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**Original Article**

# Larval condition helps explain the recent anchovy boom in an extremely warm California Current Ecosystem

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## Abstract

**Discerning the causes of boom-and-bust cycles for coastal pelagic fishes (CPF) has been a critical element in fisheries oceanography research for over a century. Although the biological and environmental conditions that drive CPF dynamics are difficult to pin down, it is clear that year-class strength (the "endpoint" when mortality rates stabilize and adult population sizes are set) is contingent on larval survival to the "pre-recruit" life history stage. Here, we test and verify whether two ideas, the Maternal Effects Hypothesis and the Growth-Survival Paradigm, can explain, at least to some degree, the exponential rise of northern anchovy (*Engraulis mordax*) off California from 2009–2019. We extracted otoliths from 127 anchovy larvae collected by the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program and measured otolith core diameter (an index of size-at-hatch), larval age, size-at-age and growth rate-at-age (indexed by otolith increment width). Both hypotheses were synergistically supported. Larvae that hatched large (a likely Maternal Effect) grew faster, were larger at age, and were more likely to survive to three weeks. In addition, in years when larvae grew faster and were more robust at age, recruitment was higher (Growth-Survival Paradigm). The oceanographic conditions that facilitated high recruitment (2015–2016) were unexpected because anchovy were previously believed to thrive when the ocean was cold and 2014–2016 was the warmest 3-year period in the California Current Ecosystem in at least a hundred years. In spite of the overall warm conditions, the anchovy larvae we examined were in better condition and had higher survival in patches of ocean with moderate temperatures and low chlorophyll in the southern portion of the sampling region. By simultaneously testing multiple hypotheses, we have come closer to discerning the mechanisms driving the abundance of an ecologically important CPF.**

**Keywords** Coastal pelagic species, northern anchovy, larval condition, maternal investment, Growth-Survival Paradigm, recruitment

## Introduction

Small coastal pelagic fishes (CPF) such as sardines and anchovies are critical economic and ecological components of many marine ecosystems around the world (Hilborn et al. 2022). For example, anchoveta (*Engraulis ringens*) off Peru and Chile was the largest fishery in the world by landed weight in 2022, the most recent year that a global assessment was conducted (FAO 2024). In the California Current Ecosystem (CCE) recent increases in northern anchovy (*Engraulis mordax*; hereby "anchovy") abundance has resonated through the marine ecosystem. On the one hand, breeding success of marine predators such as California sea lions (*Zalophus californianus*) and Brandt's Cormorant (*Phalacrocorax penicillatus*) have increased because of the availability of ample anchovy prey (McClatchie et al. 2016, Fennie et al. 2024, Thompson et al. 2024). On the other hand, an anchovy-dominant diet has been linked to thiamine deficiency and poor reproduction of coho salmon (*Oncorhynchus kisutch*; Mantua et al. 2025) and increased entanglement of humpback whales (*Megaptera novaeanglia*) in crab fishing gear as whales moved shoreward to feed on anchovy and increased interaction with crab traps (Santora et al. 2026). Given their value, it is important to discern factors affecting the population dynamics of this CPF for effective fisheries and ecosystem management.

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Coastal pelagic fishes worldwide are characterized by boom and bust cycles where abundances can change by orders of magnitude in a matter of 2–3 years (Robert et al. 2023). Many factors, including fishing mortality and predation, can affect adult CPF abundance. However, episodic strong recruitment events, where a relatively high proportion of larvae survive to the life history stage when mortality substantially decreases may be the single most important force fueling booms for most populations (Lasker 1987, Cushing 1990, Houde 2008, 2016). Analyses of otoliths or scales from radiocarbon dated sediment core samples document large population changes over the course of centuries prior to large-scale fishing off Peru (Salvatteci et al. 2022), Japan (Kuwae et al. 2017) and the United States (McClatchie et al. 2017, Jones and Checkley Jr 2019). Most CPF are short lived (e.g. anchovy live for approximately 4 years (Sydeman et al. 2020)) so just a few consecutive years of low recruitment will inevitably cause a significant drop in adult population size. Conversely, CPF are so fecund that even when adult population sizes are low it is possible to produce a large recruitment class if conditions are especially favorable for larval survival (Lasker 1987, Houde 2008). Here, we investigate potential reasons for the recent increase in northern anchovy biomass off California from a historically low abundance of $<$ 65 000 metric tons in 2015 to more than 2.7 million metric tons in 2021 (Kuriyama et al. 2022).

At the turn of the 21$^{st}$ century, it seemed that fisheries scientists had a grasp on the environmental conditions that facilitate high adult anchovy abundance. Chavez et al. (2003) published an influential paper in the realm of fisheries science (2 259 citations as of July 2025 per Google Scholar) that documented pan-Pacific rises of sardines under warm and anchovies under cool ocean regimes during the 20$^{th}$ century. However, this paradigm was not supported in the eastern North Pacific in the first quarter of the 21$^{st}$ century. The CCE was largely cooler than average from 1999–2013 (Zwolinski and Demer 2012, Thompson et al. 2017, Sydeman et al. 2020), but sardine were mostly abundant and anchovy scarce during this time. The one exception was when anchovy rose to relatively high levels during a period of brief warming from 2003–2005 (Thompson et al. 2012, Thayer et al. 2017, Hinchliffe et al. 2025). In mid-2014, ocean temperatures warmed to unprecedented highs in the CCE, and 2014–2016 turned out to be the warmest three-year period on record dating back to 1918 (Jacox et al. 2018). Anchovy recruitment was high during and after the 2014–2016 eastern Pacific Marine Heatwave (Hinchliffe et al. 2025) while sardine experienced persistently low recruitment (Allen et al. 2025). The idea that anchovy thrive in cool and sardine in warm conditions did not match reality in the 21$^{st}$ century in the CCE from 2009 to 2025 (Thompson et al. 2019, Sydeman et al. 2020, Swieca et al. 2025).

Our goal is to identify factors that contributed to the rapid rise of anchovy in the CCE over the past decade. In doing so, we test the validity of two hypotheses. The first hypothesis is that maternal effects impact recruitment. The importance of maternal effects (i.e. the idea that the environmental experience of a mother leading up to and during internal egg development can affect offspring survival after parturition; Mousseau and Fox 1998) has been gaining appreciation in fisheries science in recent years, but this concept has mostly been applied to long-lived species such as rockfishes (*Sebastes* spp.: Hixon et al. 2014, Fennie et al. 2024) and marine mammals (Beltran et al. 2025). A seminal paper by Garrido et al. (2015), however, showed that the size of European sardine (*Sardina pilchardus*) at hatch can be indexed by the size of the otolith

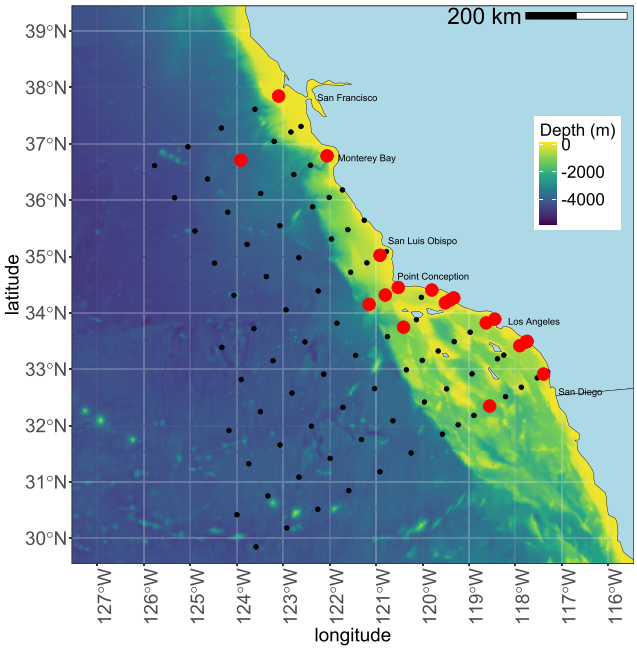


**Figure 1** Sampling region. Blue dots are core CalCOFI stations, and red dots are stations where larval anchovy were analyzed for this study.

