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Momma's larvae: Maternal oceanographic experience and larval size influence early survival of rockfishes

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Abstract

Identifying factors that affect larval mortality is critical for understanding the drivers of fish population dynamics. Although larval fish mortality is high, small changes in mortality rates can lead to large changes in recruitment. Recent studies suggest maternal provisioning can dramatically affect the susceptibility of larvae to starvation and predation, the major sources of early-life mortality. We measured otolith core width-at-extrusion and validated that this is a proxy for larval size-at-extrusion for eight species of rockfishes (genus *Sebastes*) to examine the influence of initial larval size on larval growth and survival and to understand how oceanographic conditions experienced by gestating females affect larval size (i.e., quality). Otolith core width-at-extrusion was significantly positively related to larval rockfish recent growth rate (5/7 species with sufficient sample size) and survival (all eight species). This suggests that individuals that are larger at extrusion generally grow faster and are more likely to survive early life stages. Otolith core width-at-extrusion was positively related to higher presence of Pacific Subarctic Upper Water and was negatively related to warmer, saline waters at the depths gestating mothers inhabited during the months prior to larval collection. In addition, otolith core width was larger further from fishing ports, possibly because these locations were historically less fished, contained more older, larger females, and/or had inherently better habitat quality (higher Pacific Subarctic Upper Water) than sites closer to shore. These results indicate that the

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environmental conditions female rockfish experience during gestation drive the size of the larvae they produce and impact larval growth and survival.

KEYWORDS

fish early life history, larval growth, larval quality, larval survival, maternal effects, *Sebastes*

1 | INTRODUCTION

Elucidating the mechanisms driving fish population fluctuations is a fundamental issue in fisheries science. Hjort (1914) laid the foundation of fisheries science by hypothesizing that fish population dynamics were driven by larval survival during the first few days of life. Mortality is high during this early period, but small changes to survival in early life can lead to large changes in juvenile abundance (i.e., recruitment; Houde, 1987). Numerous studies have attempted to explain recruitment drivers by examining how larval survival is impacted by processes such as advection (Hjort, 1926; Iles & Sinclair, 1982), starvation (Cushing, 1990; Lasker & Zweifel, 1978), and predation (Bailey & Houde, 1989). With over a century of research on drivers of recruitment variability, predation and/or starvation during the early life stages are considered important regulators of recruitment variability (Bailey & Houde, 1989; Hare, 2014; Houde, 2008). However, discerning the mechanism that allows some larvae to evade mortality has proven to be exceedingly difficult (Hare, 2014).

The importance of predation and starvation in governing early survival led to a focus on how early life history traits underpin year class strength. Within species, it has been hypothesized that individual larvae that are relatively large (Anderson, 1988; Miller et al., 1988), fast-growing (Meekan & Fortier, 1996; Takasuka et al., 2004), and develop more rapidly (Chambers & Leggett, 1987; Houde, 1987) should experience reduced predation and starvation and are more likely to survive the larval stage and recruit to the adult population. Prey quality and availability during the larval stage are important factors that affect growth, morphological condition, and predator encounter rates (Robert et al., 2014). When eggs and larvae are released, a combination of favorable abiotic and biotic conditions must interact to support traits that increase survival during these vulnerable early life stages and lead to high recruitment. Although most classical recruitment theories focus on the conditions encountered by larvae, it is possible that endogenous factors occurring before hatch affect early life history traits and survival (Hare, 2014; Schroeder et al., 2018).

Parental effects can influence a variety of larval fish characteristics and impact early survival (Arnold et al., 2018; Green, 2008; Grønkvær & Schytte, 1999; Meekan & Fortier, 1996). Maternal effects regulate egg size (Chambers & Leggett, 1996), oil globule size (Sogard et al., 2008), larval size-at-hatch (Heath et al., 1999), and they are associated with embryonic metabolic rate (Bang et al., 2006). Recently, it has been shown that otolith core width is an indicator of larvae size-at-hatch, and being born large is an indicator of larval

metabolic rate, growth, and survival through the larval period (Garrido et al., 2015; Grønkvær & Schytte, 1999; Meekan & Fortier, 1996). Maternal size or age can also determine the timing of reproduction and the quality of larvae produced. For example, older and larger females may produce eggs or larvae earlier in the reproductive season and provide higher lipid reserves to their embryos, leading to increased larval survival (Berkeley et al., 2004; Hixon et al., 2014; Sogard et al., 2008). Additionally, maternal environmental experience can determine egg size (Johnston & Leggett, 2002), with important consequences for larval size and survival (Chambers & Leggett, 1996; Garrido et al., 2015). Determining how maternal investment affects the early life history traits of larvae may improve our ability to understand fish population dynamics.

Rockfishes (genus *Sebastes*) are a group of economically and ecologically important groundfishes found mainly along the US west coast in the California Current Large Marine Ecosystem (CCLME; Love et al., 2002). The CCLME is characterized by highly dynamic seasonal and interannual oceanographic conditions (Checkley & Barth, 2009). Life history strategies of different rockfish species are highly variable, as some (e.g., shortbelly rockfish, *Sebastes jordani*) mature quickly (99% mature at age 3) and live short lives (95% less than 12 years; Field et al., 2007), while others (e.g., bank rockfish, *Sebastes rufus*) mature slowly (>10 years) and can live a long time (80 years; Love et al., 2002). Despite their different life histories, all rockfish species have internal fertilization of eggs and are live bearers with eggs that hatch internally before larvae are extruded (Love et al., 2002). The combination of highly variable oceanographic conditions (Hollowed et al., 1987) and high early mortality (Bailey & Houde, 1989), despite high reproductive output (Love et al., 2002), typically leads to low recruitment, which was particularly concerning for the long-lived rockfish species that were severely overfished around the end of the 20th century (Butler et al., 2003; Love et al., 1998). In fact, initial stock assessments (e.g., Butler et al., 1998) estimated that it would take several decades for the overfished stocks to recover. However, the combination of strong management actions (e.g., limiting commercial/recreational catch, establishing marine protected areas [MPAs]) and high recruitment events (Zabel et al., 2011) led to the recovery of most species in less than 20 years (Field et al., 2010; Thompson et al., 2017). Strong recruitment is important to sustain rockfish populations (Warner & Chesson, 1985), and elucidating the drivers of early survival will improve our ability to effectively manage these species.

Rockfish exhibit strong influences of maternal investment on larval quality that may affect early survival. In some species, older and/or larger females reproduce earlier in the season and contribute more lipid reserves to their larvae (Berkeley et al., 2004; Rodgveller

et al., 2012; Sogard et al., 2008). Most rockfishes in southern California spawn during winter when primary production is relatively low and thus larvae need enhanced lipid reserves to survive the first few days until they successfully feed (2–12 days depending on species; Fisher et al., 2007). Previous work examining the drivers of early rockfish survival indicated that temperature and alongshore flow during winter affected the early survival of rockfish (Ralston et al., 2013; Laidig et al., 2007). Recent work examining the influence of deeper water masses, in light of anomalous surface warming in the CCLME, found increased pelagic juvenile rockfish abundance in years when the CCLME has a higher percentage of “minty” cold, nutrient-rich, oxygen-replete Pacific Subarctic Upper Water (PSUW) compared with “spicy” equatorial or subtropical water masses that are warm, salty, and low in oxygen (Schroeder et al., 2018). Similar to previous work, this recent study suggests that the oceanographic conditions females experience during gestation may play a major role in determining rockfish year class strength (Schroeder et al., 2018). While it is hypothesized that larvae with increased maternal investment that develop or were reared in favorable oceanographic conditions are more likely to survive, few studies have examined this in the field (but see Garrido et al., 2015).

Here, we analyzed time series of oceanographic conditions and early life history traits of eight larval rockfish species from winter California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises to examine the effects of maternal environmental experience on larval size, growth rate, and survival. Notably, five species are large as adults and targeted by human fishers, while the rest are diminutive and are either not targeted or not susceptible to fishing (Love et al., 2002; Thompson et al., 2017). We used otolith microstructure analysis to validate that otolith core width-at-extrusion is a proxy for larval size-at-extrusion and used this as a metric of maternal investment. We used physical oceanographic data from conductivity, temperature, and depth (CTD) casts to characterize the water masses female rockfish experienced during gestation and larval rockfish experienced upon extrusion. Our objectives were twofold: to use larval otolith characteristics to understand how oceanographic conditions contribute to maternal investment and to test whether maternal investment contributed to faster larval growth and higher survival.

