Effects of the Blob on settlement of spotted sand bass, *Paralabrax maculatofasciatus*, to Mission Bay, San Diego, CA

Anthony Basilio¹, Steven Searcy¹*, Andrew R. Thompson²

¹ Environmental and Ocean Sciences, University of San Diego, San Diego, California, United States of America, ² Fisheries Resources Division, Southwest Fisheries Science Center, NOAA Fisheries Service, La Jolla, California, United States of America

* ssearcy@sandiego.edu

Abstract

The West Coast of the United States experienced variable and sometimes highly unusual oceanographic conditions between 2012 and 2015. In particular, a warm mass of surface water known as the Pacific Warm Anomaly (popularly as “The Blob”) impinged on southern California in 2014, and warm-water conditions remained during the 2015 El Niño. We examine how this oceanographic variability affected delivery and individual characteristics of larval spotted sand bass (*Paralabrax maculatofasciatus*) to an estuarine nursery habitat in southern California. To quantify *P. maculatofasciatus* settlement patterns, three larval collectors were installed near the mouth of Mission Bay, San Diego CA, and retrieved weekly from June–October of 2012–2015. During ‘Blob’ conditions in 2014 and 2015, lower settlement rates of spotted sand bass were associated with higher sea surface temperature and lower wind speed, chlorophyll *a* (chl *a*) and upwelling. Overall, the number of settlers per day peaked at intermediate chl *a* values across weeks. Individual characteristics of larvae that settled in 2014–2015 were consistent with a poor feeding environment. Although settlers were longer in length in 2014–15, fish in these years had slower larval otolith growth, a longer larval duration, and a trend towards lower condition, traits that are often associated with lower survival and recruitment. This study suggests that future settlement and recruitment of *P. maculatofasciatus* and other fishes with similar life histories may be adversely affected in southern California if ocean temperatures continue to rise in the face of climate change.

Introduction

A central goal of marine ecology and fisheries biology is to understand factors that contribute to variability in population size [1]. For many marine organisms understanding causes of fluctuations in abundance is complicated by a two-part life history with pelagic larvae that develop offshore and settle to benthic juvenile/adult habitats [2–5]. The number of larvae that reach settlement is a critical factor contributing to future year-class strength [3, 6–8], although post-settlement processes can also be an important source of variation [9, 10].
Settlement success is dependent on a variety of processes including egg production [11, 12] physical transport and retention of larvae [6, 13–18], and larval mortality [19]. Even small variations in larval mortality can lead to large changes in the number of individuals that survive this period [20]. Larval mortality may be caused directly by predation [21], as well as indirectly through environmental conditions such as water temperature and food supply [22–27]. Food availability is particularly important to larval survival because larvae have high metabolic rates and low energy reserves [28]. At elevated water temperatures, metabolic rates are faster, thereby increasing energetic requirements and increasing risk of starvation [22, 23, 25, 29, 30]. After only a few days without food, the larvae of some fish species reach a “point of no return” and are unable to survive [31–33].

Water temperature and food availability may also affect larval survival by influencing growth rates and physiological condition [34–37]. The growth mortality hypothesis [38] suggests that if mortality is lower for larger individuals, then faster growing individuals of a given age will have a lower probability of mortality than slower growing individuals of the same age [39]. Larger individuals may be able to detect and respond to predators more effectively [21, 40], obtain food and withstand starvation [21, 41, 42], although, some studies suggest that larger larvae may actually have higher mortality [39, 43–45]. Finally, larvae with faster growth may be exposed to overall lower levels of predation by quickly growing out of this vulnerable life history stage [38, 46, 47].

Increased sea surface temperature (SST), may also be related to poor larval growth conditions by indicating periods with low upwelling and potential stratification of the water column [48, 49]. During upwelling events, increased supply of nutrients to the surface water can spur phytoplankton growth and support a trophic pyramid that includes zooplankton and many fish species [50]. When upwelling ceases, SST and stratification increase, and there is decreased productivity [48]. Indeed, previous work indicates that during a long-term shift from a cool to a warm water regime as the result of changing Pacific Decadal Oscillation there was an overall 46% reduction in volume of phyto- and zooplankton and a corresponding decline in abundance of many species of larval rockfish (Sebastes sp.) [51].

Understanding how settlement is affected by environmental conditions such as water temperature is especially important to gain insight into how warming ocean conditions may impact marine populations. In the northeast Pacific Ocean, during the winter of 2013–14, weakened winds and unusually high sea level pressure formed a region where heat was retained in surface water. This mass of warm water, known as “the Blob”, reached coastal waters in the western United States in the spring/summer of 2014 [52] and resulted in widespread changes in the biological structure and composition of both open-ocean and coastal ecosystems [53]. Sea surface temperatures were 1–4°C higher than average along the west coast of North America [53]. A geographically distinct section of the Blob near San Diego was named the Southern California Warm Anomaly (SCWA) and increased thermal stratification which led to a reduction of vertical mixing and nutrient fluxes into the surface water [54]. This pool of warm water was partially responsible for the shift in the California Current from a productive La Niña state in 2013 to a warm area with low productivity [55].

Our objective was to examine how changes in environmental conditions over four years (2012–2015) affected daily and annual settlement success of spotted sand bass (Paralabrax maculatofasciatus) in Mission Bay, CA. We also examined how environmental conditions influenced individual characteristics at settlement (length, age, condition, larval growth rates). The sampling years included two years of relatively normal conditions (2012–13) followed by the arrival of the SCWA in 2014 and dramatic changes in chlorophyll a (chl a) and SST that continued through 2015.
Materials and methods

Ethics statement
Sampling was conducted under California Department of Fish and Wildlife scientific sampling permit SC-11846 with the approval of the University of San Diego’s Institutional Animal Care and Use Committee (IACUC).