core, and that only larvae that were born large survived to one month of age. Second, there are multiple related hypotheses postulating that larvae that grow faster (stage duration (Chambers et al. 1987); growth-selective predation (Takasuka et al. 2003)) or are larger at a given age (bigger is better (Miller et al. 1988)) are more likely to survive to become recruits. Collectively, these hypotheses have been termed the Growth-Survival Paradigm (GSP; Robert et al. 2023). In this paper, we test the GSP by evaluating if larvae were growing faster and were larger-at-age in years when recruitment was high. We also evaluate the environmental conditions that correlated with growth and body condition. The Maternal Effects and GSP hypotheses are by no means mutually exclusive, and here we determine empirically if either or both can help explain the population dynamics of anchovy in the CCE from 2009–2019.

# Methods

## Sample collection and larval characterization

Plankton samples were collected by the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program (McClatchie 2025) by dropping a 71-cm diameter dual bongo frame fitted with 505-$\mu$m mesh to 210 m and towing it obliquely through the water column while the ship was underway at 1–2 knots. CalCOFI samples were taken from a fixed-grid with 115 core sample stations between San Francisco and the U.S/Mexico border in winter and spring and 75 stations between San Luis Obispo and the U.S./Mexico border in summer and fall (Fig. 1). Plankton samples from the starboard net were preserved in 5% formalin and those from the port side in 100% ethanol. In addition, a SBE 911 plus CTD measured temperature, salinity, chlorophyll *a* and oxygen at depth intervals of 1 m. Maximal CTD depths varied by station, but

we only considered the upper 100 m because virtually all larval anchovy reside in this depth range (Ahlstrom 1959), and all casts reached that depth.

Before our project began, ichthyoplankton from the starboard net were already identified and measured to total length. We identified stations that likely contained larger anchovy (> 13 mm) in port samples based on starboard samples and sorted all anchovy out of counterpart port ethanol-preserved samples. Here, we focused on the ethanol-preserved data because otoliths are better-preserved in ethanol versus formalin. We analyzed the larger individuals because we are next planning to conduct compound specific stable isotope analysis on the larvae analyzed in this paper, and we previously found that larvae of this size had enough tissue to carry out this analysis without maternal signal interference (Swalethorp et al. 2023). In total, we sorted 127 individual anchovy larvae ranging in total length between 12.5 and 22.5 mm from 30 CalCOFI stations that were collected in 2009–2011, 2013, 2015–2017 and 2019 (Supplemental Table 1).

Larval condition was quantified by three morphometrics: standard body length (SL), muscular height at the pectoral fin (MHP) and muscular height at the anal fin (MHA) (Figure S1). To ensure the most accurate morphometric measurements, each fish was soaked in water for 20 seconds to reduce dysmorphia and brittleness caused by ethanol preservation (Sotola et al. 2019). Using tweezers, larvae were carefully straightened and measured. Standard length was measured to the nearest 10 μm as the distance from the tip of the larva's snout to the beginning of the caudal fin. MHP was the muscular height at the pectoral fin's attachment point to the body and MHA the muscular height immediately posterior to the anal fin. Both were measured to the nearest 1 μm. All dissections and measurements were done using an Olympus SZX2-ILLD dissecting microscope with a SDF Plapo 0.5xPF objective lens.

Otoliths were extracted from measured larvae following established protocols (Swalethorp et al. 2016). Each larva was decapitated using a scalpel and sagittal otoliths were removed using fine needles underneath a dissecting microscope. Once isolated under the microscope, the otolith (sometimes the left, right, or both) was placed flat-side down on a mounting slide and coated with clear nail polish.

Digital images of each otolith were taken using a LEICA Stereozoom S9i microscope camera with a 40x objective lens. An image of a calibrated slide was captured with the same camera and magnification in order to quantify the number of image pixels per $\mu$m. The calibrated slide was measured 10 times to get an average measurement of 1 $\mu$m per 4.66 pixels. For all of the otolith's increment counts, increment widths, and core diameter, the clearest digital image was analyzed, either from the right or left otolith. Otolith core diameters and increment widths were measured using ImageJ (Schneider et al. 2012).

Daily growth increments on the otoliths were counted to age each anchovy and the widths between each increment were measured to analyze the full growth rate histories and recent growth rate (RG; average of last 3 days of life). Henceforth, larval growth rates refer to the measured otolith growth (daily increment width) as a proxy for somatic growth. Otolith core diameter was used as a proxy for size-at-hatch (Garrido et al. 2015, Fennie et al. 2024).

Each otolith was read at least two times by the same reader following the methods of Swieca et al. (2023). Measurements for the number of increments and their widths were taken along the longest radius from the otolith's core to the outermost edge when possible and increment widths were quantified as the distance between two adjacent increments (Swalethorp et al. 2016) (Figure S2). For otoliths with unclear location of the first increment, the initial dark band at least 8 $\mu$m or more from the core's center was used for the first growth increment. This technique is based upon previous studies using this technique and demonstrating that the first growth increment of the otolith occurred around $10.4 \pm 1.11$ $\mu$m in European sardine and $> 6$ $\mu$m in Mediterranean anchovy (Garcia et al. 1998, Garrido et al. 2015). The outermost band for each otolith was counted as an increment. For the first read, a live image was juxtaposed with a still image to avoid counting sub-daily increments. A live image allowed for interpretation at lower magnifications, which has been shown to highlight daily-increments over sub-daily increments (Campana 1992). For the second read, only a still image was used. If the first two reads were within 5% (one or two days) of one another, the larger increment count out of the two was used to age the anchovy. If the two reads were not within 5% of each other, a third read was conducted using the same still image as the 1st and 2nd reads. If the 3rd read was within 5% of either the 1st or 2nd read, the largest increment count was used to age the anchovy. If the 3rd read differed more than 5% from the 1st and 2nd reads, the otolith and fish were not used in further analysis. Choosing a 5% threshold for all counts follows Swieca et al. (2023).

## Analyses

### Temperature, northern anchovy spawning stock biomass and recruitment dynamics

To illustrate the extreme ocean temperature fluctuations during our study period, we contrast average summer temperature within the top 10 meters from stations on the continental shelf between San Luis Obispo and the US/Mexican border from 1965–2021 using CalCOFI CTD data. To contextualize the status of the anchovy population during our study period versus the past and future years with robust data, we present spawning stock biomass (SSB) and recruitment (R) from an integrated statistical catch-at-age population dynamics model (Hincliffe et al. 2025, Fig. 2), as well as the per capita recruitment (R divided by SSB from the previous year). This time period spans the duration of the anchovy assessment conducted by Hinchliffe et al. (2025)

### Maternal and environmental effects on condition and survival

Our first objective was to identify possible factors affecting larval anchovy condition. We used age as a measure of survival (i.e. an older larvae lived for a longer period of time). We assumed that the initial distribution of traits was similar across cohorts (Chambers et al. 1987, Pepin 1991). Our condition indices were recent growth (RG), SL, MHP and MHA. Because a larva will be longer or fatter when it is older, even if it is small or emaciated given its age, we used age-adjusted values for these four dependent variables. To generate age-adjusted values, we used generalized additive models (GAMs) with three knots to fit the relationship between age and the four variables package "mgcv" (Wood 2011) in the programing platform R (R Core Team 2023). We used GAMs here instead of linear models because the rate of change in length or width with age can asymptote (Swalethorp et al. 2016) and just three

knots to prevent GAM overfitting. We then used the residuals of the GAMs as our dependent variables. We also used simple general linear models to evaluate the relationships among the four dependent variables (e.g. age-adjusted SL ~ age-adjusted MHL, etc.) to discern the degree of similarity among measures of larval condition.

