

# Source water variability as a driver of rockfish recruitment in the California Current Ecosystem: implications for climate change and fisheries management

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**Abstract:** Elucidating connections between ocean climate variability and change and recruitment of juvenile fishes to adult populations is critical for understanding variability in stock–recruit dynamics. Recruitment to adult rockfish populations in the California Current Ecosystem (CCE) is highly variable, leading to short- and long-term changes in abundance, productivity, forage availability, and potential fisheries yield. We used regional ocean model output, oceanographic data, and a 34-year time series of pelagic juvenile rockfish to investigate the interaction between changes in CCE source waters, as reflected by physical water mass properties, and recruitment variability. Specifically, variability of “spiciness” on upper water isopycnals explains a substantial fraction of the variation in pelagic juvenile rockfish abundance. High rockfish abundances correspond to cooler, fresher waters with higher dissolved oxygen (i.e., “minty”) conditions, indicative of Pacific subarctic water. By contrast, years of low rockfish abundance are associated with warmer, more saline, and more oxygen-deficient (i.e., “spicy”) conditions, reflecting waters of subtropical or equatorial origin. Transport and source waters in the CCE are key factors determining density-independent processes and subsequent recruitment to adult populations.

**Résumé :** L'élucidation des connexions entre la variabilité et les modifications du climat océanique et le recrutement de poissons juvéniles dans les populations d'adultes est essentielle à la compréhension de la variabilité de la dynamique recrues-stock. Le recrutement dans les populations de sébastes adultes dans l'écosystème du courant de Californie (CCE) est très variable, entraînant des changements à court et long terme de l'abondance, de la productivité, de la disponibilité de nourriture et du rendement potentiel des pêches. Nous avons utilisé les sorties d'un modèle océanique régional, des données océanographiques et une série chronologique de 34 années sur les sébastes juvéniles pélagiques pour étudier l'interaction entre les variations des eaux à la source du CCE reflétées dans les propriétés physiques de la masse d'eau et la variabilité du recrutement. Plus précisément, l'effet de la variabilité de la salinité et de la température sur les isopycnes supérieures de l'eau explique une fraction substantielle des variations de l'abondance des sébastes juvéniles pélagiques. De fortes abondances de sébastes correspondent à des eaux plus douces et froides à plus forte teneur en oxygène dissous indiquant de l'eau subarctique de l'océan Pacifique. En revanche, les années de faible abondance des sébastes sont associées à des conditions plus chaudes, salines et pauvres en oxygène, qui reflètent des eaux d'origine subtropicale ou équatoriale. Le transport et les sources des eaux dans le CCE sont des facteurs déterminants de processus indépendants de la densité et du recrutement subséquent dans les populations d'adultes. [Traduit par la Rédaction]

## Introduction

Contemporary fisheries management is based on the need to balance fisheries removals with the need to maintain reproductive potential among exploited populations. Typically, this leads to management objectives that seek to maintain a target level of spawning potential in a given population, despite the observation that parental biomass typically explains a small fraction of the variance in recruitment to most exploited fish populations (Myers et al. 1999; Cury et al. 2014; Szuwalski et al. 2015). Ecosystem factors, including environmental conditions and predator–prey

interactions, are generally responsible for a greater fraction of this variability, but are difficult to demonstrate mechanistically (Houde 2008; Pepin 2016). Quantifying the influence of variable environmental conditions on biologically relevant scales that reflect species life history is critical for developing a mechanistic understanding of how existing variability and future climate change will modulate changes in marine populations and productivity (Cury et al. 2008; King et al. 2011; Hare et al. 2016), particularly for populations with highly variable recruitment and subsequent population productivity (Beamish 1993; Mueter et al.

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2007; Stachura et al. 2014). For example, pelagic fish and groundfish species may experience ocean climate variability differently because ocean surface conditions can reflect physical and biological dynamics independently from conditions occurring at depth (Keller et al. 2010; Gilly et al. 2013). Oceanographic models that track depth-specific variability of physical processes may provide the critical information relating to species that occur in benthic (Huff et al. 2012) and pelagic habitats (Petersen et al. 2010; Schroeder et al. 2014; Rose et al. 2015).

Quantifying environmental drivers of recruitment processes (distribution and abundance) for commercially important groundfish within the California Current Ecosystem (CCE) aids in management of the fisheries and the food webs that rely on them as prey. Relative to the population dynamics inferred in age-structured stock assessment models, the abundance of 3- to 4-month-old pelagic juvenile rockfish has been shown to be correlated to recruitment estimates informed by fisheries data (Ralston et al. 2013). As pelagic juveniles, rockfishes are also critical, but highly variable, forage for higher trophic level predators within the CCE (Thayer et al. 2014; Szoboszlai et al. 2015; Wells et al. 2017; Warzybok et al. 2018). Rockfish from the most abundant stocks are born (via parturition) during winter. Springtime interannual and spatial variations of observed pelagic juvenile abundance is highly coherent among species (Ralston et al. 2013; Santora et al. 2014). This suggests a strong coherence in the density-independent environmental processes that drive recruitment variability. In support of this, Reilly et al. (1992) reported interannual variations in diet composition of five species of pelagic juvenile rockfish were greater than interspecific variations among the species studied, indicating that pelagic juvenile rockfish were more responsive to fluctuations in overall prey abundance than to the species composition of the forage assemblage. These observations are consistent with shifts in ecosystem productivity in the CCE and are largely a result of environmental forcing, rather than strictly biological processes (Colebrook 1977; Chelton et al. 1982; Roesler and Chelton 1987). Ralston et al. (2013) concluded from an analysis of coastal sea level height that years of high pelagic juvenile rockfish abundances are positively associated with equatorward alongshore flow. Ralston et al. (2013) also evaluated the relationship between in situ oceanographic conditions at 30 m depth based on conductivity–temperature–depth (CTD) casts conducted during the survey, but did not find a strong relationship, which they attributed to conflicting signals among source waters, upwelling dynamics, and mesoscale processes in that narrow temporal and spatial window. Specifically, they noted that the oceanographic factors that likely drove the greatest changes in year class strength likely occurred during larval stages that took place in the 3 to 4 months before the survey. Other studies also reported relationships between sea level and recruitment for settled (following the pelagic phase) juveniles in coastal waters (Laidig et al. 2007), sablefish (*Anoplopoma fimbria*) (Schirripa and Colbert 2006), and from a meta-analysis of recruitment estimates derived from groundfish stock assessments (Stachura et al. 2014). Although most of these analyses provided no conclusive mechanistic explanation for these results, most interpret the results as an indicator of greater influx of northerly source waters into the CCE that are associated with improved productivity and foraging conditions.

