# Effects of temperature and latitude on larval traits of two estuarine fishes in differing estuary types

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ABSTRACT: Variations in abiotic conditions across large latitudinal gradients can strongly influence the early life history of coastal marine organisms. We investigated the effects of temperature and latitude on the larval traits of 2 estuarine fish species. The arrow goby *Clevelandia ios* and the endangered tidewater goby *Eucyclogobius newberryi* were studied in 18 estuaries along the coast of California, spanning ~8 degrees of latitude. These 2 species were selected because of their dissimilar preferences for estuary type: the arrow goby prefers cooler, fully tidal systems, whereas the tidewater goby prefers warmer lagoons that experience some degree of seasonal isolation from the ocean. Recently settled individuals were collected from July to October 2011, and temperatures within each estuary were recorded to determine how temperature affected larval duration, settlement, and growth rates. Temperatures were more variable among estuaries inhabited by the tidewater goby (10°C range) than among those inhabited by the arrow goby (5°C range). Larval traits of both species differed among sites, but more so for the tidewater goby, a difference that was tied to the greater differences in temperatures among sites in the seasonally closed estuaries it inhabited. In both species, fish that experienced warmer temperatures had shorter larval durations and faster growth rates and were smaller at settlement. Since the length of the larval period has been related to survival and dispersal distance, future variations in temperature due to climate change could have predictable influences on population density and connectivity in estuarine species.

KEY WORDS: Temperature · Latitude · Estuarine fishes · Larval duration · Settlement · Growth rate

## INTRODUCTION

The vast majority of marine fishes begin their life as planktonic larvae, a critical stage that is highly sensitive to changes in the abiotic environment, such as temperature, which can influence larval traits associated with development, survival, and dispersal potential (Houde 1989, Cowen 1991, Gillooly 2001, Gillooly et al. 2002, Brown et al. 2004, McCormick & Hoey 2004, O'Connor et al. 2007, Takahashi et al. 2012). The predicted increases in coastal temperatures due to climate change will likely affect fish reproduction and larval development, but these effects will vary with latitude and habitat type (Pankhurst & Munday 2011). Controlled laboratory experiments have revealed effects of temperature on the pelagic larval duration (PLD), size at settlement, and growth rates in tropical reef fish, caused by as little as a 3 to 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). Since temperature naturally varies over large latitudinal gradients, studying the effects of temperature on fish larvae across these gradients may be useful in predicting some of the long-term impacts of climate change.

In regions with Mediterranean climates, 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 predicted changes in climate have already been observed in the coastal zones of southern and central California (Hayhoe et al. 2004). 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 majority of these estuaries are partially or completely isolated from marine tidal influence either seasonally or episodically due to formation of a sandbar at the estuary mouth (Jacobs et al. 2011). Such isolation typically occurs in the summer months when reduced rates of precipitation lead to reduced freshwater input (e.g. Cooper et al. 2013). In addition, the reduction of tidal exchange causes longer residence time of water, permitting warmer and more variable temperature regimes (Cousins et al. 2010). This phenomenon of estuary 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).

We studied 2 closely related species of small fish that are year-round residents of estuaries or protected coastal bays, the tidewater goby *Eucyclogobius newberryi* and the arrow goby *Clevelandia ios*. The tidewater goby is found almost exclusively in estuaries that close seasonally or episodically (Jacobs et al. 2011), whereas the arrow goby is found primarily in estuaries and protected bays that retain their connection to the ocean throughout the year. Both species do not exceed 55 to 60 mm standard length (SL) as adults (Miller & Lea 1972) and are benthic microcarnivores that feed on small invertebrates. Where they are present, these 2 fishes are often the most abundant fish in the community (Brothers 1975, Swenson 1999). Their high abundances (exceeding 100 m$^{-2}$: Steele et al. 2006, B. T. Spies pers. obs.) suggest they are important secondary consumers in the habitats they occupy and are important prey for a variety of larger species, primarily larger fishes. Both species lay demersal eggs from which larvae hatch that likely complete their entire larval development within their natal site before settling and becoming benthic juveniles (Brothers 1975, Swenson 1999).

The tidewater goby is endemic to California, where it is found in a variety of shallow, brackish water estuaries that experience seasonal closure (Swift et al. 1989, Moyle 2002). It was listed as federally endangered in 1994 (USFWS 2005), mainly due to the loss and degradation of suitable habitat. The tidewater goby is considered an annual species, with reproduction occurring year-round, typically peaking in the early spring and late summer (Swenson 1999, USFWS 2005). The estuaries that this species occupies, which are partially or completely isolated from marine tidal influence at times, have lagoonal conditions that are highly variable in salinity, water quality, and temperature. This habitat preference requires the tidewater goby to tolerate highly variable conditions, including salinities ranging from 0 to 41 ppt and temperatures from 9 to 25°C (Swift et al. 1989, Swenson 1999). Larval tidewater gobies are typically restricted to lagoonal habitats during summer months when the estuary mouth is closed (Lafferty et al. 1999a,b), which has created extensive local genetic subdivision due to lack of larval dispersal among estuaries (Barlow 2002, Earl et al. 2010). Thus, it is likely that tidewater goby larvae experience much greater variation in temperature among estuaries than arrow goby larvae, due to the isolation of the lagoons they inhabit.