To test the effects of core width (an index for size-at-birth; Garrido et al. 2015, Fennie et al. 2024), temperature, salinity, chlorophyll a, and dissolved oxygen averaged over the top 100 m (as fixed effects) on the four dependent variables we used generalized linear mixed models (GLMM) as implemented with the package "glmmTMB" (Brooks et al. 2017). Because initial examination of scatter plots indicated that some relationships may have been curvilinear, we added quadratic terms for temperature and salinity into the models. We chose to use GLMM instead of Generalized Additive Mixed Models because GAMMs have the potential to induce curved lines between independent and dependent variables that are not replicable. We also included latitude to determine if there was a geographic impact on larvae aside from temperature as previous research showed that when anchovy population sizes contract, they tend to disappear in central California but persist in southern California (Tran et al. 2025). We modeled the interaction between station and year as a random effect on the slope. Each variable was scaled mean centered (a given value subtracted from the mean value) and standardized (divided) by two standard deviations to facilitate comparison of slope coefficients among variables and to help with model convergence.

We checked model residuals with the `DHARMa` package (Hartig 2024), and collinearity between independent variables with Variance Inflation Factors, using the `performance` package (Lüdecke et al. 2021). There were no residual or collinearity issues detected in any of the models. The conditional pseudo-$R^2$ values, which can be interpreted as the variance explained by the entire GLMM model (both fixed and random effects), were calculated using the methods of Nakagawa & Schielzeth (2013).

### Growth and Recruitment

Our second objective was to discern if condition indices predicted recruitment (recruitment values were taken from Hinchliffe et al. 2025). We again used GLMM to determine if age, core width, age-adjusted SL, MHP, and MHA varied among years. Specifically, we modeled these scaled variables against year (as a factor) with station as the random effect on the slope. We conducted separate analyses for seasons. To control for sample size errors, only CalCOFI cruises with at least 5 anchovy larvae and only growth increments with a minimum of 5 replicates were chosen for this analysis. Recruitment indices from Hinchliffe et al. (2025) were largely based on young of the year anchovy collected in summer by the Rockfish Recruitment and Ecosystem Analysis Survey (Sakuma et al. 2016; Sakuma et al. 2006). Because larvae in summer and fall were collected after recruitment estimates, we restricted this analysis to include only winter and spring samples. There were enough larvae to run models for 2013 (10 larvae), 2015 (40 larvae) and 2016 (9 larvae) in winter and 2015 (15 larvae) and 2017 (13 larvae) in spring (Table S1). Serendipitously, these were years with a wide range of recruit abundances.

To determine if larvae were growing faster in above-average recruitment years, the entire otolith growth increment trajectory of each larva was examined using a Linear Mixed-Effects Model (lme function in the nmle package, Pinheiro et al. 2026). Again, because young of the year data was collected in early summer, larvae collected in summer or fall could not possibly have contributed to the sampled recruits, so growth trajectories were only analyzed from winter (2013, 2015, 2016) and spring (2015, 2017). An approach similar to that outlined in previous studies (Swalethorp et al. 2016, Malanski et al. 2020, Malca et al. 2022) was used, where the model was fit to growth increment width as the dependent variable and year as a fixed effect. Growth increment number was included as a random effect (nested by individual larvae) and applied to both intercepts and slopes. Consecutive growth increments widths tend to be autocorrelated (Campana et al. 1995, Campana 1996; Chambers and Miller 1995), and to correct for this the model was refitted with an autocorrelation structure using the corCAR1 function (also from nmle) using growth increment number as the continuous time covariate. The maximum likelihood was used to estimate slopes and level of significance to adjust for the unbalanced design as individual larvae differed in number of growth increments. The model was run separately for winter and spring and included an interaction term for growth increment number and year. If the interaction was insignificant, the term was dropped and the model re-run.

# Results

## Temperature, northern anchovy spawning stock biomass and recruitment dynamics

Temperature was mostly below average in the 1960s and early to mid-1970s (Fig. 2A). During our study, temperature was average or low from 2009–2013 before rising and remaining high from 2014–2017 and then dropping again in 2018 and 2019 (Fig. 2A). As reported in Hinchliffe et al. 2025, anchovy spawning stock biomass (SSB) was generally high from the mid-1960s to the late 1980s (Fig. 2B). It declined to low levels in the 1990s, increased briefly in the early 2000s before plummeting to record-low levels in the late 2000s. During the temporal window of our study, SSB was highly dynamic. From 2009–2015 SSB was consistently at record lows. Beginning in 2016, however, SSB rose steadily and was the highest in 2019 since the 1970s. By 2022, it was close to a record high. All told, SSB increased approximately 42-fold from the nadir in 2015 to the zenith in 2021. The surge in SSB was driven by high recruitment beginning in 2014–2015 following a decade of very low recruitment (Fig. 2B). Overall recruitment rose dramatically in 2018 and 2019 fueling the sharp rise in SSB.

Per capita recruitment (R/SSB) was also historically variable during our study years (Fig. 2C). In particular, per capita recruitment was very low in 2013, moderate in 2017 and very high in 2015 (the highest ever recorded) and 2016.

## Maternal and environmental effects on condition and survival between 2009 and 2019

Age was significantly correlated with each dependent variable (RG, SL, MHP and MHA; Fig. S3), and we thus used residuals from the GAMS as indices of age-adjusted larval growth and condition. Age-adjusted RG, SL, MHP and MHA were all highly significantly