2 | MATERIALS AND METHODS

2.1 | Sample collection

Rockfish larvae were collected during winter CalCOFI cruises from 1998 to 2013, as described in Thompson et al. (2017). Winter cruises take place in January–February, with the majority (72%–98%) of larval rockfish collected in January (Table 1). Bongo nets were deployed at fixed stations to 210 m and obliquely towed to the surface at a constant rate (Kramer, 1972; Figure 1). Plankton from the port-side net was initially preserved in 95% ethanol and changed to fresh 95% ethanol after 24 h. In the laboratory, rockfish larvae were sorted and enumerated from stations over the continental shelf (inside the yellow polygon in Figure 1). Because most rockfish larvae are not morphologically distinguishable to the species level, the mitochondrial cytochrome b gene was sequenced from each individual larva using DNA extracted from rockfish tissue (see Thompson et al., 2017 for details on sequencing), and identities were determined by comparing larval sequences to reference sequences from adults (Hyde & Vetter, 2007). After sequencing, larvae were stored individually in vials filled with 100% ethanol.

2.2 | Rockfish early life history trait measurement

We focused our analysis on eight rockfish species found throughout the Southern California Bight. Five of the species are commercially/recreationally fished (*Sebastes goodei*, *S. mystinus*, *S. paucispinis*, *S. rufus*, and *S. serranoides*) and three are non-targeted (*S. hopkinsi*, *S. jordani*, and *S. wilsoni*), although these non-target species are occasionally caught as bycatch in other fisheries. Additionally, these species vary in longevity, timing of maturity, size, and adult depth range (Table 1). Four species (*S. hopkinsi*, *S. mystinus*, *S. serranoides*, and *S. wilsoni*) have relatively shallow depth ranges, and the other four have relatively deeper ranges (*S. goodei*, *S. jordani*, *S. paucispinis*, and *S. rufus*), which may influence the strength of the influence of minty PSUW and spicy water masses on maternal habitat. A total of 5475 individuals from all eight target species were collected between 1998 and 2013. Of those, 2021 were selected for otolith extraction

TABLE 1 Rockfish life history characteristics based on information from Love et al. (2002) and Love et al. (2009). * *Sebastes paucispinis* age at maturity was not reported so length at maturity is presented in cm. There was no information on age or length at maturity for *Sebastes wilsoni*.

Species	Max age (years)	Max length (cm)	Age at maturity (years)	Depth range (m)	Fishing pressure	Targeted
<i>Sebastes goodei</i>	35	59	3–7	90–250	High	Yes
<i>Sebastes hopkinsi</i>	19	29	3–7	30–150	Low	No
<i>Sebastes jordani</i>	32	35	2–5	200–300	Low	No
<i>Sebastes mystinus</i>	44	53	4–11	0–90	High	Yes
<i>Sebastes paucispinis</i>	40+	91	36–44 cm*	50–250	High	Yes
<i>Sebastes rufus</i>	85+	55	10–20+	130–360	High	Yes
<i>Sebastes serranoides</i>	30+	61	3–8	0–120	Moderate	Yes
<i>Sebastes wilsoni</i>	26	23	NA	60–150	None	No

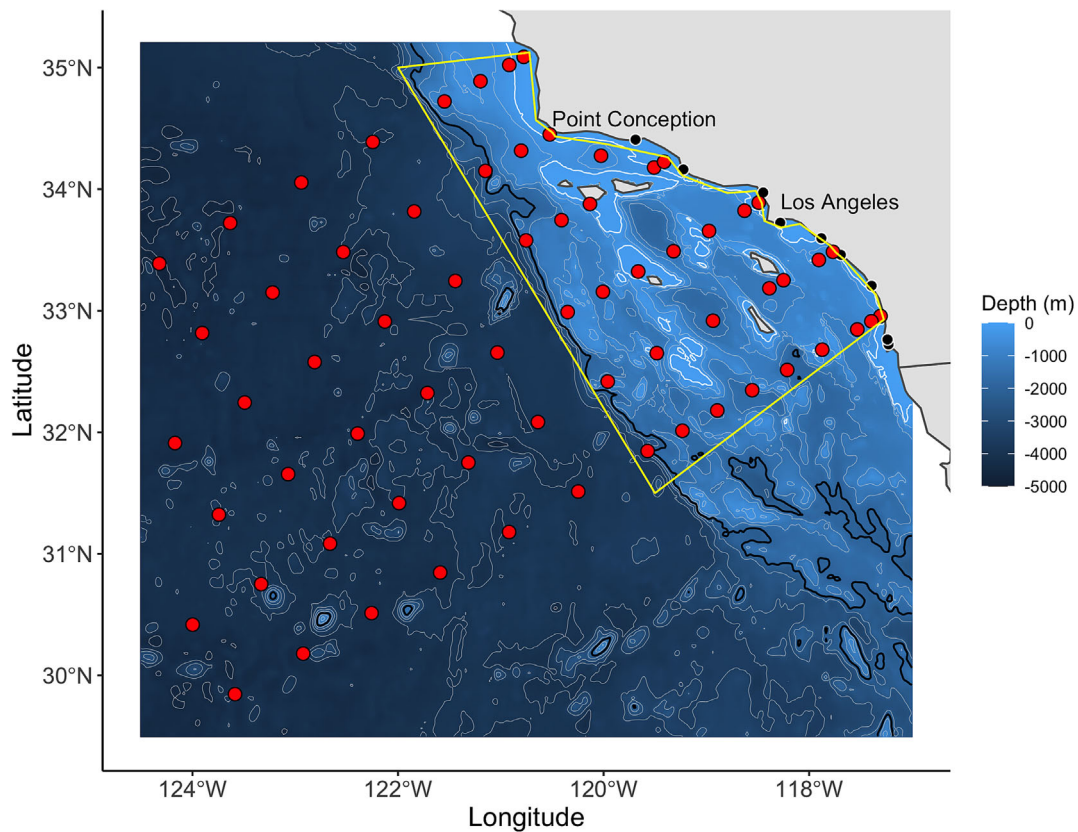


FIGURE 1 Map of sampling area in the Southern California Bight. Red circles indicate the location of California Cooperative Oceanic Fisheries Investigations (CalCOFI) stations for larval fish collection and CTD casts. The yellow polygon encompasses the larval rockfish collection area. Fishing ports are denoted by the black circles. The 200 m isobath is highlighted in white and the 2000 m isobath is highlighted in black.

(a maximum of 20 larvae from each species at a given station per year). Larvae were placed in a drop of deionized water on a microscope slide under a dissecting microscope, and the total length was measured. Sagittal otoliths were then extracted from each fish using micro-forceps and insect mounting pins. The otoliths were affixed whole to microscope slides with a drop of clear fingernail polish. Polishing was not necessary, as intact otoliths from larvae (<20 mm total length) had discernable growth increments with no further preparation.

Otoliths were photographed using a DSLR camera (Nikon D7000) mounted to a compound microscope (Leica DMLB) at 1000 \times magnification. Images were analyzed in R using the *RFishBC* package (v0.2.4; Ogle, 2022). This package facilitates measuring otolith increment widths and estimating ages by applying a known scale to defined measurements made on collected images. Otolith images were batched and analyzed by year and species. Otolith core width-at-extrusion (hereafter otolith core width) was measured from the center of the core to the postrostral edge of the extrusion check (a mark in the otolith that forms when the larva is released from the mother). Ages were obtained by increment counts beginning at the first growth increment after the extrusion check. For quality control, a randomized subsample of images was examined by an experienced reader twice, with an extended time interval between reads. If age estimates differed between the first two reads, the otolith photographs were examined

for the third time. Samples were not used in further analyses if the third reading did not agree with one of the first two. Of the 2021 otoliths aged, 1502 had agreement between reads, and 1443 were used for this study (three individuals were collected in offshore stations outside of the region of study and 56 were collected at stations where CTD casts were not performed; Table 2). Growth increments were not validated during this study. However, these counts were assumed to correspond to daily ages because the formation of daily growth increments has been validated for several of these species, including *S. jordani* (Laidig et al., 1991), *S. paucispinis*, and *S. goodei* (Woodbury & Ralston, 1991).

2.3 | Oceanographic conditions and source-water analysis

We gathered a suite of oceanographic data from basin, regional, and station scales to characterize the oceanographic conditions pregnant female rockfishes and larval rockfishes experienced. Based on previous work (Chelton et al., 1982), we hypothesized that the conditions females experience may play an important role in determining larval quality. At the basin scale, we included the Pacific Decadal Oscillation (PDO), a measure of low-frequency sea surface temperature variability throughout the northeast Pacific, the Ocean Niño Index (ONI),

TABLE 2 Sample size, otolith characteristics, percent collected in January and February, adult depth range, and larval age range of the eight rockfish species.