Study species
Spotted sand bass (*Paralabrax maculatofasciatus*) are a recreationally important fish in Southern California typically found from Santa Monica Bay, CA in the north to Mazatlan, Mexico in the south [56]. There are two main populations of *P. maculatofasciatus* along this range: one in the Gulf of California and another in the Pacific along Baja California and Southern California [57]. There is likely a high degree of larval retention as *P. maculatofasciatus* sampled near San Diego are genetically distinct from those further south along the Baja California peninsula [57]. Spotted sand bass adults are primarily found in calm, shallow, nearshore habitats such as bays and estuaries [56]. Adults spawn near the entrance of bays in the late spring and summer [56], are capable of spawning multiple times throughout the season and may even spawn daily [58]. Larvae develop in the coastal ocean for approximately 28 days [59] after which they return to settle in bays and estuaries that contain structured habitats such as eelgrass, surfgrass, and rock relief [60].

Environmental data
We measured several environmental parameters that were hypothesized to affect settlement dynamics including daily SST and chl *a*. Phytoplankton, as represented by chl *a* concentration, are consumed by zooplankton and are often used as a proxy for food availability for larval fishes [61, 62]. Significant positive relationships between chl *a* concentration and abundance of copepods have been reported in a diverse range of environments such as offshore temperate [63, 64] and tropical waters [65, 66], and in shallow estuaries [67–69].

Chl *a* concentration and SST, measured between May and October, were obtained using the R package Xtractomatic [70], which downloaded satellite measurements for SST (Pathfinder v.5, 5.5 km resolution, 8 day composite) and chl *a* (MODIS Aqua, 2.5 km resolution, 8 day composite) from NOAA’s CoastWatch Browser website (http://coastwatch.pfeg.noaa.gov). Both variables were estimated for an offshore region (34˚25’24” N and 122˚06’05”W to 29˚ 56’23”N and 115˚49’38”W) that encompassed the potential area that larvae arriving to San Diego might be spawned from [57], based on historical offshore distribution [71], as well as potential transport of larvae given a larval duration of 28 days [59] and an average net alongshore transport rate of 0.2 m/sec [72].

Mean wind speed data were obtained from San Diego International Airport provided by the Automated Surface Observation System from Weather Underground [73]. These measurements were based on 24 separate hourly measurements made throughout each day. Upwelling index was accessed from the NOAA Pacific Fisheries Environmental Laboratory database, station 93950–2097, which collects measurements of atmospheric pressure at mean sea level every six hours.

Larval fish collection and morphometric analysis
Recently settled *P. maculatofasciatus* were collected weekly from June–October in 2012, 2013, 2014 and 2015 near the Mission Bay inlet, San Diego, CA (Fig 1). Fish were collected using a modification of the standard monitoring units for the recruitment of fishes (SMURFs) design
Each collector (0.5 x 0.18 m dia.) consisted of a narrow cylinder of plastic fencing material with a 2.5 cm grid filled with giant kelp (*Macrocystis pyrifera*). The kelp attracts juvenile fish that use this habitat as a shelter, and the fencing material prevents access by larger predators. Three replicate collectors were positioned 5 m apart in approximately 4 m of water and attached to a cinder block anchor with a brass clip and floated upright with a Styrofoam float. Collectors were placed near the bottom to ensure they would not be disturbed by boat traffic, and were the only structure along the sandy bottom of the surrounding area thereby maximizing the chance that late stage larvae arriving to this area would shelter in them. Collectors were retrieved by snorkeling to depth, enclosing the collector in a 1 mm mesh bag, unclipping it and bringing it back to shore where all fishes were removed, euthanized with hypothermic shock and preserved in 70% ethanol for later identification. Following collection, the kelp was investigated and if it had started to deteriorate, the old kelp inside the collector was replaced and the collector was returned to its mooring.

In the laboratory, standard length of each fish was measured from individual digital images using Image-J analysis software [77]. Images were obtained by placing each fish on a calibrated slide and using a digital video camera attached to a dissecting microscope. Next, for age determination (see below), the sagittal otoliths were removed. Following otolith extraction, fish dry weight was obtained by placing fish into a drying oven at 60˚C for 24 h, allowing them to cool for 5 min and weighing them on an analytical balance to the nearest 0.1 mg. Finally, body condition at settlement was estimated with the equation: condition = dry weight x standard length$^3$ [78].

Otolith analysis

Sagittal otoliths were mounted on microscope slides using thermoplastic glue (Crystal Bond). One sagitta was randomly chosen and polished to the core using 200–600 grit sandpaper. All abnormally shaped and unclear (large portions with no discernable increments) otoliths were discarded (n = 9 from a total of 102). Images of sagitta were taken using a transmitted light microscope at 250x equipped with a digital camera. All otoliths were measured using an Image-Pro image analysis system [59]. Otoliths were measured along their longest radius from the core to the outer edge and distance from the core to each increment was measured and counted. Two days were added to all age estimates to account for the delay in daily growth.
ring formation in the larval otolith before yolk absorption [59]. Each sagitta was read blind, and after completing all sagittae once, they were read blind again. If counts differed by $\geq 3$ increments (~10%) between the two readings, the otolith was reread. If the third count was within 1 count of the former readings, then one of the readings was randomly chosen for analysis. Alternatively, if the difference was $> 1$ of the previous readings, the otolith was discarded [79].