The arrow goby *Clevelandia ios* is the sympatric sister species of the tidewater goby (Dawson et al. 2002). It has a much broader geographic range, extending from the Bahia Magdalena, Baja California Sur (C. Swift pers. comm.), to British Colombia (Miller & Lea 1972). Arrow gobies also have a prolonged breeding season, usually peaking between February and June (Prasad 1959, Brothers 1975), with a lifespan of 1 to 3 yr depending on locality (Brothers 1975). The open, fully tidal bays and estuaries that the arrow goby typically occupies are usually 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). However, a lack of genetic subdivision among populations does not imply frequent dispersal among them (Wang 2004) because as few as 1 migrant per

generation can cause them to be genetically homogeneous (Wright 1931, Mills & Allendorf 1996). Currently, it is unclear how frequently marine dispersal occurs in this species; however, arrow goby larvae are believed to develop and settle primarily in their natal estuarine habitats. This conclusion is based on the limited number of larvae and transitional specimens that have been collected offshore (Brothers 1975) and the common occurrence of all larval stages in estuaries (authors' pers. obs.). Therefore, in this study, we assumed that arrow gobies were collected in their natal estuaries.

The goal of our study was to determine the effects of temperature and latitude on tidewater and arrow gobies, which differ in habitat preference and larval dispersal potential. Although there is a strong correlation between temperature and latitude, which has been used to describe many patterns in larval ecology and development, there are many other environmental factors that change with latitude, including precipitation, day length, the degree of seasonality, and primary production. In this study, we treat latitude as a proxy for a suite of environmental factors that vary over a latitudinal gradient, and we measure temperature directly. We examined 3 main questions: (1) Do larval traits (larval duration, settlement, growth rate) 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? (3) Are variations in larval traits related to variations in the average temperature experienced during the larval phase or to other environmental factors related to 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. 1, Table 1). Study sites consisted of 8 fully tidal estuaries inhabited by the arrow goby and 10 seasonally closed estuaries inhabited by the tidewater goby. Study sites for the arrow goby listed from north to south were Arcata Bay, Bodega Bay, San Lorenzo River, Elkhorn Slough, Morro Bay, Carpinteria Salt Marsh, Colorado Lagoon, and Los Peñasquitos. Study sites for the tidewater goby from north to south were Ten Mile River, Salmon Creek, San Gregorio Creek, Rodeo Lagoon, Moore Creek, San Luis Obispo Creek, Santa Ynez River, Arroyo Burro Lagoon, Santa Clara River, and Las Flores Marsh. Sites were

chosen based on 2 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. 2).

### Collections and otolith analysis

Recently settled gobies were collected between August and October of 2011 (Table 1). Due to permitting logistics and to minimize temporal sampling bias, arrow goby collections began in late August and were completed within a 24 d period. Because of low initial sample sizes collected at Colorado Lagoon, an additional collection date was later added in late October. Tidewater goby collections began in late September and were completed within a 36 d period. Small (9.8 to 24.8 mm) juvenile gobies were collected from each site, though previous estimates of the length at larval to juvenile transformation for the tidewater goby (13.4–13.8 mm) and arrow goby (14.2–17.2 mm) were used as target sizes (Moser 1996). Sampling occurred for both species in water depths < 1.2 m between 05:00 and 11:00 h, using either a 3.7 × 1.2 m beach seine with a 1.6 mm mesh, or a 1-man push net with 1.6 mm mesh (Strawn
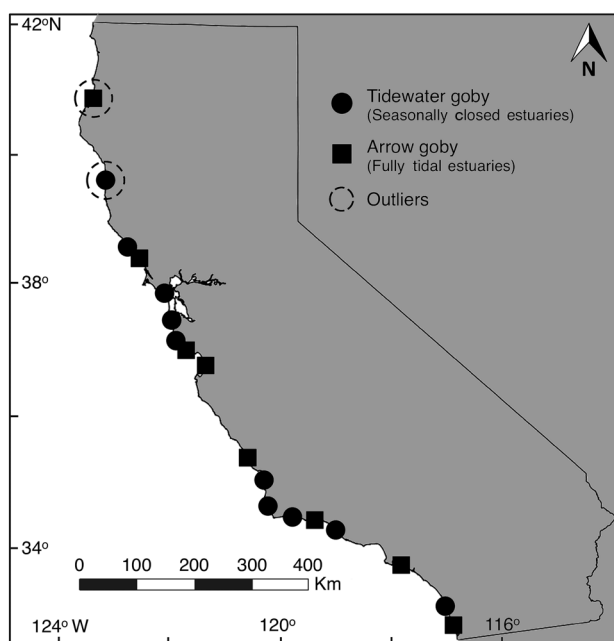


Fig. 1. California coastline showing the 18 study sites. The arrow goby (square) was collected at 8 fully tidal estuaries; the tidewater goby (circle) was collected at 10 seasonally closed estuaries. The 2 sites furthest north, Ten Mile River and Arcata Bay, were treated as outliers (broken circle) for portions of the analysis (see 'Materials and methods')