Species	n	Mean core width (μm) \pm SD	Mean first increment width (μm) \pm SD	January (%)	February (%)	Adult depth (m)	Age range (days; min, mean \pm SD, max)
<i>Sebastes goodei</i>	85	16.2 (\pm 1.86)	1.38 (\pm .60)	90.2	9.8	75–250	1, 4.3 \pm 3.8, 16
<i>Sebastes hopkinsi</i>	332	15.2 (\pm 2.2)	1.26 (\pm .37)	75.8	24.2	30–150	1, 4.0 \pm 4.2, 22
<i>Sebastes jordani</i>	276	17.1 (\pm 2.42)	1.29 (\pm .35)	80.9	19.1	200–400	1, 4.1 \pm 4.2, 21
<i>Sebastes mystinus</i>	160	13.1 (\pm 2.23)	1.47 (\pm 1.05)	97.6	2.4	0–90	1, 1.6 \pm 1.7, 13
<i>Sebastes paucispinis</i>	161	15 (\pm 2.54)	1.41 (\pm .50)	89.2	10.8	50–250	1, 2.9 \pm 3.5, 22
<i>Sebastes rufus</i>	142	14.3 (\pm 1.8)	1.22 (\pm .40)	71.7	28.3	130–360	1, 3.1 \pm 3.1, 16
<i>Sebastes serranoides</i>	92	14.8 (\pm 2.19)	1.23 (\pm .43)	88.2	11.8	0–100	1, 2.2 \pm 2.3, 14
<i>Sebastes wilsoni</i>	195	14.4 (\pm 2.92)	1.3 (\pm .49)	81	19	60–150	1, 4.2 \pm 5.2, 24

which is based on equatorial upper water temperature and is an indicator of El Niño Southern Oscillation state, and the North Pacific Gyre Oscillation (NPGO), an index of the strength of equatorward flow of the California Current, vertical mixing, and surface salinity, nutrient, and chlorophyll concentrations in the southern CCLME (Di Lorenzo et al., 2008). Regional oceanographic variables included two measures of wind-driven upwelling intensity: the Biologically Effective Upwelling Transport Index (BEUTI; Jacox et al., 2018) at 33°N and meridional winds at 33.7°N and 119.1°W (from NOAA buoy 46025).

At the local scale of the CalCOFI stations where rockfish were collected, physical oceanographic data was sampled using a SBE 911plus CTD. The CTD profiler measures temperature, salinity, and several other parameters at 1-m intervals throughout to a depth of 515 m, bottom depth permitting. At each station, we calculated the distance to the nearest fishing port (also a proxy for distance to shore) and two indicators of the source waters contributing to water column characteristics: the PSUW fraction and Spiciness (Schroeder et al., 2018). Spiciness is a state variable and is derived from temperature and salinity, with lower spice values characteristic of cooler, fresher waters (Flament, 2002). The water-mass fraction at each CalCOFI station and in the upper 500 m was obtained from an optimal multiparameter (OMP) analysis of three water masses that comprise upper waters in the CCS (Bograd et al., 2019). Spiciness has been used to describe changes in interannual variability of rockfish recruitment as abundances of pelagic juveniles (the index of recruitment in stock assessments; e.g., He & Field, 2017) were higher for most species during years with low spiciness (Schroeder et al., 2018). An OMP analysis using CalCOFI hydrographic data starting in 1984 quantifies the mixing between PSUW, Eastern North Pacific Central Water (ENPCW), and Pacific Equatorial Water (PEW) water masses (Bograd et al., 2019). Of the three water masses used in the OMP analysis, PSUW is the water mass of subarctic origin that is advected into the CCE, with the greatest percentages occurring below 100 m. PSUW has the lowest spiciness values, and we used the PSUW fraction in our analyses. Spice and PSUW fractions have been calculated for all CalCOFI stations used in this study at 5 m depth intervals from the surface to 500 m. Profiles of spice and PSUW fraction were linearly interpolated on 1-m intervals, and values were extracted on

isopycnals $\sigma_\theta = 25.5, 25.8, 26.1, 26.5,$ and 26.8 kg/m^3 , covering depths ranging between 50 and 400 m. We report the PSUW fraction as a percentage (PSUW%) at a given time (season and year), station, and depth. The combination of all three water mass fractions (PSUW, ENPCW, and PEW) will be equal to 1. OMP analysis has been calculated for all quarterly CalCOFI surveys; however, for this study, only the fall and winter quarters are considered to align with rockfish gestation in the fall and larval rockfish early life in the winter.

2.4 | Data analysis

To determine whether the otolith core width provided a proxy for larval fish size-at-extrusion, as has been demonstrated in other species (Garrido et al., 2015), we used linear regression to examine the amount of variability in length of all one-day-old rockfish larvae explained by otolith core width. While we did not have immediately-extruded (Day 0) larvae available, we assumed that one-day-old larvae provided an accurate representation of larval length-at-extrusion.

We examined the relationship between timing of extrusion and otolith core width to determine if core size was influenced by when larvae were extruded, as there is evidence that older, larger females reproduce earlier in the reproductive season (Sogard et al., 2008). We used linear regression with the date of extrusion as our explanatory variable and core width as our response variable to test this relationship. Additionally, we tested whether the date of extrusion was correlated with age-at-capture (our proxy for survival) to see if larvae born earlier (possibly due to having older mothers or due to hatch date selection) were more likely to survive. In this analysis, we used linear regression with mean birthdate as our explanatory variable and age-at-collection as our response variable. For all of the above analyses, average traits (date of birth, core size, and age-at-collection) were calculated at each station in each year for each species.

We evaluated time series of annual, species-specific, average anomalies of larval rockfish early life history traits to determine if patterns of otolith core width, recent growth, and age-at-capture were consistent across species (Figure S1). A time series of life history trait anomalies was calculated by taking the spatial average of each trait at

all stations for each year and species, then subtracting a long-term mean of each trait from the annual values. We used Spearman's rank correlation to evaluate the degree of correlation among species for each life history trait (Figures S2–S4). Additionally, we plotted the spatially averaged otolith core width size across the entire time series at each station and for each species to explore the spatial patterns of variability in otolith core width (Figure 2).

Because we expected there to be interannual and spatial variability in maternal and larval oceanographic experience, we calculated the mean core width size for each species at each station in each year and used partial least squares regression (PLSR; Carrascal et al., 2009) analysis with a suite of basin scale, regional, and local oceanographic conditions to elucidate the environmental drivers of otolith core width size. We used PLSR because it is well suited to handling multiple correlated predictor variables (Carrascal et al., 2009). All environmental variables, except PSUW% and Spiciness, were averaged from September to December to capture the fall conditions adult female rockfish experienced while they were gestating. Fall PSUW% and Spiciness were calculated from fall CalCOFI hydrographic data and were calculated along isopycnal layers (25.5, 25.8, 26.1, 26.5, and 26.8) that were matched to the adult depth range of the different rockfish species.

PLSR was used to determine how oceanographic conditions and maternal investment contribute to the recent growth rate and survival of larval rockfish. Otolith increments increase with age, and because the larval fish collected varied in age, we accounted for this in our recent growth analyses by taking the residuals of the relationship between the mean increment width of the last two growth increments and age-at-collection for each larva. Age-at-collection was used as a proxy for larval survival because mortality is high during this early period; years with older mean ages indicate higher larval survival (Garrido et al., 2015). We included the same environmental variables as in the core width analysis but averaged these from January to February (winter CalCOFI hydrographic surveys for PSUW and Spice) to capture the conditions larval rockfish experienced during early life before collection on winter CalCOFI cruises. As larval rockfish are typically found in the upper 80 m (Moser & Boehlert, 1991), we used

PSUW% and Spiciness on the 25.8 isopycnal, which is approximately 60 m deep near shore and 90 m deep offshore. We also included the mean core width for each species at each station and year to examine the influence of larval size-at-extrusion on growth and survival. Similar to the calculation of mean core width, we calculated the mean recent growth rate and mean age at each station in each year.

In each PLSR analysis, we calculated the weight squared of each predictor variable to determine the relative contribution of each variable to the PLSR components. When the weights of each variable are squared, they sum to one, providing the percent contribution of each variable to the PLSR component. We used a cutoff of PLSR weight² > .1 to identify variables that contributed significantly (more than 10%) to the first PLSR component and drivers of variability in maternal investment, larval growth rate, and age-at-capture. All otolith analyses were performed in R v4.1.2 (R Core Team, 2017) using packages *dplyr* and *plsdepot*. Figures were generated using the R package *ggplot2*.

3 | RESULTS

3.1 | Early life history traits

Otolith core width was a robust indicator of larval size-at-extrusion. Otolith core width was significantly and positively related to larval size-at-extrusion for all eight species and thus was used as a proxy for larval size-at-extrusion for the rest of this study (Table 3).

There was no strong evidence that larvae spawned earlier in the year were in better condition than those born later in the winter. Only one species, *S. wilsoni*, exhibited a significant, negative relationship between date of birth and otolith core width, explaining 5% of the variability in core width (Table S1). However, birthdate was negatively related to age-at-collection for four species (including all three non-targeted species plus *S. rufus*; Table S2). Notably, birthdate was less consistent and explained less variability than the relationship between core size and age-at-collection (Table S3).