The greatest abundance of spawning rockfish in the CCE is concentrated along the outer shelf-slope (Williams and Ralston 2002; Keller et al. 2012), coinciding with upper water physical and chemical properties between ~100 and 400 m (Huyer et al. 1998; Collins et al. 2003; Todd et al. 2012). Upper waters are important source waters for upwelling and the concomitant enhanced supply of nutrients. The upper waters of the CCE are composed primarily of four water masses (Pacific Subarctic, North Pacific Central, Coastal Upwelled, and Equatorial Pacific), each characterized by unique temperature–salinity, oxygen, and nutrient com-

positions at the time of formation (Lynn and Simpson 1987). Pacific Subarctic and Equatorial Pacific waters are the dominant water masses along the continental slope (Meinvielle and Johnson 2013; Hickey et al. 2006), and a combination of these water masses are upwelled within the 50 km coastal zone (Hickey et al. 2006; Lynn and Simpson 1987). The Pacific Subarctic water mass, formed in the North Pacific by surface cooling and freshening due to precipitation (Freeland et al. 2003), is marked by low salinity (<33.6), temperatures below 6 °C, high nutrients and dissolved oxygen (DO), and high abundances of lipid-rich zooplankton that provide the sustenance for a productive CCE with long trophic chains (Reid 1962; Roesler and Chelton 1987; Keister et al. 2011). In contrast, the Equatorial Pacific water mass is characterized by salinities greater than 34.5, high nutrients, and low DO (Bograd et al. 2015; McClatchie et al. 2016a). In the core of the California Undercurrent, DO values on the 26.5 potential density isopycnal ( $\sigma_\theta = 26.5 \text{ kg}\cdot\text{m}^{-3}$ ) vary greatly between waters entering the northern and southern parts of the CCE, with DO values at 50°N approximately five times greater than at those at 25°N (Meinvielle and Johnson 2013). Both subarctic and equatorial water masses are identifiable by the conservative properties of potential temperature ( $\theta$ ) and salinity (S) on isopycnal surfaces (Davis et al. 2008; Thomson and Krassovski 2010). “Spiciness”,  $\pi(\theta, S)$ , combines these two variables into one state variable that can be used to characterize hydrographic profiles (Flament 2002), with the profile containing a greater percentage of either cold–fresh subarctic water (i.e., negative spice values, referred to as “minty”) or warm–salty equatorial water (i.e., positive spice values, referred to as “spicy”). Isopleths of spiciness are orthogonal to potential density, and as noted by Huyer et al. (1998) this makes spiciness particularly suitable for analysis in the CCE because average temperature–salinity (T–S) curves are roughly parallel to contours of spiciness.

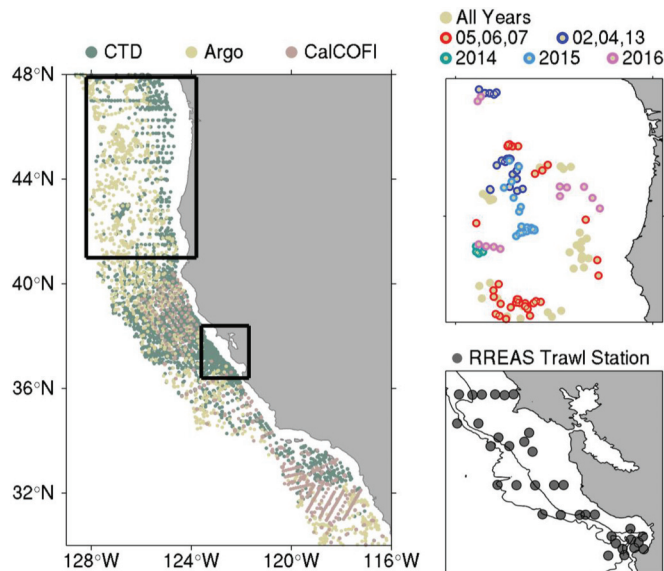
To improve our understanding of pelagic juvenile rockfish variability and their unanticipated high abundance observed during the 2014–2016 large marine heat wave (LMH) that was influenced by an El Niño event during the winter of 2015–2016 (McClatchie et al. 2016b; Fiedler and Mantua 2017; Santora et al. 2017a), we develop an indicator of upper water conditions based on modeled variations in spiciness and examine how it relates to pelagic juvenile rockfish variability during 1983–2010. We extend model results through 2016 using Lagrangian observations from Argo profiles to evaluate pelagic juvenile rockfish abundance fluctuations during the LMH of 2014–2016. We hypothesize that source water variability in the CCE is an indicator of pelagic juvenile rockfish abundance in the CCE typically and over the period of the LMH and as such represent an improvement over surface-oriented indicators.

## Methods

### Juvenile rockfish assessment survey

The Southwest Fisheries Science Center of NOAA conducts the Rockfish Recruitment and Ecosystem Assessment Survey (RREAS; Fig. 1) to assess the state of the ecosystem and, in doing so, collect 3- to 4-month-old pelagic juvenile rockfishes in a “core” area off of central California since 1983 and throughout California waters since 2004 (Ralston et al. 2013; Sakuma et al. 2016; [https://upwell.pfeg.noaa.gov/erddap/tabledap/FED\\_Rockfish\\_Catch.html](https://upwell.pfeg.noaa.gov/erddap/tabledap/FED_Rockfish_Catch.html)). Following parturition in winter months, pelagic juvenile rockfish are sampled in the late spring (late April through early June) with a midwater trawl that targets the water column between 30 to 40 m depth, as pelagic juveniles are relatively evenly distributed throughout the upper 100 m of the water column (Ross and Larson 2003). Ralston et al. (2013) highlighted the degree of interannual variability (several orders of magnitude) in pelagic juvenile rockfish abundance demonstrated by the ten most frequently occurring species of pelagic juvenile rockfish encountered, which exhibited a high degree of temporal covariation. We updated

**Fig. 1.** Study domain and distribution of conductivity–temperature–depth (CTD) stations (from World Ocean Database and the California Cooperative of Oceanic Fisheries Investigations; CalCOFI) and Argo profiles used to evaluate coherence between observed and modeled physical conditions. Inset boxes indicate (top) the location of extracted Argo profiles during April and May 2002–2016 and (bottom) Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) midwater trawling stations. The Argo profile locations for years of low (2005, 2006, 2007) and high (2002, 2004, 2013) pelagic juvenile rockfish abundances and the last 3 years of the RREAS survey (2014, 2015, 2016) are marked with colored circles.



the analysis reported by [Ralston et al. \(2013\)](#) to include catches of pelagic juvenile rockfish during the 2011–2016 time period, resulting in a 34-year time series (1983–2016; [Fig. 2](#)). We exclude fish smaller than 20 mm standard length due to size bias in the net liner. We standardize all pelagic juveniles to a common age of 100 days to account for varying abundance due to natural mortality. The process for this standardization is to age a subset of individuals, use those age observations to develop linear regressions of age as a function of standard length, estimate the ages of all fish from the length observations, and then calculate the number of 100-day-old equivalents by applying a natural mortality rate of 0.04 per day ([Ralston and Howard 1995](#); [Ralston et al. 2013](#)). Next, and as also previously described in [Ralston et al. \(2013\)](#), annual indices (year effects) for each species were estimated using a delta-generalized linear model that included year, period (season), and station (spatial) effects, and the resulting indices were analyzed using principal components analysis. We used the first principal component from that analysis ( $PC_{1,rf}$ ), which explains over 78% of the total variance in the abundance of winter spawning pelagic juvenile rockfish in the central California “core” area.