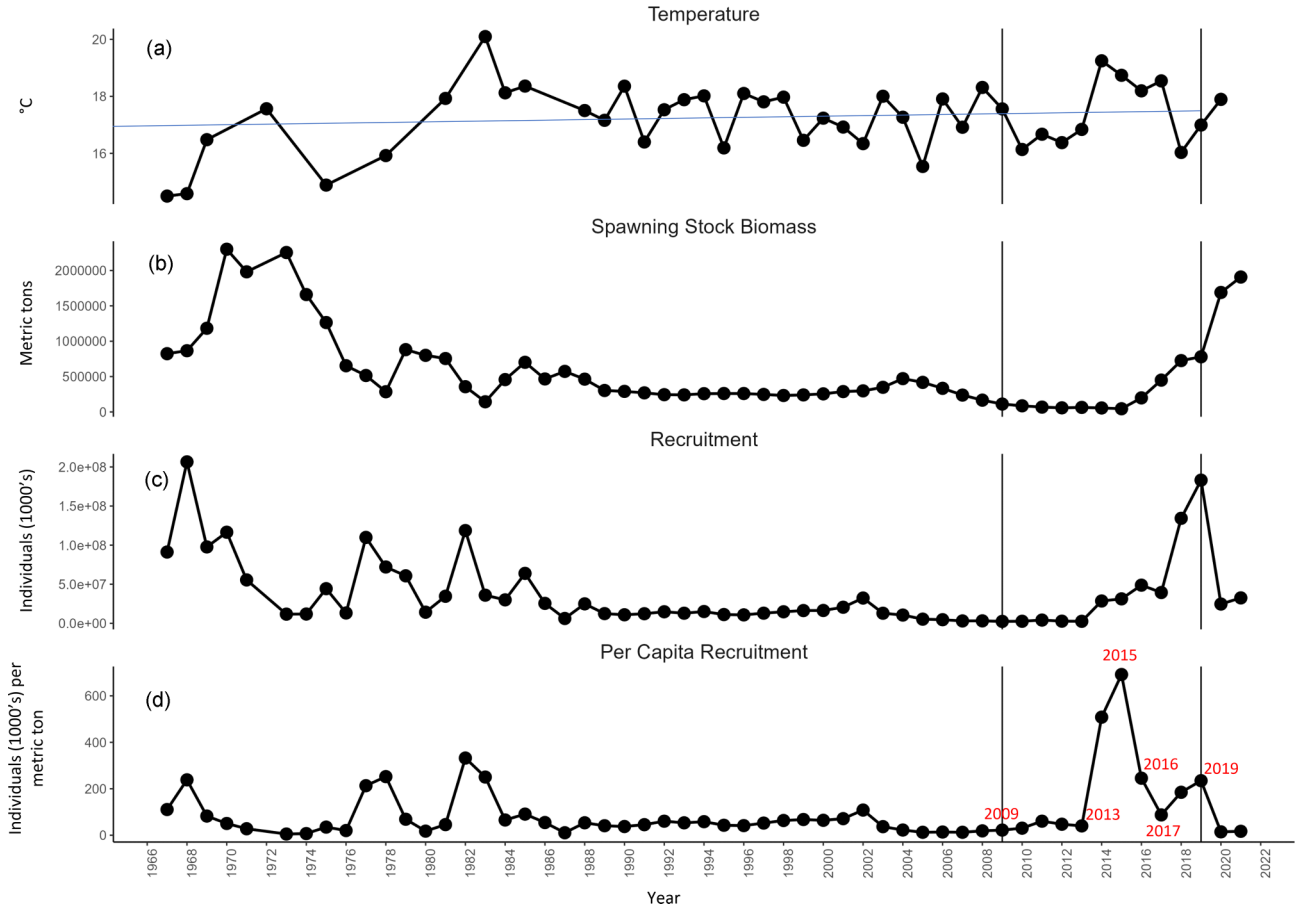


**Figure 2** A. Average temperature in the upper 10 m in summer across CalCOFI stations over the continental shelf between San Luis Obispo and the US/Mexico border. The horizontal blue line depicts the long-term mean temperature. Note that there are missing years in the late 1960s-early 1980s because CalCOFI was only conducting surveys every third year during this time period. B. Anchovy spawning stock biomass (SSB), C. recruitment (R) and D. per capita recruitment (R/SSB). The anchovy values are taken directly from Hinchliffe et al. (2025). Please see this paper to learn more about the methodology used to provide these values.

**Table 1.** Linear relationship matrix between the four dependent variables in the GLMM. RG = age-adjusted recent growth, SL = age-adjusted standard length, MHP = age-adjusted muscular height at the pectoral fin, and MHA = age-adjusted muscular height at the anal fin. Adjusted $R^2$ values are on the lower and p-values on the upper part of the matrix. All of the relationships were positive

| | RG | SL | MHP | MHA |
|---|---|---|---|---|
| RG | | 8.89E-11 | 3.72E-10 | 1.55E-08 |
| SL | 0.28 | | 2.20E-16 | 2.20E-16 |
| MHP | 0.26 | 0.45 | | 2.20E-16 |
| MHA | 0.22 | 0.52 | 0.57 | |

correlated with one another (Table 1, Figs S3-S5). However, $R^2$ from a linear model varied between 0.22 and 0.57 depending on the combination of variables. Therefore, each index tells a slightly different story and collectively these variables should better describe overall larval conditions than any index by itself.

Examining the results of the five GLMMs together implicated the variables that facilitated optimal anchovy larval condition. Four of five dependent variables were positively correlated with otolith core width (an index of birth size; Table 2, Fig. 3A-D). A close examination of the relationship between age and core width (hatch size) revealed that 28 larvae were in the upper 75$^{th}$ quantile of age (>30 days old). Of these, half (14) were in the upper 75$^{th}$ quantile of core width while only 3 were in the bottom 25$^{th}$ quantile of core width. By contrast, a much larger percentage (37%) of larvae in the bottom 25$^{th}$ quantile were in the bottom 25$^{th}$ quantile of core width. (Fig. 3A). This suggests having a wider core (an index of size-at-hatch) greatly increased the chances for surviving the first month of life.

Water temperature also correlated with larval condition but in a non-linear fashion. Age and MHA were highest at approximately 15° and 17°C, respectively (Table 2, Fig. 3 E, F). Chlorophyll *a* affected 3/5 indices of larval condition as larvae were older and thicker when chlorophyll *a* was low (Table 2, Fig. 3G). There was no relationship with salinity and oxygen (Table 2). Finally, larvae in the south grew faster, and were larger and thicker (Table 2, Fig. 3H–J).

## Growth and recruitment

Larval condition was significantly different among years with variable recruitment (Table 3, Fig. 4). In winter, core width,

**Table 2.** Generalized linear mixed model results modelling five dependent variables—age, age-adjusted recent growth, standard length, muscular height at the pectoral and anal fins against core width, temperature, temperature$^2$, salinity, salinity$^2$, oxygen, chlorophyll a and latitude.

| | independent variables | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| **Dependent varaibles** | **Core** | **Temperature** | **Temperature$^2$** | **Salinity** | **Salinity$^2$** | **Oxygen** | **Chlorophyll *a*** | **Latitude** |
| Age | **.07 (0.01)** | **−0.25 (0.009)** | **−0.34 (0.06)** | −0.002 (0.99) | .03 (0.87) | .10 (0.47) | **−0.27 (0.039)** | .17 (0.29) |
| Recent growth (age adjusted) | −0.01 (0.79) | .11 (0.33) | −0.22 (0.32) | −0.39 (0.10) | −0.31 (0.14) | .12 (0.50) | −0.05 (0.76) | **−0.37 (0.057)** |
| Standard length (age adjusted) | **.07 (0.014)** | .19 (0.055) | −0.32 (0.084) | −0.47 (0.018) | −0.12 (0.51) | .12 (0.41) | −0.086 (0.54) | **−0.38 (0.017)** |
| Muscular height at pectoral fin (age adjusted) | **.08 (0.0014)** | .12 (0.29) | −0.19 (0.39) | −0.19 (0.39) | −0.20 (0.36) | .23 (0.14) | **−0.31 (0.039)** | −0.29 (0.14) |
| Muscular height at anal fin (age adjusted) | **.071 (0.0075)** | **.26 (0.0078)** | **−0.42 (0.022)** | −0.27 (0.18) | −0.07 (0.68) | .10 (0.51) | **−0.27 (0.06)** | **−0.41 (0.016)** |

*Notes*: Values are the slope and (*P*-value). Bolded values depict relationships where the *P*-value is $< 0.10$.

age-adjusted SL, age-adjusted MHP and age-adjusted MHA were significantly higher in 2015 (the highest per capita recruitment year) than 2013 (the lowest per capita recruitment year). Age and core width were also higher in 2015 than 2016 (a medium-high per capita recruitment year). Larval age was higher in 2015 than 2016. In spring, age-adjusted RG and age-adjusted MHP and MHA were higher in 2015 than 2017 (a relatively low per-capita recruitment year).

Tracking growth over the lifetime of larvae also showed that growth histories differed between higher and lower recruitment years. In winter, larvae were growing faster (wider increments) at greater than 20 days in 2015 relative to 2016 ($df = 58$, $t = 5.177$, $P < 0.001$), and in both 2015 and 2016 larvae were growing faster on average from approximately day 10 on than in 2013 (Fig. 5; $df = 48$, $t = 2.773$, $P = 0.008$). Furthermore, the acceleration in growth rate as the larvae aged (slope) was on average greater in 2015 and 2016 compared to 2013 ($df = 1735$, $t = 2.135$, $P = 0.033$). In spring, larvae from 2015 were growing faster throughout almost their entire lives compared to 2017 (Fig. 5; $df = 30$, $t = 3.760$, $P < 0.001$).

