

CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

THE EFFECTS OF TEMPERATURE AND LATITUDE ON LARVAL TRAITS OF
THE ENDANGERED TIDEWATER GOBY (*EUCYCLOGOBIUS NEWBERRYI*) AND
ITS SISTER SPECIES THE ARROW GOBY (*CLEVELANDIA IOS*)

A thesis submitted in partial fulfillment of the requirements

For the degree of Master of Science

in Biology

By

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May, 2014

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Acknowledgements

First and foremost, I'd like to thank my advisor, Mark Steele, for his ongoing guidance and support throughout this research project. Beyond introducing me to the wonderful world of gobies, Mark's mentorship helped me develop as a scientist, and more importantly as an individual, in a way I had never imagined when I began graduate school. Mark provided a setting that allowed me to formulate and develop my own questions and ideas, even when it seemed more than I could handle. Thank you for believing in me, I am forever grateful for your support, guidance, and friendship. I'd also like to thank my committee members Larry Allen and Steve Dudgeon. Your support and guidance was essential in completing this research project. I am so grateful to you both for your encouragement and availability. Your wise words and support continuously inspired me to become a better scientist.

I would also like to thank several people who helped me with field collections, lab work, and project logistics. Berenice Tarango, you were such an instrumental part of this project. From goby dissections to otolith readings, you always worked hard and kept a positive attitude. Thanks to Brian Peña and Rando Has for your hard work in the lab dissecting otoliths out of hundreds of gobies. Aaron Dufault, Chris Dellith (USFWS), Kevin Lafferty (USGS), Darren Fong (NPS), Mike Rouse (USMC), Rhys Evans (USAF), and Rikke Kvist Preisler (ESNERR), thank you all for your help with collections, project logistics, and permitting.

Additionally, I'd like to thank Camm Swift and David Jacobs for sharing your vast amount of knowledge on gobies and California estuaries. Your expertise and direction enhanced this project tremendously. Camm, your directional road map to every goby

location was critical to completing my fieldwork in a timely fashion. Dave, you've opened up my eyes to many new and exciting questions about closing lagoons and the species that inhabit them. I look forward to continuing this work with you for my Ph.D. dissertation.

Lastly, I would like to acknowledge the funding sources that helped support this research project. Thanks to: the CSU Northridge Department of Graduate Studies and the College of Science and Mathematics, and the International Women's Fishing Association. I'd also like to thank the Council on Ocean Affairs, Science and Technology (COAST) as well as the American Society of Ichthyologist and Herpetologist (ASIH) for travel support to present my research at scientific conferences.

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Abstract

THE EFFECTS OF TEMPERATURE AND LATITUDE ON LARVAL TRAITS OF THE ENDANGERED TIDEWATER GOBY (*EUCYCLOGOBIUS NEWBERRYI*) AND ITS SISTER SPECIES THE ARROW GOBY (*CLEVELANDIA IOS*)

By

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Master of Science in Biology

In benthic associated fish species, the time an individual spends in the larval phase until settlement to a benthic substratum is a vulnerable and critical period determining survival. In many species, the length of this period can strongly influence dispersal potential, further affecting a species geographic range, population connectivity, and community structure. The type of habitat in which a fish resides can significantly influence its larval development due to variations in the abiotic environment, such as temperature. In addition, the degree of habitat isolation can strongly influence dispersal potential, as seen in seasonally closed, or isolated, estuaries in California when compared to fully tidal marine estuarine systems.

This study examines the variations in larval traits of two California endemic gobiid species found in differing estuarine habitat types. The arrow goby, *Clevelandia ios*, is commonly found in fully tidal bays, estuaries, and mudflats with consistent marine influence. The tidewater goby, *Eucyclogobius newberryi*, is the sister species to the arrow goby, and prefers estuaries and lagoons with some degree of seasonal isolation from the sea. This habitat preference exposes the tidewater goby to much greater temperatures and limits its dispersal potential.

In the first part of this study, I used otoliths to examine the larval duration, size at settlement, and pre-settlement growth rates of newly settled gobies collected in eighteen estuaries along the California coast in the summer of 2011. I found that the arrow goby, on average, had a longer larval duration than the tidewater goby, but smaller size at settlement based on back-calculated size measurement. Additionally, larval growth rate of the arrow goby was slower than that of the tidewater goby. Although variations in larval traits between these two species were significantly different, they were much more similar than initially expected.

In the second part of this study, I examined the effects of temperature and latitudinal distribution on the larval traits of the arrow and tidewater goby in eighteen study systems. Hourly temperature measurements were recorded in 18 study sites in order to determine the mean temperature experienced by each fish during its larval phase. Temperatures found in seasonally closed estuaries inhabited by the tidewater goby had greater variability among sites (10° C range) than the fully tidal marine sites inhabited by the arrow goby in (5° C range). Among site variation in larval traits was greater for the tidewater goby, likely linked to the greater temperature range of seasonally closed estuaries. On average, for both species, fish that experienced warmer temperatures had a shorter larval duration, faster growth rates, and were smaller in body size (SL) at settlement.

Projected increases in global temperatures will likely accelerate larval development for many species. For the arrow goby, tidewater goby, and related estuarine species, this can either be beneficial or damaging depending on local habitat conditions and community structure. A decrease in larval duration could potentially reduce dispersal

distance and gene flow between populations. However, decreases in larval duration could potential increase the rate of survival to settlement by reducing predator exposure. This would, in turn, decrease the size at settlement, which could prove to be detrimental in populations where a larger body size at settlement gives a greater competitive advantage in the juvenile stage. Therefore, further knowledge on the effects of temperature on endemic species can be useful for planning conservation and management strategies in the face of climate change

Chapter 1: General Introduction

The distance a benthic marine fish is able to disperse has been related to the amount of time spent in the larval phase, with longer larval duration expected to result in greater dispersal potential (O'Connor et al. 2007, Booth & Parkinson 2011). Greater dispersal potential can also be related to increased population connectivity and expanded geographic ranges (O'Connor et al. 2007, Cowen & Sponaugle 2009). For species such as the arrow goby, *Clevelandia ios*, high dispersal potential likely explains its broad geographic range and shallow phylogeographic structure (Dawson et al. 2002). These characteristics are likely due to its preference for fully tidal bays and estuarine mudflats ranging from Bahia Magdalena, Baja California Sur to British Columbia. However, the arrow goby's sister species, the federally endangered tidewater goby, appears to have limited dispersal, mainly via adult movement, with little or no marine larval dispersal (Barlow 2002, Dawson et al. 2002, Earl et al. 2010). The difference in dispersal potential is due to the preference of the tidewater goby for seasonally closed estuarine habitats, limiting its geographic range to the California coast. The isolating nature of these estuarine habitats from the sea explains why the tidewater goby is the most locally differentiated coastal vertebrate on the Pacific coast (Dawson et al. 2002, Earl et al. 2010).

Furthermore, the overall size, function, and latitudinal distribution of estuarine habitats can have a considerable effect on the abiotic factors, such as temperature, experienced in the system. Due to the broad spatial distribution (> 1000 km north to south) of the California coast, estuaries and wetland habitats experience significant temporal and spatial variability in temperature regimes. Variations in temperature have

been found to strongly influence metabolic processes in a wide range of taxa, including larval development and survival (Gillooly 2001, Gillooly et al. 2002, Brown et al. 2004, O'Connor et al. 2007). Additionally, larval duration, size at settlement, and growth rates are among many metabolically driven processes influenced by temperature (McCormick & Molony 1995, Green & Fisher 2004, O'Connor et al. 2007), as well as metamorphic success, behavior and dispersal distance (Rutherford & Houde 1995, Wilson & Meekan 2002, Meekan et al. 2003, O'Connor et al. 2007). Therefore, temperature has the potential to strongly influence species on a population and community level (Gillooly 2001, O'Connor et al. 2007).

In this thesis, I had three main research objectives: 1) to document and compare larval traits (larval duration, size at settlement, and pre-settlement growth rate) in the arrow goby and tidewater goby across their region of range overlap; 2) to evaluate the degree of temperature variation found in closed vs. tidal estuaries over a larger latitudinal distribution; and 3) to measure the effects of temperature found in different estuarine habitat types, in addition to latitudinal distribution, on the larval traits of the arrow and tidewater goby. I pursued these research objectives in 18 estuaries that spanned over eight degrees of latitude, spanning from San Diego County to Humboldt County, California. Out of the 18 study sites, 10 represented seasonally closing estuaries inhabited by the tidewater goby. The other 8 estuaries represented fully tidal marine systems inhabited by the arrow goby.

Estimates of larval duration, size at settlement, and pre-settlement growth rates were determined from daily bands and settlement marks in lapillar otoliths (ear stones) of recently settled gobies. A comparative analysis was then done to test the differences

between larval traits of these two study species, which have different habitat preferences and larval dispersal potential. I then compared larval trait measurements with hourly temperature recordings taken from each study site. This allowed me to test whether any variations found in larval traits were associated with the temperature an individual goby experienced during its larval phase, and how that varied over a large latitudinal distribution. This type of knowledge can be useful for scientists and managers planning strategies for the conservation and management of endemic and threatened species and their associated habitats.

Chapter 2

LARVAL DURATION, SIZE AT SETTLEMENT, AND LARVAL GROWTH RATES OF THE ENDANGERED TIDEWATER GOBY (*EUCYCLOGOBIUS NEWBERRYI*) AND ITS SISTER SPECIES THE ARROW GOBY (*CLEVELANDIA IOS*)

Abstract

The early life history of the federally endangered tidewater goby (*Eucyclogobius newberryi*) and its sister species the arrow goby (*Clevelandia ios*) has been poorly documented to date. Both are endemic to estuarine habitats throughout the California coast, however, habitat use differs between these two species. The arrow goby is commonly found in fully marine tidal bays and mudflats. The tidewater goby, however, prefers lagoons with some degree of seasonal isolation from the sea. Here, we used otoliths to examine the larval duration, size at settlement, and growth rates of newly settled gobies collected from eighteen estuaries in California. The arrow goby had a larval duration that was 2 days longer than the tidewater goby (26.11 vs. 23.95 days, respectively), but smaller size at settlement based on back-calculated size (10.00 vs. 12.38 mm SL), and slower larval growth rate (2.60 vs. 2.86 $\mu\text{m}/\text{day}^{-1}$). There are several reasons that could explain these differences in larval traits, such as habitat variability in temperature or food resources between populations, or the need for the tidewater goby to settle and reach maturity faster than the arrow goby due to its shorter, annual life cycle.

Introduction

Numerous fish species inhabit estuarine habitats during their early life history. These habitats are quite variable, with some remaining open to the ocean year round and others typically closing seasonally. Species that inhabit seasonally closing estuaries may exhibit different larval traits than those that inhabit permanently open estuaries, and these traits may contribute to genetic isolation by limiting dispersal (Bilton et al. 2002, Watts & Johnson 2004). For example, Dawson et al. (2002) found genetic evidence of limited dispersal in the tidewater goby, which inhabits seasonally closed estuaries, whereas its sister species the arrow goby, which inhabits open systems, lacked regional genetic differentiation. This difference is likely due to greater marine larval dispersal and gene flow between populations of arrow gobies. Larval duration, however, has long been thought to influence dispersal, and differences in larval dispersal could confound this interpretation.