#### Data-assimilative oceanographic model

The ocean modeling group at the University of California Santa Cruz developed an historical (1980–2010) reanalysis of the CCE using the ROMS four-dimensional variational data assimilation system ([Moore et al. 2011](#); <http://oceanmodeling.pmc.ucsc.edu/>). The model assimilated available satellite sea surface temperature, altimetry data, and in situ hydrographic data. The in situ hydrographic data were taken from the quality-controlled EN3 data set (v2a) maintained by the UK Met Office ([Ingleby and Huddleston](#)

[2007](#)). The model’s resolution is  $1/10^\circ$  in the horizontal, 42 terrain following  $\sigma$  levels in the vertical, and has a 15-minute time step. The model configuration is described in detail by [Veneziani et al. \(2009\)](#) and the details of the data assimilation strategy by [Neveu et al. \(2016\)](#). Six-hour snapshots of the model output were averaged to 1-day intervals for the reanalysis evaluation. As in [Neveu et al. \(2016\)](#), we refer to the particular model output used in this study as WCRA31, as it represents a data assimilative reanalysis of the US west coast that extends 31 years, starting in 1980. [Schroeder et al. \(2014\)](#) evaluated the performance of WCRA31 relative to observed hydrographic conditions (not included in the reanalysis model) and pelagic juvenile rockfish abundance collected during the RREAS and determined that the model’s prediction of the depth of the 26.0 isopycnal corresponds well for locations in the central California region from the shelf to ~50 km offshore. For use here, we extend the evaluation by [Schroeder et al. \(2014\)](#) beyond the central California region for a coastwide analysis ([Fig. 1](#)) and focus our evaluation on spiciness on isopycnal surfaces.

#### Hydrographic data for WCRA31 evaluation

The World Ocean Database (WOD; <https://www.nodc.noaa.gov/OC5/WOD13/>) and California Cooperative Oceanic Fisheries Investigations (CalCOFI, <https://www.calcofi.org/>) databases were used to extract CTD and Argo (<http://www.argo.net/>) CTD profiles for the evaluation between WCRA31 and observations. All data, starting from 1980, were extracted from the shore to 300 km offshore. Profiles were retained for the evaluation if they had temperature and salinity observations over 0–500 m. Unstable profiles were removed if more than 5% of the depths had negative buoyancy frequency values. Of the 10 279 hydrographic casts extracted from the WOD and CalCOFI databases, 9365 were used in the evaluation (3156 CalCOFI, 5084 CTD, 1125 Argo). In addition, Argo profiles from 2002 to 2016 were selected to compare with  $PC_{1,rf}$  beyond the temporal range of the ending date of WCRA31 (described below).

#### Evaluation of WCRA31 and observed physical conditions

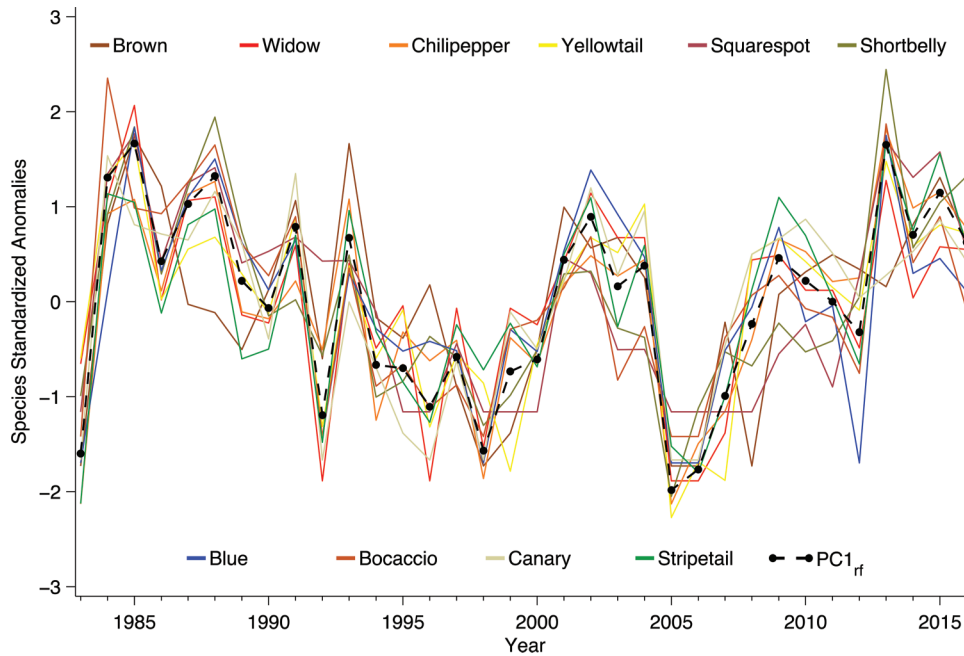
Even though the EN3 data set used in the data assimilation contains data from WOD and Argo, an evaluation is required because the isopycnal depths extracted from WCRA31 may have positive biases, with isopycnal depths deeper than observations ([Schroeder et al. 2014](#)). Our objective is to extend the water mass analysis using Argo data, and we need to be confident that there are no biases in the model isopycnal depths that could potentially result in misleading spiciness values.

For each CTD and Argo profile, the nearest WCRA31 grid point and time interval were identified and daily means of temperature and salinity profiles were extracted from the model. For both observational and WCRA31 hydrographic profiles, potential density and spiciness were calculated for isopycnal surfaces ranging from  $\sigma_\theta = 26.0$  to  $26.8 \text{ kg}\cdot\text{m}^{-3}$ . These isopycnals range between depths of 100 to 400 m, which comprise upper waters in the CCE. For each of these isopycnal surfaces, the depth of the isopycnal and spiciness on the isopycnal was grouped by season (winter: January–March, spring: April–June, summer: July–September, and winter: October–December). We evaluate WCRA31 using a combination of observed hydrographic data to determine which isopycnal surface of the model has the best fit to observational values ([Fig. 3](#); also refer to online Supplementary material, [Figs. S.1–S.2<sup>1</sup>](#)). The isopycnal surface used to define upper waters was determined based on the highest Pearson’s correlations between the observational and WCRA31 physical data ([Table S.1<sup>1</sup>](#)). Spiciness on this isopycnal is symbolized by  $\Pi$  and will be used to characterize interannual variability of source waters and how it relates to pelagic juvenile rockfish abundances.