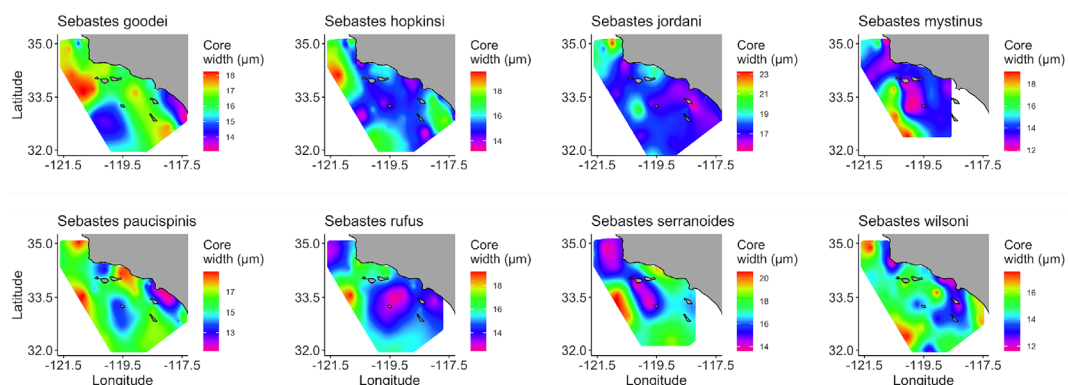


FIGURE 2 Krig map of average otolith core width at each station across the entire time series for each rockfish species. Note the scale bar is different for each species.

TABLE 3 Results of linear regressions examining the relationship between otolith radius-at-extrusion (core width) and standard length for all 1-day-old rockfish larvae. Significant *p*-values are bolded.

Species	Intercept	Core	F-stat	df	R ² adj.	<i>p</i> -value
<i>Sebastes goodei</i>	1.003	.254	4.261	1, 26	.108	.049
<i>Sebastes hopkinsi</i>	2.063	.148	9.479	1, 164	.049	.002
<i>Sebastes jordani</i>	1.969	.171	21.755	1, 111	.156	<.001
<i>Sebastes mystinus</i>	-.253	.298	106.079	1, 124	.457	<.001
<i>Sebastes paucispinis</i>	1.845	.162	6.169	1, 86	.056	.015
<i>Sebastes rufus</i>	.640	.231	9.016	1, 65	.108	.004
<i>Sebastes serranoides</i>	2.025	.139	15.671	1, 61	.191	<.001
<i>Sebastes wilsoni</i>	.996	.186	27.452	1, 103	.203	<.001

All species exhibited high spatial variability in core width, though most had larger cores in the northern (*S. goodei*, *S. hopkinsi*, *S. jordani*, *S. paucispinis*, and *S. wilsoni*) and/or offshore (*S. hopkinsi*, *S. mystinus*, *S. rufus*, *S. serranoides*, and *S. wilsoni*) regions of the Southern California Bight (Figure 2). Temporally, larval rockfish otolith core width and age (survival) were consistent across species, while growth was highly variable. Trends in core width anomalies were generally positive from 1998 to 2003, with most species peaking around 2001, declining from 2002 to 2007, and increasing from 2008 to 2013 (Figure S1a). Initially, *S. serranoides* had a different core width trend than the other species, with negative but increasing core width anomalies from 1998 to 2007, before aligning with the rest of the species from 2008 to 2013. Spearman rank correlation analysis revealed that core width patterns were positively correlated for most species (though only significantly for nine combinations; Figure S2). Rockfish recent growth was variable across time and species (Figure S1b), with weak correlations among species (only one significant; Figure S3), while age anomalies showed similar positive correlations as seen in otolith core width-at-hatch (though only five combinations were significant; Figures S1c and S4).

3.2 | Effects of oceanographic variability in maternal habitat on larval traits

The oceanographic conditions that adult rockfish experienced during the fall prior to parturition varied across space and time (Figures 3 and S5). The percent contribution of PSUW was generally lower inshore and higher offshore (Figures 3 and S5); however, high PSUW was found much closer to shore in the northern part of the region. Fall PSUW exhibited a low frequency signal in the Southern California Bight (Figure 3): PSUW was low during the start of the otolith time series (1997–1999), began to increase in 2001 and remained relatively high from 2002 to 2004, declined in 2006 and was low from 2007 to 2008, increased again from 2009 to 2010, and was moderately high from 2011 to 2013 (Figure 3).

PLSR analyses revealed that a combination of distance from fishing port (positive), PSUW% (positive), and Spiciness (negative) were the major drivers of larval rockfish core width variability. The first component of the PLSR was significant for all eight species and explained between 10% and 46.5% of the variability in core width of

larval rockfish. Increased distance from fishing port was correlated with larger core widths of all species except *S. goodei* (Figure 4, Table 4). Increased PSUW% during fall and at the depth range of each species was positively correlated with the larger core widths of six species, while spiciness was negatively correlated with five species (Figure 4, Table 4). Additionally, NPGO and meridional winds explained significant variability in the first PLSR component for *S. goodei*, *S. mystinus*, and *S. wilsoni* and *S. goodei*, *S. mystinus*, and *S. serranoides*, respectively.

3.3 | Effects of oceanographic variability in larval habitat on larval traits

The first component of the PLSR analysis explained 8%–54% of the variability in recent growth and 15%–59% of the variability in larval rockfish age-at-capture. Otolith core width was the major driver of recent growth and was significantly positively related to recent growth in five of the seven species tested (*S. mystinus* had too few fish old enough to examine growth patterns; Figure 5, Table 5), while the influence of the environment varied by species. Winter PSUW in the upper water column was also significantly related to recent growth for five species but was positively correlated with three species and negatively correlated with two species. The main finding of this study is that larval size-at-hatch (otolith core width-at-hatch) was significantly and positively correlated to survival (age-at-capture) in all eight species, indicating increased survival for individuals that were larger at extrusion (Figure 6, Table 6).

4 | DISCUSSION

Elucidating mechanisms that facilitate larval survival is a fundamental, but often elusive, tenet of fish population ecology (Hare, 2014). Here, we identify a trait of larval fish that is influenced by the oceanographic conditions experienced by their parents. This trait provides an indicator of larval quality and survival probability during the first weeks of life in oceanic marine ecosystems. We found that the otolith core width-at-extrusion of larval rockfish in the southern CCLME is tightly linked to larval growth rate and survival. Rapid larval growth and large size are frequently thought to decrease predation risk and increase

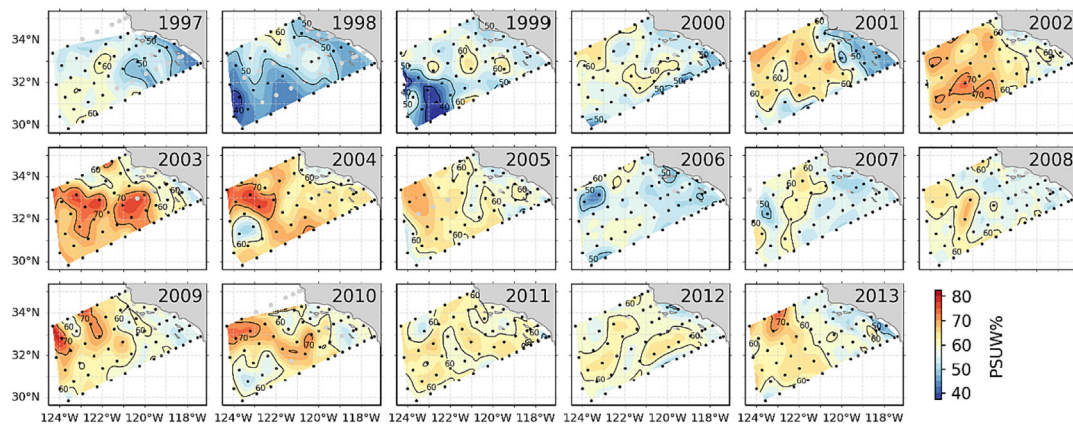


FIGURE 3 Mean percent of Pacific Subarctic Upper Water (PSUW) from 25.8 potential density isopycnal in the Southern California Bight. California Cooperative Oceanic Fisheries Investigations (CalCOFI) stations denoted by points with black points indicating stations used to calculate PSUW% and grey points indicating stations without CTD data in a given year.

survival; however, hatch timing, the strength of overlap with, as well as composition of, predator and prey fields, and the life stage where year class strength is set determine how larval growth and size influence the survival of a cohort (Robert et al., 2023). Core size has been demonstrated, in both the lab and field, to be an index of larval size-at-hatch and predicted survival of larval European sardine (*Sardina pilchardus*; Garrido et al., 2015). In addition, Robidas (2022) demonstrated that northern anchovy (*Engraulis mordax*) survival and age-adjusted morphological traits were positively correlated with otolith core width-at-hatch. Similarly, the oceanographic conditions adult walleye pollock (*Gadus chalcogrammus*) experience off the coast of Japan influence the quality of eggs and larvae produced and contribute to their early growth and survival (Kajiwara et al., 2022). The fact that fishes with very different adult life history characteristics (benthic versus pelagic, long-lived versus short-lived) that were collected in multiple oceans (Pacific and Atlantic) show the same pattern reveals a promising relationship between otolith core width-at-extrusion and survival suggests that the size of larvae at hatch/extrusion may play an important role in early survival during a life stage characterized by high mortality (Houde, 1987). Evaluation of the impact of otolith core width on larval fish survival is relatively new to fisheries science and has only been examined in a few species, but, to the best of our knowledge, every published study now demonstrates larvae with large otolith cores are more likely to survive the first few weeks of life. Larval condition at hatch/extrusion may thus be a general mechanism affecting larval survival and, potentially, population dynamics of fishes in pelagic marine ecosystems.