Closed estuaries experience greater environmental variation than seen in habitats perennially open to marine influence, and such environmental variation is known to significantly influence larval development (McCormick & Molony 1995, Green & Fisher 2004). Along the California coast, many estuaries are partially or completely isolated from tidal influence either seasonally or episodically (Jacobs et al. 2011). Opening or “breaching” is usually a function of streamflow (Rich & Keller 2013), which is driven by seasonal precipitation. Isolation, or closure, occurs when a sand bar or raised beach berm impounds systems of variable salinity during periods of lowered "summer" stream flow. Such dynamic lagoonal systems are a product of the Mediterranean climate that

characterizes California. Similar lagoonal processes are known to occur in other regions of the globe with similar climate (Jacobs et al. 2011).

The federally endangered tidewater goby is a California endemic that specializes in estuaries that experience seasonal or episodic closure (Swift et al. 1989). The tidewater goby is a small benthic fish that rarely exceeds 55 mm standard length (SL) (Miller & Lea 1972). Lagoons with seasonally closing stream mouths on the outer coast are the typical tidewater goby habitat, although they also occupy or historically occupied, naturally closing, tide-gated, or marginal pond habitats around Humboldt, Tomales & San Francisco Bays (Swift et al. 1989, Moyle 2002, U.S. Fish and Wildlife Service 2005). This species exhibits local genetic differentiation at a finer geographic scale than any other Pacific coast vertebrate (Barlow 2002, Dawson et al. 2002, Earl et al. 2010). Its preference for variable estuaries is one of the main reasons why it is predisposed to local extirpation (Lafferty et al. 1999a, b).

Dispersal of the tidewater goby is associated with high stream-flow events (Lafferty et al. 1999a,b), which cause breaching of the estuary mouth, permitting dispersal (Earl et al. 2010). Breaching events occur most frequently during winter months when reproduction is limited and larvae are generally absent. As confirmed by genetic differentiation, marine larval dispersal appears to be extremely limited if it occurs at all (Barlow 2002, Dawson et al 2002, Earl et al. 2010). Presumably this is due to the isolated nature of these lagoonal habitats during the summer peak reproductive months (Swenson 1999). Thus, dispersal appears limited to adult movement over sandy substrate following breaching events (Earl et al. 2010).

The arrow goby is the sister species to the tidewater goby, and it ranges from Bahia Magdalena, Baja California Sur (C. Swift, pers com) to British Columbia (Miller and Lea 1972). Similar to the tidewater goby, the arrow goby is a small benthic fish that rarely exceeds 60 mm SL (Miller & Lea 1972, Hart 1974). The arrow goby prefers more open, fully tidal estuaries and mudflats that are typically cooler and higher in salinity. This preference for open estuaries is thought to facilitate marine larval dispersal.

Here, we compare the early life history of the arrow goby and the tidewater goby collected from eighteen California estuaries. Larval traits were determined from daily bands and settlement marks in lapillar otoliths of recently settled gobies. Larval duration, size at settlement, and pre-settlement growth rates were compared between the two species.

Materials and methods

Study Sites

Gobies were collected from eighteen estuaries in California (Fig. 2.1). Sites were chosen based on the presence of healthy and abundant populations of the arrow goby or tidewater goby, in addition to their mouth dynamics (closed vs. open estuary mouth). The tidewater goby was collected at ten seasonally closing estuaries: Ten Mile River (39°32'43.86"N, 123°45'25.04"W); Salmon Creek (38°21'10.87"N, 123°03'57.19"W); San Gregorio (37°19'14.29"N, 122°24'03.38"W); Rodeo Lagoon (37°49'54.41"N, 122°31'43.31"W); Moore Creek (36°57'4.50"N, 122°03'29.85"W); San Luis Obispo Creek (35°11'13.35"N, 120°43'33.47"W); Santa Ynez River (34°41'30.57"N, 120°35'00.70"W); Arroyo Burro Lagoon (34°24'11.77"N, 119°44'35.12"W); Santa Clara

River (34°14'07.19"N, 119°15'27.46"W); and Las Flores Marsh (33°17'25.79"N, 117°27'53.91"W). The arrow goby was collected at eight estuaries that are typically fully tidal: Arcata Bay (40°51'30.57"N, 124°06'00.08"W); Bodega Bay (38°18'59.42"N, 123°02'43.12"W); San Lorenzo River (36°57'56.41"N, 122°00'45.46"W); Elkhorn Slough (36°48'40.14"N, 121°44'38.77"W); Morro Bay (36°57'56.41"N, 122°00'45.46"W); Carpinteria Salt Marsh (34°23'52.97"N, 119°32'16.72"W); Colorado Lagoon (33°45'10.52"N, 118°07'47.37"W); and Los Peñasquitos (32°55'57.84"N, 117°15'29.11"W). Due to the differences in habitat preference of the arrow goby and tidewater goby, none of the eighteen study sites had both species present at the time of collection.

Collection Methods

Larval, transitional, and recently settled gobies (Fig. 2.2) were collected between August and October of 2011. Both species were collected using a 3.7 x 1.2 m beach seine with a 1.6-mm mesh, and in some cases, a one-man push net with 1.6-mm mesh (Strawn 1954). The arrow goby was collected at low tide in both study sites. The ten study sites where the tidewater goby was collected were both completely closed to marine tidal influence at the time of collection. Once collected, the fishes were euthanized and preserved in 95% ethanol.

Otolith Analysis

Otoliths were used to measure larval traits of the study species. Otoliths have been used for these purposes in a wide variety of fishes, including many species in the family

Gobiidae (Sponaugle & Cowen 1994, Hernaman et al. 2000, Radtke et al. 2001, Yamasaki & Maeda 2007, Wilson et al. 2009, Samhoury et al. 2009). Both the sagittal and lapillar otoliths were extracted from all individuals using standard techniques (Brothers 1987, Hellmair 2010) and placed in immersion oil for >30 days to clear (Samhoury et al. 2009). For the two species, the smaller lapilli were used because they were clearer and easier to interpret than the sagittae, and they did not require sectioning or polishing. Lapilli were read whole from images on a computer monitor that were captured by a digital camera mounted on a compound microscope at 200× magnification, with a polarizing filter placed between the light source and the first stage. Increment measurements were made along the longest axis, from the core to the outermost complete ring using Image-Pro Plus image analysis software.

Larval duration, size at settlement, and growth rates were estimated from the otoliths. Previous work has validated daily otolith increment deposition in the tidewater goby (Hellmair 2010), and increments were assumed to be daily in the arrow goby. Settlement was recorded in the otolith structure as a distinct transition in increment widths (Fig. 2.3), as noted in other gobies by Sponaugle and Cowen (1994). Larval duration was determined from a count of the rings from the hatch mark (first band from otolith core) to the settlement mark. Average pre-settlement growth rates were estimated as average increment width between the hatch mark and the settlement mark (McCormick & Molony 1995). All otoliths were read twice by one person (B.T. Spies), and all unclear and abnormally shaped otoliths were discarded. If the two readings were more than 10% different, the readings were not included in any analysis. If the two readings were less than 10% different but not the same, then the second reading was used for the analysis.

Data Analysis

To validate that the presumed settlement mark actually corresponded to settlement, the number of presumed post-settlement bands was regressed against body length for both species. The x-intercept of the linear regression equation estimates size at settlement, which was compared to the size of fish known to have recently settled based on their morphology. Further regression analyses examined the relationship between body length and age (days) to determine whether otolith measurements provide accurate proxies of somatic traits (Booth & Parkinson 2011). Back calculation was used to estimate body size at settlement for each fish using the equation calculated by ordinary least square linear regression of body size (mm SL) on otolith radius, of the form $L = mx + b$; where L represents the body length, m represents the slope, x represents the otolith radius at settlement, and b represents the y-intercept. A nested ANOVA with the factors Species (fixed effect) and Site nested within species (random effect) was used to test whether larval traits differed between species and collection sites.

Results

Otolith-based estimates appeared to be appropriate for both the tidewater goby and arrow goby due to the fact that body length was tightly related to age as estimated from otoliths (Fig. 2.4: arrow goby $n=317$, $r^2=0.75$; tidewater goby $n=406$, $r^2=0.71$) for both species, as was the number of post-settlement otolith bands and body length (Fig. 2.5: arrow goby $n=317$, $r^2=0.79$; tidewater goby $n=406$, $r^2=0.73$). This result indicates that the distinguishable transition zone in the otolith is the settlement band (Fig. 2.3A), and that all bands between the core and the settlement mark indicate the larval duration

(Sponaugle and Cowen 1994). Otolith radius was a good proxy for body length, as indicated by a strong linear relationship between body length and otolith radius (Fig. 2.6: arrow goby $n=317$, $r^2=0.80$; tidewater goby $n=406$, $r^2=0.78$). Based on back-calculation, mean \pm SD size at settlement was 11.45 ± 0.23 mm SL for the tidewater goby and 9.32 ± 0.63 mm for the arrow goby (Table 2.1).

The arrow goby had a significantly longer larval duration ($F_{1,705}=227.3$, $p<0.0001$), larger otolith radius at settlement ($F_{1,705}=28.39$, $p<0.0001$), and slower growth rates ($F_{1,705}=399.75$, $p<0.0001$) than the tidewater goby (Table 2.1). Size at settlement (back calculated) of the tidewater goby was larger than that of the arrow goby ($F_{1,705}=5360.1$, $p<0.0001$). All larval traits varied significantly among sites for both species (larval duration: $F_{16,705}=42.5$, $p<0.0001$; otolith radius at settlement: $F_{16,705}=43.9$, $p<0.0001$; pre-settlement growth rate: $F_{16,705}=33.53$, $p<0.0001$; back calculated body size at settlement: $F_{16,705}=25.9$, $p<0.0001$).

Discussion

Analysis of lapillar otoliths revealed that larval duration, size at settlement, and pre-settlement growth rates of the two sister species, the arrow goby and tidewater goby, were statistically different, though not dramatically different. The similarity between the two species in larval duration is somewhat surprising given known differences in their habitat usage and methods of dispersal. Despite inhabiting two different kinds of estuaries, “open” versus “closed”, and dispersing as larvae (arrow goby) versus adults (tidewater goby), the duration of the larval phase was only 8.63% shorter in the tidewater

goby. Due to faster larval growth rates, the tidewater goby settled at larger size than did the arrow goby.