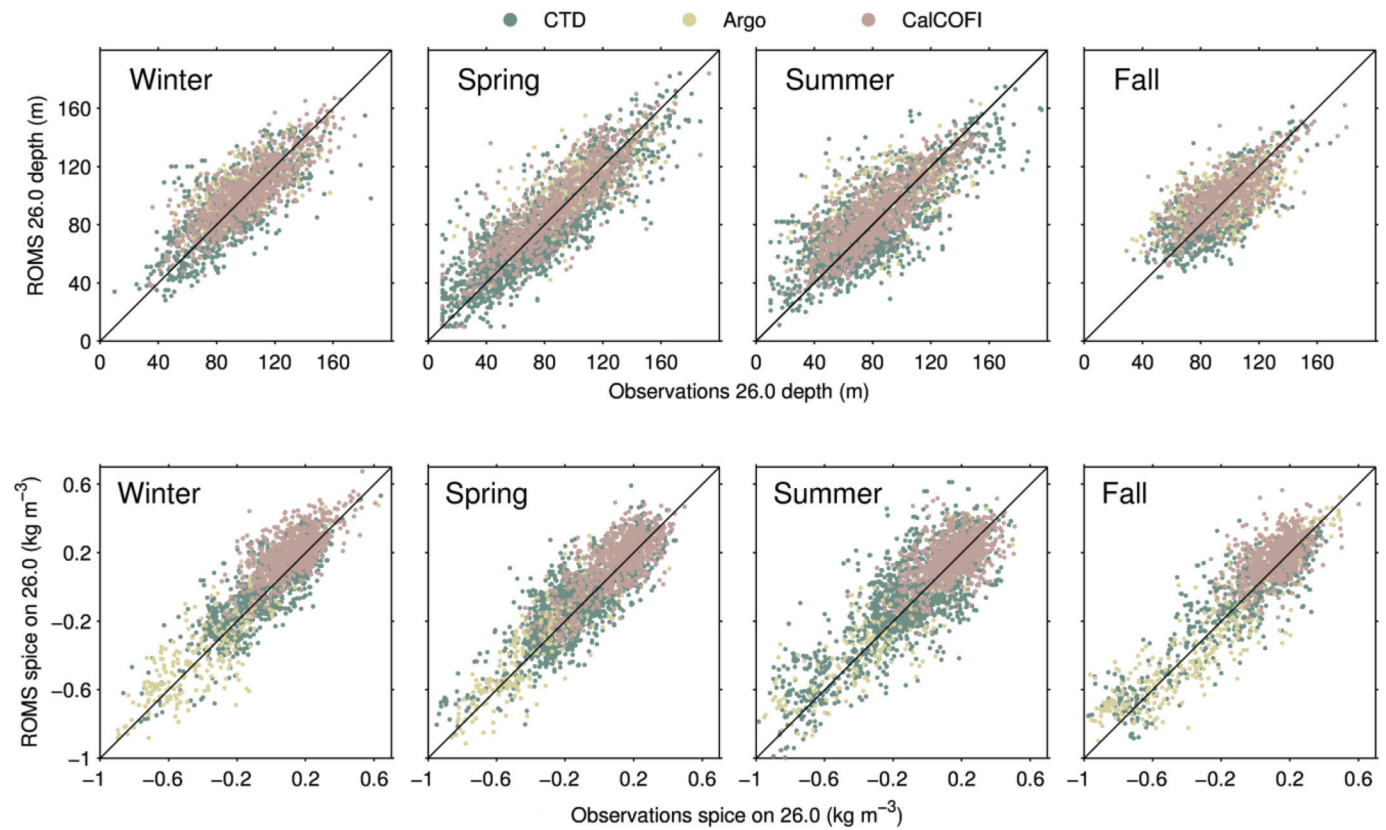
<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0480>.



**Fig. 2.** Standardized abundance of the top ten most abundant pelagic juvenile rockfish species and the common trend ( $PC1_{rf}$ ) sampled by the RREAS midwater trawls (see Fig. 1 inset for sampling locations) during May and June.  $PC1_{rf}$  was normalized by the square root of the first eigenvalue.



**Fig. 3.** (Top row) Relationships between observed and modeled depth of the 26.0 potential density isopycnal, per season. (Bottom row) Relationships between observed and modeled spiciness at the depth of the 26.0 isopycnal, per season (see Fig. 1 for spatial domain). The modeled data were extracted from the WCRA31 ROMS reanalysis over the 1980–2010 time period.



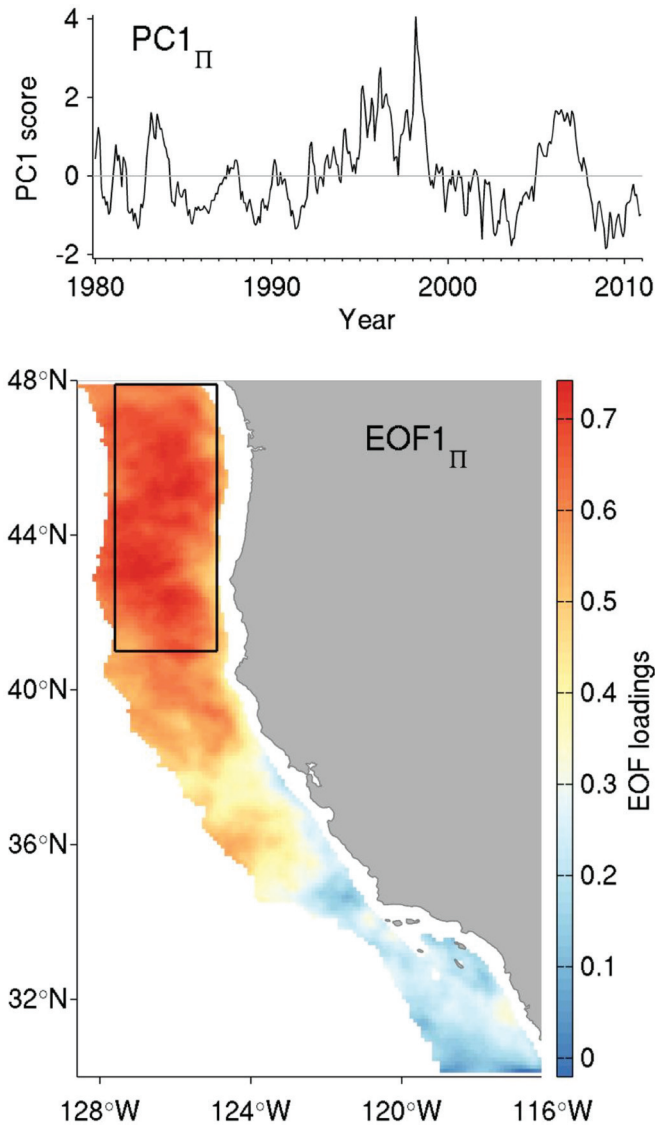
**Source water aspects and variability in the CCE**

Large-scale variations of source waters are characterized by the first mode of the empirical orthogonal function (EOF) analysis of II. The domain for the EOF analysis is from 30°N to 48°N and for

ROMS grid points extending to 300 km offshore and for depths greater than 500 m. The 300 km offshore extent is an estimate of the annual mean boundary for the California Current (Auaud et al. 2011), and the domain roughly covers the area from the shelf

