Pelagic Larval Duration and Amphidromy
Not Linked to Endemism in *Stiphodon* Gobies

A Thesis

by

Macaulay White

Submitted to the College of Graduate Studies of Texas A&M University and Texas A&M University -Corpus Christi in partial fulfillment of the requirements for the joint degree

of

MASTER OF SCIENCE

Approved as to style and content by:

Dr. Frank Pezold
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December, 2015

Major Subject: Marine Biology

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ABSTRACT

PELAGIC LARVAL DURATION AND AMPHIDROMY NOT LINKED TO ENDEMISM IN *STIPHODON* GOBIES

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Chair of Advisory Committee: Dr. Pezold

Sicydiine gobies are a diverse group of freshwater fishes characterized by a unique life history and morphological features that allow them to inhabit oceanic island streams throughout tropical and sub-tropical regions (Taillebois et al. 2012; Keith and Lord 2011). Larval dispersal is achieved by an amphidromous life history in which adults live and spawn in fresh water and larvae develop at sea (Radtke et al. 1988). Sicydiine gobies often account for the majority of freshwater fauna in island streams, and many are endemic to particular regions. The subfamily Sicydiinae currently consists of nine genera of which the genus *Stiphodon* exhibits the most diversity and is widespread throughout the western Pacific. Many species of *Stiphodon* have very large distributional ranges, while others are more restricted. Dispersal plays a large role in the distribution of species, greater dispersal capabilities can lead to larger range sizes and vice versa. Variations in the number of individuals migrating to the sea may influence the dispersal capabilities, as well as the duration of time that larvae spend at sea. Variation in these traits may influence the geographic range size for a given species. To test these hypotheses, we counted daily growth rings from otoliths to determine the pelagic larval duration and used otolith chemistry to determine migratory behaviors of different *Stiphodon* species exhibiting different range sizes.

Introduction

Dispersal is achieved by many organisms at some point in their lifecycle whether it be adults, juveniles, or larvae (Sale et al. 2005). Organismal dispersal is driven by a variety of ecological and evolutionary processes such as environmental factors, body size, population abundance, latitude, and colonization and extinction dynamics (Lester et al. 2005). Dispersal plays a key role in exploitation of essential resources necessary for the overall survival of a species. Dispersal benefits populations by enabling gene flow, increases species range to help cope with fragmentation and habitat loss, and increase the ability to respond to changing environment (Clobert et al. 2009). Many fishes have evolved migration traits that allow them to move between very different environments. Diadromy refers to migrations by adult fishes between freshwater and marine environments for spawning (McDowall, 2007). Diadromous lifecycles are of interest because of the extreme adaptations needed for migrations as well as being a source of connectivity, which has significant influence on the evolutionary ecology and biogeography of diadromous fishes. Diadromous lifecycles can have significant effects on gene flow and genetic diversity and play an important role in connectivity of oceanic islands (Bloom and Lovejoy, 2014). A type of diadromy known as amphidromy has been extremely influential in colonizing freshwater streams of oceanic islands. Oceanic islands provide unique habitats and are the most remote sources for resource exploitation and colonization. These islands are relatively young compared to continental land masses and are usually formed by underwater volcanoes. Oceanic islands are characterized by having special niches, high endemism, and extreme isolation (Gellespie, 2007). Amphidromy is a life history that is widespread among phyla that inhabit oceanic island streams. It is known that amphidromy is an ecological link between island rivers and coastal waters and theoretically aids in species' range expansions (Keith, 2003; Cook et al., 2009). Amphidromous taxa of fishes include gobies, galaxiids, some members of the family Cottidae, and Rhyacichthyids (McDowall 2010).

Freshwater gobies belonging to the subfamily Sicydiinae and the family Gobiidae (Gill & Mooi, 2012; Taillebois et al. 2013), are a group of freshwater fishes that inhabit rivers on oceanic island streams throughout tropical and sub-tropical regions. With over 170 species, Sicydiine gobies are thought to be the most diverse group of fishes occurring on oceanic island. These fishes are highly adapted for island living due to their amphidromous life history and unique morphological characteristics (Keith and Lord 2011). Amphidromy refers to a life history in which adults live and spawn in fresh water and the larvae are washed into the ocean where they spend the duration of the larval stage feeding in the marine environment. After a period of time at sea (several weeks to many months), juveniles must locate freshwater and migrate back upstream where they live the remainder of their lives (McDowall 2009). Another significant feature of sicydiine gobies is the modification of the pelvic fins to form a suction disc. This suction disc, used in combination with powerful oral suction, enables them to migrate up river with ease (Schoenfuss and Blob 2007). These powerful pelvic fins also help individuals of the genus *Lentipes* to reach parts of stream that are less utilized by other aquatic species. *Lentipes concolor* uses its pelvic disc to climb waterfalls in Hawai'i to inhabit rivers above (Blob et al. 2006). The climbing abilities of *L. concolor* allows them to scale even one of the highest falls in Hawai'i, the Hi'ilawe Waterfall, which reaches just over 1,200 feet high. It is features like these that have possibly allowed stream gobies to diversify and utilize specialized niches of island rivers (Maie et al. 2009).