Larval durations of other related goby species (e.g. *Gillichthys mirabilis*, *Ilypnus gilberti*, *Lepidogobius lepidus*, *Quietula y-cauda*), commonly referred to as the “Bay gobies” (Teleostei: Gobionellidae) (Thacker 2009, Ellingson et al. 2014) have not yet been determined. In fact, detailed knowledge of early life history characteristics is unknown for many native fishes that occupy estuaries and wetlands in California. Larval traits have been studied more regularly in tropical gobies (Teleostei: Gobiidae), which on average, tend to exhibit more prolonged larval stages than those of the species in this study. Yamasaki et al. (2007) documented a 78-146 day larval duration in *Stiphodon percnopterygionus*, a stream-associated goby found in Okinawa Island, Southern Japan. *Lentipes concolor*, an endemic Hawaiian amphidromous goby was found to have a larval duration between 63-106 days (Radtke et al. 2001). The goldspot goby (*Gnatholepis thompsoni*), commonly found on coral reefs in the Caribbean, was found to have a larval duration between 45-80 days (Samhuri et al. 2009), with the potential of reaching 112 days (Sponaugle & Cowen 1994). Another common goby in the Caribbean (*Coryphopterus glaucofraenum*), however, had a much shorter larval duration of 27 days (Sponaugle & Cowen 1994), similar to that found in this study for the arrow goby.

Previous estimates of larval characteristics of these two study species have varied widely, presumably due to methodological limitations. Estimates of larval duration for the tidewater goby have ranged from as little as several days (Capelli 1997) to a few weeks (Dawson et al. 2002). Past research on the arrow goby has provided a broad estimate of larval duration using both field collected and laboratory-reared specimens.

However, none of these estimates were obtained from otolith analysis. Brothers (1975) estimated larval duration at approximately 30 days from the timing of annual reproduction and recruitment. Dawson et al. (2002) estimated a 2–4 week larval duration by extrapolating the time to reach 7 mm (10 days; Hart 1973) to the time to reach the average size at settlement of 13.1 ± 1.3 mm (range 10.0–16.6 mm) observed by Kent & Marliave (1997) for newly settled arrow gobies from British Columbia. Our back-calculated estimate of size at settlement (10.00 ± 0.6 mm) falls just on the lower end of Kent & Marliave's (1997) range of size at settlement, but overlaps with measurements of nearshore postlarve collected by Brothers (1975). Morphological descriptions of transitional juveniles (12.5 mm SL) from British Columbia are consistent with the morphology of juveniles in Southern California estuaries that settled at a much smaller size, perhaps indicating regional differences in size at settlement.

The larval traits investigated in this study could vary between populations due to differences in habitat such as temperature, water quality, or food resources. In addition, it is also possible that the tidewater goby has adapted the ability to settle and reach maturity faster than the arrow goby due to its shorter, annual life cycle. This could be one explanation for the different estimates of settlement size from this study, done in Southern California, and that of Kent & Marliave (1997) conducted in British Columbia. Brothers (1975) found that the arrow goby lives for approximately one year in southern California, similar to the annual lifespan of the tidewater goby throughout its range, but has an extended lifespan in the more northern portions of its range (2-3 years). Swenson (1999) found that the average size of the tidewater goby was significantly larger in marsh habitats than in lagoons or creeks. She speculated that this was due to the more stable

physical conditions of the marsh, which fosters improved growth, perhaps due to a more consistent or abundant supply of prey. It is also worth noting that, given genetic isolation of populations (e.g. Earl et al. 2010), adaptation to local conditions is also possible in the tidewater goby. Our findings provide baseline estimates of some of the early life history traits of the tidewater goby and the arrow goby, but these attributes are likely to vary with environmental parameters.

Tables

Table 2.1. Estimated larval duration, settlement size, and growth rate for the tidewater goby and arrow goby from otolith analysis and back-calculations pooled over all 18-study sites

Species	Larval Duration		Settlement		Growth Rate	N
	Range (d)	Mean \pm SD (d)	Otolith Radius (μm)	Length - SL(mm)	Mean \pm SD ($\mu\text{m}/\text{day}-1$)	
<i>E. newberryi</i>	18 - 31	23.95 \pm 2.71	75.62 \pm 6.40	12.38 \pm 0.36	2.86 \pm 0.23	406
<i>C. ios</i>	20 - 33	26.11 \pm 2.40	77.61 \pm 6.37	10.00 \pm 0.71	2.60 \pm 0.22	317

Figures

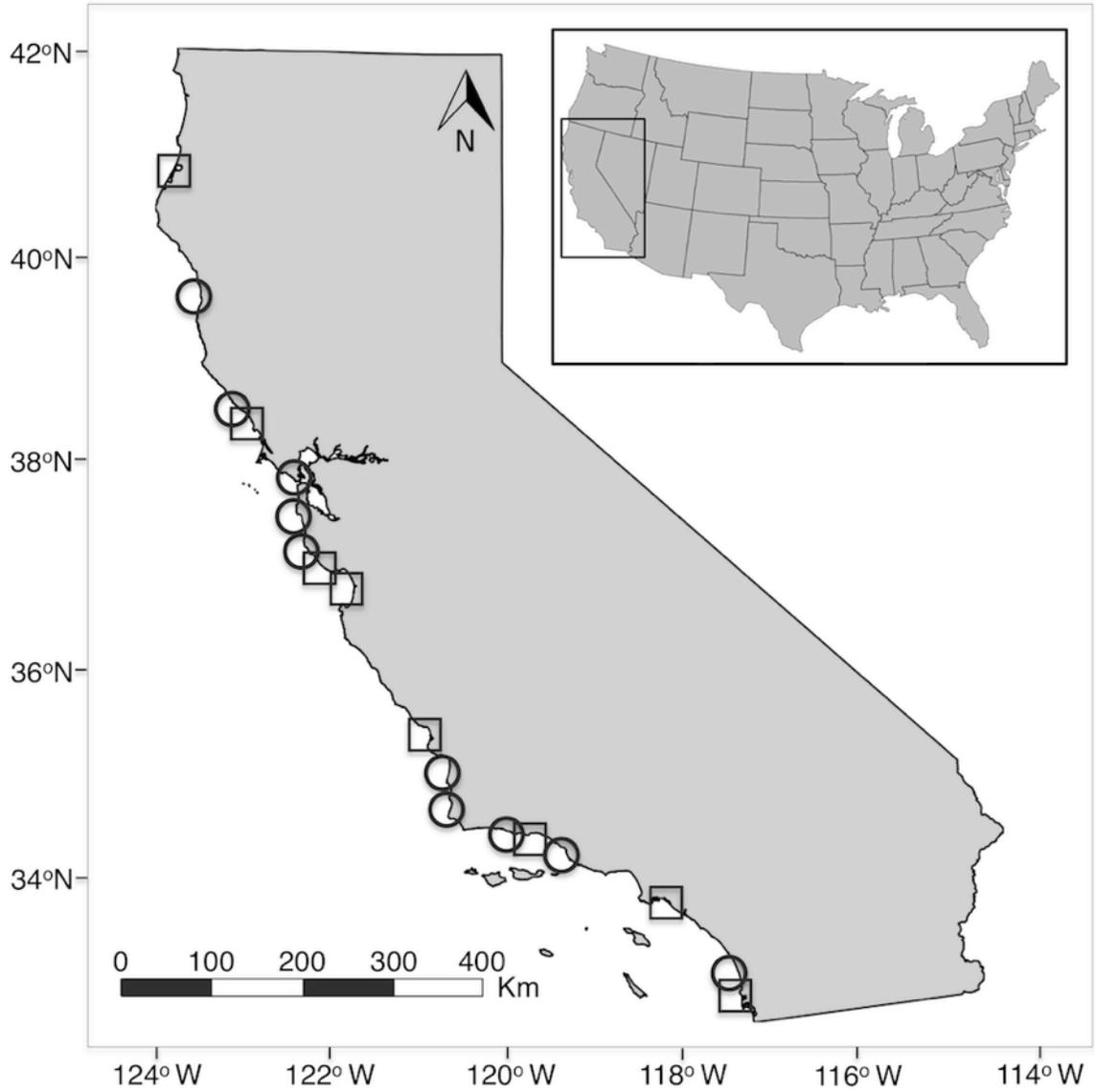


Figure 2.1. Map of 18 study sites located along the California coastline. The arrow goby (square) was collected at 8 sites, the tidewater goby (circle) was collected at 10 sites.

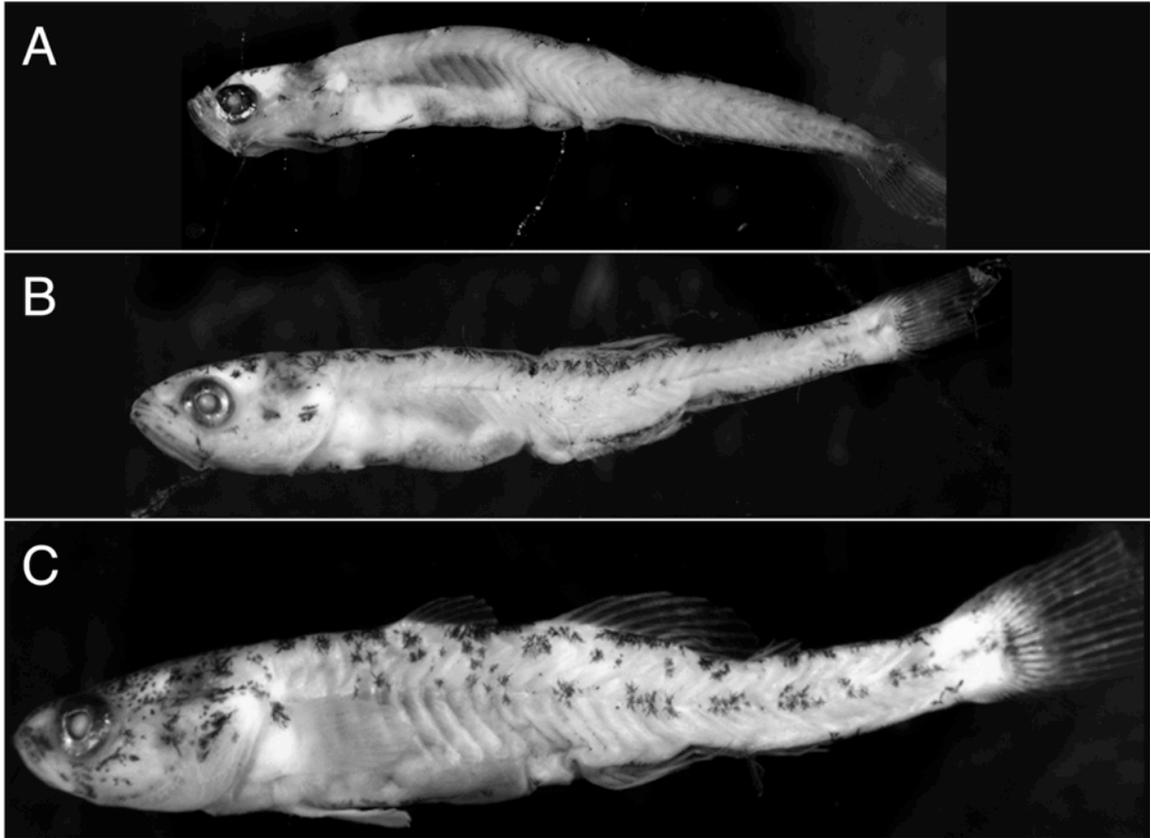


Figure 2.2. Photos showing the rapid development of the tidewater goby exhibiting the transition from (A) 20-day-old postflexion larva (9.3 mm SL), (B) 25-day-old transitional juvenile captured prior to settlement (10.8 mm), and (C) 34-day-old settled juvenile (13.7 mm).