Table 1. Collection and habitat information for the tidewater goby and arrow goby. The 18 study sites are listed from north to south for each species

| Collection date | Study site | Latitude (°N) | Habitat size[*] | Closed/Open @ collection | Temp. (°C) Mean ± SD | Std. length (mm) Mean ± SD | n |
|---|---|---|---|---|---|---|---|
| **Tidewater goby** | | | | | | | |
| 10/15/11 | Ten Mile River | 39° 32′ 43.86″ | Large | Open | 15.33 ± 0.14 | 14.69 ± 1.16 | 39 |
| 09/25/11 | Salmon Creek | 38° 21′ 10.87″ | Medium | Closed | 18.70 ± 0.34 | 14.93 ± 1.36 | 40 |
| 09/30/11 | Rodeo Lagoon | 37° 49′ 54.41″ | Medium | Closed | 17.40 ± 0.31 | 15.48 ± 1.15 | 40 |
| 10/16/11 | San Gregorio Creek | 37° 19′ 14.29″ | Medium | Closed | 18.86 ± 0.32 | 14.48 ± 1.60 | 40 |
| 10/07/11 | Moore Creek | 36° 57′ 04.50″ | Small | Closed | 21.59 ± 0.20 | 16.17 ± 1.31 | 40 |
| 10/07/11 | San Luis Obispo Creek | 35° 11′ 13.35″ | Large | Closed | 18.92 ± 0.30 | 18.47 ± 2.78 | 39 |
| 09/22/11 | Santa Ynez River | 34° 41′ 30.57″ | Large | Open | 18.51 ± 0.32 | 16.53 ± 1.96 | 40 |
| 10/07/11 | Arroyo Burro Lagoon | 34° 24′ 11.77″ | Medium | Closed | 24.95 ± 0.44 | 20.53 ± 1.53 | 40 |
| 09/25/11 | Santa Clara River | 34° 14′ 07.19″ | Large | Closed | 21.47 ± 0.21 | 13.68 ± 0.95 | 38 |
| 10/28/11 | Las Flores Marsh | 33° 17′ 25.79″ | Large | Closed | 25.11 ± 0.18 | 18.58 ± 1.48 | 39 |
| **Arrow goby** | | | | | | | |
| 09/17/11 | Arcata Bay | 40° 51′ 30.57″ | Large | Open | 20.41 ± 0.10 | 13.85 ± 1.33 | 41 |
| 09/02/11 | Bodega Bay | 38° 18′ 59.42″ | Large | Open | 16.12 ± 0.33 | 14.33 ± 1.49 | 42 |
| 09/10/11 | San Lorenzo River | 36° 57′ 56.41″ | Large | Open | 17.62 ± 0.12 | 16.13 ± 1.84 | 40 |
| 09/09/11 | Elkhorn Slough | 36° 48′ 40.14″ | Large | Open | 18.37 ± 0.18 | 13.84 ± 2.22 | 41 |
| 08/25/11 | Morro Bay | 35° 20′ 34.52″ | Large | Open | 17.96 ± 0.07 | 14.50 ± 2.02 | 40 |
| 08/24/11 | Carpinteria Salt Marsh | 34° 23′ 52.97″ | Medium | Open | 19.70 ± 0.12 | 13.10 ± 1.96 | 43 |
| 08/28/11; 10/31/11 | Colorado Lagoon | 33° 45′ 10.52″ | Large | Open | 20.50 ± 1.00 | 18.01 ± 3.01 | 29 |
| 08/27/11 | Los Peñasquitos | 32° 55′ 57.84″ | Large | Open | 21.37 ± 0.34 | 13.21 ± 2.09 | 41 |

[*](USFWS 2005) Habitat size classification: large = systems of >2 hectares (5 acres) in surface area; medium = systems with a surface area <2 ha but >0.4 ha (1 acre); small = systems with surface area < 0.4 ha

1954). This size mesh likely selected for individuals on the larger end of our target size range, and smaller gobies were seen passing through the net at times. We used this mesh because it was large enough to allow algae and other material to pass through the net while still capturing fish spanning the targeted size range. Although our nets were size selective, which could bias estimates of density and assemblage composition (Weinstein & Davis 1980), our tests for correlations between larval traits and temperature or latitude are unlikely to be similarly biased because the same mesh size was used at all study sites. Once the fishes were collected, they were euthanized and then preserved in 95% ethanol. This preservation technique is considered the best choice when using otoliths to assess life history traits, despite the possibility that specimens can shrink over time (Fowler & Smith 1983).

The standard length of each goby was measured to the nearest 0.01 mm using a digital caliper before extraction of lapillar otoliths. Lapilli were used for all otolith analyses because they were clearer and required less processing than sagittal otoliths. Previous work has validated daily increment deposition in sagittal otoliths for the tidewater goby (Hellmair 2010), and we found no differences in increment counts between sagittal and lapillar otoliths based on

a small subsample in this study. Due to the similarity and close phylogenetic relationship with the tidewater goby (Ellingson et. al 2014), it was assumed that increments in otoliths of the arrow goby were also deposited daily. Furthermore, otolith-based estimates of larval traits appear to be suitable for both species due to a strong relationship between body length and age (Spies et al. 2014).

A total of 712 otoliths (arrow goby: n = 317; tidewater goby: n = 395) were prepared using techniques similar to Samhouri et al. (2009), which included placing the otoliths in immersion oil for >30 d to clear them to facilitate interpretation. Otoliths were then viewed under a compound microscope with a polarizing filter and camera at 200× magnification. Any otoliths that were irregularly shaped or unreadable were discarded from the study (tidewater goby n = 5; arrow goby n = 8). The remaining otoliths were viewed and measured twice by the same individual (B. T. Spies). Following methods from Wilson et al. (2009), if the 2 readings were >10% different, they were not included in any analysis. If the 2 readings were <10% different, but not the same, then the second reading (which we considered more accurate) was used for the analysis.