Fish collectors were only retrieved once a week, therefore records of daily settlement required us to back calculate settlement dates. Fortunately, *P. maculatofasciatus* have a ‘settlement check’ on their otoliths, identified as an abrupt change in the width of daily bands at the time of settlement [59]. This check is likely the result of stress or changes in growth or metabolic rate associated with the transition from a pelagic to a demersal life style [80]. If no check was apparent, the fish was considered to be collected during its initial process of settlement. From these measurements, larval duration and average pre-settlement otolith growth were determined. Finally, to estimate standard length at settlement for all fish collected, we calculated separate linear regressions for 2012, 2013, and 2014–2015 for the relationship between standard length at collection to age at collection and then used the equation of the line to back-calculate standard length at settlement [39]. Data for 2014–2015 were pooled due to low sample size in 2015 (n = 5).

**Data analysis**

**Annual scale.** To determine whether there were significant differences in environmental conditions, average weekly settlement among years, and larval traits (age-, length-, condition-at-settlement), we first examined these factors for normality and homogeneity of variance. To test for significance among years, we used an ANOVA or the nonparametric counterpart (Kruskal-Wallis). When significant differences in these factors occurred among years, Tukey’s HSD means comparison test or the nonparametric equivalent (Wilcoxon rank sum test) were performed. Small sample sizes in 2014 and 2015 made it difficult to determine statistical differences in larval traits among years. Therefore, to estimate the minimum sample size required, post-hoc power analysis was run (alpha = 0.05).

All annual means of environmental variables were calculated by averaging conditions from May–October to incorporate the period from first potential spawning (approximately 1 month prior to our first sample) until the final retrieval of collectors.

**Daily scale.** To determine the importance of SST and chl $a$ on settlement, we tested the plausibility of 6 *a priori* candidate models that included combinations of environmental parameters for all four years combined. We included both linear and quadratic terms for SST and chl $a$ because we hypothesized that optimal settlement may occur at intermediate values. Because the settlement data were not normally distributed, we explored the fit of alternative distributions with generalized linear models (negative binomial, Poisson, zero-inflated) and determined that a negative binomial distribution with a log link best fit the data. Preliminary model exploration also indicated that it was not necessary to add year as a random effect under a mixed model platform. However, residuals from the negative binomial models were temporally autocorrelated at lags (days) 1–8, violating the assumption that each settlement sample was independent [81]. We thus utilized negative binomial models that accounted for serial temporal autocorrelation as implemented by the R package tscount [82]. Preliminary analyses revealed that the tscount models eliminated low-order residual temporal autocorrelation. Relative model plausibility was evaluated based on Akaike’s Information Criterion (AIC) scores (e. g., [83]). Overall model fit was determined by calculating the proportion of deviance explained by the most plausible model.
Results

Annual scale

Oceanographic and wind conditions were significantly different among years (Table 1). Annual mean SST was significantly lower in 2012 and 2013 relative to 2014 and 2015 (Fig 2A), whereas chl a, upwelling index and wind speed were significantly higher in 2012–13 compared to 2014–15 (Fig 2B–2D).

The abundance and individual characteristics of *P. maculatofasciatus* settlers also varied significantly among years (Table 2). Significantly more settlers were collected in 2012 and 2013 than 2014 and 2015 (Fig 3A). Individual characteristics also varied annually with mean standard length on the day of collection as well as back-calculated length at settlement lowest in 2012 and 2013 and increasing in 2014 and 2015 (Fig 3B and 3C). Body condition, a measure of body fatness, showed a trend of fish with higher condition in 2012 and 2013 than 2014 and 2015 (Fig 3D). Otolith derived traits also had mixed trends with fish in 2012 and 2013 settling at a younger average age than fish in 2014 and 2015 (Fig 3E). Due to the high degree of error associated with the small sample size in 2015 (n = 5), mean pelagic larval duration in that year overlapped with both 2013 and 2014. Finally, daily larval otolith growth had a non-significant trend to be lower in 2014 than in 2012 and 2013 settling at intermediate levels of chl a. With these same parameters, using the 2014 sample size (n = 12) would still need to be approximately n = 30 for all groups.

Daily scale

The only models that received support based on AIC scores contained (chl a)^2, indicating that settlement was highest at intermediate values of chl a (Table 3). The best model, which had a weight of 79%, explained 22% of the total deviance. All terms in the best model had slope estimates that did not overlap 0 (Table 4). The second most plausible model contained sst + sst^2 in addition to chl a + (chl a)^2 and had a weight of 21%. Examination of slope estimates, however, revealed that 95% confidence intervals of slopes for both sst and sst^2 overlapped 0 indicating that there was no effect of temperature on daily settlement abundances. Examination of time-series plots (Fig 4) and scatter plots of chl a and settlement (Fig 5) indicated that peak chl a was observed approximately two weeks prior to the onset of settlement and that peak settlement occurred at intermediate levels of chl a.

Discussion

Settlement of spotted sand bass to Mission Bay was higher in 2012–13 than in 2014–15. We attribute the overall reduction in settlement in 2014 and 2015 to the arrival of the Blob.
(SCWA) in 2014 and continued warm conditions in association with El Niño in 2015. The Blob, which formed in the northeast Pacific in 2013, and then spread south and impinged upon southern California in May of 2014, brought with it unusually warm surface water and low chl $a$ \([49, 52, 84]\). Low chlorophyll can likely be attributed to increased thermal stratification and reduction in nutrient fluxes from colder deep waters \[53\]. During the SCWA, compared to the previous 30 years, stratification was the strongest, surface nutrient levels of nitrate were approximately 0.02 $\mu$M lower, and chl $a$ values were the lowest observed over the entire time period \[49\]. Similar patterns have been observed in previous work which suggests there is an inverse relationship between SST and productivity in the California Current Ecosystem (CCE) \[85, 86\], as well as more generally in the oceans \[48\].