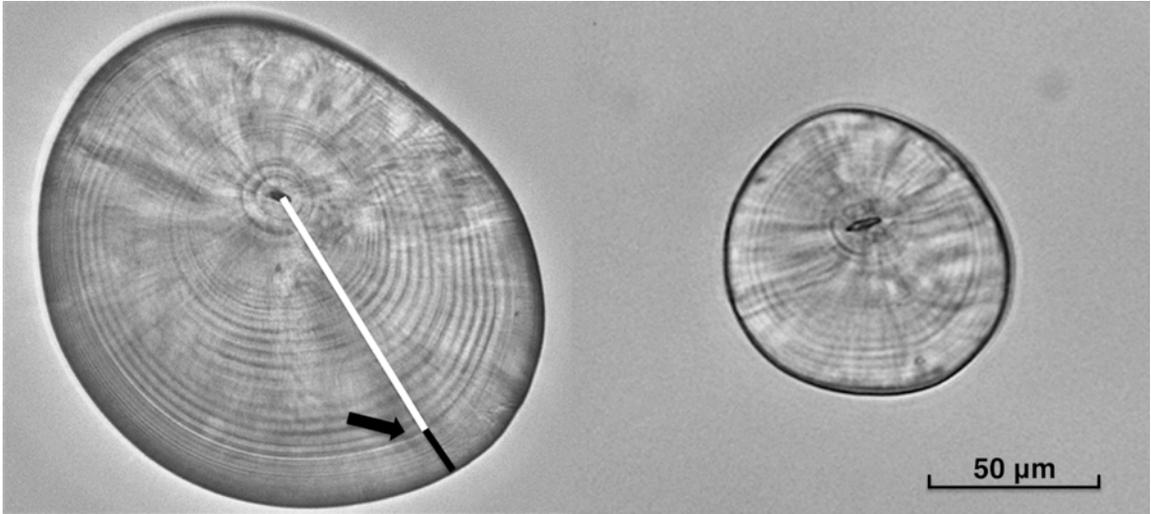


Figure 2.3. Lapillar otolith of a juvenile tidewater goby (A), and a larval tidewater goby (B) with visible daily bands viewed at 200x magnification. Black arrow indicates the settlement band. The white line indicates pre-settlement bands, and the black line represents post-settlement bands.

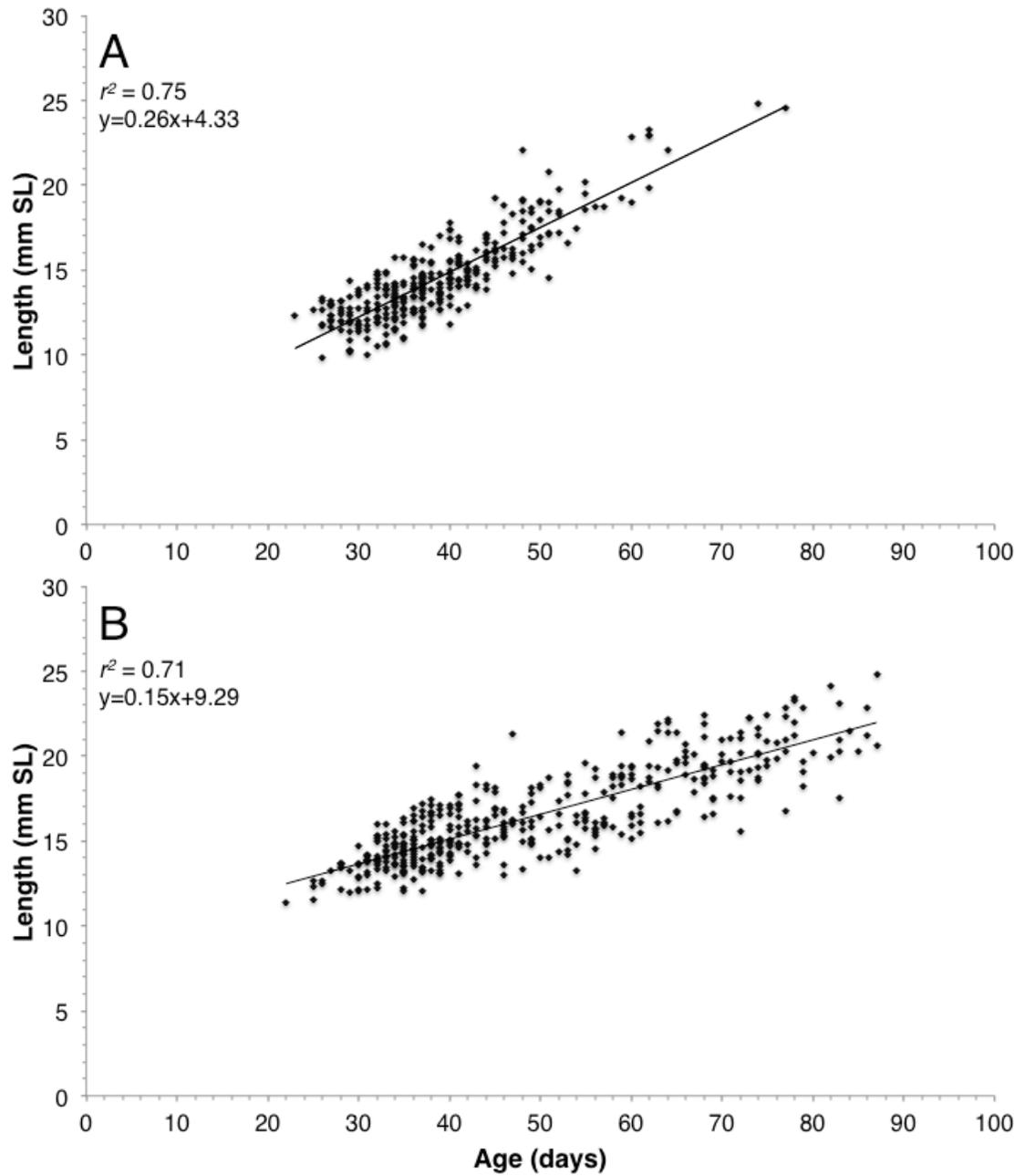


Figure 2.4. Relationship between body length and age for the arrow goby (A) and tidewater goby (B).

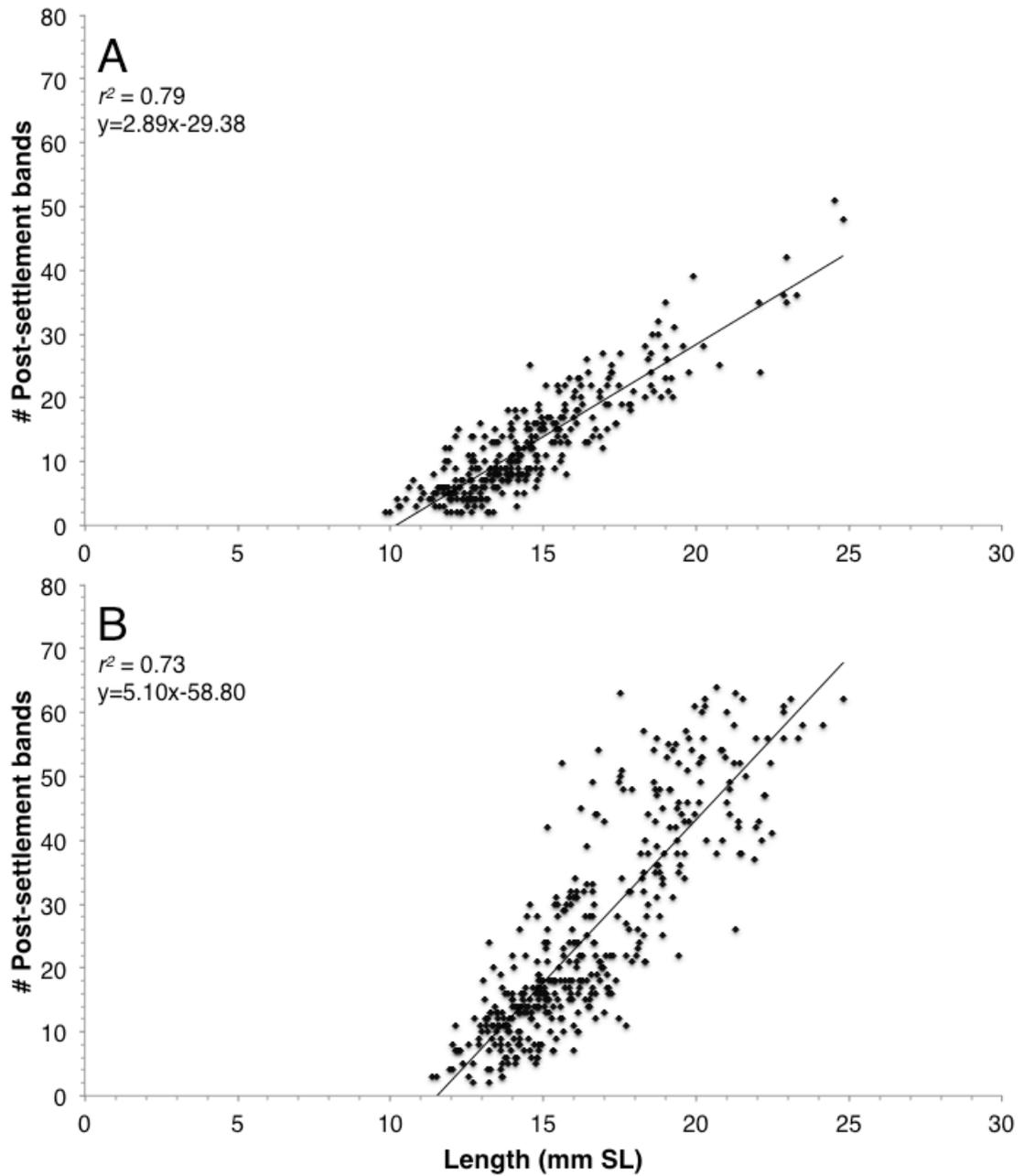


Figure 2.5. Relationship between post-settlement age and body length for (A) the arrow goby and (B) tidewater goby.