Amphidromy is an important trait promoting the colonization of freshwater streams of isolated oceanic islands. Freshwater gobies oftentimes are the only native species of freshwater fauna in island streams, and many become localized to small geographic regions (McDowall, 2004). With no other connection to land, an amphidromous way of life seems required for many gobioids living within oceanic islands. The subfamily Sicydiinae currently consists of nine genera of which the genus *Stiphodon* exhibits the most diversity (Taillebois et al. 2013). *Stiphodon* is found throughout the Indo-Pacific from Sri Lanka to French Polynesia. There are more than thirty nominal species of *Stiphodon*, yet little is known about the true diversity of this genus and what factors influence their diversity and distribution (Maeda and Tan 2013).

Currently, life history studies have only been documented for *Stiphodon percnopterygionus,* describing breeding behavior, egg characteristics, and larval transitions to and from the sea. Life histories of the remainder of *Stiphodon* species have yet to be examined (Maeda and Tan 2013). Although little is known about the ecology and behavior of larvae at sea, it is well understood that this phase allows species to disperse to new locations and maintain connectivity among scattered island populations. Many species of *Stiphodon* have very large distributions, while others are found only in localized regions. For example, *S. pelewensis* (which likely includes *S. ornatus*, *S. atratus*, and *S. weberi*, (Pezold et al. unpubl. data)) has a wide distribution from western Indonesia to the Ryukyu Islands, northeastern Australia, and Micronesia. In contrast, *S. annieae* is only known from Halmahera (Keith and Hadiaty 2014) and Ambon Island in the Maluku province of Indonesia (M. White pers. obs.). It is unclear if endemism of some species of *Stiphodon* is a natural phenomenon or if it is a result of under sampling and misidentifications.

Range sizes have often been attributed to pelagic larval dispersal abilities. It is often assumed that organisms with restricted dispersal capabilities have smaller range sizes than organisms with greater dispersal capabilities (Lester and Ruttenberg 2005). Many benthic reef fishes rely solely on the larval phase for dispersal through open water given that adults would not be able to inhabit pelagic conditions (Ruttenberg and Lester 2015). Oceanic dispersal is also essential for sicydiine gobies due to the amphidromous nature of the larvae. As a result of the adults being restricted to freshwater on oceanic islands, the larvae provide the only means of dispersal to other locations and many researchers believe that pelagic larval durations (PLD) are the key determinants affecting range size (Taillebois et al. 2012).

Variations in range sizes are also exhibited in other related genera of sicydiine gobies. *Sicyopterus lagocephalus, Sicyopterus aiensis* and *Sicyopterus sarasini* all occur in in New Caledonia and Vanuatu. However, *Sicyopterus lagocephalus* ranges throughout the Indo-Pacific while *S. aiensis* is endemic to Vanuatu and *S. sarasini* is endemic to New Caledonia. Lord et al. (2012) analyzed the pelagic larval durations of all three species by counting daily rings on otoliths to determine if there were any differences in the number of days each species spent at sea. It was found that *S. lagocephalus* spent more days at sea than the two endemic species. Although there is conflicting evidence about whether pelagic larval durations affect range size, it can be a useful tool in learning more about certain aspects the life histories of these amphidromous fishes. Pelagic larval duration and ranges size studies on reef fishes, in the genus *Xyrichtys*, conclude that PLD does not affect range size for members of this genus. Some members of this genus such as *Xyrichtys pavo* are widespread from East Africa to California while *Xyrichtys wellingtoni* is believed to be endemic to the very small region of the Clipperton Atoll (Victor and Wellington 2000). Another example of this occurrence of endemism to the Clipperton Atoll is also exhibited in the *Thalassoma* genus of wrasses. *Thalassoma purpureum* is a widespread species that ranges from South Africa to South and Central America. However, one of its closely related counterparts (*Thalassoma robertsoni*) is endemic to the Clipperton Atoll (Ruttenburg and Lester 2015). The authors of these studies believe that larval dispersal is not the only source of range size determination (Victor and Wellington 2000). Pelagic larval durations do however show strong correlations to overall ocean wide dispersal. For example, fishes that have the ability to cross the Pacific Ocean to Hawai'i tend to have longer pelagic larval duration (Victor and Wellington 2000). This correlation however is limited to a few instances. More recent research suggests that there are many factors that determine range size. Larval fishes have relatively strong swimming and orientation abilities which may aid in how far they can disperse. Rafting has also been known to aid in larval dispersal. Many species of marine vertebrates and invertebrates have been known to stay in the pelagic environment longer when rafting (Jokiel 1990; Ruttenberg and Lester 2015).