Increment measurements were made along the longest axis, from the core to the outermost complete

Fig. 2. (A) Moore Creek, located in Santa Cruz County, represents a seasonally closed estuary inhabited by the tidewater goby. (B) Carpinteria Salt Marsh, located in Santa Barbara County, represents a fully tidal system inhabited by the arrow goby

ring, using Image-Pro Plus image analysis software. The settlement band was interpreted as the point where the daily increment transitioned distinctly in band width (Wilson & McCormick 1999, Spies et al. 2014). 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. The first dark ring outside the core was considered to be the hatch mark (Hellmair 2010), although this interpretation has not been validated. Average pre-settlement growth rates (larval growth rate) were estimated from otolith growth as a proxy for larval somatic growth, by dividing the otolith radius to the settlement mark by the age at settlement (McCormick & Molony 1995, Spies et al. 2014).

## Temperature measurement

Hourly temperature measurements were recorded at all 18 sites, from 10 July to 3 October 2011, allowing for at least 6 wk of temperature data to be recorded before fish collections began on 24 August 2011. At 17 of the 18 sites, iButton thermocron temperature recorders (model DS1921G with 0.5°C resolution) were used. Before placement in the field, 10 iButtons were randomly chosen to test for accuracy and precision in controlled laboratory conditions. All hourly temperature measurements were within the stated 0.5°C resolution range. iButtons were then waterproofed using ¾ inch (1.9 cm) 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 and spaced approximately 100 m apart to provide representative measurements of temperature ranges around the area where goby collections would occur. The site where iButtons were not used (Elkhorn Slough) had multiple, fixed, long-term temperature loggers already put in place and maintained by the Elkhorn Slough National Estuarine Research Reserve. At the time of fish collections, water temperature was also measured, using a YSI 556 water quality meter, and these data were compared to the temperature measurements of the fixed loggers to assess their accuracy. In addition, 2 other sites (Arcata Bay and Morro Bay) also had fixed, long-term temperature loggers in place during this study. Temperature measurements from the fixed loggers and iButton recorders were very similar (within 1.0°C). The fixed loggers were located much closer to where fish collections took place and had a much finer resolution; therefore, we used temperature measurements from them instead of iButton data recorders at those 2 sites. Those data were provided by the US Fish and Wildlife Service (Arcata Bay) and the San Luis Obispo Science and Ecosystem Alliance (Morro Bay).

Hourly temperature recordings were used to calculate the mean temperature experienced by each fish through its larval phase. The date of hatching and the date of settlement for each fish were estimated from otolith-derived age estimates and the date of capture. This allowed us to calculate the mean temperature history for each individual fish during its larval phase (McCormick & Molony 1995). The mean temperature experienced by each fish was then used to calculate the mean temperature for each study site. Additionally, temperature variance was calculated for each site as a possible additional temperature metric for analysis. However, preliminary analysis showed that temperature variance was not a good predictor of differences in larval traits, so it was not used in the analyses reported.

### Statistical analysis

To test the effects of temperature and latitude on 3 larval traits (larval duration, otolith based size at settlement, and growth rate) and whether these effects differed between the 2 species (i.e. test whether slopes differed between the 2 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 2 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 (covariates) were sequentially eliminated if p > 0.05, following Winer et al. (1991).

In addition to the GLM, linear regression was used to test the fit of larval trait data for the 2 species to temperature or latitude. This was done, in addition to GLM models mentioned above, to evaluate whether the extent to which temperature or latitude predicted variation in larval traits differed between the 2 species. The GLM analyses tested whether 2 slopes were equal (via the interaction term), and if the slopes were equal, whether the pooled slope differed from zero, but those analyses did not test whether the fits to those 2 lines were equal. These linear regressions were used only to generate $r^2$-values, not p-values (because doing so would increase the probability of Type I error by testing the same hypothesis — that the slope was equal to zero — with the same data set twice). Linear regression was also used to examine the relationship between temperature and latitude of the 18 study sites. For all analyses, assumptions of normality and homogeneity of variance were checked by inspection of normal probability plots and residual plots.

The 2 most northern sites (Arcata Bay and Ten Mile River) were unusual, and all analyses were conducted with and without them (i.e. treating them as outliers) to evaluate their influence on the results. Thus, all GLM and linear regressions were analyzed under 2 alternative conditions: (1) a full model with all study sites (n = 18) and (2) a reduced model with both unusual sites removed (n = 16). Ten Mile River is typically a seasonally closed estuary that is inhabited by the tidewater goby, but it remained open to tidal influence throughout the duration of this project, while maintaining an abundant population of tidewater gobies. This unexpected occurrence could bias results for the tidewater goby since this estuary was more similar to the fully tidal sites occupied by arrow gobies. Arcata Bay, a site occupied by the arrow goby, was a major outlier in the relationship between temperature and latitude because it was much warmer than predicted. We are confident that our estimate of temperature is accurate because both fixed data loggers and iButtons measured essentially the same temperature. This site is shallow and has extensive sun-exposed mudflats, which probably accounts for its warm temperature.

## 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 ~10°C from the coolest to warmest site (range: 15.33 ± 0.14 to 25.11 ± 0.18, n = 10), whereas those occupied by the arrow goby differed by only ~5°C (range: 16.12 ± 0.33 to 21.27 ± 0.34, n = 8). Removal of the 2 unusual sites slightly reduced the temperature range to 7.7°C for tidewater goby sites but did not change the temperature range of arrow goby sites.