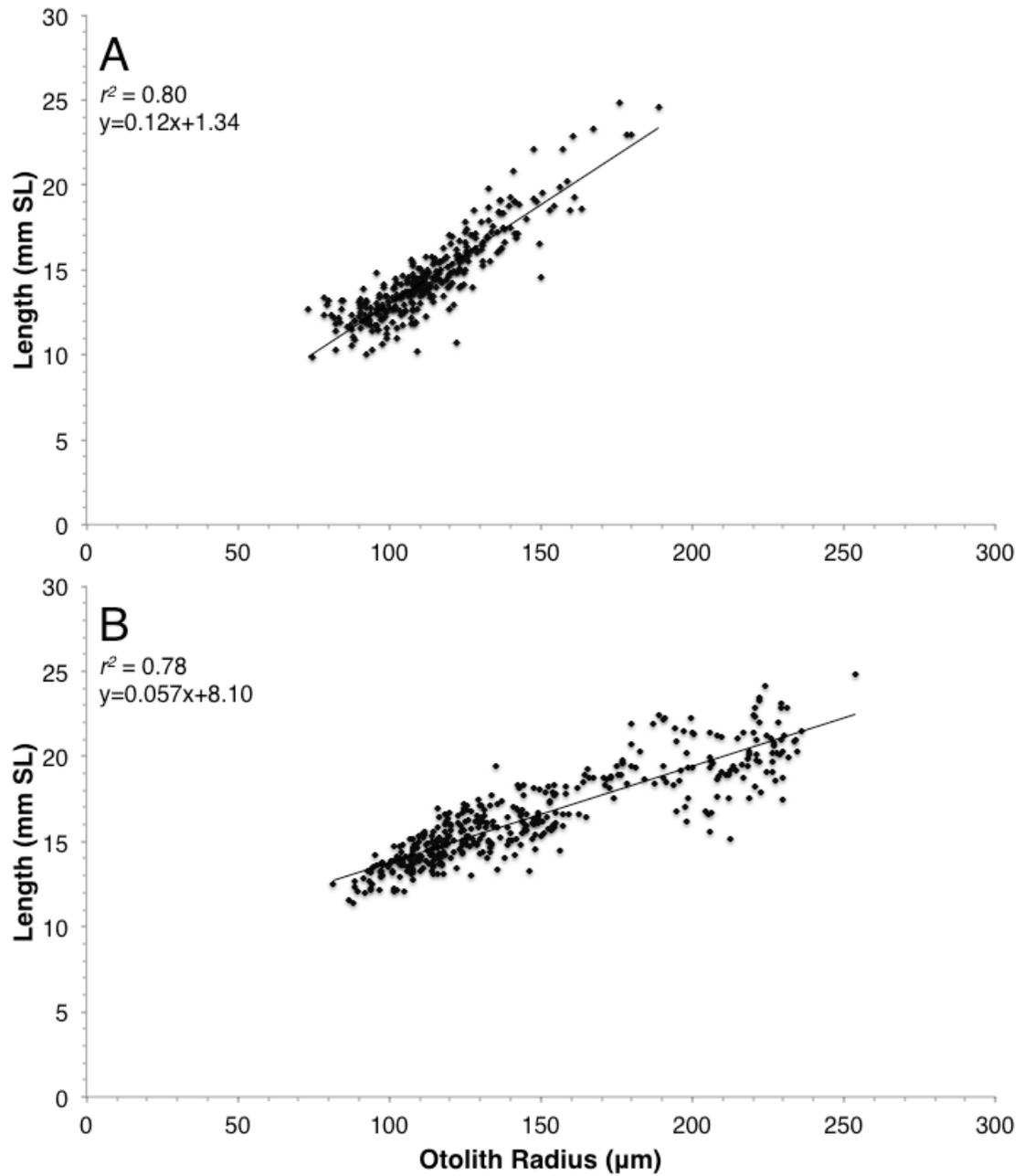


Figure 2.6. Relationship between otolith radius and body length for the arrow goby (A) and tidewater goby (B).

Chapter 3

EFFECTS OF TEMPERATURE AND LATITUDE ON LARVAE TRAITS OF TWO ESTUARINE FISHES IN DIFFERING ESTUARY TYPES

Abstract

Variations in abiotic conditions across large latitudinal gradients have been found to strongly influence the early life history of marine organisms. This study investigates the effects of temperature and latitude on the larval traits of two native estuarine fish species. The arrow goby (*Clevelandia ios*) and the federally endangered tidewater goby (*Eucyclogobius newberryi*) were studied in 18 estuaries along the coast of California, spanning approximately 8 degrees of latitude. These two species were selected because of their dissimilar preference for estuary type: the arrow goby prefers cooler, fully tidal bays and mudflats, whereas the tidewater goby prefers warmer estuaries and lagoons that experience some degree of seasonal closure, or isolation, from the sea. Recently settled individuals were collected from July-October 2011 and temperatures within each estuary were recorded hourly in order to determine how temperature variations affect larval duration, settlement, and growth rates. Temperatures were more variable among sites for estuaries inhabited by the tidewater goby (10° C range) than for those inhabited by the arrow goby (5° C range). Larval traits of both species varied significantly among sites, but among site variation was greater for the tidewater goby, a difference that was tied to the greater differences in temperatures among sites in the seasonally closed estuaries it inhabited. On average, for both species, fish that experienced warmer temperatures had a shorter larval duration, faster growth rates, and were smaller at settlement. Since the

length of the larval period has been related to dispersal distance for some species, and survival in others, future variations in temperature due to climate change could have a direct and predictable influence on population connectivity and community interactions of estuarine associated species.

Introduction

It is unclear how the predicted increases in coastal temperatures due to climate change will affect the larval development of estuarine fish species. Studies to date have shown that the effects of temperature on the metabolic rates of marine fish species can greatly affect larval development and survival (Gillooly 2001, Gillooly et al. 2002, Brown et al. 2004, O'Connor et al. 2007). Controlled laboratory experiments have revealed effects of temperature on the pelagic larval duration (PLD), size at settlement, and growth rates in tropical reef fish with as little as a 3-5°C variation (McCormick & Molony 1995, Green & Fisher 2004). In addition, variations in temperature have been found to significantly affect metamorphic success, behavior, and dispersal distance in marine fish species (Rutherford & Houde 1995, Wilson & Meekan 2002, Meekan et al. 2003, O'Connor et al. 2007), which has the potential to significantly influence population dynamics and community level processes (Gillooly 2001, O'Connor et al. 2007).

In Mediterranean regions, such as California, climate variations are predicted to increase with accelerated human population growth and continued climate change, resulting in warmer, drier, and more variable weather patterns (Valiela et al. 2009, Klausmeyer & Shaw 2009). These climate patterns have become more noticeable over the past decade, especially in the coastal zones of Southern and Central California. As a

consequence of their broad spatial distribution (> 1000 km north to south) and tidal patterns, California's estuarine habitats experience significant variability in temperature, both spatially and temporally.

The vast majority of these estuaries are partially or completely isolated from marine tidal influence either seasonally or episodically due to a formation of a sandbar at the estuary mouth (Jacobs et al. 2011). This event typically occurs in the warmer summer months when reduced rates of precipitation lead to reduced freshwater input (Cooper et al. 2012). In addition, the reduction of tidal exchange causes longer resident time of water, permitting warmer and more variable temperature regimes (Cousins et al. 2010). This phenomenon of closure provides beneficial conditions for a number of endemic and endangered species that use the closed estuaries at some point during their life history (Swift et al. 1989, 1993, Bond et al. 2008).

In this study, I examine the effects of temperature on the larval traits of two estuarine fish species, the arrow goby and the federally endangered tidewater goby. The tidewater goby is a small (<55 mm standard length, SL), benthic fish endemic to California that is found in a variety of shallow estuarine habitats (Miller & Lea 1972, Swift et al. 1989, Moyle 2002). The tidewater goby was listed as federally endangered in 1994 (U.S. Fish and Wildlife Service 2005), mainly due to the loss and degradation of suitable habitat. This species occupies estuarine habitats that are partially or completely isolated from marine tidal influence either seasonally or episodically (Jacobs et al. 2011). A high degree of mouth closure yields distinct lagoonal conditions that are highly variable, and can strongly influence salinity, water quality, and temperature. This unique habitat preference requires the tidewater goby to tolerate highly variable conditions, including

salinities ranging from 0-41 ppt, and temperatures from 9-25° C (Swift et al. 1989, Swenson 1999a). However, larval tidewater gobies are typically restricted to their lagoonal habitats during summer months when the estuary mouth is closed (Lafferty, Swift, & Ambrose 1999a, b). Thus, it is likely that the tidewater goby larvae experience much greater variation in temperature than arrow goby larvae.

The arrow goby is the sympatric sister species of the tidewater goby (Dawson et al. 2002). Similar to the tidewater goby, the arrow goby is also a small (<60 mm SL) benthic fish, however it has a broader geographic range that extends from the Bahia Magdalena, Baja California Sur (C. Swift, pers. com.) to British Columbia (Miller and Lea 1972). This broader range is likely due to its preference for more open, fully tidal, bays and estuaries that are typically cooler and higher in salinity than those occupied by the tidewater goby. This differing habitat preference of the arrow goby provides it with a greater dispersal potential via marine larvae, which likely explains its broader geographic range and shallow phylogeographic structure (Dawson et al. 2002).

In order to determine the effects of temperature and latitude in these two gobiid species with differing habitat preference and larval dispersal potential, I examined three main questions: 1) Do larval traits vary latitudinally in both species across their geographic range of overlap; 2) How do temperature regimes vary latitudinally in seasonally closed vs. fully tidal systems; and 3) Are variations in larval traits related to variations in the average temperature experienced during the larval phase or latitude?

Materials and methods

Study sites

A total of 18 study sites along the California coast were sampled from July to October of 2011 (Fig. 2.1, Table 3.1). Study sites consisted of eight fully tidal estuaries inhabited by the arrow goby, and ten seasonally closed estuaries inhabited by the tidewater goby. Study sites for the arrow goby listed from north to south include: Arcata Bay (40°51'30.57"N, 124°06'00.08"W); Bodega Bay (38°18'59.42"N, 123°02'43.12"W); San Lorenzo River (36°57'56.41"N, 122°00'45.46"W); Elkhorn Slough (36°48'40.14"N, 121°44'38.77"W); Morro Bay (36°57'56.41"N, 122°00'45.46"W); Carpinteria Salt Marsh (34°23'52.97"N, 119°32'16.72"W); Colorado Lagoon (33°45'10.52"N, 118°07'47.37"W); and Los Peñasquitos (32°55'57.84"N, 117°15'29.11"W). Study sites for the tidewater goby listed from north to south include: Ten Mile River (39°32'43.86"N, 123°45'25.04"W); Salmon Creek (38°21'10.87"N, 123°03'57.19"W); San Gregorio (37°19'14.29"N, 122°24'03.38"W); Rodeo Lagoon (37°49'54.41"N, 122°31'43.31"W); Moore Creek (36°57'4.50"N, 122°03'29.85"W); San Luis Obispo Creek (35°11'13.35"N, 120°43'33.47"W); Santa Ynez River (34°41'30.57"N, 120°35'00.70"W); Arroyo Burro Lagoon (34°24'11.77"N, 119°44'35.12"W); Santa Clara River (34°14'07.19"N, 119°15'27.46"W); and Las Flores Marsh (33°17'25.79"N, 117°27'53.91"W). Sites were chosen based on two characteristics: 1) the presence of healthy and abundant populations of the arrow goby or tidewater goby, and 2) estuary mouth dynamics: fully tidal or seasonally closing (Fig. 3.2).