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**Fig. 4.** Results of an empirical orthogonal function (EOF) analysis assessing the integrated spatiotemporal variability of spiciness at the depth of the 26.0 potential density isopycnal ( $\Pi$ ): (top) the first principal component time series; (bottom) the spatial loadings of the first mode. The first mode of the EOF analysis captures 26% of the total variance. The black box ( $41^{\circ}\text{N}$ – $48^{\circ}\text{N}$ ,  $127.6^{\circ}\text{W}$ – $124.9^{\circ}\text{W}$ ) contains the area of the highest EOF1 loadings.



break and continental slope. For grid points within this domain, the data matrix for the EOF analysis consists of monthly means of  $\Pi$  from 1980 to 2010. Each time series of the data matrix had a long-term trend removed and was normalized by the standard deviation of the time series. The first principal component ( $\text{PC1}_{\Pi}$ ) of the EOF analysis is used as a monthly index of source water variation within the California Current. Because of the Lagrangian nature of the Argo data, the extension of the upper water variability analysis to 2016 is not possible using EOF analysis. Instead, two monthly time series of  $\Pi$  are constructed from the WCRA31 (1980–2010) and Argo (2002–2016) data sets. These time series are the area average of all profiles contained within the box ( $41^{\circ}\text{N}$ – $48^{\circ}\text{N}$ ,  $127.6^{\circ}\text{W}$ – $124.9^{\circ}\text{W}$ ) of highest loadings of the first empirical orthogonal function ( $\text{EOF1}_{\Pi}$ ; Fig. 4). This time series extension is important because it provides two independent assessments for using spiciness of upper waters to evaluate the common trend of pelagic juvenile rockfish abundance variability.

To determine the extent to which source waters vary among low and high pelagic juvenile rockfish abundance years, we perform a mixing analysis on the  $\sigma_{\theta} = 26.0 \text{ kg}\cdot\text{m}^{-3}$  density surface. For the mixing analysis, we will follow Thomson and Krassovski (2010) and Meinvielle and Johnson (2013) and assume that mixing occurs along isopycnals and is primarily defined by two end-member source water masses: Pacific Subarctic Upper Water (PSUW; in Meinvielle and Johnson (2013), this water mass is referred to as North Pacific Water) and Pacific Equatorial Water (PEW). PSUW and PEW potential temperature, salinity, and DO end-member values on the  $\sigma_{\theta} = 26.0 \text{ kg}\cdot\text{m}^{-3}$  isopycnal were defined by taking regional averages in the Pacific Subarctic ( $47.5^{\circ}\text{N}$ – $53.5^{\circ}\text{N}$ ,  $149.5^{\circ}\text{W}$ – $139.5^{\circ}\text{W}$ ) and the eastern Equatorial Pacific ( $0.5^{\circ}\text{N}$ – $10.5^{\circ}\text{N}$ ,  $109.5^{\circ}\text{W}$ – $99.5^{\circ}\text{W}$ ); annual averages were obtained from the World Ocean Atlas (Locarnini et al. 2010; data downloaded from ERDDAP server at [https://upwell.pfeg.noaa.gov/erddap/griddap/noaa\\_pmel\\_bef7\\_52b0\\_a333.html](https://upwell.pfeg.noaa.gov/erddap/griddap/noaa_pmel_bef7_52b0_a333.html)). Since temperature and salinity are conservative tracers, the percentage of PSUW along the  $\sigma_{\theta} = 26.0 \text{ kg}\cdot\text{m}^{-3}$  isopycnal can be determined by a simple linear relationship between the PSUW and PEW end-members on a T–S diagram. Data for the T–S diagram are taken from Argo profiles occurring in the area of highest  $\text{EOF1}_{\Pi}$  loading (Fig. 4) for the months of April and May. We compared T–S properties relative to source water aspects for years of high (2002, 2004, 2013) and low (2005, 2006, 2007) pelagic juvenile rockfish abundance (Ralston et al. 2013) and during the last 3 years (2014–2016).

#### Assessment of juvenile rockfish variability

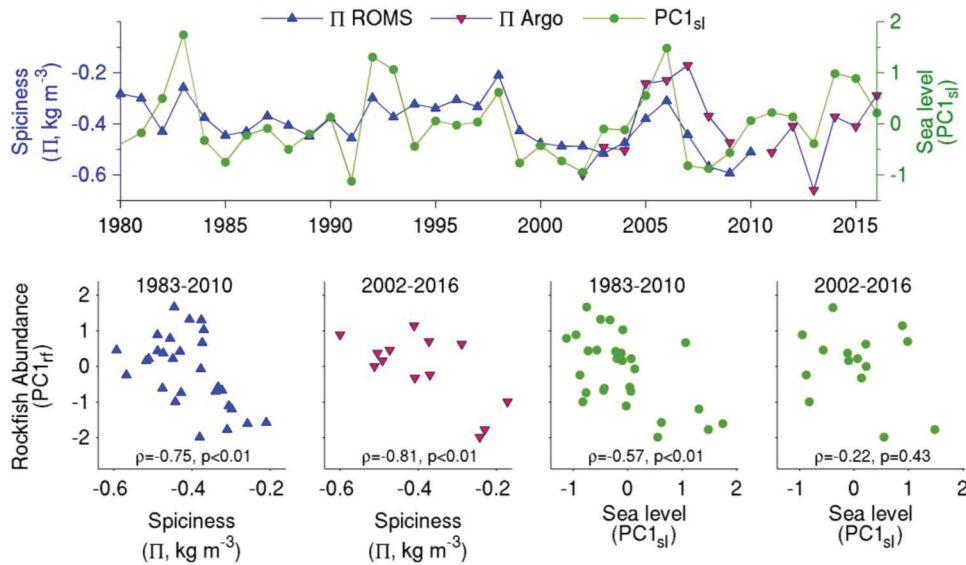
To test our hypothesis, we used Spearman's rank correlation coefficients ( $\rho$ ) on detrended time series to assess the coherence between  $\text{PC1}_{\text{rf}}$  with monthly values of  $\text{PC1}_{\Pi}$ , sea level anomaly ( $\text{PC1}_{\text{sl}}$ ; Ralston et al. 2013), upwelling index at  $39^{\circ}\text{N}$  (Bakun 1973; Schwing et al. 1996), and a variety of basin-scale ocean climate indicators (e.g., Pacific Decadal Oscillation, Mantua et al. 1997; Multivariate El Niño Southern Oscillation Index, Wolter and Timlin 1998; and the North Pacific Gyre Oscillation, Di Lorenzo et al. 2008). Previously, Ralston et al. (2013) compared these indices with their  $\text{PC1}_{\text{rf}}$  index for the 1983–2010 period. They found that the sea level anomaly index ( $\text{PC1}_{\text{sl}}$ ) had the best agreement with the rockfish index during April–May and that the relationship was negative (see Results), indicating that environmental conditions during years of implied increased equatorward flow (i.e., southerly flow) are associated with greater recruitment in rockfish populations. We reevaluated the strength of the relationship to the sea level anomaly index to determine the extent to which their results held true during the recent LMH. Importantly, to evaluate the difference between surface and subsurface conditions during the LMH period (2014–2016), we compared the  $\text{PC1}_{\text{rf}}$  with spiciness of upper waters during two different but overlapping time periods: (a) WCRA31 from 1980 to 2010 and (b) Argo profiles from 2002 to 2016.