The study sites showed the expected trend of lower temperature at higher latitude, but when all sites were included in the regression models, this trend was only statistically significant for estuaries inhabited by the tidewater goby (Table 1, Fig. 3: tidewater goby n = 10, $r^2$ = 0.603, p = 0.008; arrow goby n = 8, $r^2$ = 0.167, p = 0.315). The removal of the 2 unusual sites, however, strengthened the temperature-latitude relationship such that it was significant for estuaries inhabited by both species (Table 1, Fig. 3; tidewater goby: n = 9, $r^2$ = 0.465, p = 0.043; arrow goby: n = 7, $r^2$ = 0.936, p < 0.001).

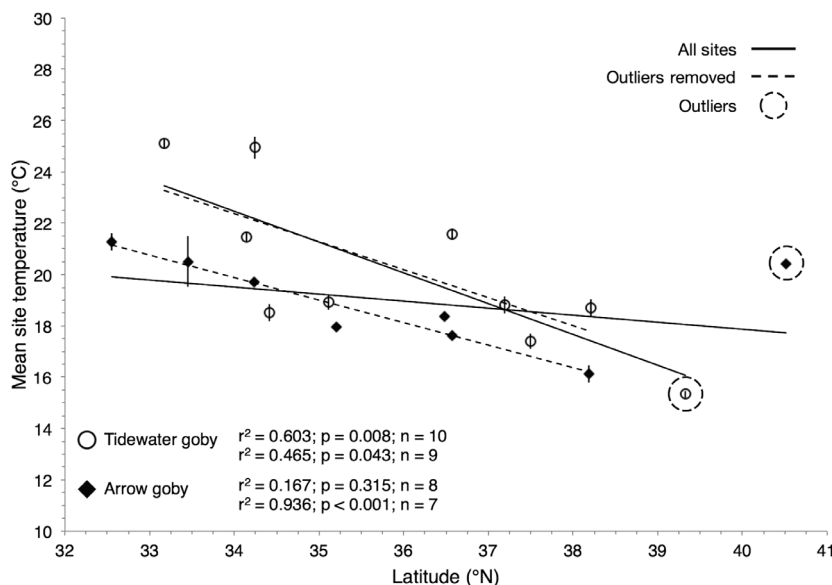### Effects of temperature and latitude on larval traits

Larval traits were significantly related to temperature, but not latitude, and these relationships between larval traits and temperature were stronger in the tidewater goby than the arrow goby. This variation between species was likely due to the larger range of temperatures in estuaries inhabited by the tidewater goby (10 or 7.7°C with an outlier removed), compared to those inhabited by the arrow goby (5°C). There were no significant Species × Temperature or Species × Latitude interactions found in the full model (Species × Temperature: larval duration $F_{1,10}$ = 0.25, p = 0.63; size at settlement $F_{1,10}$ = 2.75, p = 0.13; growth rate $F_{1,10}$ = 0.73 p = 0.41; Species × Latitude: larval duration $F_{1,10}$ = 0.36, p = 0.56; size at settlement $F_{1,10}$ = 2.99, p = 0.11; growth rate $F_{1,10}$ = 0.61, p = 0.45; Figs. 4 & 5) or in the model with outliers removed (Species × Temperature: larval duration $F_{1,8}$ = 2.46, p = 0.16; size at settlement $F_{1,8}$ = 0.92, p = 0.37; growth rate $F_{1,8}$ = 0.48, p = 0.51; Species × Latitude: larval duration $F_{1,8}$ = 3.43, p = 0.10; size at settlement $F_{1,8}$ = 1.28, p = 0.29; growth rate $F_{1,8}$ = 0.68, p = 0.44; Figs. 4 & 5). Thus, there was no statistical evidence for a difference in the pattern of response of the 2 species to the effects of temperature and latitude. All 3 larval traits were significantly related to temperature (Table 2). Larval duration decreased as temperature increased (full model: p = 0.001; outliers removed: p = 0.01; Fig. 4A), as did size at settlement (p = 0.03 and p = 0.056; Fig. 4B), whereas larval growth rates increased with temperature (full model: p = 0.04; outliers removed: p = 0.05; Fig. 4C). However, latitude was not related to the 3 larval traits: larval duration (p = 0.76 and p = 0.95 for full and reduced models, respectively; Fig. 5A), settlement at size (p = 0.15 and p = 0.92; Fig. 5B), or growth rate (p = 0.07 and p = 0.71; Fig. 5C).