Collections and otolith analysis

Larval and juvenile gobies (Fig. 3.3) were collected between August and October of 2011 (Table 3.1). Both species were collected using either a 3.7 x 1.2 m beach seine with a 1.6-mm mesh, or a one-man push net with 1.6-mm mesh (Strawn 1954). Once the fishes were collected, they were euthanized and then preserved in 95% ethanol. Length and weight measurements were taken for each goby before extraction of lapillar otoliths (Brothers 1987). Lapilli (Fig. 3.3A) were used for all otolith analysis because they were clearer and required less processing than sagittal otoliths. Previous work has validated daily increment deposition in sagittal otoliths (Fig. 3.3B) for the tidewater goby (Hellmair 2010), and I found no differences in increment counts between sagittal and lapillar otoliths in this study. Due to the similarity and close phylogenetic relationship with the tidewater goby, it was assumed that increments in otoliths of the arrow goby were also deposited daily.

A total of 723 otoliths (arrow goby: $n=317$; tidewater goby: $n=406$) were prepared using techniques similar to Samhuri et al. (Samhuri et al. 2009), which included placing the otoliths in immersion oil for >30 days to clear them to facilitate interpretation. Otoliths were then viewed under a compound microscope with a polarizing filter and camera at 200 \times magnification. Any otoliths that were irregularly shaped or unreadable were discarded from the study. The remaining otoliths were viewed and measured twice by the same individual (B.T. Spies). If the two readings were more than 10% different, the readings were not included in any analysis. If the two readings were less than 10% different, but not the same, then the second reading was used for the analysis.

Increment measurements were made along the longest axis, from the core to the outermost complete ring, using Image-Pro Plus image analysis software. The settlement band was interpreted as a distinct transition in increment widths (Fig 3.3A). Date of settlement was found by subtracting the number of post-settlement increments counted for each otolith from the date the fish was collected. Larval duration was estimated as the number of rings from the hatch mark to the settlement mark. Average pre-settlement growth rates were estimated from otolith growth as a proxy for somatic growth, by dividing the otolith radius to the settlement mark by the age at settlement (McCormick & Molony 1995).

Temperature measurement

Hourly temperature measurements were recorded at all 18 sites. At 15 out of the 18 sites, ibutton thermocron temperature recorders (model DS1921G with 0.5° C resolution) were used. Ibuttons were waterproofed using $\frac{3}{4}$ inch schedule 40 PVC male and female caps with silicone thread tape and a small dehydration packet inserted to absorb moisture. Two ibutton recorders were placed within each site in the beginning of July 2011, allowing for at least four weeks of temperature data to be recorded before fish collections took place. Ibuttons were spaced approximately 100 m apart in order to provide representative measurements of temperature ranges around the area where goby collections would occur. The three sites where ibuttons were not used (Arcata Bay, Elkhorn Slough, and Morro Bay) had fixed, long-term temperature loggers already in place. Temperature data for these sites was provided by the U.S. Fish and Wildlife

Service (Arcata Bay), the Elkhorn Slough National Estuarine Research Reserve, and the San Luis Obispo Science and Ecosystem Alliance (Morro Bay).

Hourly temperature recordings were used to calculate the mean hourly temperature experienced by each fish through its larval phase. Daily otolith increments were used to estimate the date of hatching and the date of settlement for each fish. This allowed me to calculate the mean temperature history for each individual fish during its larval phase (McCormick and Molony 1995). The mean temperature experienced by each fish was then used to calculate the mean temperature for each study site.

Statistical analysis

To test the effects of temperature and latitude on three larval traits (larval duration, otolith based size at settlement, and growth rate) and whether these effects differed between the two species, a general linear model (GLM) was used in SYSTAT 13. The model included Species as a categorical factor and Temperature and Latitude as continuous variables. Whether the effects of temperature or latitude were consistent between species was tested by the interaction terms between these two covariates and the factor Species. To allow unbiased tests of the main effects of Species, Temperature, and Latitude, all non-significant interaction terms involving the continuous variables were sequentially eliminated (Winer et al. 1991). In addition, linear regression was used to examine the relationship between temperature and latitude of the study sites.

Results

Mean site temperature and latitude

Larval tidewater gobies experienced a greater range of average temperatures at the study sites than did larvae of the arrow goby. Average temperatures at the sites occupied by the tidewater goby differed by approximately 10° C from the coolest to warmest site (range = 15.33 ± 0.14 to 25.11 ± 0.18). Mean site temperatures occupied by the arrow goby differed by only approximately 5° C from the coolest to warmest site (range = 16.12 ± 0.33 to 21.27 ± 0.34).

Sites inhabited by the arrow goby and tidewater goby showed the expected trend of decreasing average temperature with latitude, but this trend was not statistically significant in both estuary types (Table 3.1, Fig. 3.3). In sites inhabited by the arrow goby, the latitudinal trend was not statistically significant (Fig. 3.3: $n=8$, $r^2=0.03$, $p=0.32$), whereas it was significant for sites inhabited by the tidewater goby (Fig 3.3: $n=10$, $r^2=0.55$, $p=0.008$). Estuaries inhabited by the arrow goby followed the expected latitudinal temperature trend for 7 out of the 8 sites, but the northernmost site deviated from this trend.

Effects of temperature and latitude on larval traits

Larval traits were significantly affected by temperature, not latitude, and the effects of temperature on larval traits varied between species. This variation between species is likely due to the mean temperature difference experienced in estuaries inhabited by the tidewater goby (10°C) compared to the arrow goby (5°C). There were no significant Species \times Temperature or Species \times Latitude interactions (larval duration $F_{1,10}=0.24$,

$p=0.64$; size at settlement $F_{1,10}=3.05$, $p=0.11$; growth rate $F_{1,10}=0.82$, $p=0.39$; Figs. 3.4 and 3.5), indicating that there was no statistical evidence for a difference in the pattern of response of the two species to the effects of temperature and latitude. All three larval traits were significantly related to temperature (Table 3.2). Larval duration decreased as temperature increased ($F_{1,14}=18.9$, $p=0.001$; Fig. 3.4A), as did size at settlement ($F_{1,14}=6.1$, $p=0.03$; Fig. 3.4B), whereas growth rates increased with temperature ($F_{1,14}=5.3$, $p=0.04$; Fig. 3.4C) of larval fish. Variations in larval traits, however, did not follow a latitudinal trend, as no significant effect of latitude was found on the larval duration ($F_{1,14}=0.1$, $p=0.76$; Fig. 3.5A), settlement at size ($F_{1,14}=2.3$, $p=0.15$; Fig. 3.5B), or growth rate ($F_{1,14}=3.8$, $p=0.07$; Fig. 3.5C).

Linear regressions were used to inspect the fit of the larval trait response variables to the temperature and latitude data; examining the species-specific relationship between larval traits and both the mean site temperature (Fig. 3.4) and latitude (Fig. 3.5). There was a strong negative relationship between larval duration (Fig. 3.4A: $n=10$, $r^2=0.72$) and settlement size (Fig. 3.4B: $n=10$, $r^2=0.71$) as a function of temperature for the tidewater goby. This finding indicates that larval tidewater gobies are significantly larger at settlement and spend more time in their larval phase in cooler environments. Conversely, the arrow goby did not show strong linear relationships between larval duration (Fig. 3.4A: $n=8$, $r^2=0.40$) or settlement size (Fig. 3.4B: $n=8$, $r^2=0.08$) as a function of temperature. These findings suggest that the effects of temperature on larval duration and settlement sized found in the GLM analysis was driven by the greater range of temperatures experienced by the tidewater goby in seasonally closed estuaries. Larval

growth rate had a weak positive relationship with temperature for both the tidewater goby (Fig. 3.4C: $n=10$, $r^2=0.10$) and the arrow goby (Fig. 3.4C: $n=8$, $r^2=0.09$).

Overall, the tidewater goby had approximately 35% shorter larval durations in the warmest sites, as well as being 27% smaller in body size, and growing 24% faster. In comparison, the arrow goby had an approximate 3.62 day (15%) difference in larval duration in warmer sites, and was 14% smaller in body size, with a 16% faster growth rate.

Discussion

This study demonstrates the variable nature of temperature in estuarine habitats, and how it can strongly influence larval fish growth. Larval duration, settlement size, and growth rate were significantly affected by temperature, with no significant effects of latitude. Temperature, however, had a stronger effect on larvae of the tidewater goby than the arrow goby, presumably due to the larger difference temperatures this species experienced. Nonetheless, in warmer estuarine environments, both the tidewater arrow goby and tidewater goby spent fewer days in their larval phase, were smaller in size at settlement, and exhibited faster growth rates.

The smaller, seasonally closed systems inhabited by the tidewater goby exhibited a greater range of mean temperature (10°C). While seasonally closed estuaries had a stronger linear relationship between temperature and latitude than tidal estuaries, closed estuaries exhibited greater latitudinal variability in mean site temperature than tidal estuaries. Thus, the strong linear relationship found between temperature and latitude in closed estuaries was mainly driven by the significant difference in temperature found

between the coldest and warmest sites located at the extremes of latitude. It is worth noting that the coldest and most northern study site for the tidewater goby was in fact open to tidal influence at the time of collection, thus, water temperatures there did not represent closed estuarine conditions.

A number of studies have found similar effects of temperature on larvae of a variety of temperate and tropical marine species, using both field and laboratory approaches. Several species of flatfish (*Pseudopleuronectes americanus*, *Solea solea*, *Platichthys stellatus*, *Paralichthys olivaceus*; *Paralichthys californicus*, *Paralichthys dentatus*) in temperate systems have exhibited shorter larval durations with increased temperature in controlled laboratory experiments (Laurence 1975, Fonds 1979, Policansky 1982, Seikai et al. 1986, Gadomski & Caddell 1991, Keefe 1993). Green and Fisher (Green & Fisher 2004) found that a decrease of 3° C resulted in a slower swimming development in laboratory reared tropical anemone fish *Amphiprion melanopus*, including longer larval duration and reduced growth rates. Similar results were found in the tropical goatfish *Upeneus tragula*, which showed a significant negative relationship between water temperature and size and age at metamorphosis both in the field and laboratory experiments (McCormick and Molony 1995). Furthermore, water temperature in the upper Florida Keys was found to explain 78% of the variation in the pelagic larval duration (PLD) in the Caribbean reef fish *Thalassoma bifasciatum* (Sponaugle et al. 2006), with larval growth explaining 85% of the variation in PLD. This resulted in warmer water cohorts exhibiting a shorter pelagic larval duration as a product of faster growth rates. Warmer-water fish were larger at age, but due to the shorter time spent in the larval phase they were smaller in body size at settlement. However, size at settlement

was found to be largest at intermediate temperatures, not the expected colder temperatures where larval duration was found to be highest. Larvae of Hawaiian amphidromous goby *Lentipes concolor* settled after a shorter PLD and at smaller sizes during months of warmer ocean temperature (Radtke et al. 2001).

Physiological responses to temperature commonly follow a dome-shaped relationship where a maxima is reached as rates increase with temperature, but thereafter decrease rapidly if temperatures exceed the thermal optimum (Munday et al. 2009). The thermal optima for the arrow goby and tidewater goby larvae are unknown, but it is likely different for these species given what is known about their natural history. This difference could be a result of local adaption or acclimation to site-specific temperature regimes (Hawkins 1996). Elevated temperatures have the potential to cause a decline in reproductive output if water temperature rises above the optimum for reproduction (Munday et al. 2008). A decline in adult reproductive output could result in significant consequences for population connectivity (Munday et al. 2009).