Another potential factor affecting range size may be variations within the amphidromous life histories of these fishes. Hogan et al. (2014) and Closs et al. (2003) reveal some facultative species that have the ability to survive when access to the sea becomes lost. The eleotrid species *Gobiomorphus cotidianus* is considered amphidromous but has also been known to survive in landlocked lakes with no access to the sea (Closs et al. 2003) Using otolith microchemistry analysis (measurement of strontium: calcium ratios measured throughout the larval and adult life), Closs et al. (2003) were able to determine there are *Gobiomorphus cotidianus* that do not go to sea even if there is no barrier. Similar results were observed in a goby species endemic to the Hawaiian Islands. *Awaous stamineus* was believed to be an obligatory amphidromous species until otolith microchemistry revealed that only about 40% of juveniles went to sea as larvae (Hogan et al. 2014). This variation in the percent of individuals traveling to the sea may influence the dispersal capacity which in turn may ultimately dictate the geographic range size for a given species. For example, species with a high proportion of individuals that stay in freshwater may be less likely to disperse and more likely to be endemic to a small region. Conversely, obligate amphidromous species may have larger distributional ranges. Therefore, the intention of this study is to examine otoliths to gain more insight about the varying distributional ranges of *Stiphodon* species and what the contributing factors are to those range size differences. By examining otoliths, pelagic larval durations can be obtained by counting daily growth rings and microchemistry analysis of otoliths can reveal characteristics associated with amphidromy.

Materials and Methods

Geographic and Taxon Sampling

Stiphodon species used for this study were collected from multiple streams in Ambon, Indonesia, Solomon Islands, and the Federated States of Micronesia. Fishes for otolith extraction were fixed in 95% ethanol before the sagittal otoliths (ear stones) were extracted. To account for varying ranges of *Stiphodon*, species that exhibit wide distributional ranges as well as ones with smaller ranges were used. Areas in which *Stiphodon* are located are outlined in Figure 1.

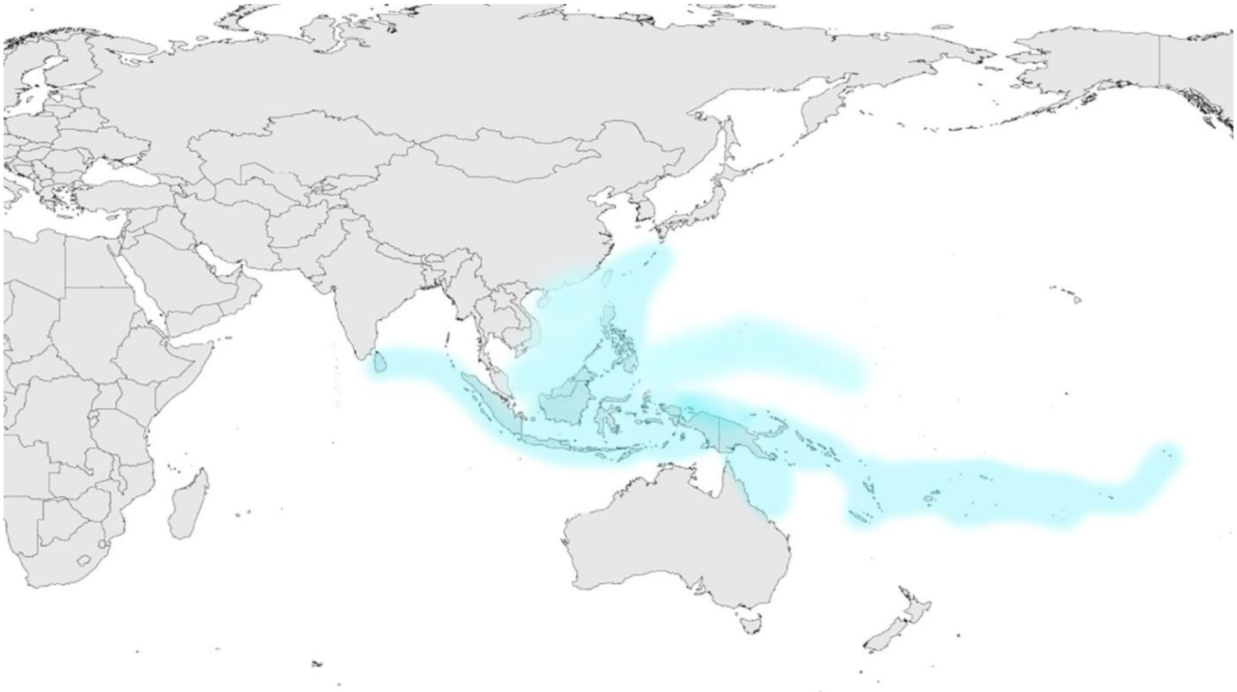

Figure 1. Map of distributional ranges of *Stiphodon*.