Linear regressions evaluating the fit of the larval traits to temperature and latitude including all study sites revealed that traits of the tidewater goby were more predictable based on temperature or latitude than were those of the arrow goby. Strong negative relationships with temperature predicted 73% and 71% of the variation in larval duration and settlement size, respectively, for the tidewater goby but only 40% and 8% in the arrow goby (Fig. 4). Positive linear rela-
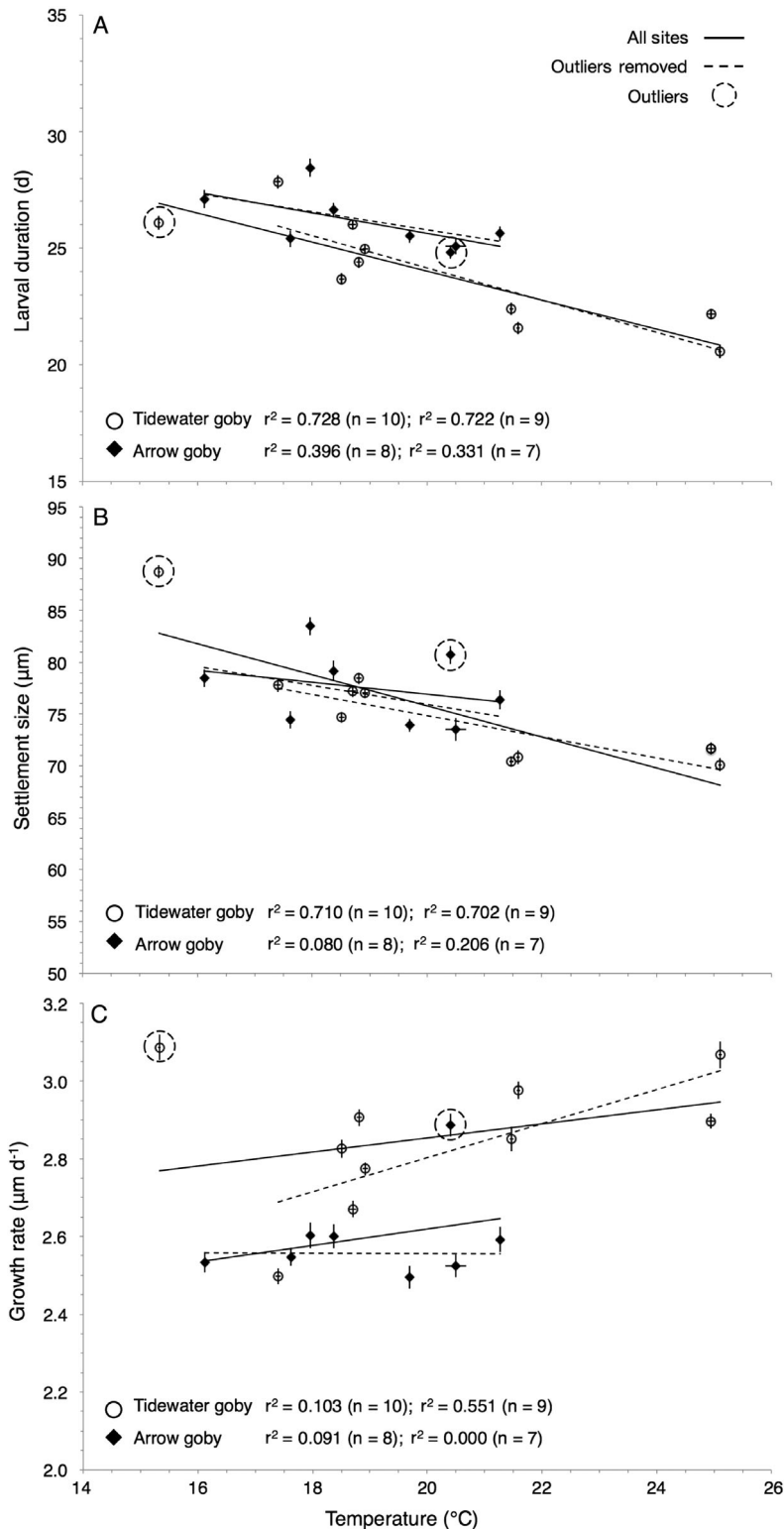


Fig. 3. Temperatures for each site (°C, mean hourly ± 1 SD) as a function of latitude. Solid trend lines represent relationships for all 18 study sites inhabited by the tidewater goby and arrow goby (n = 10 and 8 sites, respectively). Dashed trend lines represent relationships for 16 study sites with the 2 outlier sites removed (n = 9 and 7 sites, respectively)

Fig. 4. Relationships between site temperature (°C, mean hourly ± 1 SD) and (A) larval duration, (B) size at settlement, and (C) and pre-settlement growth rate for the tidewater goby and arrow goby in all 18 study sites (solid lines: n = 10 and 8 sites, respectively) and with outlier sites removed (dashed lines: n = 9 and 7 sites, respectively). Error bars for all 3 response variables represent ±1 SE

tionships with latitude predicted a somewhat smaller fraction of the variation in larval duration and settlement size, 56% and 64%, respectively, for the tidewater goby, and <1% and 23% for the arrow goby (Fig. 5). The better fits of the relationships with temperature rather than latitude suggest that temperature was a stronger driver of larval duration and settlement size. Also, these findings suggest that the effects of temperature on larval duration and settlement size found in the GLM analyses were driven mostly by the tidewater goby, which experienced a greater range of temperatures than the arrow goby.

Larval growth rate was not strongly predicted by temperature in either species: tidewater goby ($r^2 = 0.10$; Fig. 4C) or arrow goby ($r^2 = 0.09$). However, the removal of an outlier site significantly improved this relationship for the tidewater goby ($r^2 = 0.55$; Fig. 4C). Furthermore, larval growth rate had a moderately strong positive relationship with latitude for the arrow goby ($r^2 = 0.46$; Fig. 5C) but a weak negative relationship for the tidewater goby ($r^2 = 0.03$). When the 2 outlier sites were removed from the analyses, there was no relationship between growth rate and latitude for the arrow goby ($r^2 = 0.00$), but the strength of the negative relationship increased for the tidewater goby ($r^2 = 0.36$).

Overall, considering all 18 study sites, the tidewater goby had a larval duration that was approximately 35% shorter in the warmest sites, as well being 27% smaller in body size and growing 24% faster in those sites. In comparison, the arrow goby had an approximately 15% shorter larval duration in the warmest sites, was 14% smaller in body size, and grew 16% faster.