In our study, low chl $a$ levels were related to low settlement success, which supports the idea that larval food availability and larval survival are tightly linked \[24, 87, 88\]. Further, there was a delay between peak chl $a$ and settlement. This likely reflects the time between the onset of primary production (phytoplankton) and development of secondary production (zooplankton) upon which larval fishes feed. Low offshore chl $a$ levels, like those observed during the SCWA, are thought to indicate a poor feeding environment for larval fishes which consume small zooplankton such as copepods. Indeed, areas with high chl $a$ have been related to enhanced recruitment of larvae that consume phytoplankton directly (e.g. barnacles) and indirectly (e.g. rockfish) across the entire CCE \[62\]. A recent study examining recruitment of a temperate wrasse, *Coris julis*, in the Azores archipelago found a strong relationship between ocean productivity and year-class strength at two different spatial scales and over a six year period \[26\]. One of the main differences between the current study and previous work is that

**Table 2. Summary of inter-annual comparisons of individual larval characteristics for 2012, 2013, 2014, and 2015.**

| Measure                  | Test          | $F$ (ANOVA) or $\chi^2$ (Kruskal-Wallis) | df | $p$-value |
|-------------------------|---------------|----------------------------------------|----|-----------|
| Standard length at settlement | ANOVA         | 6.07                                   | 3  | <0.0001   |
| Standard length at collection | ANOVA         | 5.56                                   | 3  | <0.001    |
| Pelagic larval duration      | ANOVA         | 6.07                                   | 3  | <0.0001   |
| Larval otolith growth       | Kruskal-Wallis| 17.47                                  | 3  | <0.001    |
| Body condition             | Kruskal-Wallis| 4.70                                   | 3  | 0.19      |

https://doi.org/10.1371/journal.pone.0188449.t002
in addition to annual trends, we were able to examine daily settlement pattern in relation to environmental conditions that each larva experienced. The shorter temporal scale allows for greater understanding of why settlement may vary over an entire recruitment season.

Although observed inter-annual variation in individual characteristics may be due to differences in selective mortality across years [41, 44, 45], we suggest that there is a close relationship between the larval feeding environment and individual larval characteristics. The idea that chl\textsubscript{a} reflects the feeding environment that larvae are exposed to is consistent with the individual characteristics of larvae that we measured. For example, settlers in 2014 and 2015, years characterized by low chl\textsubscript{a} levels, had a non-significant trend towards lower body condition which suggests that larvae may have had trouble finding sufficient food. In addition, in 2014 and 2015 larvae settled at an older age which may indicate that they needed to extend their larval duration, thereby increasing the time that larvae are vulnerable to high mortality [39, 89].

Interestingly, larval otolith growth rates in 2014 and 2015 were mixed, with lower otolith growth in 2014 and higher otolith growth in 2015. Lower otolith growth rates in 2014 are consistent with a poor feeding environment, whereas, higher otolith growth rates in 2015 may reflect warmer water temperatures or a decoupling between otolith growth and somatic growth [90].

The increased larval duration in 2014–15 may also be the result of changing current patterns with the introduction of the SCWA, which could prevent larvae from reaching the coast and delay settlement. A recent study in the CCE examined how movement of the warm

**Table 3. Model selection results for parameters explaining variation in settlement.**

| model          | AIC  | delta AIC | k  | model weight |
|----------------|------|-----------|----|--------------|
| chl\textsubscript{a} + (chl\textsubscript{a})\textsuperscript{2} | 469.5 | 0.0       | 3  | 0.79         |
| sst + sst\textsuperscript{2} + chl\textsubscript{a} + (chl\textsubscript{a})\textsuperscript{2} | 472.2 | 2.7       | 5  | 0.21         |
| sst + sst\textsuperscript{2} | 502.2 | 32.6      | 3  | 0            |
| sst            | 503.2 | 33.6      | 2  | 0            |
| sst + chl\textsubscript{a} | 505.2 | 35.7      | 3  | 0            |
| chl\textsubscript{a}       | 509.8 | 40.2      | 2  | 0            |

Delta AIC is the difference in AIC between a particular model and the most plausible model. k is the number of parameters in a model.
anomaly to coastal waters in 2014 changed current patterns and altered settlement in 30 species of nudibranchs [91]. Northward ranges of typically southern nudibranch species may have been facilitated by increased poleward and onshore transport of their planktonic larvae [91]. This stronger poleward current is expected during periods of reduced upwelling, which was observed in 2014 off northern Baja California and southern California [55]. We expect a poleward shift in the CCE would not affect settlement of \textit{P. maculatofasciatus} in Mission Bay, because Mission Bay is located near the northern end of their range. Any poleward movement alongshore would likely bring larvae to the bay from populations further south.

The lack of a strong link between SST and settlement does not preclude the idea that water temperature may indirectly affect larval survival by modifying plankton distribution and abundance, as well as by influencing larval metabolic rates and the amount of food required to survive [26]. Interestingly, previous studies have found a positive relationship between annual

| Table 4. Summary of results from the most plausible daily settlement model (chl a + (chl a)²). |
|-----------------|--------|--------|--------|--------|
|                | slope  | se     | lower 95% CI | upper 95% CI |
| intercept       | -5.1   | 0.6    | -6.3          | -3.9          |
| beta 1          | 0.9    | 0.4    | 0.1           | 1.6           |
| chl a           | 7.0    | 1.4    | 4.2           | 9.8           |
| chl a²          | -3.2   | 0.7    | -4.6          | -1.7          |
| sigma squared   | 2.9    | NA     | NA            | NA            |

Beta 1 is the autocorrelation parameter and sigma squared the negative binomial overdispersion factor. se is standard error.

anomaly to coastal waters in 2014 changed current patterns and altered settlement in 30 species of nudibranchs [91]. Northward ranges of typically southern nudibranch species may have been facilitated by increased poleward and onshore transport of their planktonic larvae [91]. This stronger poleward current is expected during periods of reduced upwelling, which was observed in 2014 off northern Baja California and southern California [55]. We expect a poleward shift in the CCE would not affect settlement of \textit{P. maculatofasciatus} in Mission Bay, because Mission Bay is located near the northern end of their range. Any poleward movement alongshore would likely bring larvae to the bay from populations further south.