Distribution Maps

Geographic distribution maps were generated for each species based on several sources of data. First, species occurrences were document from a search of the Fishnet2 (www.fishnet2.com) database, which queries major museum collection databases around the world. These records were supplemented with collection records from additional museums outside the Fishnet2 database, such as the American Museum of Natural History and the Western Australia Museum. Lastly, additional data points were considered from uncatalogued field collections and genetically confirmed species records (Pezold et al. unpubl. data).

Otolith Preparation

Otoliths were taken from 10-12 individuals of each species. All specimens utilized were males except for four females of *Stiphodon pelewensis*. *Stiphodon* males are sexually dimorphic which makes species confirmation more accurate. However, the females used in this study were confirmed genetically. After extraction, otoliths were mounted to glass slides using crystal bond glue and the surfaces polished with diamond lapping films (3M^{TM}) that range from 30 micron grit size down to .5 micron grit size. Otoliths were intermittingly rinsed with milliQ water after each grit size was used and again when poling was completed. Polishing was considered to be finished when growth rings were clearly visible under a compound microscope and the otolith primordium was visible close to the surface of the otolith (Hogan et al. 2014).

Pelagic Larval Duration

Polished otoliths from five species of *Stiphodon* were photographed with a NIKON LV150N light microscope in order to count daily growth rings. Rings were counted from the primordium (core/nucleus) to the metamorphosis mark (Figure 2). The metamorphosis mark is clearly visible on these otoliths as a relatively broad ring having high optical density that arises during metamorphosis from the larval form into the post-larval form (Radtke et al. 1988). The mean and standard deviation of pelagic larval duration (PLD) were then calculated for each species. To test whether the PLD differs among species, a one-way ANOVA was used with Tukey-HSD post-hoc tests using a critical value of alpha = 0.05.

Otolith Microchemistry

Analyses of otolith microchemistry were performed to determine if individuals went to sea as larvae by detecting concentrations of strontium and calcium. The ratio of Sr:Ca is utilized to determine amphidromy in these fishes. Saltwater residency is indicated by elevated Sr:Ca ratios, and has been widely used to identify marine habitat use in diadromous fishes (Hale and Swearer 2008; Michel et al. 2008). Samples were analyzed with laser ablation (New Wave esi 193nm NWR) inductively coupled plasma mass spectrometry (Agilent 7500 Series) at the Jackson School of Geology at University of Texas at Austin. A laser transect with a laser width of 25µm was ablated on each sample starting at one edge of the otolith, bisecting the primordium (core), and ending at the other edge of the otolith (Figure 2A), resulting in a palindromic signal for all samples (Hogan et al. 2014). The laser was set at 50% power with a frequency of 10 Hz and a speed of 5µm per second. The carrier gas consisted of a concentration of 700mL/min of Argon and 650mL/min of Helium. High Sr:Ca ratios (typically 6 – 12 mmol/mol) in the core of the otolith, prior to the metamorphosis mark, indicate a marine migration in the larval period. The percentage of individuals that undergo marine migration as larvae indicates whether a species is obligate amphidromous (100% of individuals), facultative amphidromous (100% > X > 0%), or not amphidromous (0%). Raw data were first analyzed in individual Excel files and data were grouped into areas of where the laser was on and were the otolith started. The data that only encompassed the otolith material where then compiled into one Excel file to be read in R to produce graphs of Strontium and Calcium ratios.

