al.*, 2014; Smith & Kwak, 2014; Tsunagawa & Arai, 2008). In the case of *Rhinogobius* again, loss of migration appears linked with land-locked populations (Yamasaki *et al.*, 2015). Owing to other observations of flexibility, we thought it likely that *E. sandwicensis* and *S. hawaiiensis* exhibit partial migration. Consistent with this expectation, we found that a considerable proportion of individuals from both species exhibited lifelong freshwater residency (*E. sandwicensis* 40%, *S. hawaiiensis* 29%). Neither species is able to climb waterfalls due to the lack of fused pelvic fins in *E. sandwicensis* (Kinzie, 1990) and the limited adhesive strength of the sucker of *S. hawaiiensis* (Maie *et al.*, 2012). Both species upstream migrations are limited by large cascades and even small waterfalls. Consequently, they tend to inhabit lower elevation reaches closer to the stream mouth, where banks are often relatively wide, surface flow is slow and in some cases where tidal salt water can intrude. Despite the fact that they live closer to the river mouths, there appears to be a mechanism to retain larvae within the streams, perhaps during period of low flow such as droughts.

Biogeographic processes may also be a factor in the propensity for migration flexibility in the Hawai'ian fishes. Many of the observations of migration flexibility are associated with barriers to downstream migration such as land-locked populations [e.g., *Gobiomorphus* Gill 1863 (Michel *et al.*, 2008), *Rhinogobius* (Tsunagawa & Arai, 2008)] or large continental river systems which may retain larvae (e.g.,

Awaous; Huey *et al.*, 2014). If migration flexibility has evolved in these taxa in response to selection for non-migrants then a similar process could be happening in Hawai'i. Hawai'ian populations are not land-locked, nor are the rivers particularly large to prevent larval egress, however, Hawai'i is extremely remote and larvae that migrate to sea in Hawai'i must return to a stream in Hawai'i or else will be lost at sea. Theory predicts that when habitat patchiness increases, species should evolve shorter dispersal distances to retain more larvae in natal habitats (Pinsky *et al.*, 2012). Due to the high degree of patchiness in Hawai'ian stream habitats and the risk of larval loss, it is possible that the native Hawai'ian taxa have adapted to cope through the evolution of migration flexibility. Alternatively, the habitat patchiness selects for species that are pre-adapted for migration flexibility such that inflexible species are unlikely to persist.

The question remains how precisely do the larvae of the Hawai'ian taxa survive in the stream environments, specifically what do they feed on? At first-feeding these Hawai'ian freshwater species are known to be planktivorous (Schoenfuss & Blob, 2007) with unicellular algae, small rotifers, copepods and other plankton identified in the gut (Lindstrom, 1998). *Sicyopterus stimpsoni* is unique in that a ventral mouth and feeding position occurs rapidly only after the transition from salt water to fresh water (Schoenfuss *et al.*, 1997), which may indicate the required cue for development provided by a shift between the two aquatic environments. For the other species, however, if larvae can physiologically cope with a freshwater environment without a saltwater requirement for development, dynamic stream processes may facilitate adequate nutrient cycling and access to prey allowing for survival through the larval phase. Tropical streams are mostly categorised as oligotrophic but nutrient delivery increases during periodic flooding, which can increase larval survival in streams (Kerr and Secor, 2010). Alternatively, during periodic drought, disconnected freshwater pools can form and concentrate larvae and their phytoplankton prey, (Rypel, 2009) which may provide access to adequate nutrition sources for larval development. Additionally, closely related species of *Stenogobius* Bleeker 1874 have shown egg size variation that may reduce larval starvation for land-locked types when compared with the smaller eggs of migratory counterparts (Maruyama *et al.*, 2003). Lindstrom *et al.* (2012) found that there were two larval morphologies for *Awaous stamineus* (large and small), but it is unknown whether these different larval forms are linked to migrant and non-migrant forms of this species. Further examination is needed to explore larval development and the mechanisms that may allow for survival of resident types in the Hawai'ian freshwater environments.