It is not clear how climate change will affect temperature regimes in closed vs. open estuarine habitats along the coast of California, because variations in climate patterns over large latitudinal scales can have considerable effects on the overall size, function, and distribution of estuarine habitats (Scavia et al. 2002, Day et al. 2008). A rise in global temperature is expected to shift the evaporation/precipitation regime, causing increased evaporation at lower latitudes and increased precipitation in the higher latitudes (Roessig et al. 2005). This could cause longer durations of estuary closure in southern California, and more frequent opening conditions in northern California. Increased global temperatures will likely accelerate larval development for many species. This could prove

to be positive or negative for some species depending on their local conditions and community structure. For example, if a species such as the arrow goby experienced a decrease in larval duration, this change could decrease the spatial scale over which it disperses, reducing connectivity (O'Connor et al. 2007, Munday et al. 2009). However, reductions in larval duration could potentially increase survival to settlement by reducing exposure to mortality agents in the plankton. This change could prove beneficial in habitats where there are numerous predators of larvae, but could be detrimental in habitats where increased body size at settlement gives a competitive advantage in the juvenile and adult stage (Fontes et al. 2010).

In summary, larval traits of the two estuarine gobies in this study differed, both between species and within species among estuaries spanning the coast of California. Differences in larval traits between species followed the pattern proposed by Dawson et al. (2002), with the tidewater goby predicted to have a shorter larval duration than the arrow goby, based on an apparent lack of marine larval dispersal in the tidewater goby. However, variation in larval traits for both species was strongly related to differences in the mean temperature experienced during larval development, and not strongly influenced by latitude. These findings reveal the variable nature of estuarine habitats and their abiotic conditions. Closed estuaries exhibited a much greater range of thermal environments than did estuaries open to the ocean, but these systems have not been studied much. Further research on them is needed to provide a better understanding of how local abiotic conditions can effect population dynamics of endangered taxa, as well as provide vital information on the ability of endemic and threatened species to acclimate or adapt to the projected increases in temperature due to climate change.

Tables

Table 3.1: Study sites with corresponding latitudes, mean (\pm SD) temperatures experienced by larval gobies, and numbers of gobies sampled, listed from north to south for the tidewater goby and arrow goby.

Species	Study Site	Latitude	Mean \pm SD Temp.	N
<i>E. newberryi</i>	Ten Mile River	39°32'43.86"N	15.33 \pm 0.14	39
	Salmon Creek	38°21'10.87"N	18.70 \pm 0.34	40
	Rodeo Lagoon	37°49'54.41"N	17.40 \pm 0.31	40
	San Gregorio Creek	37°19'14.29"N	18.82 \pm 0.33	44
	Moore Creeke	36°57'04.50"N	21.59 \pm 0.20	40
	San Luis Obispo Creek	35°11'13.35"N	18.92 \pm 0.30	39
	Santa Ynez River	34°41'30.57"N	18.51 \pm 0.32	40
	Arroyo Burro Lagoon	34°24'11.77"N	24.92 \pm 0.50	47
	Santa Clara River	34°14'07.19"N	21.47 \pm 0.21	38
	Las Flores Marsh	33°17'25.79"N	25.11 \pm 0.18	39
<i>C. ios</i>	Arcata Bay	40°51'30.57"N	20.41 \pm 0.10	41
	Bodega Bay	38°18'59.42"N	16.12 \pm 0.33	42
	San Lorenzo River	36°57'56.41"N	17.62 \pm 0.12	40
	Elkhorn Slough	36°48'40.14"N	18.37 \pm 0.18	41
	Morro Bay	35°20'34.52"N	17.96 \pm 0.07	40
	Carpenteria Salt Marsh	34°23'52.97"N	19.70 \pm 0.12	43
	Colorado Lagoon	33°45'10.52"N	20.50 \pm 1.00	29
	Los Peñasquitos	32°55'57.84"N	21.27 \pm 0.34	41

Table 3.2: Results of general linear models (GLM) testing for effects of temperature, latitude, and species on larval duration, settlement size, and pre-settlement growth rate.

Larval trait	Source	df	SS	F	p	r2
Larval duration	Species	1	8.52	5.93	0.03	0.75
	Latitude	1	0.14	0.10	0.76	
	Mean Temp.	1	27.20	18.92	0.00	
	Error	14	20.12			
Settlement size	Species	1	2.98	0.27	0.61	0.60
	Latitude	1	25.27	2.30	0.15	
	Mean Temp.	1	66.50	6.05	0.03	
	Error	14	153.79			
Growth rate	Species	1	0.19	9.47	0.01	0.60
	Latitude	1	0.08	3.85	0.07	
	Mean Temp.	1	0.11	5.26	0.04	
	Error	14	0.28			

Figures



Figure 3.1. (A) Moore Creek, located in Santa Cruz County, represents a seasonally closed estuary inhabited by the tidewater goby. (B) Bodega Bay, located in Sonoma County, represents a fully tidal bay inhabited by the arrow goby. Photograph by Chris Saulit.

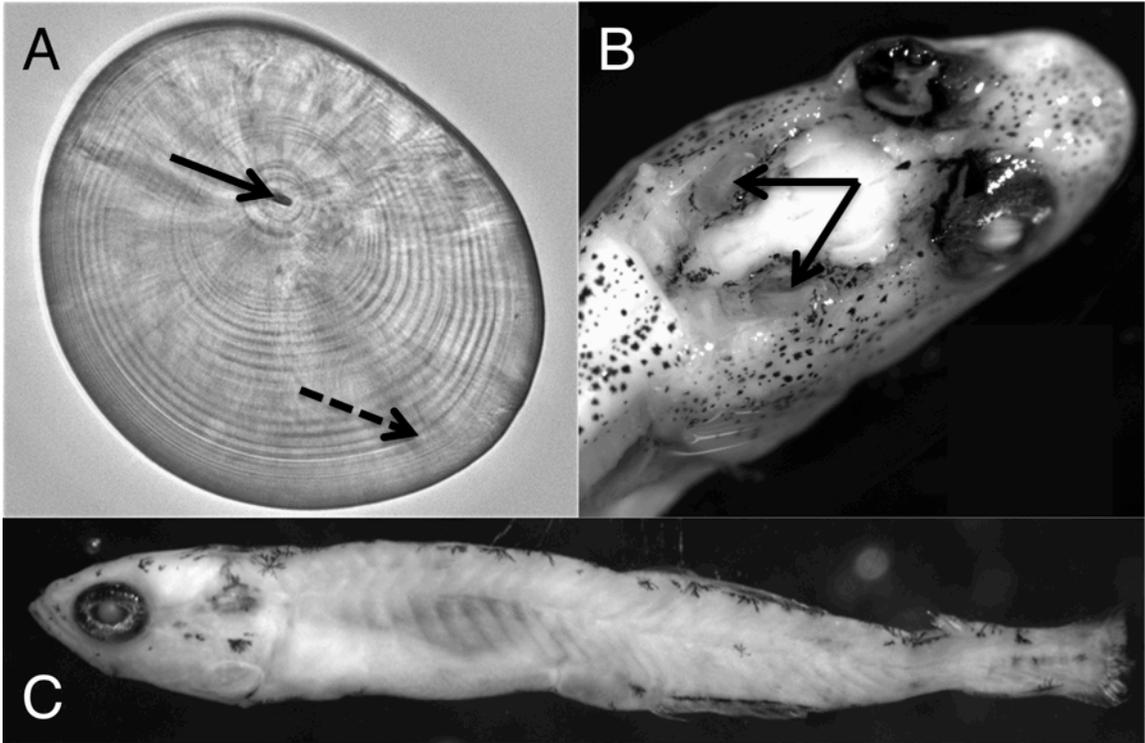


Figure 3.2. (A) Lapillar otolith from a juvenile tidewater goby with visible daily growth bands viewed at 200 \times magnification. The otolith core is located at the tip of the solid black arrow. The settlement band is located at the tip of the broken arrow. (B) Photo of a juvenile tidewater goby with sagittal otoliths indicated by black arrows. (C) Photo of a larval tidewater goby SL= 9.95mm.

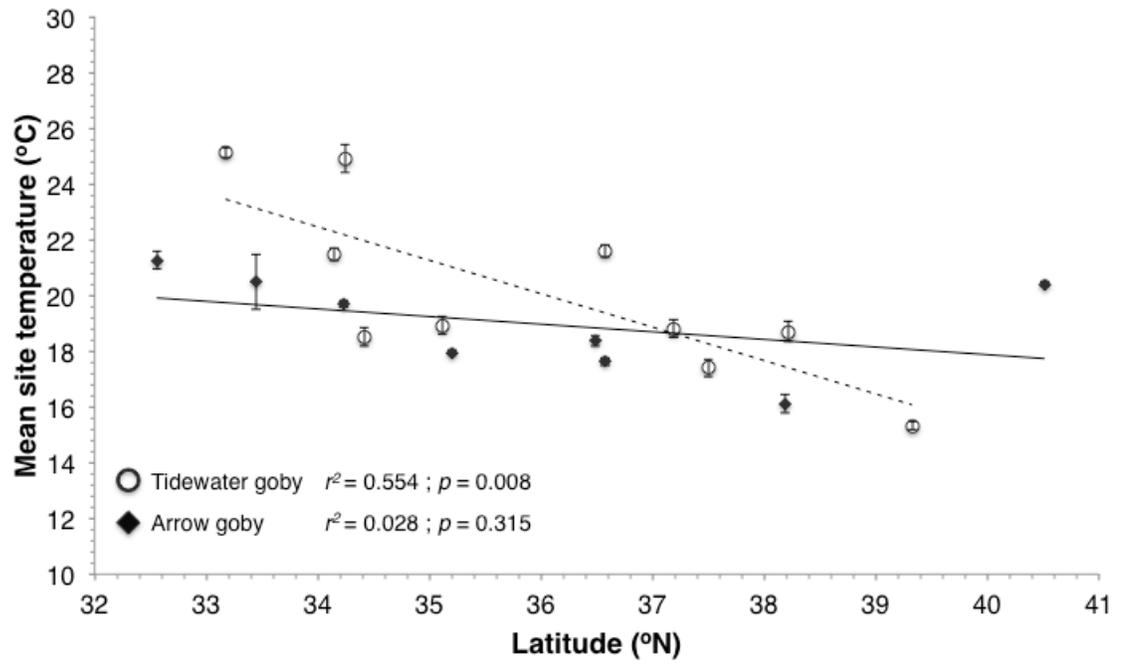


Figure 3.3. Mean hourly temperatures (°C) for each site as a function of latitude (°N). Study sites inhabited by the arrow goby spanned greater latitude and were on average cooler.