We found that parental environmental experience during gestation drove variability in the quality of rockfish larvae. Larvae that were collected further from fishing ports during years when parents were exposed to relatively high amounts of PSUW, which is cool, fresh, oxygen and nutrient-rich, in the months leading to parturition, had larger otolith core widths. This strongly suggests that the parental environment (likely maternal investment) impacts early growth and survival. We thus identify important environmental characteristics

experienced by adults that may drive population dynamics and improve our understanding of how and when oceanographic variability influences larval survival.

4.1 | What impacts larval survival?

Enhanced maternal investment may explain why higher-quality larvae are found further from fishing ports and, in some species, higher-quality larvae were born earlier. Several studies found that older, larger female rockfishes reproduce earlier in the year, produce higher-quality larvae with increased resistance to starvation (Arnold et al., 2018; Berkeley et al., 2004; Rodgveller et al., 2012; Sogard et al., 2008; Stafford et al., 2014), and that larger adults are the targets of fishers. In southern California, fish stocks were serially depleted, beginning with locations close to fishing ports and then moving progressively offshore through time (Miller et al., 2014). A consequence of intense fishing pressure nearshore is that larger rockfish are found further from fishing ports (Bellquist & Semmens, 2016). More recently, Keller et al. (2019) found that 10/14 rockfish species were larger in the Cowcod Conservation Area (CCA, a mostly offshore MPA in southern California) than in non-MPA locations that tended to be closer to shore, demonstrating how decreased fishing pressure is associated with larger fishes. Areas further from fishing ports in southern California are found offshore and therefore may provide fish with at least some physical, de facto, natural refuge from the strongest fishing effects, allowing for the accumulation of older, larger females and the production of higher-quality larvae. Additionally, of the eight rockfish species we examined, three (*S. jordani*, *S. hopkinsi*, and *S. wilsoni*) are diminutive and not targeted by fishers (although *S. hopkinsi* are often caught in the recreational fishery sector in southern California; Love et al., 2002), and all three (as well as *S. rufus*—a targeted species) had a pattern of larvae born earlier in the reproductive season experiencing higher survival. This pattern may demonstrate that these species have a large enough population of older/

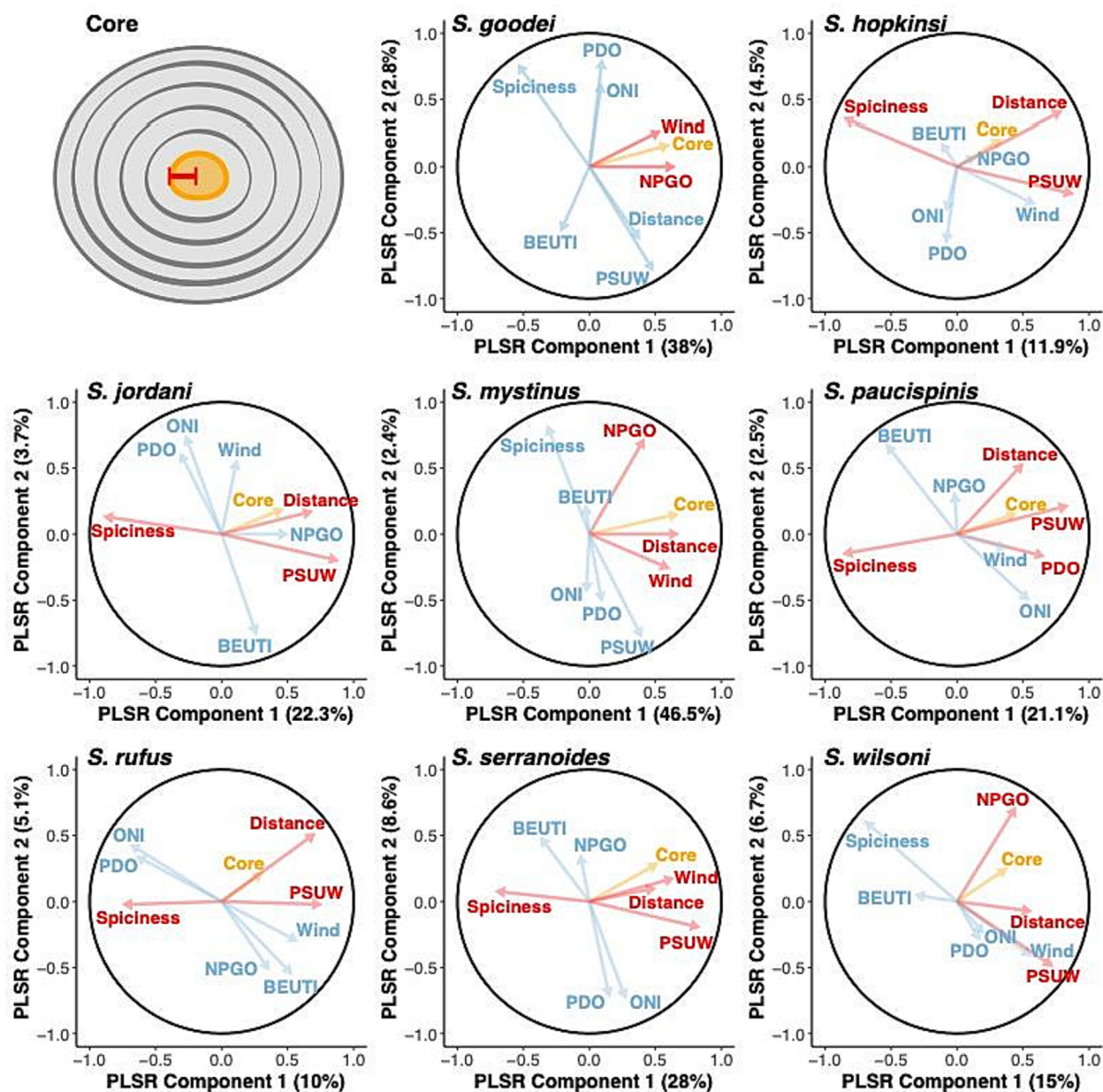


FIGURE 4 Results of partial least squares regression (PLSR) analyses of the major drivers of larval rockfish otolith core width variability for each species. Circle plots demonstrate the contribution of each fall environmental driver (including Biologically Effective Upwelling Transport Index (BEUTI), distance from nearest port (Distance), meridional wind (Wind), North Pacific Gyre Oscillation (NPGO), Ocean Niño Index (ONI), Pacific Decadal Oscillation (PDO), percent Pacific Subarctic Upper Water (PSUW), and Spiciness). The PLSR score of each variable indicated by colored lines with the length of the lines indicating higher scores. The horizontal component of each line indicates the loading on the first PLSR component and the vertical component of each line representing the loading on the second PLSR component. Variables that accounted for significant variation in otolith core width variability are indicated by red lines, while blue lines indicate variables that did not account for significant variability in otolith core width (orange line). The amount of variability captured in otolith core size by each component is indicated in (%) on each axis label. The upper left panel depicts how otolith core width is measured.

larger females to produce high-quality young earlier in the year and/or that there was selection for early hatch dates for these species (via environmental conditions or predator/prey abundance), increasing early survival.

Fishing pressure, however, is clearly not the only factor influencing larval quality. All three non-targeted species (*S. jordani*, *S. hopkinsi*,

and *S. wilsoni*) had larger otolith core widths in locations further from fishing ports. This indicates that being born further from fishing ports may inherently augment the probability of survival of larval rockfish in southern California and may play an important role in determining larval quality. Offshore habitats in the southern CCLME are more likely to be exposed to PSUW than inshore habitats in this region (Bograd

TABLE 4 Partial least squares regression (PLSR) weight² results for the basin, regional, and local oceanographic conditions influencing otolith core width-at-extrusion. Weights of oceanographic variables that contributed to more than 10% of the variability in the first PLSR component for a particular species are bolded. The sign of the correlation is indicated in ().