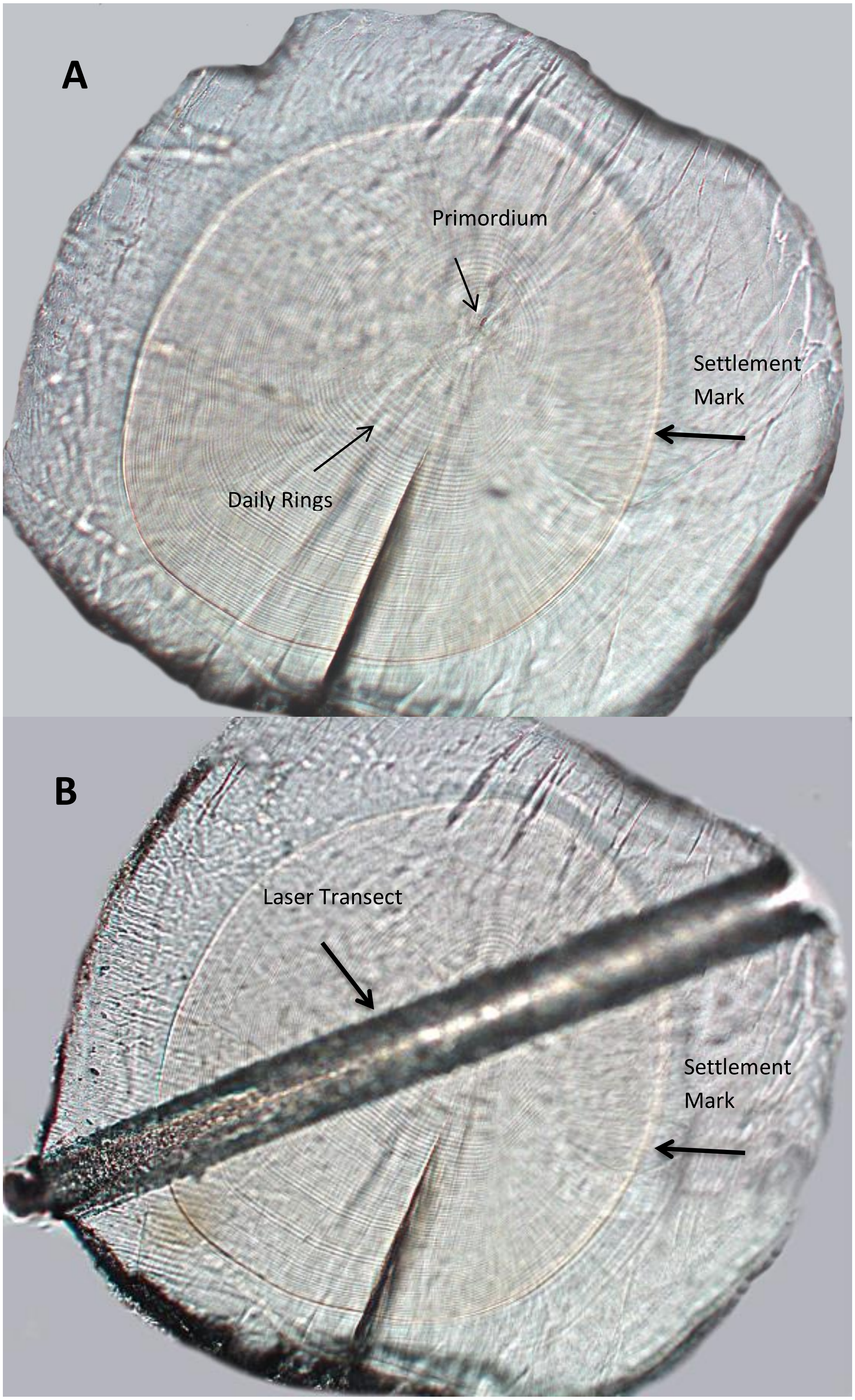

Figure 2A-2B. (A) Polished otolith from *Stiphodon annieae* showing daily growth rings, primordium, and settlement mark. (B) Laser transect line through otolith.