4.2 | Larval duration

Our study reinforces earlier work and fills gaps in understanding of LD in all five native Hawai'ian amphidromous gobies. Though the LD of three species were assessed in earlier work, estimates for only two were based on robust sample sizes (*L. concolor* (Radtke *et al.*, 2001) and *A. stamineus* (Hogan *et al.*, 2014)). Our mean ($\pm$ SD) LD estimate of 87 ± 11.52 days with a range of 70–106 days for *L. concolor* is consistent

with Radtke *et al.*, (2001) estimate of a mean LD of 86.2 ± 8.5 days with a range of 63–106 days. On the other hand, our mean LD estimate of 114 ± 17.68 days for *S. hawaiiensis* is lower than the estimate of 135 ± 9.2 days reported by Radtke *et al.* (1988), but our estimate is based on a larger sample size and a wider range of age estimates. We estimated a mean LD of 102 ± 7.64 days for *E. sandwicensis*, which overlaps with previous reports of c. 60–120 days for two *Eleotris* spp. in Japan (Maeda *et al.*, 2008), but it is longer than that of *Eleotris perniger* (Cope 1871) (65 ± 11 days) in the Caribbean (Engman *et al.* 2017) and *E. fusca* in the Pacific Ocean (90 ± 19.2 days) and Indian Ocean (63.3 ± 11 days; Mennesson *et al.*, 2015). We also estimated a mean LD of 120 ± 26.42 days for *S. stimpsoni*, which is similar to the mean LD of *S. lagocephalus* (131 ± 3.4 days) from Vanuatu and New Caledonia, which is longer than *Sicyopterus aiensis* Keith, Watson & Marquet 2004 (79.2 ± 4.6 days) and *Sicyopterus sarasini* Weber & de Beaufort 1915 (76.5 ± 3.9 days; Lord *et al.*, 2010).

The extended LD found in all of the Hawai'ian species is consistent with the premise that an extended larval stage can translate to greater dispersal distances through the marine environment. Marine-larval dispersal facilitates colonisation of available habitat and population connectivity among disjunct locations (Alda *et al.*, 2016; Murphy & Cowan, 2007; Radtke *et al.*, 2001). Prolonged LD, however, can expose fish to greater predation pressure, which might favour variation in LD according to life history (i.e., resident v. migrant), but we did not find evidence of differentiation. This finding is consistent with the expectation that a long LD can help separate periods of intraspecific resource use between different life stages, thereby reducing inter-generational competition (Lord *et al.*, 2010; Murphy & Cowan, 2007). Although it has been noted that a short LD might promote the rise of endemic species by constraining dispersal (Murphy & Cowan, 2007; Radtke *et al.*, 2001), all of the amphidromous species found in Hawai'ian streams are endemic, including those that have a relatively long LD (Hogan *et al.*, 2014; Lindstrom *et al.*, 2012; McDowall, 2007a). While this probably has limited the rise of adaptive radiations among islands within archipelagos (Alda *et al.*, 2016), it suggests that other factors determine species endemism. Our findings point to migration flexibility as a potential factor that may limit dispersal among widely separated oceanic islands.

This study underscores the importance of understanding the propensity and nature of migration in order to sustain native Hawai'ian amphidromous gobies (Hogan *et al.*, 2014). Larvae, especially early-stage larvae, are thought to experience high mortality rates as a consequence of exposure to heterogeneous and dynamic conditions in both marine and stream ecosystems (Cushing, 1977; Cushing, 1990; Hjort, 1914; Houde, 2008; Lasker, 1978; Moody *et al.*, 2019). Increasing pressures in both environments may further depress survival and recruitment (Cushing, 1975; Hjort, 1914, 1926; Lisi *et al.*, 2018; Moody *et al.*, 2017; Walter *et al.*, 2012). Marine and freshwater conditions are becoming even more dynamic with shifting mean climate conditions and intensification of natural climatic cycles (Chu & Chen, 2005; IPCC, 2014). Along with experiencing climate-driven shifts in surface flow (Clilverd *et al.*, 2019; Oki, 2004; Walter *et al.*, 2012), Hawai'ian streams have also been subject to alteration from human