Weight	<i>Sebastes goodei</i>	<i>Sebastes hopkinsi</i>	<i>Sebastes jordani</i>	<i>Sebastes mystinus</i>	<i>Sebastes paucispinis</i>	<i>Sebastes rufus</i>	<i>Sebastes serranoides</i>	<i>Sebastes wilsoni</i>
Distance	.089 (+)	.366 (+)	.272 (+)	.375 (+)	.135 (+)	.361 (+)	.235 (+)	.247 (+)
BEUTI	.028 (-)	.004 (-)	.001 (-)	.001 (-)	.053 (-)	.007 (+)	.022 (-)	.097 (-)
ONI	.036 (+)	.001 (+)	.001 (-)	.002 (-)	.070 (+)	.074 (-)	.008 (+)	.002 (+)
PDO	.094 (+)	.031 (-)	.013 (-)	.001 (+)	.211 (+)	.071 (-)	.013 (-)	.011 (+)
NPGO	.343 (+)	.018 (+)	.070 (+)	.251 (+)	.001 (+)	.001 (-)	.021 (+)	.423 (+)
Wind	.383 (+)	.104 (+)	.066 (+)	.317 (+)	.029 (+)	.031 (+)	.262 (+)	.038 (+)
Spice	.011 (-)	.136 (-)	.294 (-)	.005 (-)	.219 (-)	.221 (-)	.108 (-)	.024 (-)
PSUW	.015 (+)	.338 (+)	.280 (+)	.048 (+)	.279 (+)	.232 (+)	.328 (+)	.158 (+)

Abbreviations: BEUTI, Biologically Effective Upwelling Transport Index; NPGO, North Pacific Gyre Oscillation; ONI, Ocean Niño Index; PDO, Pacific Decadal Oscillation; PSUW, Pacific Subarctic Upper Water.

et al., 2015; Bograd et al., 2019; Lynn & Simpson, 1987). PSUW is transported to southern California via the equatorward-flowing California Current, infusing the region with low temperature, low salinity, and high oxygen water (Figure S5). North of Point Conception (at 35°N), the California Current flows relatively close to shore, but within the Southern California Bight, the coast abruptly curves eastward, and inshore areas are largely shielded from the California Current (Hamilton et al., 2010; Thompson et al., 2016). Conversely, spicy (Pacific Equatorial) water masses are advected into the Southern California Bight by the California Undercurrent that transports high temperature, high salinity, and low oxygen waters around the continental slope (Bograd et al., 2019; Lynn & Simpson, 1987). The cross-shelf gradient of spicy waters nearshore and high PSUW offshore creates vastly different conditions for adult rockfish living in the Southern California Bight and may play an important role in determining the quality of larvae they produce (Figure 7).

Our work strongly suggests that exposure to high PSUW during gestation leads to rockfish larvae with large otolith core widths-at-hatch, which translates to faster growth rates and higher survival. We propose three non-mutually exclusive mechanisms to explain the role of PSUW on rockfish larvae. First, PSUW is high in nutrient concentration and has been associated with increased zooplankton biomass (Chelton et al., 1982) and zooplankton that are higher in lipids (Miller et al., 2017), which might enhance adult rockfish feeding conditions. If females are well fed, they will have higher lipid reserves and be able to better provision their offspring with lipids. Second, because PSUW is low in temperature and high in oxygen, females in high PSUW areas may experience reduced metabolic rates, while higher oxygen concentrations reduce metabolic costs, leaving more energy available to provision eggs. This may be especially true for larger, older females who allocate a larger portion of their energy to reproduction and provide higher lipid reserves to their larvae (Berkeley et al., 2004). Third, higher PSUW creates vertical expansion of habitat, allowing rockfish to access additional habitats that would otherwise be too low in oxygen (Meyer-Gutbrod et al., 2021), thus increasing feeding success and/or reducing metabolic costs. It is possible/likely that these proposed mechanisms interact to increase the energy available to provision young, thereby increasing size-at-hatch and improving larval growth and survival.

4.2 | Recruitment drivers?

Identifying the mechanisms driving rockfish recruitment variability in the CCLME is critically important to the management of these species now and in the face of climate change. The CCLME is highly dynamic, and climate change is already impacting oceanographic conditions (Thompson et al., 2022), leading to changes in fish phenology with potential consequences for population dynamics (Asch, 2015). Previous work identified a link between sea level anomalies (an indicator of the relative strength of alongshore flow and a proxy for the transport of cold, nutrient-rich, subarctic water) and pelagic juvenile rockfish abundance (Ralston et al., 2013). However, the CCLME experienced

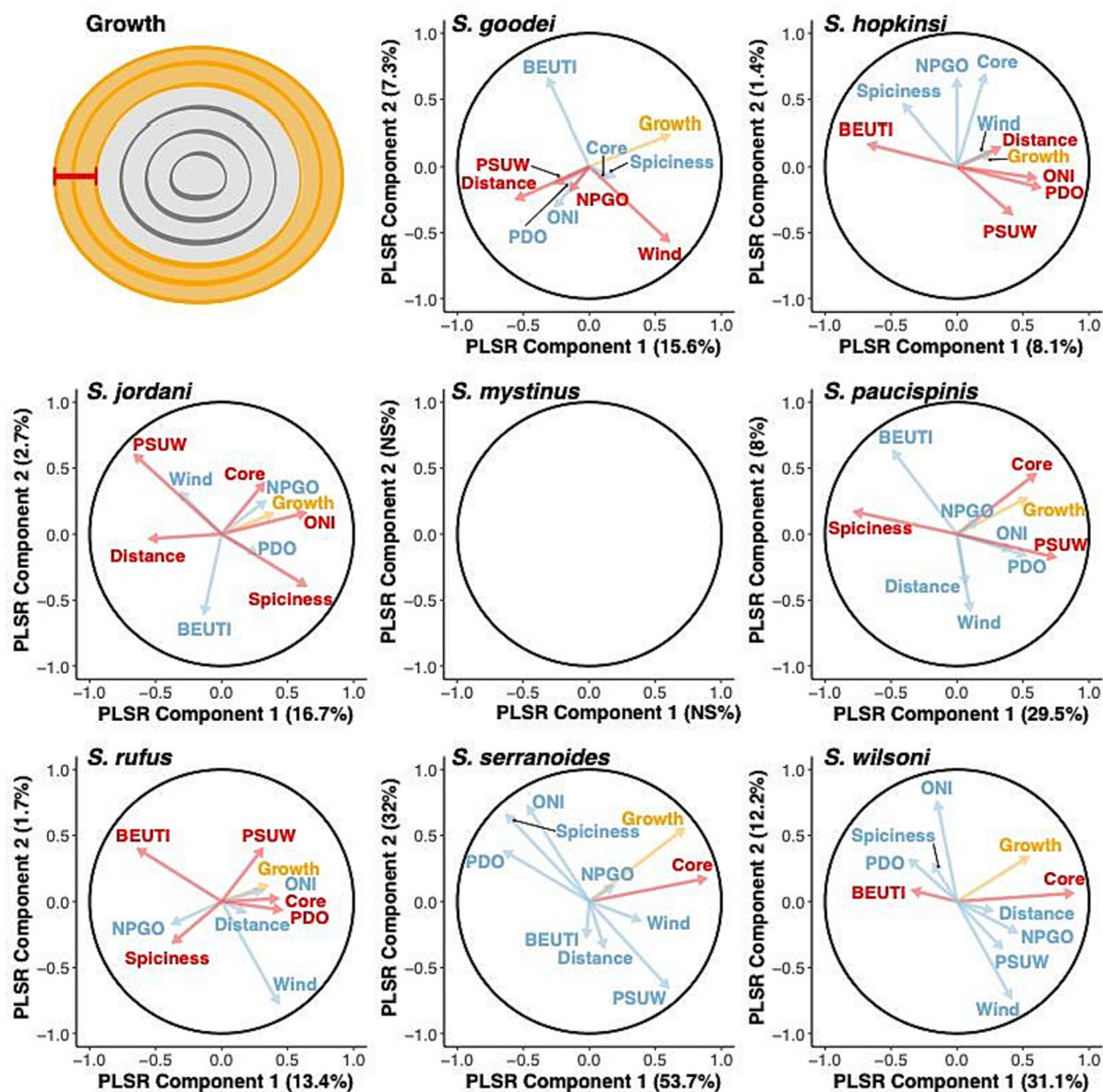


FIGURE 5 Results of partial least squares regression (PLSR) analyses of the major drivers of larval rockfish recent growth (residuals of the average last 2 days of growth) variability for each species. Circle plots demonstrate the contribution of each winter environmental driver including Biologically Effective Upwelling Transport Index (BEUTI), core width anomaly (Core), distance from nearest port (Distance), meridional wind (Wind), North Pacific Gyre Oscillation (NPGO), Ocean Niño Index (ONI), Pacific Decadal Oscillation (PDO), percent Pacific Subarctic Upper Water (PSUW), and Spiciness. Variables that accounted for significant variation in recent growth variability are indicated by red lines, while blue lines indicate variables that did not account for significant variability in growth (orange line). We did not have sufficient sample size of *Sebastes mystinus* of at least 3 days old to run a PLSR for recent growth rate. The upper left panel depicts how recent growth is measured from the mean of the last two increments for each larva.