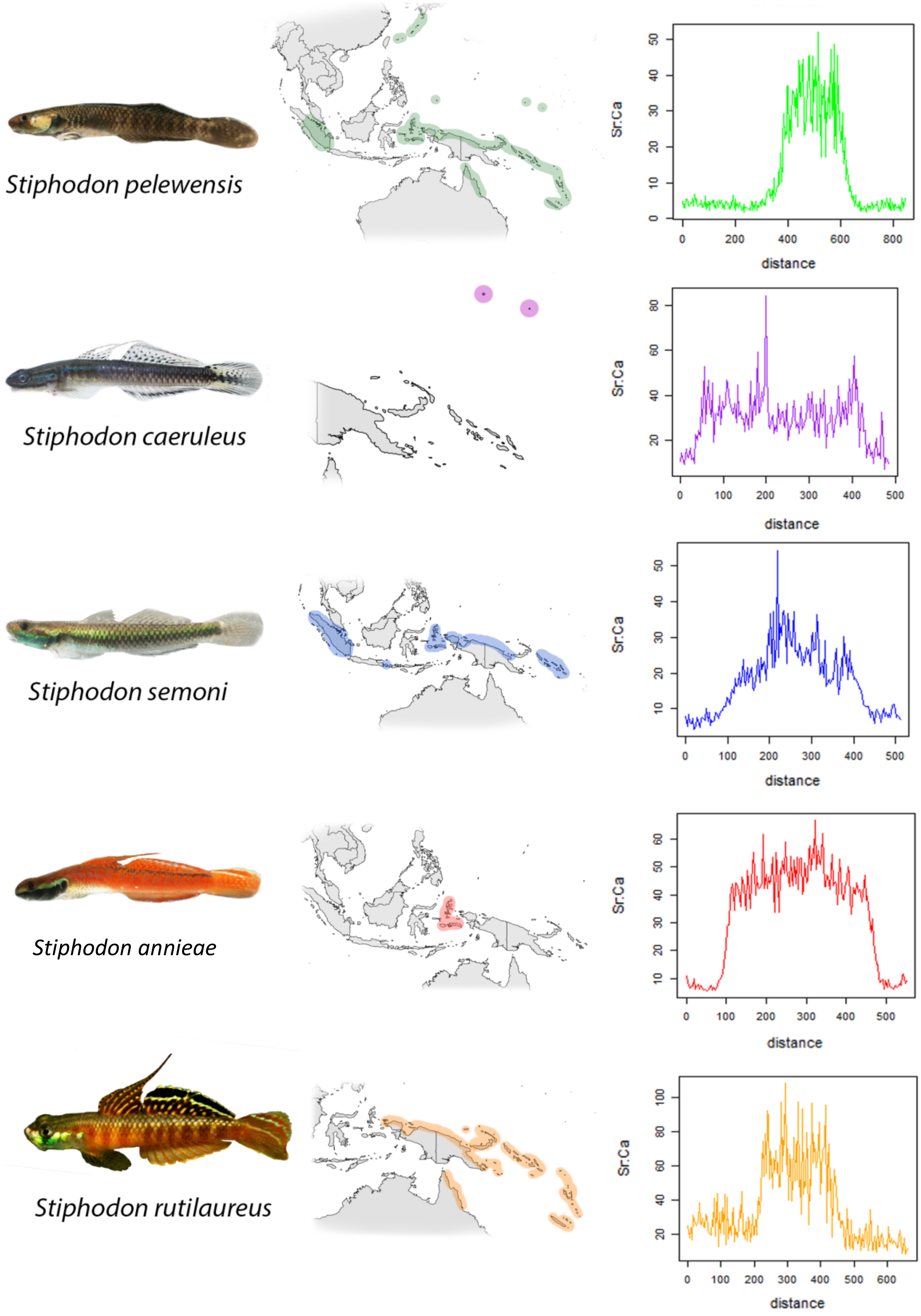

Figure 3. Distribution maps and Sr:Ca peaks from single representative otolith samples of five species of *Stiphodon*.

Results

LA-ICP-MS

Otolith microchemistry analyses revealed that all individuals of all *Stiphodon* species analyzed went to sea as larvae. The five species selected showed consistent patterns of strontium peaks in the larval period of the otolith (Figure 3).

Pelagic Larval Duration

Daily rings were counted for 3-16 individuals from each of the five species (Table 1). *S. caereuleus* had the highest average PLD at 82.75 days followed by *S. annieae* at 75.63 days, S. rutilaureus at 72.67 days, *S. semoni* at 71.23 days, and lastly *S. pelewensis* with 66.29 days. The resulting mean ring counts and standard deviations are shown are in A boxplot depicting the PLD was generated using the program R (Figure 4). The one-way ANOVA indicated an overall p value of 0.038, indicating a statistically significant difference in pelagic larval duration among species. The Tukey-HSD post-hoc pairwise tests indicated that the only significant difference was between *S. pelewensis* and *S. caeruleus* (Figure 4). This difference however, is not consistent with our hypothesis that

Table 1. Summary of pelagic larval duration from otolith daily ring counts for five species of *Sitphodon*.

Species	Number of Individuals	Average PLD count	Standard Deviation	Range
S. caeruleus	8	82.75	7.55	72-92
S. semoni	13	71.23	13.42	50-92
S. pelewensis	7	66.29	10.47	54-82
S. annieae	16	75.63	8.85	61-89
S. rutilaureus	3	72.67	2.52	70-75

the PLD is affecting range size, as *S. atratus* appears to have a shorter PLD but larger range size than *S. caeruleus*.