## Results

### Evaluation of observed and modeled ocean conditions

Isopycnal depths and spiciness on isopycnals derived from WCRA31 in the upper waters have the best agreement with WOD observations on the 26.0 isopycnal (Figs. 3, S.1<sup>1</sup>, S.2<sup>1</sup>; Table S.1<sup>1</sup>). Modeled isopycnal depths and spiciness have small biases across seasons, with winter and spring values displaying small biases in both isopycnal depth and spiciness. The isopycnal depths for the deeper isopycnals (e.g.,  $>26.5$ ) have biases of larger than 20 m, where the observed isopycnals are much deeper than the WCRA31 model results (Fig. S.1<sup>1</sup>). In general, the correlations for spiciness are low ( $<0.4$ ) for isopycnals greater than 26.4 and for latitudes greater than  $39^{\circ}\text{N}$  (Fig. S.2<sup>1</sup>). On the 26.0 isopycnal, biases between observation and WCRA31 are  $\sim 0.1 \text{ kg}\cdot\text{m}^{-3}$ , with observations greater than the model. The WCRA31 model corresponds best

**Fig. 5.** (Top) Time series of April–May averages of spiciness on the 26.0 isopycnal ( $\Pi$ ) and sea level anomaly ( $PC1_{sl}$ ). Spiciness was calculated from WCRA31 ROMS, and Argo profiles were area-averaged over  $41^{\circ}\text{N}$ – $48^{\circ}\text{N}$ ,  $127.6^{\circ}\text{W}$ – $124.9^{\circ}\text{W}$ . The sea level anomaly ( $PC1_{sl}$ ) is derived from tide gauge measurements along the California coast. (Bottom) Relationships between pelagic juvenile rockfish abundance ( $PC1_{rf}$ ) and the time series displayed in the top plot for two different time periods: 1983–2010 and 2002–2016.



with observations in the southern portion of the CCE ( $<39^{\circ}\text{N}$ ), which may be attributed to the southern portion having more than twice the number of observations than in the north (Fig. S.3<sup>1</sup>). Since the 26.0 isopycnal evaluations displayed the highest correlation and least overall bias of all the upper water isopycnals, it was selected to represent  $\Pi$  for additional assessment with  $PC1_{rf}$ .

Long-term trends (1980–2010) of  $\Pi$  from the ROMS model are negative offshore and positive along shore for areas between  $32^{\circ}\text{N}$ – $38^{\circ}\text{N}$  and  $40^{\circ}\text{N}$ – $48^{\circ}\text{N}$  (Fig. S.4<sup>1</sup>), which are similar to the spiciness trends over 1950–2012 reported by Meinville and Johnson (2013). The first mode of the EOF analysis for  $\Pi$  explains 26% of the total variance. The first principal component ( $PC1_{\Pi}$ ) is dominated by low frequencies and has the largest positive values during major El Niño events (1983 and 1998) and other warm events (2005–2007) in the CCE (Fig. 4). The highest loadings of  $PC1_{\Pi}$  occur in the north, especially between  $41^{\circ}\text{N}$ – $48^{\circ}\text{N}$  for distances between 50 and 280 km offshore (Fig. 4). Negative values of  $PC1_{\Pi}$  are associated with lower spice values (i.e., minty) in these northern waters of highest loadings and are indicative of  $\Pi$  containing a greater fraction of subarctic upper waters.

We extracted  $\Pi$  values from both the WCRA31 and Argo profiles in the region of the highest EOF $_{1\Pi}$  loadings ( $41^{\circ}\text{N}$ – $48^{\circ}\text{N}$ , 50–280 km offshore) to evaluate the coherence between observed and modeled values (Figs. 1 and 5). Within this region, time series of  $\Pi$  for the WCRA31 model and from the Argo profiles were averaged over April and May to conduct another evaluation of the model to examine variation of  $\Pi$  for years beyond 2010. The time series of  $\Pi$  for WCRA31 has a significant long-term (1980–2010) negative trend of  $-0.0049 \text{ kg}\cdot\text{m}^{-3}\cdot\text{year}^{-1}$  ( $p < 0.01$ ). The three highest values of this time series occurred in El Niño years (1983 and 1998), and the three lowest values occurred at the end of the time series from 2008 to 2010. For the overlapping time period (2002–2010) for WCRA31 and Argo time series, the 3 years of highest values occurred for the same years, 2005–2007; the 3 years of lowest values, 2008–2010, were only covered by the Argo data in 2008 and 2009, and these 2 years of Argo data are low but not the lowest values of the time series. The 2013 value is the lowest of the Argo  $\Pi$  time series. The values during 2014–2015 are low, with spice values around  $-0.4 \text{ kg}\cdot\text{m}^{-3}$ . During 2016 the value of  $\Pi$  is high,  $\sim -2.5 \text{ kg}\cdot\text{m}^{-3}$ , but lower than those during the high years of 2005–2007.

#### Indicators of rockfish recruitment variability

A monthly lagged correlation analysis between  $PC1_{\Pi}$  and  $PC1_{rf}$  indicates significant ( $p < 0.01$ ) negative correlations for January through June. The correlations strengthen with month (Fig. S.5<sup>1</sup>), where January has the lowest correlation ( $\rho = -0.59, p < 0.01$ ), and April, May, and June have the highest correlations ( $\rho = -0.78, -0.73, -0.76, p < 0.01$ , respectively). The negative correlations suggest that greater juvenile rockfish abundances occur when source waters are more minty.

The time series of April–May  $\Pi$  values derived from the WCRA31 model for 1980–2010 have similarly high negative correlation ( $\rho = -0.76, p < 0.01$ ) with the rockfish index (Fig. 5). The April–May  $\Pi$  values derived from the Argo profiles during 2002–2016 also have similar correlation to the rockfish index ( $\rho = -0.81, p < 0.03$ ; Fig. 5). The time series constructed from the Argo profiles should be interpreted with some caution, since the number of profiles for a given year is highly variable (e.g., 2010 had zero profiles, 2011 had only three profiles, 2006 had the maximum number with 20).