anomalous warming from 2014 to 2016 (McClatchie et al., 2016), but pelagic juvenile rockfish abundance was very high from 2013 to 2016 (Schroeder et al., 2018), revealing that recruitment was not linked to sea level anomalies. Recent work examining the relative contributions of PSUW and spicy water masses at the depths of adult rockfish provided a more robust link to recruitment that persisted through the marine heatwave (Schroeder et al., 2018). Surprisingly, some of

the highest volumes of PSUW and abundances of pelagic juveniles on record occurred before (2013) and during the 2014–2016 marine heatwave (Santora et al., 2017; Schroeder et al., 2018). In the past, PSUW tended to decline during warm years, so the combination of high PSUW with warm Central Pacific and California Undercurrent waters was highly unusual during 2014–2016 (Zaba et al., 2020; Zaba & Rudnick, 2016). These findings point to the importance of

TABLE 5 Partial least squares regression weight² results for how basin, regional, local oceanographic conditions, and larval quality (core column) influence recent growth rate. Variables that contributed to more than 10% of the variability in the first PLSR component are bolded. The sign of the correlation is indicated in 0.

Weight	<i>Sebastes goodei</i>	<i>Sebastes hopkinsi</i>	<i>Sebastes jordani</i>	<i>Sebastes myxistinus</i>	<i>Sebastes paucispinis</i>	<i>Sebastes rufus</i>	<i>Sebastes serranoides</i>	<i>Sebastes wilsoni</i>
Core	.040 (+)	.088 (+)	.100 (+)	NA	.247 (+)	.163 (+)	.843 (+)	.701 (+)
Distance	.398 (-)	.134 (+)	.203 (-)	NA	.014 (-)	.001 (+)	.001 (-)	.039 (+)
BEUTI	.024 (-)	.218 (-)	.031 (-)	NA	.035 (-)	.228 (-)	.028 (-)	.118 (-)
ONI	.089 (-)	.232 (+)	.305 (+)	NA	.052 (+)	.098 (+)	.001 (-)	.024 (+)
PDO	.026 (-)	.154 (+)	.003 (+)	NA	.056 (+)	.141 (+)	.035 (-)	.072 (-)
NPGO	.107 (-)	.010 (+)	.078 (+)	NA	.014 (+)	.095 (-)	.017 (+)	.020 (+)
Wind	.176 (+)	.045 (+)	.040 (-)	NA	.018 (-)	.026 (+)	.059 (+)	.006 (-)
Spice	.038 (+)	.012 (-)	.138 (+)	NA	.356 (-)	.126 (-)	.009 (-)	.003 (-)
PSUW	.100 (-)	.104 (+)	.101 (-)	NA	.204 (+)	.119 (+)	.007 (+)	.017 (+)

Abbreviations: BEUTI, Biologically Effective Upwelling Transport Index; NPGO, North Pacific Gyre Oscillation; ONI, Ocean Niño Index; PDO, Pacific Decadal Oscillation; PSUW, Pacific Subarctic Upper Water.

evaluating conditions below the surface mixed layer to better understand the oceanographic drivers of rockfish recruitment variability. We found that basin scale indices were not consistently strongly correlated with otolith core width nor with larval growth or survival, likely because the basin scale indicators do not reflect well the local oceanographic conditions experienced by the larvae. In addition, the relationship between basin-scale processes described by large-scale climate indices and local physical and ecological conditions in the North Pacific has been changing (Litzow, Hunsicker, et al., 2020). For example, the correlation between the PDO and salmon catch in the Gulf of Alaska has changed dramatically in recent decades; salmon catch was strongly positively correlated with the PDO from 1965 to 1988, not correlated from 1989 to 2014, and then negatively correlated from 2014 to 2019 (Litzow, Malick, et al., 2020). Additionally, the majority of rockfish recruitment research has focused on the pelagic juvenile stage not only because it is a good indicator of recruitment (Field et al., 2010; Ralston et al., 2013) but also because larval rockfish are difficult to distinguish morphometrically. Directly examining the influence of oceanographic conditions on larval traits and early survival is needed to better understand what regulates rockfish population dynamics now and as climate change progresses.

The influence of PSUW on the CCLME may provide a new indicator of rockfish recruitment that is robust to large-scale changes in surface conditions. Our work demonstrates the importance of PSUW in the fall, when females are gestating, on the growth and early survival of larval rockfish born during winter in the southern CCLME. While this study is limited to the early larval period and does not link through to recruitment, our findings combined with those that show pelagic juveniles in the central CCLME are more abundant when PSUW is the main source water for the CCLME (Schroeder et al., 2018), indicate that PSUW plays an important role in rockfish population dynamics. Although there are surveys that provide recruitment data in southern California, none match the temporal and spatial resolution of our study (Field et al., 2021; Meyer-Gutbrod et al., 2021). To obtain a more holistic understanding of rockfish recruitment dynamics in southern California, it would be helpful to better coordinate sampling efforts focused on larval, juvenile, settlement, and adult life stages.

Given the importance of PSUW to rockfish larval condition and recruitment (Schroeder et al., 2018), it is vital to understand the environmental conditions that control the input of this water mass to the southern CCLME. The California Current, which transports PSUW equatorward, forms when the eastern-flowing North Pacific Current (NPC) bifurcates near the North American coast, and the latitude of that bifurcation can impact both the physical and biological characteristics of the California Current System (Sydeman et al., 2011). Climate models project a poleward shift of the NPC (e.g., Rykaczewski et al., 2015) and its bifurcation, which will likely alter the source region and characteristics of PSUW advected into the region. Future research should focus on the link between the NPC bifurcation, the characteristics and transport of PSUW to the CCLME, and the implications for rockfish survival.