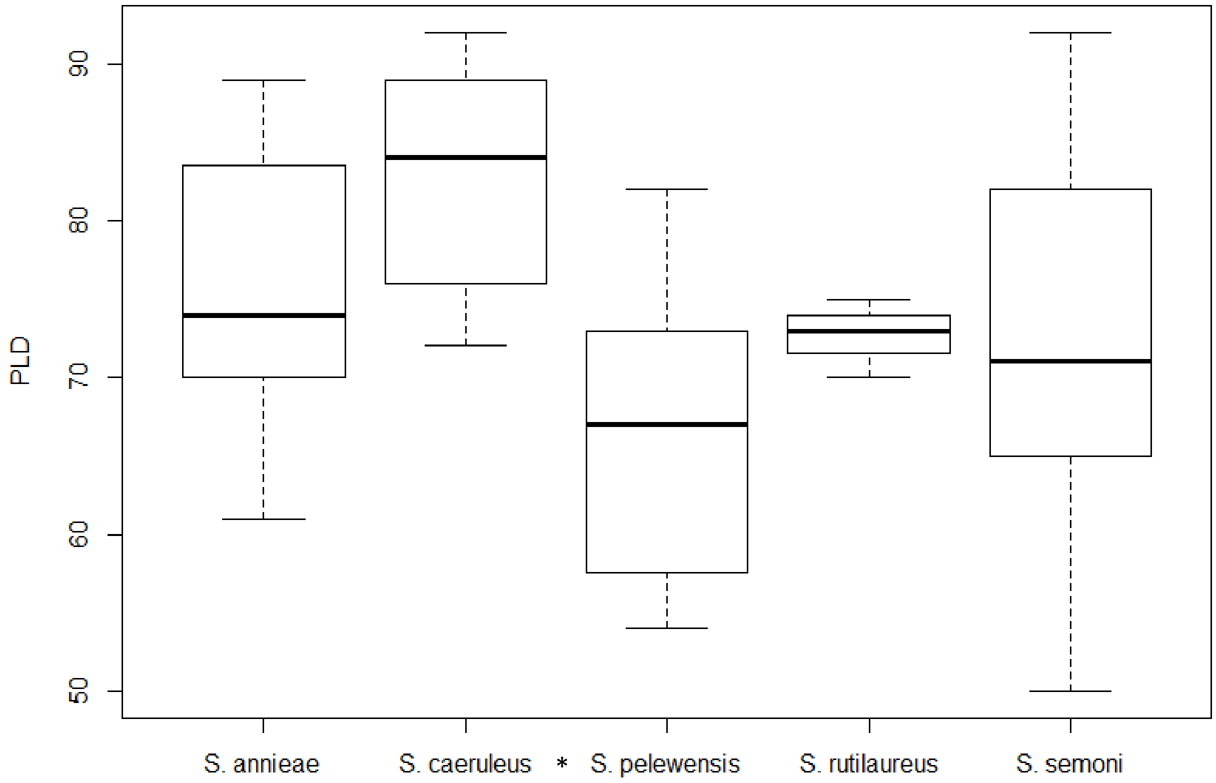

Figure 4. Pelagic larval duration (PLD) of five species of *Stiphodon*. The * indicates the only species pair where mean PLD differed significantly between species based on the ANOVA and Tukey-HSD post-hoc analysis. P-value =0.038.

Discussion

The genus *Stiphodon* is one of the most diverse genera of sicydiine gobies and is widespread throughout the Indo-Pacific (Keith and Hadiaty 2014). Many species of *Stiphodon* have been described from only a few islands or are only known from small regions. It is unclear as to why some *Stiphodon* species such as *S. caeruleus* are only found in localized regions (Chabarria et al. 2013) while other similar species such as *S. pelewensis* have very large widespread ranges (Maeda and Tan 2013). In marine species, dispersal potential is mostly achieved by larvae. Some organisms have the potential for movement as adults to expand range size (Ruttenberg and Lester 2015). For Sicydiiane gobies however, the adult phase is restricted to freshwater, so dispersal potential, to different islands, is achieved only in the marine larval phase. Like other sicydiine gobies, *Stiphodon* has an amphidromous life history which allows for dispersal via oceanic currents. With this type of dispersal capabilities, it would seem as though all *Stiphodon* species would have the potential to disperse widely. Recent findings of facultative abilities in amphidromy of some *Awaous* species led to the question of whether or not all amphidromous species go to sea as larvae (Hogan et al. 2014). If some individuals do not go to sea, then dispersal would be limited and could potentially lead to smaller range sizes due to fewer individuals dispersing. Risks are also involved for obligate amphidromous species. Species that require access to the ocean are more susceptible to possible blockages, from human or naturally induced damming, which can lead to reduced population sizes (Crook et al. 2006). Many freshwater gobies and basal goby members such as *Awaous* and *Gobiomorphus* have facultative abilities that allow them to complete their lifecycle in freshwater. There are known landlocked populations of amphidromous *Rhinogobius* species that are able to complete their lifecycle in those landlocked bodies of water. Many other *Rhinogobius* species such as *Rhinogobius flumineus* also show a trend of loss in amphidromy and reside in fully freshwater environments their whole life (Tsunagawa et al. 2010). However, of the studies conducted on members of Sicydiinae, none show facultative abilities in amphidromy. There is strong evidence suggesting that all larval members of Sicydiinae require access to the ocean in order to develop (Wantanabe et al. 2014). To investigate this assumption for *Stiphodon*, Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS) was used to compare strontium and barium elements of otoliths of selected species of *Stiphodon,* a sicydiine genus exhibiting a spectrum of species ranges. Strontium elevation and barium decreases were apparent from the core through the settlement mark for all samples of *Stiphodon* used for this study, which implies that these individuals lived in the marine environment as larvae.