# Discussion

CalCOFI has been systematically monitoring larval fish abundance and oceanography in the CCE since 1951, and events from 2009–2019 were unprecedented. The CCE warmed appreciably beginning in 2014, 2014–2016 was on average the warmest 3-year period on record (Jacox et al. 2018), and warm conditions have largely persisted through at least 2026 (Thompson et al. 2024, Leising et al. 2025, Hunsicker et al. 2026). The overall larval fish assemblage changed significantly around 2015 as the abundance of southern mesopelagic fishes and anchovy spiked to record levels in the CCE (Thompson et al. 2022). The rise in mesopelagic fishes was relatively easy to explain as it is well-known that these species reside in water masses that move shoreward and north during warming periods (Moser et al. 1987, Hsieh et al. 2009, Thompson et al. 2012, Moser and Smith 1993a, b); their increase in abundance was mostly likely a function of redistribution. The causes of the large increase in anchovy abundance are more complex. Here we provide clues from empirical data that may shed light on the most recent anchovy boom in the northeast Pacific Ocean.

Houde (2008) referred to the cumulative sum of mechanisms occurring from egg development to recruitment as an "integrative process," whereby no single mechanism consistently controls recruitment strength. Instead, it is important to appreciate the many mechanisms working in concert to deliver recruitment strength for a given year. Mechanisms spanning the pre-fertilization to initial feeding transition have been recognized to coarsely influence recruitment strength (Houde 2016), and when modulated by a concomitant positive late-larval to juvenile stage survival (Peterman & Bradford 1987, Peterman et al. 1988, Baumann et al. 2006), have the potential to lift a population out of a multi-year low. Our approach to elucidating drivers of the recent anchovy boom in the CCE was to evaluate the condition of the fish at hatch and between 10 and 55 days of age to determine if this could explain recruitment variability. In addition, we attempt to tie larval condition to the oceanographic conditions in which larvae were collected.

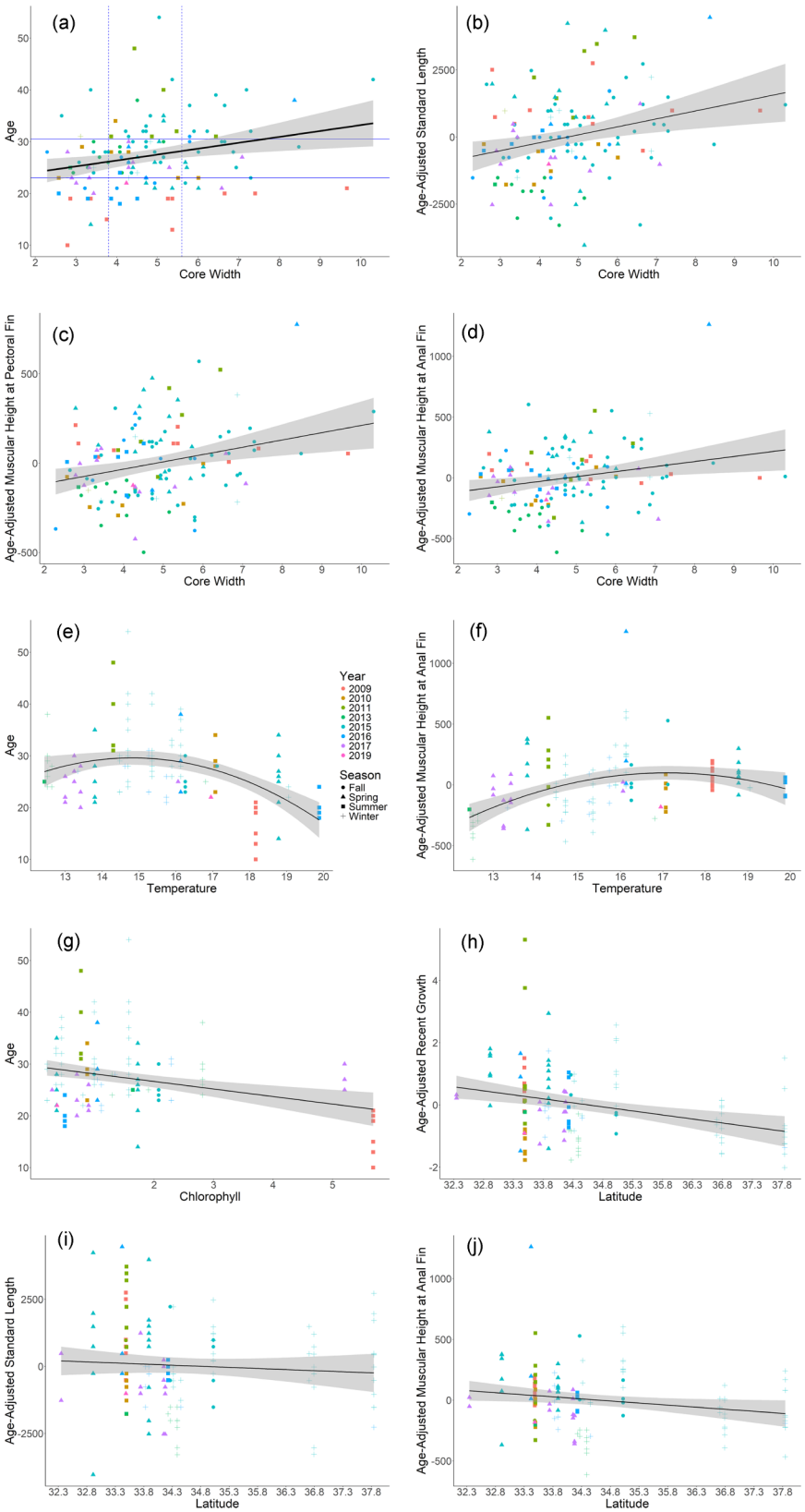


**Figure 3** Univariate relationships between indices of larval condition and core width (μm)/environment that were significant in the Generalized Linear Mixed Models (Table 2). a. Core width vs. age (days) with dashed vertical lines depicting 25$^{th}$ and 75$^{th}$ quantile of core width and solid lines of age. b. Temperature (°C) vs. age. c. Chlorophyll *a* vs. age, d. Latitude (decimal degrees) vs. Age-Adjusted Recent Growth (μm). e. Core vs. Age-Adjusted Standard Length (μm), f. Latitude vs. Age-Adjusted Standard Length (μm), g. Core vs. Age-Adjusted Muscular Height at the Pectoral Fin (μm). h. Core vs. Age-Adjusted Musculature Height at the Anal Fin (μm). i. Temperature vs. Age-Adjusted Muscular Height at the Anal Fin. j. Latitude Versus Age-Adjusted Musculature Height at the Anal Fin.