activities, including water abstraction, increased land-use and the introduction of invasive species (Brasher 2003; Lisi *et al.*, 2018; Moody *et al.*, 2017; Walter *et al.*, 2012). Considering the prevalence of partial migration among native Hawai'ian gobies, management plans organised around migration flexibility might help dampen exposure risk in both environments and consequently reduce the likelihood of localised extirpation (McIntyre *et al.*, 2016). For example, an in-stream resident contingent might persist when cohorts of marine immigrants are lost due to unstable marine conditions, and *vice versa* (Hogan *et al.*, 2014). Management approaches could be adopted that recognise this possibility. Accordingly, it would be prudent to protect, improve, or create in-stream habitat for non-migratory residents in order to buffer against unfavourable marine environs, which are not as responsive to management interventions (i.e., due to a mismatch in scale). Appropriate actions might include restoring base flows, maintaining water quality, removing invasive species that compete or prey upon native larvae, preserving habitat diversity so that non-migrant fishes of multiple species can complete their life cycles in-stream (Blum *et al.*, 2014; Brasher, 2003; Hain *et al.*, 2016, 2019; Heim-Ballew, 2019; Lisi *et al.*, 2018; Walter *et al.*, 2012). Care should, of course, be taken to focus efforts on key stream segments in order to deliver the greatest benefits to local populations. While this might call for targeting habitat used by stream residents for feeding and reproduction, it might be necessary to focus on downstream migratory corridors, including estuarine and near-shore coastal areas that may influence immigration and recruitment (Blum *et al.*, 2014; Hain *et al.*, 2019; Walter *et al.*, 2012).

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REFERENCES

- Alda, F., Gagne, R. B., Walter, R. P., Hogan, J. D., Moody, K. N., Zink, F., ... Blum, M. J. (2016). Colonization and demographic expansion of freshwater fauna across the Hawai'ian archipelago. *Journal of Evolutionary Biology*, 29, 2054–2069.