The lack of a strong link between SST and settlement does not preclude the idea that water temperature may indirectly affect larval survival by modifying plankton distribution and abundance, as well as by influencing larval metabolic rates and the amount of food required to survive [26]. Interestingly, previous studies have found a positive relationship between annual

| Fig 4. Relationship between chlorophyll a and number of settlers. Daily measurements of chlorophyll a (green line, left axis) and number of settlers in A. 2012, B. 2013, C. 2014, and D. 2015. |
|---------------------------------|-----------------|-------|
|                                | chl a (μg L⁻¹)  | no settlers |
|                                | Jun  | Jul  | Aug  | Sep  | Oct  | Nov  | Jun  | Jul  | Aug  | Sep  | Oct  | Nov  |
| A                              | 3.0  | 2.0  | 1.5  | 1.0  | 0.5  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  |
| B                              | 7.5  | 5.0  | 2.5  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  |
| C                              | 2.5  | 1.0  | 0.5  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  |
| D                              | 5.0  | 3.0  | 2.0  | 1.0  | 0.5  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  |

https://doi.org/10.1371/journal.pone.0188449.g004

https://doi.org/10.1371/journal.pone.0188449.t004
recruitment of spotted sand bass and mean summer SST off southern California [56, 92]. In particular, annual abundance was greater during times of higher SST, such as the El Niño events of 1977–78 and 1982–83 [56, 92]. The opposite trends between our study and the previous work may be due to the other studies surveying older fish, in contrast to our study which examined initial settlement of larvae, or may simply be due to factors associated with the SCWA that were not observed in previous years.

Another possible explanation for the decreased settlement in our study involves increased SST affecting reproduction. Although reproduction and recruitment rates are positively associated with SST in Pacific sardine (Sardinops sagax) [93], increased SST has been shown to negatively affect spawning success and egg production in demersal species in southern California such as the blackeyed goby (Rhinogobiops nicholsii) and garibaldi (Hypsypops rubicundus, [92]). H. rubicundus actually left their shallow nests within a harbor due to increased water temperature [92]. Although it is possible that P. maculatofasciatus may also abandon their spawning grounds for deeper areas as water temperatures rise, spotted sand bass are typically considered a warm water species. In San Diego, spotted sand bass are at the northern end of their range which extends into much warmer waters throughout the Gulf of California [56]. Furthermore, P. maculatofasciatus typically produces more eggs throughout the summer as water temperature increases, with the highest egg production occurring during July when the water is warmest [56, 94]. Also, unlike other members of Paralabrax common in southern

---

**Fig 5. Scatterplot between chlorophyll a value and settlement for each day of the study.** Green points are from 2012, blue from 2013, red from 2014, and yellow from 2015.

https://doi.org/10.1371/journal.pone.0188449.g005
California such as kelp bass (*P. clathratus*) and barred sand bass (*P. nebulifer*), spotted sand bass adults typically remain in shallow coastal embayments their entire lives and may be especially resistant to higher water temperatures [56].

We propose that in 2014–15 increased SST associated with the Blob and an El Niño, combined with decreased food availability due to nutrient stratification, formed an environment that limited survival of larval *P. maculatofasciatus*. The appearance of Blob conditions is highly unusual in the northeastern Pacific since detailed oceanographic monitoring began in the late 1940s. However, warming of surface waters is consistent with predicted ocean warming with climate change [95–97]. Although caution should be used to avoid over-interpreting our data due to the one study species and location that were examined, this study gives us insight into how increasing water temperatures and decreasing upwelling and chl a may affect settlement and recruitment patterns of fishes in southern California.

Supporting information

S1 File. Larval and environmental characteristics. Individual characteristics of recently settled larvae and corresponding physical environmental variables. (XLSX)

Acknowledgments

Constructive comments were provided by N. Reynolds and two anonymous reviewers. Fieldwork was accomplished with the help of University of San Diego undergraduates (Tom Remington, Connell Ford, Matt Ray, Caroline Leinung, Colin Phillips, Craig Foxhoven, Diana Fontaine). Help with image analysis was provided by Jenny McDaniel and Emmanis Dorval at Southwest Fisheries Science Center. Funding was provided by a faculty research grant from the University of San Diego to Steven Searcy as well as from support by the Department of Environmental and Ocean Sciences at the University of San Diego.

Author Contributions

Conceptualization: Steven Searcy.

Data curation: Steven Searcy.

Formal analysis: Anthony Basilio, Andrew R. Thompson.

Funding acquisition: Steven Searcy.

Investigation: Anthony Basilio, Steven Searcy.

Methodology: Steven Searcy.

Project administration: Steven Searcy.

Resources: Steven Searcy, Andrew R. Thompson.

Software: Anthony Basilio, Andrew R. Thompson.

Supervision: Steven Searcy.

Validation: Anthony Basilio, Steven Searcy, Andrew R. Thompson.

Visualization: Anthony Basilio, Steven Searcy, Andrew R. Thompson.

Writing – original draft: Anthony Basilio.