We revisited the analysis of Ralston et al. (2013) to include the LMH during 2014–2016. This was done by performing correlations on the Pacific Decadal Oscillation, Multivariate ENSO Index, North Pacific Gyre Oscillation,  $PC1_{sl}$ , upwelling index at  $39^{\circ}\text{N}$  (UI  $39^{\circ}\text{N}$ ), and  $\Pi$  for two time periods, 1983–2010 and 2002–2016 (Table 1). We found the relationship between April and May  $PC1_{sl}$  for 2002–2016 is considerably weaker than that previously reported for the 1983–2010 period ( $\rho = -0.22, p = 0.43$ ). This degradation of the previous relationship is primarily driven by the higher values of  $PC1_{sl}$  (indicative of high coastal sea level and weak southerly transport) during 2014–2016 period, which were years of high rockfish abundances (Fig. 5; Table 1). Specifically, 2014 and 2015 represented the second and fourth highest years of the (truncated) 2002–2016 rockfish index, while also representing the second and third highest observations for relative sea level height during this time period. Of the other variables, only the upwelling index (UI  $39^{\circ}\text{N}$ ) and  $\Pi$  have higher correlations for the 2002–2016 time period compared with 1983–2010. However, the correlations between UI  $39^{\circ}\text{N}$  and the rockfish index for both time periods were not significantly correlated (1983–2010:  $\rho = 0.27, p = 0.17$ ; 2002–2016:  $\rho = 0.41, p = 0.13$ ). The correlations between  $\Pi$  and the rockfish index was  $\rho = -0.76$  ( $p < 0.01$ ) during 1983–2010 and  $\rho = -0.81$



**Table 1.** Spearman's rank correlation  $\rho$  values ( $p$  values are in parentheses) between time series of juvenile rockfish abundance ( $PC1_{rf}$ ) and April–May time series of ocean climate state indicators (Pacific Decadal Oscillation (PDO), Multivariate El Niño Southern Oscillation Index (MEI), and North Pacific Gyre Oscillation (NPGO)), coastal sea level height ( $PC1_{sl}$ ), upwelling index at 39°N (UI 39°N; Northern California, Pt. Arena), and spiciness at the depth of the 26.0 potential density isopycnal ( $\Pi$ ).

Time period	PDO	MEI	NPGO	$PC1_{sl}$	UI 39°N	$\Pi$
1983–2010	-0.37 (0.06)	-0.20 (0.30)	0.53 (<0.01)	-0.57 (<0.01)	0.27 (0.17)	-0.76 (<0.01)
2002–2016	-0.06 (0.84)	0.17 (0.56)	0.11 (0.70)	-0.22 (0.43)	0.41 (0.13)	-0.81 (<0.01)

**Note:** The 1983–2010 spiciness time series is derived from the WCRA31 ROMS reanalysis, and the 2002–2016 spiciness time series is derived from Argo profiles.

( $p < 0.01$ ) during 2002–2016, suggesting that the influence of the marine heat wave did not dramatically reduce rockfish productivity.

### Recruitment variability relative to patterns in source waters

Our results regarding the relationship of upper water provide context to understand the impacts of source water variability on rockfish recruitment in the CCE (Fig. 6). To evaluate source water variability and juvenile rockfish abundance patterns, we plotted T–S curves of PSUW and PEW against T–S curves derived from Argo profiles during April and May (Fig. 1 inset) found within the box of highest EOF1 loadings (Fig. 4) for years of high (2002, 2004, 2013), low (2005, 2006, 2007)  $PC1_{rf}$  values and for the last 3 years 2014–2016 (Figs. 6 and S.6'). The composite T–S curve of the 3 years of high  $PC1_{rf}$  values is skewed towards more minty waters of the PSUW end-member, composed of ~78% PSUW concentration on the 26.0 isopycnal. The coldest and freshest profiles from Argo occurred during 2002 (Fig. S.6'). The composite T–S curve of the lowest  $PC1_{rf}$  years is skewed towards spicier waters of the PEW end-member, with PSUW concentrations of ~66%. During 2005, unusual warmer and saline waters were observed in the northern CCE, and T–S curves were similar to those experienced during 1993. The T–S curves of the last 3 years lay between the high and low year composites, with 2014–2015 at ~74% and 2016 at ~70% PSUW concentrations. The warm waters of the 2014–2016 LMH were surface-oriented with the largest temperature deviations above the 25.5 isopycnal isopleth. Since mixing occurs mostly along isopycnals, intrusions of subarctic water (representing a greater percentage of PSUW concentrations) occur during years of greater juvenile rockfish abundances.