- Augspurger, J. M., Warburton, M., & Closs, G. P. (2017). Life-history plasticity in amphidromous and catadromous fishes: A continuum of strategies. *Reviews in Fish Biology and Fisheries*, 27, 177–192.
- Ayers, S.D. (2010). A review of the species status of the Angayukaksurak charr (*Salvelinus anaktuvukensis*) of northern Alaska: Perspectives from molecular and morphological data (PhD thesis). University of Alaska Fairbanks, Fairbanks.
- Benbow, M. E., Burky, A. J., & Way, C. M. (2004). Morphological characteristics and species separation of Hawaiian postlarval amphidromous fishes. *Micron*, 37, 129–144.
- Berrebi, P., Cattaneo-Berrebi, G., Valdae, P., Ricou, J. F., & Hoareau, T. (2005). Genetic homogeneity in eight freshwater populations of *Sicyopterus lagocephalus*, an amphidromous gobiid of La Réunion Island. *Marine Biology*, 148, 179–188.
- Bickford, N., & Hannigan, R. (2005). Stock identification of walleye via otolith chemistry in the eleven Point River, Arkansas. *North American Journal of Fisheries Management*, 25, 1542–1549.
- Blob, R. W., Bridges, W. C., Ptacek, M. B., Maie, T., Cediell, R. A., Bertolas, M. M., ... Schoenfuss, H. L. (2008). Morphological selection in an extreme flow environment: Body shape and waterfall-climbing success in the Hawaiian stream fish *Sicyopterus stimpsoni*. *Integrative and Comparative Biology*, 48, 734–749.
- Blob, R. W., Kawano, S. M., Moody, K. N., Bridges, W. C., Maie, T., Ptacek, M. B., ... Schoenfuss, H. L. (2010). Morphological selection and the evaluation of potential tradeoff between escape from predators and the climbing of waterfalls in the Hawaiian stream goby *Sicyopterus stimpsoni*. *Integrative and Comparative Biology*, 50, 1185–1199.
- Blum, M. J., Gilliam, J. F., & McIntyre, P. B. (2014). Development and use of genetic methods for assessing aquatic environmental condition and recruitment dynamics of native stream fishes on Pacific Islands. In *United States Department of Defense, SERDP RC-1646*. New Orleans, LA: Tulane University.
- Brasher, A. M. (2003). Impacts of human disturbances on biotic communities in Hawaiian streams. *AIBS Bulletin*, 53, 1052–1060.
- Chapman, B. B., Skov, C., Hulthén, K., Brodersen, J., Nilsson, P. A., Hansson, L. A., & Brönmark, C. (2012). Partial migration in fishes: Definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*, 81, 479–499.
- Chu, P. S., & Chen, H. (2005). Interannual and interdecadal rainfall variations in the Hawaiian islands. *Journal of Climate*, 18, 4796–4813.
- Chubb, A. L., Zink, R. M., & Fitzsimons, J. M. (1998). Patterns of mtDNA variation in Hawaiian freshwater fishes: The phylogeographic consequences of amphidromy. *Journal of Heredity*, 89, 8–16.
- Ciliverd, H. M., Tsang, Y. P., Infante, D. M., Lynch, A. J., & Strauch, A. M. (2019). Long-term streamflow trends in Hawai'i and implications for native stream fauna. *Hydrological Processes*, 33, 699–719.
- Closs, G. P., Smith, M., Barry, B., & Markwitz, A. (2003). Non-diadromous recruitment in coastal populations of common bully (*Gobiomorphus cotidianus*). *New Zealand Journal of Marine and Freshwater Research*, 37, 301–313.
- Cook, B. D., Bernays, S., Pringle, C. M., & Hughes, J. M. (2009). Marine dispersal determines the genetic population structure of migratory stream fauna of Puerto Rico: Evidence for Island-scale population recovery processes. *Journal of the North American Benthological Society*, 28, 709–718.
- Cushing, D. H. (1975). *Marine Ecology and Fisheries*. Cambridge, England: CUP Archive.
- Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. In *Advances in Marine Biology* (Vol. 26, pp. 249–293). Cambridge, MA: Academic Press.
- Cushing, J. M. (1977). Periodic time-dependent predator-prey systems. *SIAM Journal on Applied Mathematics*, 32, 82–95.
- England, R., & Filburt, R. (1997). Discovery of the native goby, *Lentipes concolor*, above Hawaii's highest waterfall, Hi'ilawe falls. *Bishop Museum Occasional Papers*, 49, 62–64.
- Engman, A. C., Kwak, T. J., & Fischer, J. R. (2017). Recruitment phenology and pelagic larval duration in Caribbean amphidromous fishes. *Freshwater Science*, 36, 851–865.
- Enright, J. T. (1970). Ecological aspects of endogenous rhythmicity. *Annual Review of Ecology and Systematics*, 1, 221–238.
- Fitzsimmons, J. M., & Nishimoto, R. T. (1995). Use of fish behavior in assessing the effects of hurricane Iniki on the Hawaiian islands of Kaua'i. *Environmental Biology of Fishes*, 43, 39–50.
- Frotté, L., Ringelstein, J., Monti, D., Robert, M., Pécheyran, C., Améziane, N., & Tabouret, H. (2020). Detection of full and limited amphidromous migratory dynamics of fish in Caribbean rivers. *Ecology of Freshwater Fish*, 29, 132–144.
- Hain, E. F., Kennen, J. G., Caldwell, P. V., Nelson, S. A., Sun, G., & McNulty, S. G. (2018). Using regional scale flow-ecology to identify catchments where fish assemblages are most vulnerable to changes in water availability. *Freshwater Biology*, 63, 928–945.
- Hain, E. F., Lamphere, B. A., Blum, M. J., McIntyre, P. B., Nelson, S. A., & Gilliam, J. F. (2016). Comparison of visual survey and mark-recapture population estimates of a benthic fish in Hawaii. *Transactions of the American Fisheries Society*, 145, 878–887.
- Hain, E. F., Moody, K. N., Lamphere, B. A., Nelson, S. A., McIntyre, P. B., Gilliam, J. F., & Blum, M. J. (2019). Migratory gauntlets on oceanic islands: Watershed disturbance increases the cost of amphidromy. *Ecology of Freshwater Fish*, 28, 446–458. <https://doi.org/10.1111/eff.12467>.
- Hamer, P. A., & Jenkins, G. P. (2007). Comparison of spatial variation in otolith chemistry of two fish species and relationships with water chemistry and otolith growth. *Journal of Fish Biology*, 71, 1035–1055.
- Heim-Ballew, H. (2019). *Identifying migration flexibility and the environmental factors that influence variation in recruitment success in partially migratory Hawaiian fishes* (Doctoral dissertation). Texas A&M University-Corpus Christi, Corpus Christi, Texas.
- Hicks, A. (2012). *Facultative amphidromy in galaxiids and bullies: The science, ecology and management implications* (PhD thesis). University of Otago, Dunedin, New Zealand.
- Hjort, J. (1914). *Fluctuations in the great fisheries of northern Europe viewed in the light of biological research*. Oxford, England: ICES.
- Hjort, J. (1926). Fluctuations in the year classes of important food fishes. *ICES Journal of Marine Science*, 1, 5–38.
- Hogan, J. D., Blum, M. J., Gilliam, J. F., Bickford, N., & McIntyre, P. B. (2014). Consequences of alternative dispersal strategies in a putatively amphidromous fish. *Ecology*, 95, 2397–2408.
- Hogan, J. D., Kozdon, R., Blum, M. J., Gilliam, J. F., Valley, J. W., & McIntyre, P. B. (2017). Reconstructing larval growth and habitat use in an amphidromous goby using otolith increments and microchemistry. *Journal of Fish Biology*, 90, 1338–1355.
- Houde, E. D. (2008). Emerging from Hjort's shadow. *Journal of Northwest Atlantic Fishery Science*, 41, 53–70.
- Huey, J. A., Crook, D. A., Macdonald, J. I., Schmidt, D. J., Marshall, J. C., Balcombe, S. R., ... Hughes, J. M. (2014). Is variable connectivity among populations of a continental gobiid fish driven by local adaptation or passive dispersal? *Freshwater Biology*, 59, 1672–1686.
- Iida, M., Watanabe, S., Yamada, Y., Lord, C., Keith, P., & Tsukamoto, K. (2010). Survival and behavioral characteristics of amphidromous goby larvae of *Sicyopterus japonicus* (Tanaka, 1909) during their downstream migration. *Journal of Experimental Marine Biology and Ecology*, 383, 17–22.
- IPCC (2014). In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, et al. (Eds.), *Climate change 2014: Impacts, adaptation and vulnerability. Part A: Global and Sectoral Aspects contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change* (p. 1132). Cambridge, UK and New York, NY: Cambridge University Press.