**Table 3.** Generalized linear mixed model results comparing larval anchovy attributes between pairs of years within seasons. Figure 4 is the accompanying plot.

| | | winter | | | |
|---|---|---|---|---|---|
| **Variable** | **Comparison** | **Estimate** | **Std error** | **z value** | ***P*** |
| Age | 2013 vs. 2015 | 0.28 | 0.16 | 1.70 | 0.09 |
| | 2013 vs. 2016 | −0.22 | 0.21 | −1.04 | 0.30 |
| Core width | 2013 vs. 2015 | **0.50** | **0.17** | **2.97** | **0.003** |
| | 2013 vs. 2016 | 0.16 | 0.21 | 0.73 | 0.46 |
| Age-adjusted final ring width | 2013 vs. 2015 | **0.51** | **0.22** | **2.26** | **0.02** |
| | 2013 vs. 2016 | 0.39 | 0.26 | 1.47 | 0.14 |
| Age-adjusted body length | 2013 vs. 2015 | **0.81** | **0.15** | **5.44** | **0.0 000 001** |
| | 2013 vs. 2016 | **0.52** | **0.19** | **2.67** | **0.01** |
| Age-adjusted pectoral depth | 2013 vs. 2015 | **0.57** | **0.20** | **2.81** | **0.01** |
| | 2013 vs. 2016 | 0.26 | 0.25 | 1.06 | 0.29 |
| Age-adjusted anal depth | 2013 vs. 2015 | **0.75** | **0.21** | **3.65** | **0.0003** |
| | 2013 vs. 2016 | 0.43 | 0.24 | 1.76 | 0.08 |
| Age | 2015 vs. 2016 | **−0.47** | **0.17** | **−2.79** | **0.01** |
| Core width | 2015 vs. 2016 | **−0.34** | **0.18** | **−1.87** | **0.06** |
| Age-adjusted final ring width | 2015 vs. 2016 | −0.13 | 0.22 | −0.60 | 0.55 |
| Age-adjusted body length | 2015 vs. 2016 | −0.33 | 0.19 | −1.71 | 0.09 |
| Age-adjusted pectoral depth | 2015 vs. 2016 | −0.34 | 0.22 | −1.53 | 0.13 |
| Age-adjusted anal depth | 2015 vs. 2016 | −0.37 | 0.22 | −1.67 | 0.09 |
| | | spring | | | |
| Variable | comparison | estimate | std error | z value | *P* |
| age | 2015 vs. 2017 | −0.093 | 0.19 | −0.49 | 0.622 |
| Core width | 2015 vs. 2017 | −0.249 | 0.18 | −1.35 | 0.176 |
| Age-adjusted final ring width | 2015 vs. 2017 | **−0.558** | **0.16** | **−3.56** | **0.0004** |
| Age-adjusted body length | 2015 vs. 2017 | −0.339 | 0.18 | −1.90 | 0.057 |
| Age-adjusted pectoral depth | 2015 vs. 2017 | **−0.577** | **0.22** | **−2.63** | **0.009** |
| Age-adjusted anal depth | 2015 vs. 2017 | **−0.496** | **0.16** | **−3.02** | **0.0026** |

## Maternal effects

We found that anchovy larvae with larger otolith cores (i.e. those hatched at larger sizes) experienced increased early survival and that recruitment was higher in years when larvae were born large. Previous work demonstrated that maternal effects influenced early survival in fish as larger and/or older females produced larger and/or better provisioned larvae that were more likely to get through vulnerable early life stages (Berkeley et al. 2004, Hixon et al. 2014). This initial work largely focused on fishes that grow to be relatively large and live for decades. For example, Hixon et al. (2014) called for the conservation of "big old fat female" (BOFF) rockfishes that may disproportionately contribute to strong recruitment classes and ensure population viability. In addition, maternal provisioning was recently shown to impact larval growth potential in large and long-lived Atlantic bluefin tuna (*Thunnus thynnus*) in the Gulf of Mexico (Quintanilla et al. 2024). Here, we provide evidence that maternal provisioning may affect larval survival of a small, short-lived fish.

Our findings suggest that maternal impacts can affect the viability of anchovy larvae, a relatively small (maximal length is rarely greater than 18 cm; (Kuriyama et al. 2022)), and short-lived fish (adults older than four years are rare (Sydeman et al. 2020)). In addition to our work, size-at- parturition was recently found to affect the condition of rockfish larvae in the CCE from 1997–2013 (Fennie et al. 2024). The life history of adult rockfishes run the gamut from species that resemble CPF and are small and short lived to those that are apex predators and can live over a hundred years (Love et al. 2002). Adult life history, however, did not determine if maternal effects were manifest, as larval size-at- parturition was positively correlated with growth rate at the time of capture for both small (*Sebastes jordani*, *S. serranoides* and *S. wilsoni*) and large (*S. paucispinis* and *S. rufus*) rockfishes (Fennie et al. 2023). Further, Garrido et al. (2015) found that survival of another relatively small fish, European sardine (*Sardina pilchardus*) was positively correlated with size-at-hatch both in a hatchery and in the ocean. Collectively, these recent findings suggest that maternal effects may generally be an important factor impacting the survival of marine fishes with myriad life histories.

## Growth-survival paradigm

Fisheries oceanographers have been attempting to understand the mechanisms governing recruitment dynamics for over a century. These efforts have produced many hypotheses including the