Understanding what factors are important in determining range size and dispersal in fishes can be daunting (Ruttenberg and Lester 2015). Many theories have been suggested about what factors influences range sizes. Most commonly, larval dispersal abilities are suggested to explain range size variations for many coral reef species. Why range size variations occurs in amphidromous fishes, such as of *Stiphodon,* can also be difficult to determine. *Stiphodon* species are widespread throughout the Indo-Pacific yet some are listed as endemic to certain regions, one to two islands, and even to a single stream on an individual island (Keith et al. 2009) With the dispersal capabilities provided by amphidromy, it is baffling as to why some species of *Stiphodon* such as *S. pelewensis*, have very widespread distributional ranges while others like *S. annieae* appear more limited and possibly endemic to a few islands. In addition to all *Stiphodon* species examined exhibiting complete amphidromy, results from otolith ring counts and the one-way ANOVA testing indicated no significant differences in the PLDs. In fact, the species with the shortest PLD (*S. pelewensis*) has the largest distributional range. Even though PLD has been linked with range size for some time, evidence suggests that PLD does not majorly influence range sizes unless it is at large scales and only if range sizes span large dispersal barriers (Ruttenberg and Lester 2015). For example, PLD and range size correlations have been found in reef fishes when sampling taxonomic subsets in one or a few families. Other correlations of PLD and ranges have also been found in longitudinal ranges of snappers in the eastern Pacific. However, this example fails to compare PLD to overall range size. Comparatively, Thresher et al. (1989) state that pelagic larval durations correlate to the ability of larvae being able to cross major dispersal barriers in the west Indo-Pacific. Thresher et al. (1989) also notes that pomacentrids endemic to Hawai'i tend to have a much shorter PLD than related genera found throughout the Pacific (Thresher et al. 1989). In the case of the endemic *Sicyopterus* species, such as *S. aiensis* and *S. sarasini*, it was found that *Sicyopterus lagocephalus* indeed has a longer PLD than the endemic species, but the authors conclude that there are other factors such as swimming and orientation abilities affect range size more so than PLD.

Although longer pelagic larval durations allow more time for dispersal, the PLD of endemic species is still long enough for wider ranges of dispersal. Therefore, other potential larval behavior factors must be contributing to restrictions in range sizes (Victor and Wellington, 2000). There is plenty of support for larval swimming abilities and behavior influencing range sizes (Lord et al. 2012; Ruttenberg and Lester 2015).

Some sicydiines such as *Sicyopterus japonicus* inhabit temperate regions of Japan and respond to seasonal cues for migrations. It is possible that other members of this group of fishes also rely on environmental stimuli, during migrations and dispersal, which might influence range size. *Sicyopterus japonicus* larvae tend to prefer low salinity haloclines during downstream migrations. This halocline is postulated to aid in their swimming ability (Iida et al. 2009; Lord et al. 2012). Lord et al. (2012) speculates that endemic *Sicyopterus* species such as *S. sarasini* is relying on certain behavioral traits that allow them to choose specific habitat types, such as a nickel rich substrate, similar to those that they are adapted to (Lord et al. 2012).

Body size has been shown to facilitate wider range sizes among terrestrial organisms such as mammals, insects, and birds. Recent studies have also linked body size to range size in several groups of marine fishes (Ruttenberg and Lester 2015). Bowen et al. (1996) expresses that an organism with a large body size is unlikely to have a small geographic range. This may be due to larger species requiring more resources and occupying wider ranges of habitats. Larger organisms may also have fewer predators and be able to adapt to utilizing a variety of food sources which in turn may result in faster growth rate and higher reproductive output leading to increased chances of colonization (Ruttenberg and Lester 2015).

Why endemism occurs on islands, when dispersal through the ocean is feasible, remains unclear. Studies have found that island endemics are similar to their non-endemic counterparts in that their biological functions do not differ greatly. It has also been noted that the pelagic larval durations of island endemics are sometimes longer than those of the related widespread species. *Lentipes concolor*, a sicydiine species endemic to Hawai’i, has a pelagic larval duration range of 63-106 days; which is relatively long compared to other closely related species of similar in body size (Radtke et al. 2001). Also, species with smaller ranges may be more abundant in their locality (Ruttenberg and Lester 2015). A 1976 study of endemic fish abundance in the Hawaiian Islands, Lord Howe Island, and Easter Island, indicated that the most abundant fishes in these regions were species that are unique to those islands (Randall 1976). Local abundance was also observed for *Stiphodon annieae*, a recently described species and which was only known from Halmahera, Indonesia (Keith and Hadiaty 2014). During collections in Ambon, *Stiphodon annieae* was one of the most abundant species collected. This finding supports the claim of endemics being abundant in their regions. A longer PLD was also observed for this species compared to the widespread species in this study. However, it also raises questions about sampling. Some species may have been described multiple times and some may be under sampled resulting in inaccurate descriptions of endemism and range sizes (Maeda et al. 2015).

From this study it can be concluded that amphidromy and pelagic larval duration do not correlate with endemism and range sizes of *Stiphodon*. However, there is still more information to be determined, but through these analyses we now have a better understanding about the life history and pelagic larval durations of several *Stiphodon* species. Future studies should aim to broadly sample *Stiphodon* species as well as other sicydiines to determine amphidromous traits and PLDs of all species. Studying lifespan, population sizes, and reproductive output has also been suggested to further understanding endemism (Ruttenberg and Lester 2015).

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