- Kano, Y., Iida, M., Tetsuka, K., Saitoh, T., Kato, F., Sato, T., & Nishida, S. (2014). Effect of waterfalls on fluvial fish distribution and landlocked *Rhinogobius brunneus* populations on Yakushima Island, Japan. *Ichthyological Research*, 61, 305–316.
- Kerr, L. A., & Secor, D. H. (2010). Latent effects of early life history on partial migration for an estuarine-dependent fish. *Environmental Biology of Fishes*, 89, 479–492.
- Kinzie, R. A., III. (1990). *Species profiles: Life histories and environmental requirements of coastal vertebrates and invertebrates Pacific Ocean region: Amphidromous macrofauna of Hawai'ian Island streams* (Technical report EL-89-10, 20314). Washington, DC: Department of the Army.
- Kinzie, R. A. (1988). Habitat utilization by Hawai'ian stream fishes with reference to community structure in oceanic Island streams. *Environmental Biology of Fishes*, 22, 179–192.
- Kuang, T., Tornabene, L., Li, J., Jiang, J., Chakrabarty, P., Sparks, J. S., ... Li, C. (2018). Phylogenomic analysis on the exceptionally diverse fish clade Gobioidae (Actinopterygii: Gobiiformes) and data-filtering based on molecular clocklikeness. *Molecular Phylogenetics and Evolution*, 128, 192–202.
- Lasker, R. (1978). The relation between oceanographic conditions and larval anchovy food in the California current: Identification of factors contributing to recruitment failure. *Rapports et Proces-verbaux des Reunions Conseil International pour l'Exploration de la Mer*, 173, 212–230.
- Lindstrom, D. P. (1998). *Reproduction, early development and larval transport dynamics of amphidromous Hawaiian gobioids* (Doctoral dissertation). University of Hawaii, Manoa.
- Lindstrom, D. P., Blum, M. J., Walter, R. P., Gagne, R. B., & Gilliam, J. F. (2012). Molecular and morphological evidence of distinct evolutionary lineages of *Awaous guamensis* in Hawai'i and Guam. *Copeia*, 2012, 293–300.
- Lisi, P. J., Childress, E. S., Gagne, R. B., Hain, E. F., Lamphere, B. A., Walter, R. P., ... McIntyre, P. B. (2018). Overcoming urban stream syndrome: Trophic flexibility confers resilience in a Hawai'ian stream fish. *Freshwater Biology*, 63, 492–502.
- Lord, C., Brun, C., Hauteceur, M., & Keith, P. (2010). Insights on endemism: Comparison of the duration of the marine larval phase estimated by otolith microstructural analysis of three amphidromous species (Gobioidae: Sicydiinae) from Vanuatu and New Caledonia. *Ecology of Freshwater Fish*, 19, 26–38.
- Lord, C., Tabouret, H., Clavier, F., Pécheyran, C., & Keith, P. (2011). Femtosecond laser ablation ICP-MS measurement of otolith Sr:Ca and Ba: Ca composition reveal differential use of freshwater habitats for three amphidromous *Sicyopterus* (Teleostei: Gobioidae: Sicydiinae) species. *Journal of Fish Biology*, 79, 1304–1321.
- Luton, C. D., Brasher, A. M., Durkin, D. C., & Little, P. A. I. G. E. (2005). Larval drift of amphidromous shrimp and gobies on the Island of Oahu, Hawaii. *Micronesica-Agana*, 38, 1.
- Maeda, K., Yamasaki, N., Kondo, M., & Tachihara, K. (2008). Reproductive biology and early development of two species of sleeper, *Eleotris acanthopoma* and *Eleotris fusca* (Teleostei: Eleotridae). *Pacific Science*, 62, 327–340.
- Maie, T., Schoenfuss, H. L., & Blob, R. (2012). Performance and scaling of a novel locomotor structure: Adhesive capacity of climbing gobiid fishes. *Journal of Experimental Biology*, 215, 3925–3936.
- Maruyama, A., Rusuwa, B., & Yuma, M. (2003). Interpopulational egg-size variation of a landlocked *Rhinogobius* goby related to the risk of larval starvation. *Environmental Biology of Fishes*, 67, 223–230.
- McDowall, R. M. (2007a). On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish and Fisheries*, 8, 1–13.
- McDowall, R. M. (2007b). Hawai'ian stream fishes: The role of amphidromy in history, ecology and conservation biology. *Bishop Museum Bulletin in Cultural and Environmental Studies*, 3, 3–9.
- McDowall, R. M. (2009). Early hatch: A strategy for safe downstream larval transport in amphidromous gobies. *Reviews in Fish Biology and Fisheries*, 19, 1.