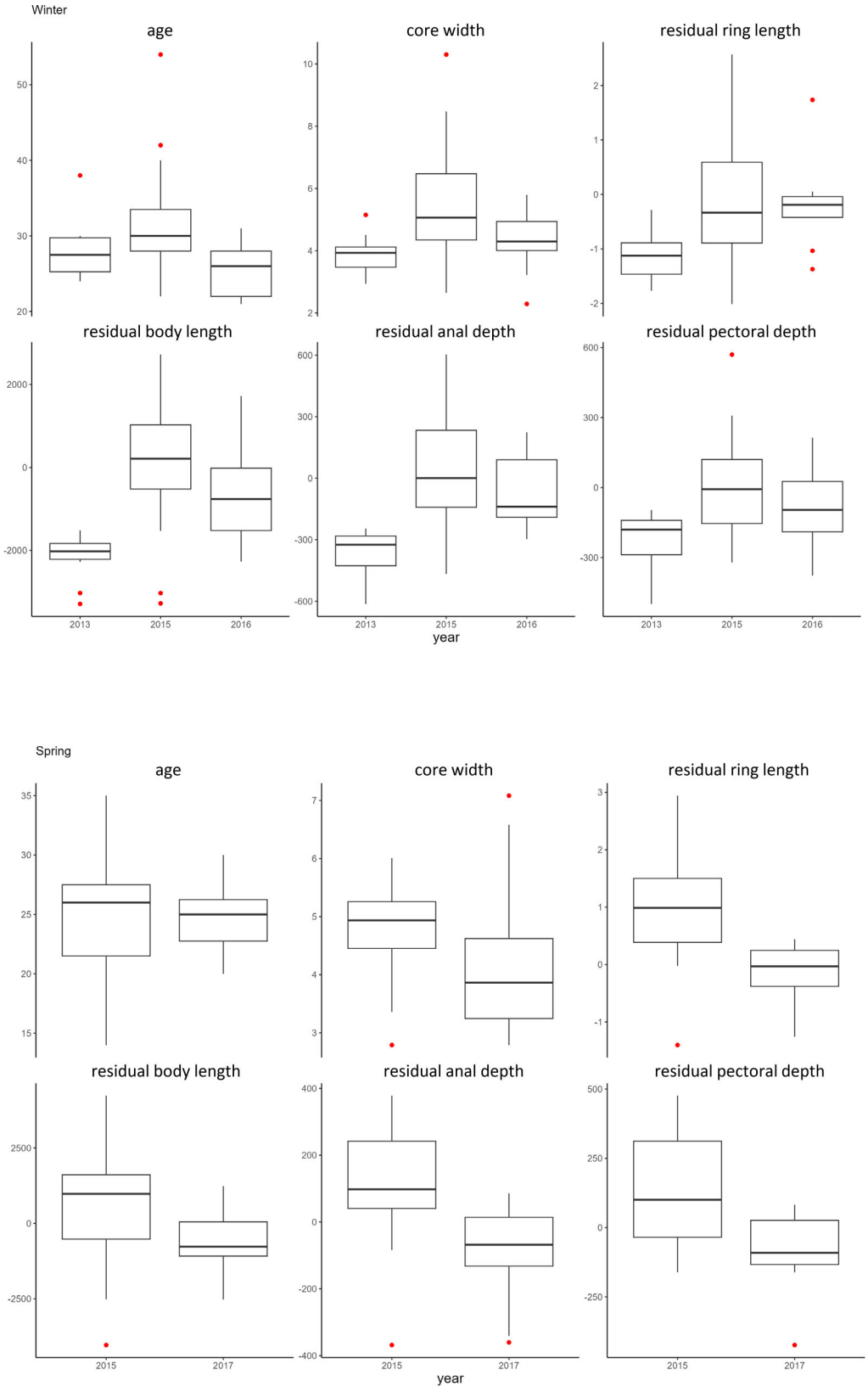


**Figure 4** Box and whisker plots showing indices of larval conditions in winter (top) and spring (bottom) in years with variable per capita recruitment. The thick horizontal line depicts the median, the lighter horizontal upper line the 75 quartile and the lighter horizontal line the lower 25$^{th}$ quantile. The whiskers (vertical lines) depict 1.5$*$ the distance between the 75$^{th}$ and 25$^{th}$ quantile. Points are measurements lower or higher than the outer range of the whiskers. Units for age are in days and the rest are μm.

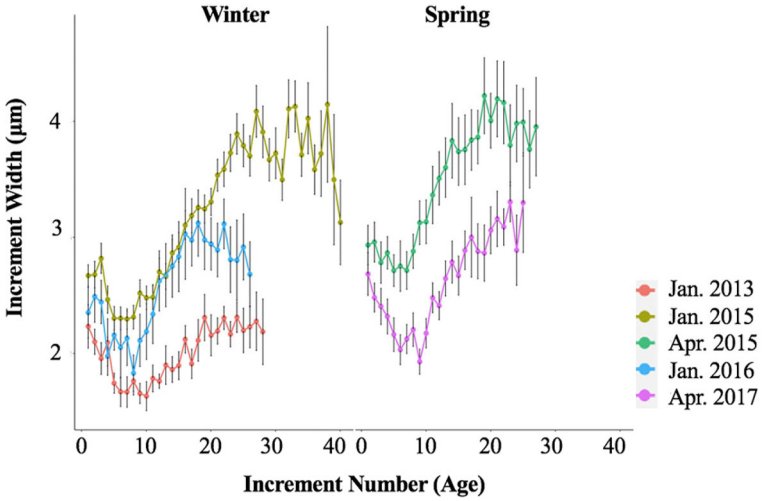


**Figure 5** Growth trajectories across the lifespan of anchovy larvae in years with different per capita recruitment. Mean increment width at age (± 95% confidence interval) in winter 2015 (high recruitment year), winter 2016 (medium recruitment), winter 2013 (low recruitment), spring 2015 (high recruitment) and spring 2017 (medium recruitment).

critical period (Hjort 1914), match-mismatch (Cushing 1990), stable ocean (Lasker 1978), and trophic efficiency in early life (TEEL; Swalethorp et al. 2023) hypotheses. While focusing on different aspects of the life-experience of a larval fish, they are all underpinned on the notion that larvae need to obtain adequate nutrition to avoid incurring negative impacts on physiological condition that would make them vulnerable to starvation or predation. This idea aligns with the Growth-Survival Paradigm (GSP) which postulates that fast-growing larvae are more likely to survive to an "endpoint" where the probability of mortality decreases to a level similar to the adult life stage (Robert et al. 2023). The main rationale behind the GSP is that a larva is more likely to become a recruit if it gets through early life quickly, when mortality rate per day can approach 80% (Pepin & Marshall 2016). In a recent literature review and modeling study, however, Robert et al. (2023) found that approximately 25% of studies in marine systems found no evidence for the GSP and that in some cases slow-growing larvae were more likely to survive to the endpoint (e.g. Fuiman 1989, Litvak and Leggett 1992, Pepin et al. 1992). Thus, the GSP is probably context-dependent.

Our work firmly supported the GSP for anchovy between 2009 and 2019 in central and southern California. In 2015, per capita larval survival was by far the highest since the time series began in 1965 (Hinchliffe et al. 2025). Furthermore, both growth rates and age-adjusted larval condition were highest in 2015 when per capita recruitment was very high, and lowest in 2013 when recruitment was also low. Condition and growth rate tended to be moderate in 2016 and 2017 when recruitment was higher than 2009 but lower than 2015. In the northern CCE, the GSP was also supported off Oregon (Takahashi et al. 2012). Here, 2005 upwelling was long delayed, productivity was low, anchovy larvae grew slowly and recruitment was low. By contrast, upwelling was normal in 2006, larvae grew faster, and recruitment was higher (Takahashi et al. 2012). More recently, Swieca et al. (2025) found that anchovy larvae off Oregon grew faster within upwelling fronts where copepods were moderately abundant, but the location of the upwelling fronts and overall growth rates varied among years.

Notably, the Maternal Effects hypothesis and GSP are entirely compatible. Several studies have shown that daily somatic growth rates are autocorrelated in larval fish from species such as Atlantic mackerel *Scomber scombrus*, radiated shammy *Ulvaria subbifurcata*, and capelin *Mallotus villosus* (Robert et al. 2014a, Dower et al. 2009, Pepin et al. 2014, Murphy et al. 2018). This means that, for example, if a larva was growing faster than average on day 5, it also grew at an accelerated rate on day 15. Our finding that core width (i.e. size-at-hatch) correlates with survival and body condition at the time of capture strongly suggests that pre-hatch processes resonate through the life of a larval fish. Larvae that are hatched large likely have a better chance to consume prey at first feeding when the yolk sac is absorbed, and this enhanced condition may propagate to the endpoint in agreement with the GSP. When larvae are large at hatch, they may also possess the capability to be more selective in their feeding and target more nutritious prey (Walsh et al. 2024). Assessing multiple hypotheses that attempt to explain CPF recruitment in concert has the potential to provide more explanatory power than focusing on just one hypothesis at a time (Hare 2014).

## Oceanographic experience

Anchovy recruitment in the CCE between 2009 and 2019 was higher in years when larvae were growing faster and were more robust, but what environmental conditions facilitated this phenomenon? We found that maximal age and/or growth rate occurred at locations with intermediate temperatures (15–17°C) and lower chlorophyll. This conceptually agrees with past work in the CCE suggesting that larval northern anchovy survival is highest under "moderate" ocean conditions when there is adequate larval prey but the ocean is not so turbulent that it is exceedingly difficult to catch prey (Lasker 1985, Peterman and Bradford 1987, Cury & Roy 1989). Empirical studies in the northern CCE also found relationships between upwelling and larval survival. Takahashi et al. (2012) showed that larval anchovy growth was suppressed off Oregon when upwelling was

very low but individuals grew faster when upwelling began later in the year, and Litz et al. (2008) demonstrated that anchovy year class strength was positively correlated with copepod abundance. From a modeling perspective, higher anchovy population growth was associated with higher per-capita egg production fueled by higher prey availability for age 1 fish (Fiechter et al. 2015). Overall, it appears that in the CCE relatively calm oceanographic conditions coupled with adequate prey foster higher recruitment.