Writing – review & editing: Steven Searcy, Andrew R. Thompson.
References

1. Levin PS. Recruitment in a temperate demersal fish: Does larval supply matter? Limnol Oceanogr. 1996; 41(4):672–9.
2. Navarrete SA, Broitman B, Wieters EA, Finke GR, Venegas RM, Sotomayor A. Recruitment of intertidal invertebrates in the southeast Pacific: Interannual variability and the 1997–1998 El Nino. Limnol Oceanogr. 2002; 47(3):791–802.
3. Wing SR, Botsford LW, Morgan LE, Diehl JM, Lundquist CJ. Inter-annual variability in larval supply to populations of three invertebrate taxa in the northern California Current. Estuar Coast Shelf Sci. 2003; 57(5–6):859–72.
4. Wilson JR, Broitman BR, Caselle JE, Wendt DE. Recruitment of coastal fishes and oceanographic variability in central California. Estuarine Coastal and Shelf Science. 2008; 79(2):483–90.
5. Watson JR, Mitarai S, Siegel DA, Caselle JE, Dong C, McWilliams JC. Realized and potential larval connectivity in the Southern California Bight. Mar Ecol Prog Ser. 2010; 401:31–48.
6. Caselle JE, Kinlan BP, Warner RR. Temporal and spatial scales of influence on nearshore fish settlement in the southern California Bight. Bull Mar Sci. 2010; 86(2):355–85.
7. Ralston S, Sakuma KM, Field JC. Interannual variation in pelagic juvenile rockfish (Sebastes spp.) abundance—going with the flow. Fish Oceanogr. 2013; 22(4):288–308.
8. Doherty PJ. Variable replenishment and the dynamics of reef fish populations. In: Sale PF, editor. Coral Reef Fishes: dynamics and diversity in a complex ecosystem. San Diego: Academic Press; 2002. p. 327–55.
9. Hixon MA, Webster MS. Density dependence in reef fish populations. In: Sale PF, editor. Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. San Diego, CA, USA.: Academic Press; 2002. p. 303–25.
10. Anderson TW, Carr MH, Hixon MA. Patterns and mechanisms of variable settlement and recruitment of a coral reef damselfish, Chromis cyanea. Mar Ecol Prog Ser. 2007; 350:109–16.
11. Meekan MG, Milich MJ, Doherty PJ. Larval production drives temporal patterns of larval supply and recruitment of a coral reef damselfish. Mar Ecol Prog Ser. 1993; 93:217–25.
12. Robertson DR, Green DG, Victor BC. Temporal Coupling of Production and Recruitment of Larvae of a Caribbean Reef Fish. Ecology. 1988; 69(2):370–81.
13. Cowen RK. Larval dispersal and retention and consequences for population connectivity. In: Sale PF, editor. Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem. San Diego, California. USA.: Academic Press; 2002. p. 149–70.
14. Criales MM, Yeung C, Jones DL, Jackson TL, Richards WJ. Variation of oceanographic processes affecting the size of pink shrimp (Farfantepeneaus duorarum) postlarvae and their supply to Florida Bay. Estuar Coast Shelf Sci. 2003; 57(3):457–68.
15. Milich MJ. Dynamic coupling of reef fish replenishment and oceanographic processes Mar Ecol Prog Ser. 1994; 110:135–44.
16. Vargas CA, Valenzuela GS, Núñez S, Arcos DF. Role of oceanographic topographic factors in the retention of hake (Merluccius gayi gayi) larvae in the upwelling system off central-southern Chile. Arch of Fishery and Marine Research. 1997; 45(3):201–22.
17. Logenwell EA, Smith PE. Mesoscale eddies and survival of late stage Pacific sardine (Sardinops sagax) larvae. Fish Oceanogr. 2001; 10(1):13–25.
18. Hutchins JB, Pearce AF. Influence of the Leeuwin current on recruitment of tropical reef fish at Rottnest Island, Western Australia. Bull Mar Sci. 1994; 54(1):245–55.
19. Houde ED. Patterns and trends in larval-stage growth and mortality of teleost fish. J Fish Biol. 1997; 51:52–83.
20. Houde ED. Subtleties and episodes in the early life of fishes. J Fish Biol. 1989; 35:29–38.
21. Bailey KM, Houde ED. Predation on Eggs and Larvae of Marine Fishes and the Recruitment Problem. In: Blaxter JHS, Southward AJ, editors. Adv Mar Biol, Volume 25: Academic Press; 1989. p. 1–83.
22. Sponaugle S, Grorud-Colvert K, Pinkard D. Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish Thalassoma bifasciatum in the Florida Keys. Mar Ecol Prog Ser. 2006; 308:1–15.
23. Houde ED. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish Bull. 1989; 87:471–95.
24. Platt T, Fuentes-Yaco C, Frank KT. Spring algal bloom and larval fish survival. Nature. 2003; 423(6938):398–9.
25. Stige LC, Langangen Ø, Yaragina NA, Vikebø FB, Bogstad B, Ottersen G, et al. Combined statistical and mechanistic modelling suggests food and temperature effects on survival of early life stages of Northeast Arctic cod (Gadus morhua). Prog Oceanogr. 2015; 134:138–51.

26. Fontes J, Semmens B, Caselle JE, Santos RS, Prakya SR. Ocean Productivity May Predict Recruitment of the Rainbow Wrasse (Coris julis). PLOS ONE. 2016; 11(11):e0165648. https://doi.org/10.1371/journal.pone.0165648 PMID: 27824889

27. Voss R, Clemmesen C, Baumann H, Hinrichsen H. Baltic sprat larvae: coupling food availability, larval condition and survival. Mar Ecol Prog Ser. 2006; 308:243–54.

28. Fuiman LA. Special considerations of fish eggs and larvae. In: Fuiman LA, Werner RG, editors. Fishery Science: The Unique Contributions of Early Life Stages. Oxford, U.K.: Wiley-Blackwell; 2002.