- McIntyre, P. B., Reidy Liermann, C., Childress, E., Hamann, E. J., Hogan, J. D., Januchowski-Hartley, S. R., ... Pracheil, B. M. (2016). *Conservation of migratory fishes in freshwater ecosystems* (pp. 324–360). Cambridge, UK: Cambridge University Press.
- Mennesson, M. I., Tabouret, H., Pécheyran, C., Feunteun, E., & Keith, P. (2015). Amphidromous life cycle of *Eleotris fusca* (Gobioidae: Eleotridae), a widespread species from the indo-Pacific studied by otolith analyses. *Cybiu: Revue Internationale days'Ichtyologie*, 39, 249–260.
- Michel, C., Hicks, B. J., Stölting, K. N., Clarke, A. C., Stevens, M. I., Tana, R., ... Van den Heuvel, M. R. (2008). Distinct migratory and non-migratory ecotypes of an endemic New Zealand eleotrid (*Gobiomorphus cotidianus*) – implications for incipient speciation in Island freshwater fish species. *BMC Evolutionary Biology*, 8, 49.
- Moody, K. N., Gagne, R. B., Heim-Ballew, H., Alda, F., Hain, E. F., Lisi, P., ... Blum, M. J. (2017). Invasion hotspots and ecological saturation of streams across the Hawai'ian islands. *Cybiu*, 4, 127–156.
- Moody, K. N., Hunter, S. N., Childress, M. J., Blob, R. W., Schoenfuss, H. L., Blum, M. J., & Ptacek, M. B. (2015). Local adaptation despite high gene flow in the waterfall-climbing Hawai'ian goby, *Sicyopterus stimpsoni*. *Molecular Ecology*, 24, 545–563.
- Moody, K. N., Wren, J. L., Kobayashi, D. R., Blum, M. J., Ptacek, M. B., Blob, R. W., ... Childress, M. J. (2019). Evidence of local adaptation in a waterfall-climbing Hawai'ian goby fish derived from coupled biophysical modeling of larval dispersal and post-settlement selection. *BMC Evolutionary Biology*, 19, 88.
- Murphy, C. A., & Cowan, J. H. (2007). Production, marine larval retention or dispersal and recruitment of amphidromous Hawai'ian gobioids: Issues and implications. *Bishop Museum Bulletin in Cultural and Environmental Studies*, 3, 63–74.
- Nordlie, F. G. (2012). Life-history characteristics of eleotrid fishes of the western hemisphere and perils of life in a vanishing environment. *Reviews in Fish Biology and Fisheries*, 22, 189–224.
- Oki, D. S. (2004). *Trends in streamflow characteristics at long-term gaging stations, Hawai'i* (Vol. 120). United States Geological Society.
- Pinsky, M. L., Palumbi, S. R., Andréfouët, S., & Purkis, S. J. (2012). Open and closed seascapes: Where does habitat patchiness create populations with high fractions of self-recruitment? *Ecological Applications*, 22, 1257–1267.
- Radtke, R. L., & Kinzie, R. A., III. (1996). Evidence of a marine larval stage in endemic Hawai'ian stream gobies from isolated high-elevation locations. *Transactions of the American Fisheries Society*, 125, 613–621.
- Radtke, R. L., Kinzie, R. A., III, & Shafer, D. J. (2001). Temporal and spatial variation in length of larval life and size at settlement of the Hawai'ian amphidromous goby *Lentipes concolor*. *Journal of Fish Biology*, 59, 928–938.
- Radtke, R. L., Kinzie, R. A., & Folsom, S. D. (1988). Age at recruitment of Hawai'ian freshwater gobies. *Environmental Biology of Fishes*, 23, 205–213.
- Radtke, R. L., Townsend, D. W., Kinzie, R. A., III, & Fey, D. (1999). Two-dimensional X-ray mapping of otoliths, a high-resolution technique for determining amphidromy in the tropical goby *Lentipes concolor* (gill). *Journal of Experimental Marine Biology and Ecology*, 238, 21–27.
- Rosenfeld, J. S., & Hatfield, T. (2006). Information needs for assessing critical habitat of freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 63, 683–698.
- Rypel, A. L. (2009). Climate-growth relationships for largemouth bass (*Micropterus salmoides*) across three southeastern USA states. *Ecology of Freshwater Fish*, 18, 620–628.
- Schoenfuss, H. L. (1997). *Metamorphosis of the Hawai'ian stream goby Sicyopterus stimpsoni: A structural, functional and behavioral analysis* (Doctoral Dissertation). Louisiana State University, Baton Rouge, Louisiana.
- Schoenfuss, H. L., & Blob, R. W. (2007). The importance of functional morphology for fishery conservation and management: Applications to Hawai'ian amphidromous fishes. *Biology of Hawai'ian Streams and Estuaries*, 3, 125–141.