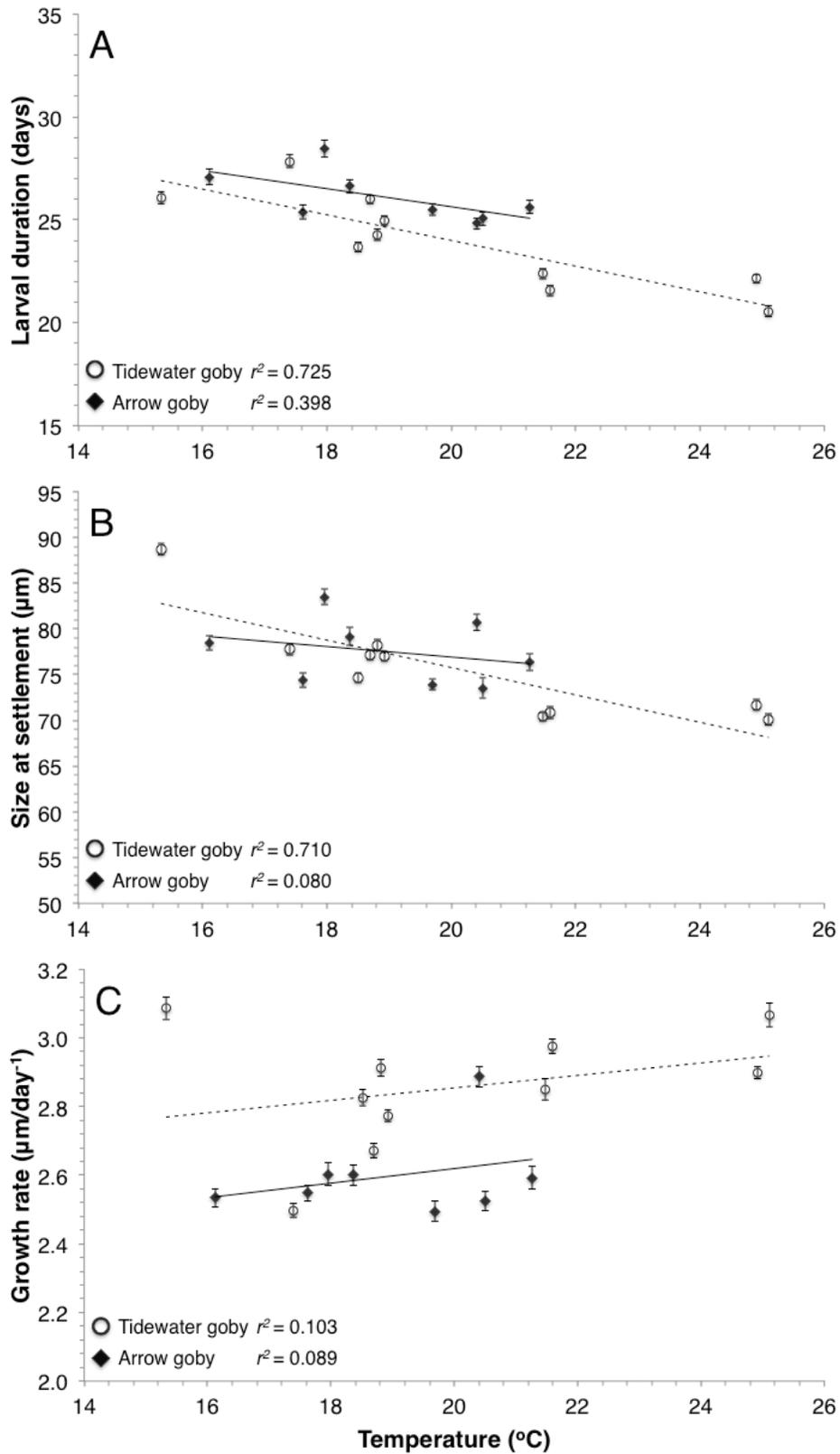


Figure 3.4. Relationships between mean site temperature and (A) larval duration, (B) size at settlement, and (C) pre-settlement growth rate for the tidewater goby and arrow goby

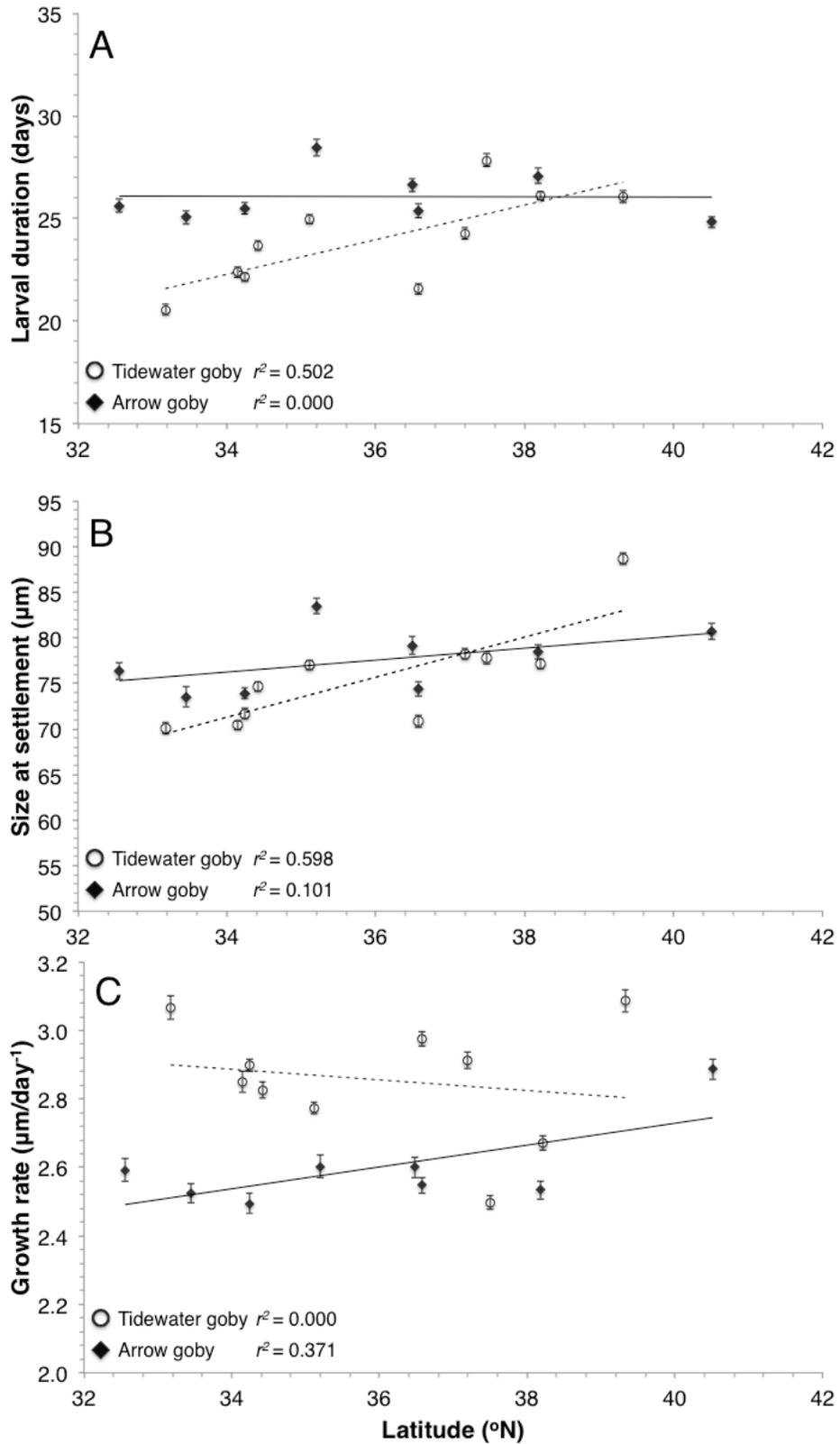


Figure 3.5. Relationships between latitude and (A) larval duration, (B) size at settlement, and (C) and pre-settlement growth rate for the tidewater goby and arrow goby.

Chapter 4: Conclusions

This research was the first to document the larval life history of the federally endangered tidewater goby, and was the first detailed study of arrow goby larvae using otolith analysis. A total of 18 collection sites (10 tidewater goby; 8 arrow goby) that spanned over 8° of latitude provided a detailed understanding of the variation in larval traits between these two sister species throughout their region of range overlap. Although significantly different, larval traits were surprising similar given the differences in their habitat preferences and methods of dispersal. The approach used by Dawson et al. (2002) to predict the estimated larval duration of the arrow goby (2-4 weeks) based on extrapolating the time to reach 7 mm (10 days; Hart 1973) to the time to reach the average size at settlement of 13.1 ± 1.3 mm observed by Kent & Marliave (Kent & Marliave 1997) was fairly accurate. However, from my analysis a 3-4 week range of larval duration appears more accurate, and seems unlikely to extend as low as 2-weeks. Furthermore, estimates of larval duration for the tidewater goby have ranged from as little as several days (Capelli 1997) to a few weeks (Dawson et al. 2002). Using lapillar otoliths, I found that the larval duration of tidewater goby is quite similar to arrow goby (3-4 weeks), but on average 3 days shorter than the arrow goby. In addition, arrow gobies were found to have a slightly larger otolith radius at settlement, slower growth rates, and were smaller in body size at settlement than the tidewater goby along the California coast.

The larval duration of these two study species falls on the shorter end of other related gobiid species (Sponaugle & Cowen 1994, Radtke et al. 2001, Yamasaki & Maeda 2007, Samhuri et al. 2009), potentially due to the isolating and variable nature of estuarine

habitats as documented and discussed in this study. Seasonally closed estuaries inhabited by the tidewater goby exhibited a wider range of temperatures (10°C) than fully tidal marine systems (5°C) inhabited by the arrow goby. While there was a larger difference in the mean temperatures experienced by the tidewater goby than those experienced by the arrow goby, variations in larval traits for both species were strongly influenced by differences in the mean temperature experienced during larval development. Gobies in warmer estuarine environments had shorter larval durations, were smaller in size at settlement, and exhibited faster growth rates. Similar results have been documented in a wide range of taxa (McCormick & Molony 1995, Green & Fisher 2004, Sponaugle et al. 2006, O'Connor et al. 2007), and have been associated with the relationship between temperature and metabolic processes.

Differences in estuarine habitat type can cause variations in the abiotic environment, which explains the differences in temperature ranges (5°C – 10°C) found between closed vs. open estuaries in this study. Warmer temperatures often increase metabolic rates and reduce the duration of time spent in the larval phase. A decrease in larval duration could potentially reduce dispersal distance and gene flow between populations. This would not affect the tidewater goby as much as the arrow goby, which relies on marine larval dispersal to maintain population connectivity. However, decreases in larval duration could potentially increase the rate of survival to settlement by reducing predator exposure (Shima & Findlay 2002). This decreased in larval duration would likely decrease the size at settlement, which could prove to be detrimental in populations where a larger body size at settlement gives a greater competitive advantage in the juvenile stage.

Very little research to date has focused on California's seasonally closed estuaries and lagoons. These variable and highly productive ecosystems are prominent components of the coast, where many have suffered degradation or destruction. The endangered tidewater goby is one of several endangered or threatened taxa (e.g. Southern steelhead, red-legged frog, three-spined stickleback) that utilize closed estuarine habitat at some point in their life history. It is unclear how these unique and highly impacted habitats will respond to future climate change and increased coastal development. Further research on these systems will benefit agencies responsible for recovery of endangered taxa, and aid in the development of appropriate standards and management practices for closing systems.

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