We also found that larvae tended to be in better condition in the southern part of the sampling region in a manner not explained purely by the oceanographic parameters we analyzed. The idea that anchovy population dynamics may be fueled by recruitment in southern rather than central or northern California was supported by midwater trawl surveys that provide the only consistent empirical time series of young of the year anchovy in the CCE (Sakuma et al. 2016, Thompson et al. 2019). In 2015, anchovy young of the year (recruit) abundance jumped abruptly in southern, central and northern California (Thompson et al. 2019). From 2016–2019, recruitment remained very high in southern California but dropped off in central and northern California (Thompson et al. 2019). By contrast, adult anchovy abundance was higher north of Point Conception from 2017–2021 (Thompson et al. 2024), suggesting that southern California may be a hotbed of recruitment while adults may disperse north with age where feeding conditions may be better. Tran et al. (2025) also found support for the idea that southern California is particularly important for anchovy recovery from bust to boom periods. They showed that the geographic extent of anchovy distribution increased with abundance in line with MacCall's Basin Model (MacCall 1990) and that when populations collapsed, they remained at low levels in southern California and that when population sized increased, the population expanded out of southern California. Another possibility for higher recruitment in the south is that larvae in the north may experience higher mortality due to cannibalism of eggs and larvae as adult density can be higher in the north (MacCall 1990). Southern California thus seems to provide important habitat in a way that was not fully captured by our analysis, and future work should strive to identify the environmental features that support high anchovy recruitment in southern California.

Globally, there has been substantial research seeking to discern the oceanographic conditions that drive anchovy recruitment both within Eastern Boundary Upwelling Systems (EBUS; California, Humboldt (*E. ringens*), Benguela (*E. capensis*) and Canary (*E. encrasicolus*) Currents) and outside of EBUS (e.g. Europe, Japan, Australia) (Checkley et al. 2017) . Conditions that favor higher recruitment (adequate prey, a relatively calm ocean and larval retention) seem to overlap among EBUS and align with our study. For example, *E. ringens* in the Humboldt Current had high recruitment in years with moderate winds (Artega et al. 2024), *E. capensis* larval survival in the Benguela Current was predicted to be higher when moderate upwelling fueled primary and secondary production but was not so severe that larvae were advected offshore (Mullon et al. 2002, Lett et al. 2006), and in the Canary Current, moderate upwelling and mesoscale retention favored *E. encrasicolus* recruitment (Brochier et al. 2009a, 2009b). In non-EBUS, anchovy recruitment seems to be associated with moderate warming, seasonal stratification, and retentive circulation features, rather than specifically with wind-driven upwelling. For example, stability and recruitment of *E. encrasicolus* in the Bay of Biscay was linked to stratified spawning habitats and off-shelf transport (Motos et al. 1996, Irigoien et al. 2008), Japanese anchovy (*E. japonicus*) recruitment was predicted to correlate with temperature and rates of larval growth (Xing et al. 2021) in the Yellow Sea (Xing et al. 2021), and Australian anchovy (*E. australis*) recruitment reflected cross-shelf transport and retention dynamics (Dimmlich et al. 2004; Condie et al. 2011). Further research is needed to understand anchovy population dynamics at a global scale.

## Future research

We found that size at birth and fast growth in early life contributed to recruitment success in northern anchovy in the CCE between 2009 and 2019. However, we recognize that this is one piece of the puzzle that may help us understand drivers of recruitment dynamics of anchovy in the CCE. To better unravel the mechanisms that impact fish populations in the CCE we are following several paths of inquiry.

Although we did not have data on potential larval predators, it is important to note that variability in the predator field can have a substantial impact on larval mortality and recruitment. For example, Akinora Takasuka and colleagues demonstrated that while faster-growing anchovy larvae were more likely to survive overall, there were important exceptions (Takasuka et al. 2003, 2007, 2017). Specifically, when raptorial predators were abundant, faster-growing larvae that were more active were selectively consumed. By contrast, when filter-feeding predators were prevalent, the less active, slower growing larvae were more likely to be consumed (Takasuka et al. 2004). Research in the CCE also provided insight on the role of predation on larval fish survival. Using video equipment towed behind a research vessel, Swieca et al. (2025) found that northern anchovy larvae growth rate was positively correlated with the abundance of gelatinous predators off Oregon, likely because slower-growing individuals incurred higher rates of predation. In addition, European anchovy recruitment correlated negatively with the abundance of adult European sardine as egg and larval predation by sardine may have curtailed anchovy survival in early life (Ferreira et al. 2024). To gain a more complete picture of the conditions that facilitated high anchovy recruitment in the CCE it will be necessary to better account for shifting predator assemblages. In the near future, we are planning to deploy autonomous gliders with optical capabilities in conjunction with CalCOFI sampling to better observe the interaction of larval with their predators.

Another need is to better understand how the larval prey field and environmental variability impact anchovy recruitment. In addition to the upcoming glider work, which has the potential to directly observe larval prey *in situ*, we are planning to conduct compound-specific stable isotope analysis (CSSIA) on the larvae that were analyzed in this study. Swalethorp et al. (2023) found that anchovy spawning stock biomass was higher between 1960 and 2005 in years when larvae fed on prey that were at low trophic level. This study postulated that consuming lower trophic level prey facilitates efficient energy transfer and optimizes growth. Discerning whether larvae in recent high recruitment years (2015-present) again fed on low trophic position prey will be an impor-

tant step towards more fully understanding drivers of anchovy recruitment.

We are also building on Individual Based Models that previously modeled anchovy dynamics in the CCE from 1959–2008 (Fiechter et al. 2015). These results should provide better insight on the environmental conditions that correlated with the rise in anchovy over the past decade and inform whether the recent oceanographic parameters were similar or different from past years when anchovy were high in the CCE.

In addition, we are planning to conduct a thorough analysis to correlate the recently developed indices of anchovy recruitment with environmental drivers. Hinchliffe et al. (2025) synthesized multiple anchovy time series in the CCE to produce the first long-term quantitative estimates of anchovy SSB and recruitment in this marine ecosystem. This data can serve as a dependent variable to discern the independent oceanographic variables that may affect overall anchovy abundance in the CCE over six decades. Here, we will include several covariates (e.g. habitat compression, upwelling, basin scale conditions) that we were not able to use in this paper due to the relatively small sample size of our data.

Perhaps the single most valuable piece of information that can further understanding of the conditions that facilitate recruitment failure or success for fishes in the CCE may come from our recent capability to detect the presence of life in the ocean with environmental DNA (eDNA; (Satterthwaite et al.2023). Recent improvements in genetics technology have enabled us to identify every component of life that deposits DNA in a parcel of water. Because all life on earth contains DNA, and life is constantly sloughing parts of itself into the environment, we can track, at least to some degree, every organism that has been in contact with the larval fish we are sampling. This tool has great potential to enable us to discern which predators and prey interact with the larval fish *in situ*. CalCOFI has been conducting eDNA sampling since 2014 (James et al. 2022), and there is great potential to use this new data to better inform the biological oceanographic conditions that impact fish recruitment.

Finally, our results suggest that maternal condition affected larval quality at hatch and in early life. In another regular survey out of the Southwest Fisheries Science Center, NOAA has been collecting and freezing adult anchovy in the CCE during approximately the past two decades (Zwolinski and Demer 2012). A careful examination of these adults could discern if gravid females were in better condition during high recruitment years.

# Conclusion

In the 2014 ICES Journal of Marine Science Special Issue: 'Commemorating 100 years since Hjort's 1914 treatise on fluctuations in the great fisheries of northern Europe' Jonathan Hare contributed a paper titled: 'The future of fisheries oceanography lies in the pursuit of multiple hypotheses' (Hare 2014). We wholeheartedly agree with this sentiment and hope that this paper provides one of multiple inquiries into the grand attempt to finally and truly elucidate the mechanisms that caused anchovy abundance to increased exponentially in the California Current Ecosystem between 2009 and at least 2026.

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# Author contributions

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# Supplementary material

Supplementary material is available at *ICES Journal of Marine Science* online.

## Conflicts of interest

There is no conflict of interest involved with this manuscript.

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## Data availability

All data analyzed for this study is publicly available on Dryad.

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