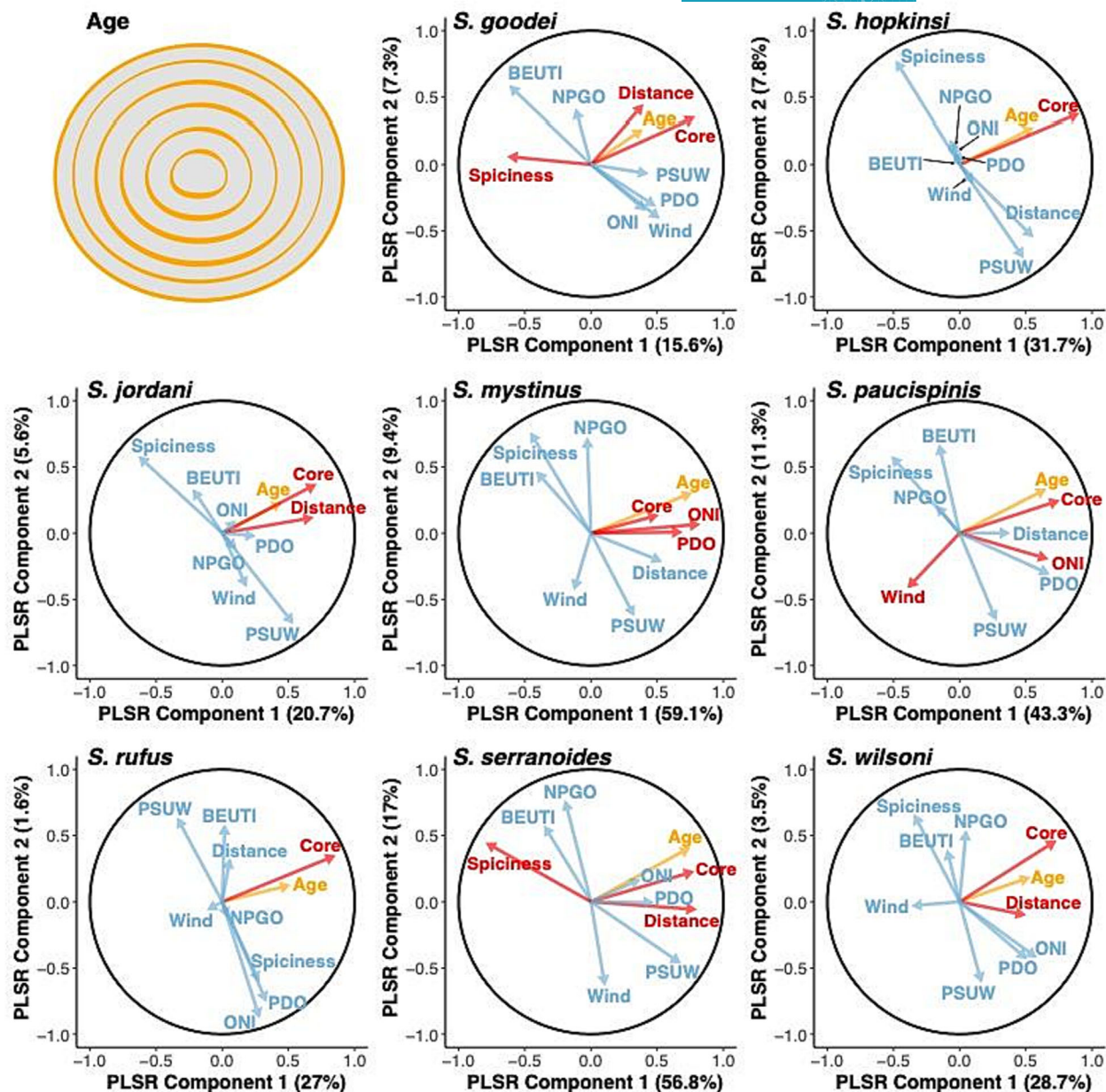


FIGURE 6 Results of partial least squares regression (PLSR) analyses of the major drivers of larval rockfish age variability for each species. Circle plots demonstrate the contribution of each winter environmental driver including Biologically Effective Upwelling Transport Index (BEUTI), Core, distance, wind, North Pacific Gyre Oscillation (NPGO), Ocean Niño Index (ONI), Pacific Decadal Oscillation (PDO), Pacific Subarctic Upper Water (PSUW), and Spiciness. Variables that accounted for significant variation in core width variability are indicated by red lines, while blue lines indicate variables that did not account for significant variability in age (orange line). The upper left panel indicates how otolith increments were counted to determine the age of each larva.

4.3 | Management implications

Our finding that larval quality was significantly higher further from fishing ports in southern California has important management implications. In the United States, fisheries managers are mandated under the Magnuson–Stevens Fisheries Management and Conservation Act (2006) to designate essential fisheries habitat (EFH) to help enhance sustainable fisheries. At present, the entire continental shelf off southern California is designated as groundfish EFH. However, our work shows that different regions within the shelf have different

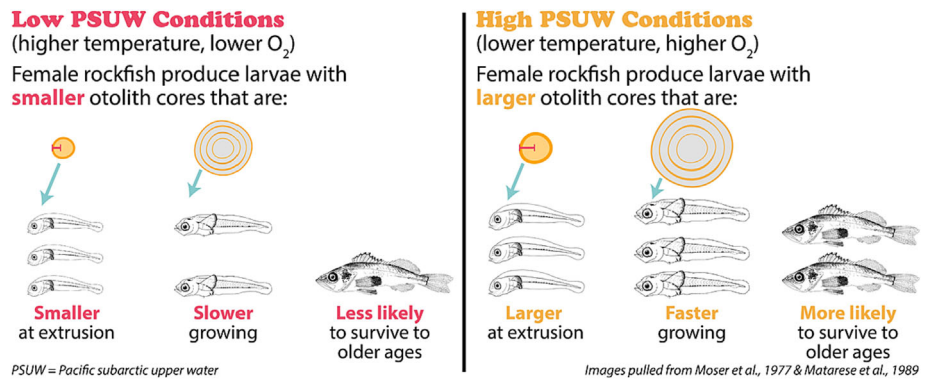
values for rockfish. This knowledge could be important if there is a need to establish rockfish conservation areas (RCAs) off southern California. For example, the CCA, the largest RCA in the United States, was established in 2002 to facilitate the rebuilding of overfished cowcod rockfish (*Sebastes levis*; Butler et al., 2003). The footprint of the CCAs was based upon California Department of Fish and Game catch block records indicating where the most cowcod were historically caught in southern California (Butler et al., 2003). However, it is possible that catch records are not the best metric of habitat quality if fishing effort is not equal throughout the potential EFH. Our work shows

TABLE 6 Partial least squares regression weight² results for how basin, regional, local oceanographic conditions, and larval quality (otolith core width) influence age-at-capture. Variables that contributed to more than 10% of the variability in the first PLSR component are bolded. The sign of the correlation is indicated in ().

Weight	<i>Sebastes goodiei</i>	<i>Sebastes hopkinsi</i>	<i>Sebastes jordani</i>	<i>Sebastes mystinus</i>	<i>Sebastes paucispinis</i>	<i>Sebastes rufus</i>	<i>Sebastes serranoides</i>	<i>Sebastes wilsoni</i>
Core	.484 (+)	.901 (+)	.487 (+)	.158 (+)	.508 (+)	.857 (+)	.366 (+)	.543 (+)
Distance	.124 (+)	.034 (+)	.348 (+)	.094 (+)	.089 (+)	.001 (+)	.291 (+)	.144 (+)
BEUTI	.085 (-)	.001 (-)	.012 (-)	.053 (-)	.001 (-)	.019 (+)	.012 (-)	.001 (-)
ONI	.052 (+)	.001 (-)	.013 (+)	.408 (+)	.158 (+)	.001 (+)	.070 (+)	.095 (+)
PDO	.030 (+)	.004 (-)	.020 (+)	.179 (+)	.068 (+)	.032 (+)	.058 (+)	.089 (+)
NPGO	.002 (-)	.010 (-)	.008 (-)	.034 (+)	.012 (-)	.001 (-)	.027 (+)	.006 (+)
Wind	.011 (+)	.001 (+)	.003 (+)	.045 (-)	.118 (-)	.001 (-)	.006 (-)	.077 (-)
Spice	.194 (-)	.014 (-)	.060 (-)	.007 (-)	.044 (-)	.037 (+)	.105 (-)	.038 (-)
PSUW	.015 (+)	.034 (+)	.046 (+)	.019 (+)	.001 (+)	.043 (-)	.064 (+)	.006 (-)

Abbreviations: BEUTI, Biologically Effective Upwelling Transport Index; NPGO, North Pacific Gyre Oscillation; ONI, Ocean Niño Index; PDO, Pacific Decadal Oscillation; PSUW, Pacific Subarctic Upper Water.

FIGURE 7 Schematic demonstrating how the conditions female rockfish experience during gestation affect the otolith derived proxies for size-at-extrusion, recent growth, and survival.



that offshore areas with increased exposure to PSUW may disproportionately contribute to rockfish larval survival and may be exceptionally valuable to conservation efforts. Understanding the interaction between oceanographic conditions and fish vitality is an important component of marine spatial planning, and our results provide insight on habitat suitability for rockfishes in southern California.

5 | CONCLUSION

To recruit to the adult population, fish larvae must survive a gauntlet of death at multiple early life history stages (Hare, 2014; Houde, 1987, 2008). Since Hjort articulated the critical period hypothesis, multiple prominent ideas have emerged to help explain recruitment variability (reviewed in Hare, 2014). A common thread among these hypotheses is that exogenous events (e.g., prey availability, predation pressure) impact the recruitment potential of larvae. Further, each is underpinned by the idea that larvae must feed to avoid starvation and elude predators. Here, we found that an endogenous event, the exposure of gestating adults to PSUW in areas far from fishing ports, enhanced larval quality at extrusion, which translated to faster larval growth and increased the probability of survival during the larval stage. In addition to our empirical work, recent modeling efforts showed that female preconditioning impacts recruitment of sablefish (*Anoplopoma fimbria*; Tolimieri et al., 2018) and petrale sole (*Eopsetta jordani*; Haltuch et al., 2020). Given recent lab, modeling and now field (Arnold et al., 2018) results pointing to the importance of maternal effects on fish population dynamics, we encourage future recruitment research to assess whether otolith core width-at-extrusion is a universal proxy for maternal contribution and to discern if maternal contributions prior to hatch, in conjunction with feeding and predation post-hatch/extrusion, are a general driver of early survival of fishes worldwide. While we still need to understand the mechanism by which oceanographic, habitat, and maternal characteristics determine larval quality and survival through the juvenile stage, our work strongly suggests larval rockfish otolith core width-at-extrusion is an indicator of larval rockfish quality and early survival, representing an important step to holistically understand how environmental variability translates to recruitment variability.

AUTHOR CONTRIBUTIONS

Andrew R. Thompson, Noah Ben-Aderet, H. William Fennie, Garfield T. Kwan, Jarrod A. Santora, Isaac D. Schroeder, and Steven J. Bograd designed the research. Noah Ben-Aderet and Andrew R. Thompson performed the research. H. William Fennie, Noah Ben-Aderet, and Isaac D. Schroeder analyzed the data. H. William Fennie, Andrew R. Thompson, Noah Ben-Aderet, Garfield T. Kwan, Jarrod A. Santora, Isaac D. Schroeder, and Steven J. Bograd wrote the paper.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Data and code for this manuscript are stored in the dryad data repository: <https://doi.org/10.7291/D1Q96H>.

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