29. Clarke A, Fraser KPP. Why does metabolism scale with temperature? Funct Ecol. 2004; 18(2):243–51.

30. Comerford S, Brophy D, Fox CJ, Taylor N, van der Veer HW, Nash RDM, et al. Temperature effect on growth and larval duration of plaice Pleuronectes platessa in three regions of the Northeast Atlantic. Mar Ecol Prog Ser. 2013; 476:215–26.

31. McGurk MD. Effects of delayed feeding and temperature on the age of irreversible starvation and on the rates of growth and mortality of Pacific herring larvae. Mar Biol. 1984; 84(1):13–26.

32. Rana KJ. Influence of egg size on the growth, onset of feeding, point-of-no-return, and survival of unfed Oreochromis mossambicus fry. Aquaculture. 1985; 46(2):11–31.

33. Eldridge MB, Whipple JA, Eng D, Bowers MJ, Jarvis BM. Effects of Food and Feeding Factors on Laboratory-Reared Striped Bass Larvae. Trans Am Fish Soc. 1981; 110(1):111–20.

34. Gurod-Colvert K, Sponaugle S. Variability in water temperature affects trait-mediated survival of a newly settled coral reef fish. Oecologia. 2011; 165:675–86. https://doi.org/10.1007/s00442-010-1748-4 PMID: 20714906

35. Searcy SP, Sponaugle S. Selective mortality during the larval-juvenile transition in two coral reef fishes. Ecology. 2001; 82(9):2452–70.

36. Hoey AS, McCormick MI. Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. Oecologia. 2004; 139(1):23–35. https://doi.org/10.1007/s00442-004-1490-9 PMID: 15025706

37. Takahashi M, Watanabe Y. Effects of temperature and food availability on growth rate during late larval stage of Japanese anchovy (Engraulis japonicus) in the Kuroshio–Oyashio transition region. Fish Oceanogr. 2005; 14(3):223–35.

38. Anderson JT. A review of size dependant survival during pre-recruit stages of fishes in relation to recruitment. J Northwest Atl Fish Sci. 1988; 8:55–66.

39. Leggett WC, Debois E. Recruitment in marine fishes: Is it regulated by starvation and predation in the egg and larval stages? Netherlands Journal of Sea Research. 1994; 32(2):119–34.

40. Fuiman LA, Magurran AE. Development of predator defences in fishes. Rev Fish Biol Fish. 1994; 4(2):145–83.

41. Miller TJ, Crowder LB, Rice JA, Marschal EA. Larval Size and Recruitment Mechanisms in Fishes: Toward a Conceptual Framework. Can J Fish Aquat Sci. 1988; 45(9):1657–70.

42. China V, Holzman R. Hydrodynamic starvation in first-feeding larval fishes. Proceedings of the National Academy of Sciences of the United States of America. 2014; 111(22):8083–9. https://doi.org/10.1073/pnas.1323205111 PMID: 24843180

43. Litvak MK, Leggett WC. Age and size-selective predation on larval fishes, the bigger is better hypothesis revisited. Mar Ecol Prog Ser. 1992; 81:13–24.

44. Pepin P, Shears TH, de Lafontaine Y. Significance of body size to the interaction between a larval fish (Malloplus villosus) and a vertebrate predator (Gasterosteus aculeatus). Mar Ecol Prog Ser. 1992; 81:1–12.

45. Bertram DF, Leggett WC. Predation risk during the early life history periods of fishes: separating the effects of size and age Mar Ecol Prog Ser. 1994; 109:105–14.

46. Rankin TL, Sponaugle S. Characteristics of Settling Coral Reef Fish Are Related to Recruitment Timing and Success. PLOS ONE. 2014; 9(9):e108871. https://doi.org/10.1371/journal.pone.0108871 PMID: 25250964

47. Cushing DH. Plankton Production and Year-class Strength in Fish Populations: an Update of the Match/Mismatch Hypothesis. In: Blaxter JHS, Southward AJ, editors. Adv Mar Biol. Volume 26: Academic Press; 1990. p. 249–93.

48. Behrenfeld MJ, O’Malley RT, Siegel DA, McClain CR, Sarmaeinto JL, Feldman GC, et al. Climate-driven trends in contemporary ocean productivity. Nature. 2006; 444(7120):752–5. https://doi.org/10.1038/nature05317 PMID: 17151666
49. Leising AW, Schroeder ID, Bograd SJ, Abell J, Durazo R, Gaxiola-Castro G, et al. State of the California current 2014–15: Impacts of the warm-water “blob”. California Cooperative Oceanic Fisheries Investigations Reports. 2015; 56:31–68.

50. Ryther JH. Photosynthesis and Fish Production in the Sea. Science. 1969; 166(3901):72–6. PMID: 5817762

51. Moser HG, Charter RL, Watson W, Ambrose DA, Butler JL, Charter SR, et al. Abundance and distribution of rockfish (Sebastes) larvae in the Southern California Bight in relation to environmental conditions and fishery exploitation. California Cooperative Oceanic Fisheries Investigations Reports. 2000; 41:132–47.

52. Bond NA, Cronin MF, Freeland H, Mantua N. Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys Res Lett. 2015; 42(9):3414–20.

53. Cavole LM, Demko AM, Diner RE, Giddings A, Koester I, Pagniello CMLS, et al. Biological Impacts of the 2013–2015 Warm-Water Anomaly in the Northeast Pacific: Winners, Losers, and the Future. Oceanography. 2016; 29.

54. Zaba KD, Rudnick DL. The 2014–2015 warming anomaly in the Southern California Current System observed by underwater gliders. Geophys Res Lett. 2016; 43(3):1241–8.

55. Leising AW, Schroeder ID, Bograd SJ, Bjorkstedt EP, Field J, Sakuma K, et al. State of the California current 2013–14: El Nino looming. California Cooperative Oceanic Fisheries Investigations Reports. 2014; 55:51–87.