- Shen, K. N., Lee, Y. C., & Tzeng, W. N. (1998). Use of otolith microchemistry to investigate the life history pattern of gobies in a Taiwanese stream. *Zoological Studies-Taipei*, 37, 322–329.
- Sinclair, D. J. (2005). Correlated trace element "vital effects" in tropical corals: A new geochemical tool for probing biomineralization. *Geochemical et Cosmochimica Acta*, 69, 3625–3284.
- Smith, W. E., & Kwak, T. J. (2014). Otolith microchemistry of tropical diadromous fishes: Spatial and migratory dynamics. *Journal of Fish Biology*, 84, 913–928.
- Tabouret, H., Tomadin, M., Taillebois, L., Iida, M., Lord, C., Pecheyran, C., & Keith, P. (2014). Amphidromy and marine larval phase of ancestral gobiids *Rhyacichthys guilberti* and *Protogobius attiti* (Teleostei: Rhyacichthyidae). *Marine and Freshwater Research*, 65, 776–783.
- Tsunagawa, T., & Arai, T. (2008). Flexible migration of Japanese freshwater gobies *Rhinogobius* spp. as revealed by otolith Sr: Ca ratios. *Journal of Fish Biology*, 73, 2421–2433.
- Walter, R. P., Hogan, J. D., Blum, M. J., Gagne, R. B., Hain, E. F., Gilliam, J. F., & McIntyre, P. B. (2012). Climate change and conservation of endemic amphidromous fishes in Hawai'ian streams. *Endangered Species Research*, 16, 261–272.
- Walther, B. D., & Nims, M. K. (2015). Spatiotemporal variation of trace elements and stable isotopes in subtropical estuaries: I. Freshwater endmembers and mixing curves. *Estuaries and Coasts*, 38, 754–768.
- Yamasaki, Y. Y., Nishida, M., Suzuki, T., Mukai, T., & Watanabe, K. (2015). Phylogeny, hybridization and life history evolution of *Rhinogobius* gobies in Japan, inferred from multiple nuclear gene sequences. *Molecular Phylogenetics and Evolution*, 90, 20–33.

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