## DISCUSSION

This study demonstrates the variable nature of temperature in estuarine habitats and the influence temperature can have on the traits of larval fishes. Larval duration, settlement size, and growth rate were significantly affected by temperature,
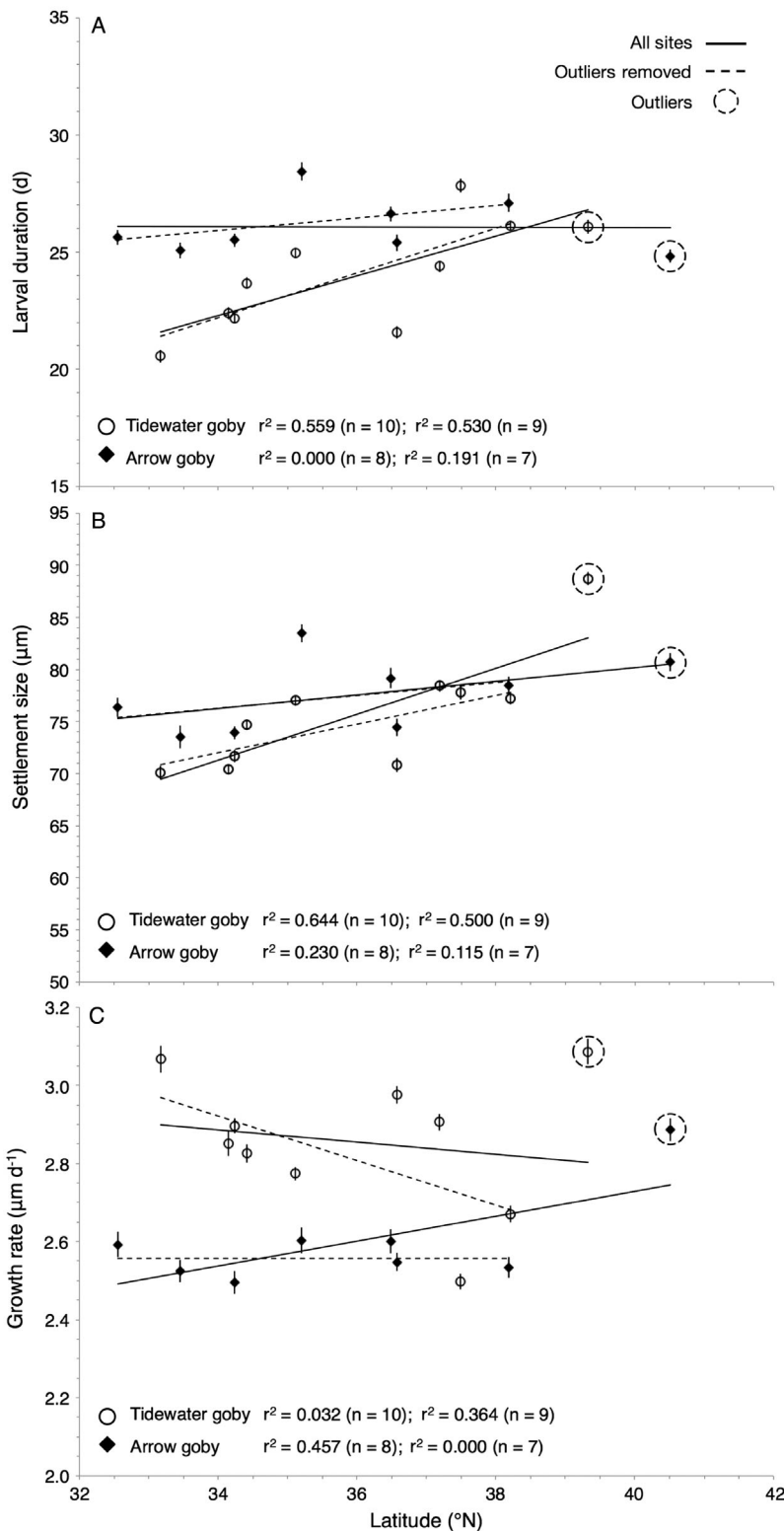
Fig. 5. Relationships between latitude and (A) larval duration, (B) size at settlement, and (C) and pre-settlement growth rate for the tidewater goby and arrow goby in all 18 study sites (solid lines: n = 10 and 8 sites, respectively) and with outlier sites removed (dashed lines: n = 9 and 7 sites, respectively). Error bars represent ±1 SE

with no statistically 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 among sites in temperatures this species experienced. Nonetheless, in warmer estuarine environments, both the arrow goby and tidewater goby spent fewer days in the larval phase, were smaller in size at settlement, and exhibited faster growth rates.

The smaller, seasonally closed estuaries inhabited by the tidewater goby exhibited a greater range of mean temperature (10°C) than the larger, tidal estuaries inhabited by the arrow goby (5°C). Excluding the unusually warm Arcata Bay, temperature was also better predicted by latitude in the tidal estuaries inhabited by arrow gobies than in the seasonally closed estuaries inhabited by tidewater gobies. However, in testing the relationships between larval traits and temperature, including Arcata Bay was useful because doing so helped to remove the covariance between temperature and latitude. Models with and without the 2 unusual sites (Arcata Bay and Ten Mile River) showed generally similar results, strengthening the conclusion that variation in all 3 larval traits was more closely linked to temperature than to other attributes that change with latitude.