56. Allen LG. Planktonic Larval Duration, Settlement, and Growth Rates of the Young-of-the-Year of Two Sand Basses (Paralabrax maculatofasciatus) within the Southern California Bight. CALCOFI Reports. 1995; 36:193–203.

57. Tranah GJ, Allen LG. Morphologic and Genetic Variation Among Six Populations of the Spotted Sand Bass, Paralabrax maculatofasciatus, from Southern California to the Upper Sea of Cortez. Bull South Calif Acad Sci. 1999; 98(3):103–18.

58. Oda DL, Lavenberg RJ. Reproductive biology of three California species of Paralabrax (Pisces: Serranidae). California Cooperative Oceanic Fisheries Investigations Reports. 1993; 34:122–32.

59. Woodson CB, McManus MA, Tyburczy JA, Barth JA, Washburn L, Caselle JE, et al. Coastal fronts set recruitment and connectivity patterns across multiple taxa. Limnol Oceanogr. 2012; 57(2):582–96.

60. Durbin EG, Durbin AG, S-mayda TJ, Verity PG. Food limitation of production by adult Acartia tonsa in Narragansett Bay, Rhode Island1. Limnol Oceanogr. 1983; 28(6):1199–213.

61. Ambler JW. Effect of food quantity and quality on egg production of Acartia tonsa Dana from East Lagoon, Galveston, Texas. Estuar Coast Shelf Sci. 1986; 23(2):183–96.

62. Beckman BR, Peterson WT. Egg production by Acartia tonsa in Long Island Sound. J Plankton Res. 1986; 8(5):917–25.

63. Mendelssohn R. Xtracomatic: extracts environmental data from ERD’s ERDDAP web service. 2015. Mendelssohn R. Xtracomatic: extracts environmental data from ERD’s ERDDAP web service. 2015.
73. Cogliani E. Air pollution forecast in cities by an air pollution index highly correlated with meteorological variables. Atmos Environ. 2001; 35(16):2871–7.

74. Ammann AJ. SMURFs: standard monitoring units for the recruitment of temperate reef fishes. J Exp Mar Biol Ecol. 2004; 299(2):135–54.

75. Connell SD. The relationship between large predatory fish and recruitment and mortality of juvenile coral reef-fish on artificial reefs. J Exp Mar Biol Ecol. 1997; 209(1–2):261–78.

76. Kahle D, Wickham H. ggmap: Spatial visualization with ggplot2. The R journal. 2013; 5:144–61.

77. Hinaux H, Pottin K, Chalhoub H, Pere S, Eliop Y, Legendre L, et al. A Developmental Staging Table for Astyanax mexicanus Surface Fish and Pachon Cavefish. Zebrafish. 2011; 8(4):155–65. https://doi.org/10.1089/zeb.2011.0713 PMID: 22181659

78. Wootton RJ. Ecology of Teleost Fishes. London: Chapman and Hall; 1990.

79. Searcy SP, Eggleston DB, Hare JA. Is growth a reliable indicator of habitat quality and essential fish habitat for a juvenile estuarine fish? Can J Fish Aquat Sci. 2007; 64(4):681–91.

80. Wilson DT, McCormick MI. Microstructure of settlement-marks in the otoliths of tropical reef fishes. Mar Biol. 1999; 134(1):29–41.

81. Bullmore E, Brammer M, Williams SC, Rabe-Hesketh S, Janot N, David A, et al. Statistical methods of estimation and inference for functional MR image analysis. Magn Reson Med. 1996; 35(2):261–77. PMID: 8622592

82. Liboschik T, Fokianos K, Fried R. tscount: An R Package for Analysis of Count Time Series Following Generalized Linear Models. Vignette of R package tscount version 130. 2016.

83. Burnham K P., Anderson D R. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. USA: Springer; 2002.

84. Whitney FA. Anomalous winter winds decrease 2014 transition zone productivity in the NE Pacific. Geophys Res Lett. 2015; 42(2):428–31.

85. McGowan JA, Bograd SJ, Lynn RJ, Miller AJ. The biological response to the 1977 regime shift in the California Current. Deep-Sea Research Part II-Topical Studies in Oceanography. 2003; 50(14–16):2567–82.

86. Palacios DM, Bograd SJ, Foley DG, Schwing FB. Oceanographic characteristics of biological hot spots in the North Pacific: A remote sensing perspective. Deep Sea Research Part II: Topical Studies in Oceanography. 2006; 53(3–4):250–69.

87. Baumann H, Peck M, Herrmann J-P. Short-term decoupling of otolith and somatic growth induced by food level changes in postlarval Baltic sprat, Sprattus sprattus2005. 539–47 p.

88. Jacobson LD, MacCall AD. Stock-recruitment models for Pacific sardine (Sardinops sagax). Can J Fish Aquat Sci. 1995; 52(3):566–77.

89. Miller EF, Allen LG. Captive breeding of spotted sand bass, Paralabrax maculofasciatus, in southern California. Calif Fish Game. 2006; 92:98–105.

90. Nixon SW, Granger S, Buckley BA, Lamont M, Rowell B. A one hundred and seventeen year coastal water temperature record from Woods Hole, Massachusetts. Estuaries. 2004; 27(3):397–404.

91. Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, et al. Coral Reefs Under Rapid Climate Change and Ocean Acidification. Science. 2007; 318(5857):1737–42. https://doi.org/10.1126/science.1152509 PMID: 18079392

92. Howell P, Auster PJ. Phase Shift in an Estuarine Finfish Community Associated with Warming Temperatures. Marine and Coastal Fisheries. 2012; 4(1):481–95.