A number of studies have found similar effects of temperature on larvae of a variety of temperate and tropical marine fishes, using both field and laboratory approaches. Several species of flatfish 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 & 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

Table 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 for all study sites (n = 18) and with 2 unusual sites removed (n = 16)

| n | Source | df | SS | $F$ | p | $r^2$ |
|---|---|---|---|---|---|---|
| **Larval duration** | | | | | | |
| 18 | Species | 1 | 8.523 | 5.931 | 0.029 | 0.745 |
| | Latitude | 1 | 0.140 | 0.097 | 0.760 | |
| | Mean temp. | 1 | 27.195 | 18.923 | 0.001 | |
| | Error | 14 | 20.12 | | | |
| 16 | Species | 1 | 5.067 | 3.132 | 0.102 | 0.748 |
| | Latitude | 1 | 0.007 | 0.005 | 0.948 | |
| | Mean temp. | 1 | 13.825 | 8.545 | 0.013 | |
| | Error | 12 | 19.415 | | | |
| **Settlement size** | | | | | | |
| 18 | Species | 1 | 2.979 | 0.271 | 0.611 | 0.603 |
| | Latitude | 1 | 25.267 | 2.300 | 0.152 | |
| | Mean temp. | 1 | 66.498 | 6.054 | 0.027 | |
| | Error | 14 | 153.785 | | | |
| 16 | Species | 1 | 3.100 | 0.412 | 0.533 | 0.560 |
| | Latitude | 1 | 0.088 | 0.012 | 0.916 | |
| | Mean temp. | 1 | 33.713 | 4.479 | 0.056 | |
| | Error | 12 | 90.332 | | | |
| **Growth rate** | | | | | | |
| 18 | Species | 1 | 0.191 | 9.473 | 0.008 | 0.597 |
| | Latitude | 1 | 0.078 | 3.847 | 0.070 | |
| | Mean temp. | 1 | 0.106 | 5.261 | 0.038 | |
| | Error | 14 | 0.283 | | | |
| 16 | Species | 1 | 0.106 | 8.925 | 0.011 | 0.736 |
| | Latitude | 1 | 0.002 | 0.141 | 0.714 | |
| | Mean temp. | 1 | 0.055 | 4.650 | 0.052 | |
| | Error | 12 | 0.143 | | | |

water temperature and size and age at metamorphosis both in the field and in laboratory experiments (McCormick & Molony 1995). Furthermore, water temperature in the upper Florida Keys explained 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 PLD as a product of faster growth rates. Fish from warmer periods were larger at age, but due to the shorter time spent in the larval phase, they were smaller in body size at settlement. Larvae of the Hawaiian amphidromous goby *Lentipes concolor* settled after a shorter PLD and at smaller sizes during months of warmer ocean temperature (Radtke et al. 2001).

Although temperature was a good predictor of larval traits in this study, these traits are likely influenced by other biotic or abiotic factors (e.g. water quality, predator abundance, and food availability). For example, variations in precipitation and stream flow are 2 of the main hydrological drivers of mouth dynamics (open or closed) in seasonally closed estuaries throughout California (Rich & Keller 2013). During the summer months when precipitation is typically low in California, which is when this study took place, a net increase in evaporation can lead to hypersaline environments (Largier et al. 1997). Salinity can influence nutrient availability, physiological rates, and behavior responses (Cowen & Sponaugle 2009). For example, unusually low or high salinity can interfere with egg development and the hatching process and reduce survival of larvae (Fonds 1979). In seasonally closed estuaries, dissolved oxygen levels can drop precipitously, especially during warm months (Collins & Melack 2014). Lower than normal levels of dissolved oxygen can lead to reduced growth rates (Boeuf et al. 1999, Pichavant et al. 2001, Ekau et al. 2010) and altered swimming behavior (Ciuhandu et al. 2007). Increased flow rates when estuary mouths are open, and the resulting turbulence, could enhance prey encounters and, thus, ingestion rates (Kiørboe & MacKenzie 1995). In addition, genetic differences among populations can contribute to latitudinal differences in larval traits, as Billerbeck et al. (2001) found for growth of the Atlantic silverside *Menidia menidia*.

Due to the permitting and logistical constraints, we were unable to examine the temporal variation in larval traits. This would be an interesting topic for future research. Temporal variability in the abiotic environment can differ strongly between fully tidal estuaries and seasonally closed estuaries, depending on their frequency and degree of closure/breaching. Temperature changes of only a few degrees Celsius, as might occur during a breaching event, have been found to strongly influence key physiological processes in fish, such as developmental rate, growth rate, swimming ability, and reproductive performance (Munday et al. 2008, 2009). Physiological responses to temperature commonly follow a dome-shaped relationship where a maximum is reached as rates increase with temperature, but responses 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 are likely different given what is known about the natural history of these 2 species. Such a difference could be a result of local adaption or acclimation to site-specific temperature regimes (Hawkins 1996). However, if water temperature rises above the thermal optimum for reproduction, this could potentially cause a decline in adult reproductive output, which could result in significant consequences for population connectivity (Munday et al. 2008, 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 affect 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 alter the evaporation/precipitation regime, causing increased evaporation at lower latitudes and increased precipitation in the higher latitudes (Roessig et al. 2004). 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 be beneficial or harmful for an individual 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 2 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. Variation in larval traits for both species was strongly related to differences in the mean temperature experienced during larval development and not strongly related to latitude per se. Our findings also reveal the variable nature of estuarine habitats and their abiotic conditions. Closed estuaries exhibited a greater range of thermal environments than did estuaries open to the ocean. These systems, however, have not been studied in great detail. We know relatively little about latitudinal trends in the abiotic environment and even less about biotic interactions. For example, how do the types and abundance of prey for larval fishes change with latitude, and are these changes similar between open and seasonally closed estuaries? What about predators of larvae, and densities of conspecifics? Further research on these systems is needed to better understand how local biotic and abiotic conditions can affect 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.

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