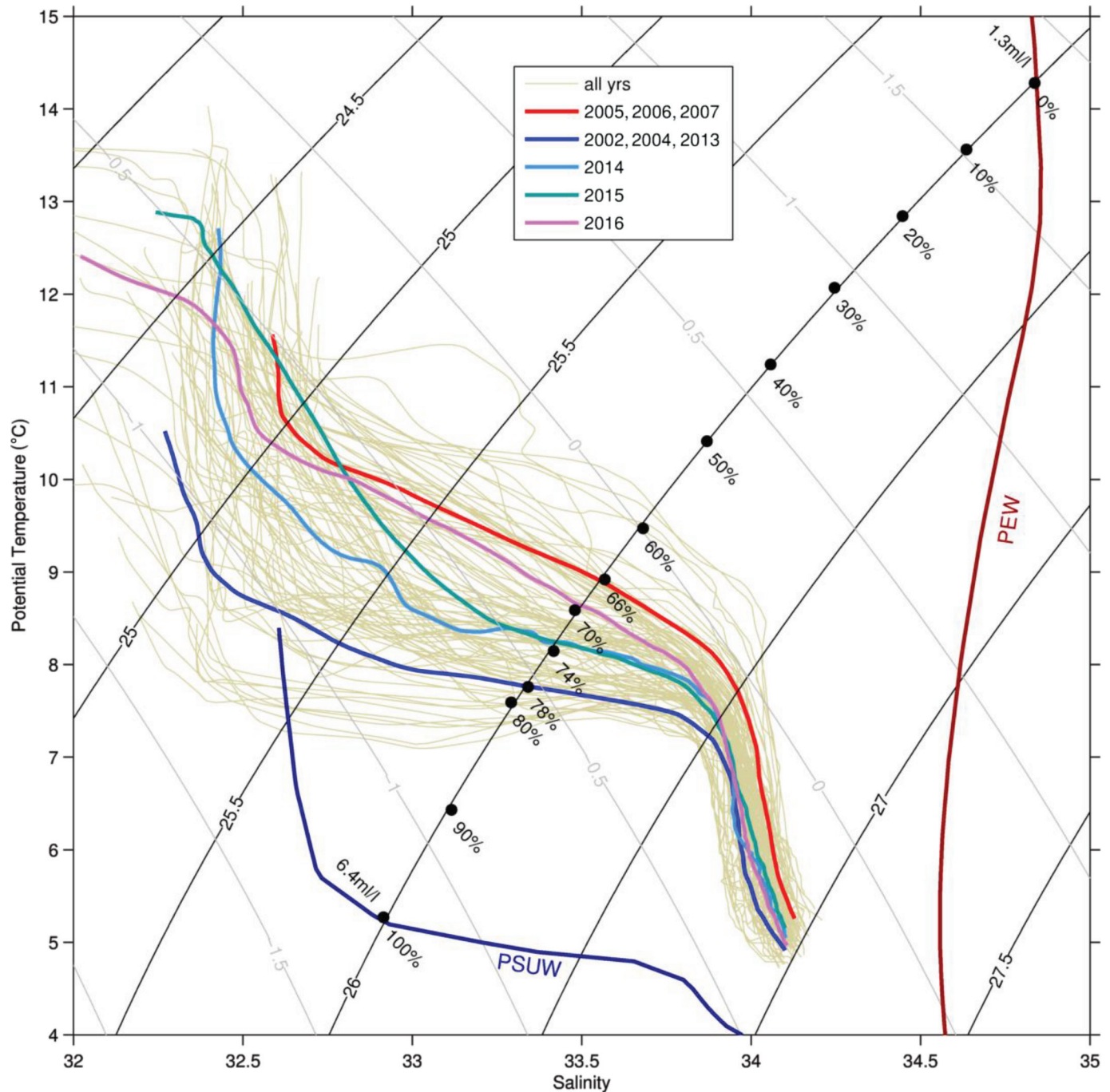
### Discussion

During 2013–2016, the North Pacific Ocean experienced episodes of unusually warm sea surface temperatures (Bond et al. 2015; Di Lorenzo and Mantua 2016; Leising et al. 2015) and an El Niño that influenced the region during winter of 2015–2016. The vertical extent of the heating of the LMH in the water column appeared to be within the upper 100 m, and observations suggest it had substantial ecosystem impacts, with major changes in community structure of copepod composition (Leising et al. 2015; McClatchie et al. 2016b), the species composition and diversity of the epipelagic micronekton (forage) assemblage (Sakuma et al. 2016; Santora et al. 2017a), toxic algal blooms, and California sea lion (*Zalophus californianus*) mortalities (Leising et al. 2015; McCabe et al. 2016). The high abundances of pelagic juvenile rockfish during the LMH and 2016 El Niño event are contrary to many of these surface-oriented negative ecosystem impacts (i.e., subtropical warm water influences) and are inconsistent with the results of Ralston et al. (2013) due to the combined observations of high pelagic juvenile rockfish abundance with high relative coastal sea level height. However, the results are consistent with the interpretation of Ralston et al. (2013), namely, that rockfish recruitment is observed to be considerably greater during years of more subarctic water mass conditions in the CCE. Thus, while the nominal indicator evaluated by Ralston et al. (2013) did not persist (by virtue of extraordinarily unusual environmental conditions), the conceptual relationship proposed in that analysis, the relationship between California Current source waters and rockfish recruit-

ment, has been shown here to be robust upon the development of a more appropriate indicator for this process. It is worth noting that in a later paper Ralston et al. (2015) attempted to characterize source water variability and its effect on trawl catches by estimating spiciness from CTD data collected in situ during surveys conducted in central California. While they found no significant relationship between spiciness and faunal catch rates, their calculations were based on water properties at the depth of trawl sampling (30 m), which supports our conclusion that conditions much deeper in the water column in the months preceding the survey and upstream from the survey area in the northern part of the CCE (e.g., off Oregon and Washington; Fig. 4) are key to understanding variability in rockfish recruitment. Specifically, our approach addresses interannual variability of water masses in the CCE and potentially relates strongly to ocean condition at the depth at which adult rockfish inhabit. This improved indicator is therefore more robust compared with indicators derived from ocean surface conditions.

In the CCE, coastal upwelling plays a critical role in providing nutrients essential for primary productivity and population growth of secondary and tertiary consumers, which extends to midwater to benthic species, as well as to air-breathing predators (Checkley and Barth 2009; Jacox et al. 2016; Santora et al. 2017b). However, there has long been a perceived interaction between source waters to the CCE and productivity, which presumably relates to the nutrient and oxygen content of those waters being upwelled (Chelton et al. 1982; Lynn and Simpson 1987). Productivity within the CCE, on interannual time scales, is partially a function of latitudinal shifts in the position of the North Pacific Current (Parrish et al. 2000; Sydeman et al. 2011). Similarly, decadal-scale variability of low-salinity upper waters within the core of the North Pacific Current may propagate downstream into the CCE and bring source waters high in DO onto the continental shelf (Pozo Buil and Di Lorenzo 2017). These years will also have a greater DO content due to the larger fraction of PSUW water (Meinvielle and Johnson 2013), which should have consequences for the biological productivity within the CCE. Because of climate change, increased ocean surface warming may impede the effectiveness of upwelling to deliver nutrients to the surface because of increased stratification (Gilly et al. 2013; Bakun et al. 2015). However, the interaction of biological production as a result of the distribution of source waters and regional ocean climate and upwelling processes can be complex. An example was a summer 2002 hypoxic event (Grantham et al. 2004) on the Oregon inner shelf that was associated with increased respiration due to the input of nutrient-rich subarctic water (Freeland et al. 2003). Consequently, it is difficult to predict how climate change may alter the conditions that drive early life history processes for benthic species, such as adult rockfish. The ecosystem state during the LMH might give us some indication of what we might expect, with a wide range of ecosystem impacts for the pelagic community complex and with benthic production different from surface conditions. Therefore, monitoring source water variability may improve our understanding of ecosystem dynamics and in turn benefit management of ecosystem services in the face of ongoing climate variability and future climate change.

**Fig. 6.** Temperature–salinity (T–S) diagram showing Argo profiles sampled between 41°N–48°N and 127.6°W–124.9°W during April and May 2002–2016. Also shown are characteristic curves of Pacific Subarctic Upper Water (PSUW) and Pacific Equatorial Water (PEW) and dissolved oxygen content on the 26.0 potential density isopycnal. T–S curves during high rockfish abundance years (blue) have higher percentage of PSUW, while during low abundance years (red) have a higher percentage of PEW. T–S curves are also shown for the years of the large marine heat wave (2014–2015) and the 2016 El Niño. Gray contours are constant spiciness and black contours are constant potential density. Black circles along the 26.0 potential density isopycnal mark various percentages of PSUW with the assumption that mixing occurs along the isopycnal.



#### Importance of deriving depth-specific physics for groundfish

The rockfish species in this study are primarily the winter-spawning, shelf-break-associated species that make up the majority of both the biomass and the fisheries targets in the CCE (Hilborn et al. 2012; Miller et al. 2014). Our analysis strongly indicates that transport and source waters in the CCE are a key factor in determining density-independent processes leading to subsequent recruitment to adult populations for these species, although the exact mechanism itself remains elusive. The connec-

tion to transport (primarily as aliased by sea level) has long been acknowledged as a key driver of productivity and recruitment success in the CCE (Parrish et al. 1981; Chelton et al. 1982) and indeed has been strongly linked to both pelagic juvenile abundance (Laidig et al. 2007; Ralston et al. 2013) and realized recruitment to adult populations based on stock assessments (Schirripa and Colbert 2006; Stachura et al. 2014). For sablefish, one of the most valuable groundfish in the CCE and a stock that also demonstrates very high recruitment variability, Schirripa and Colbert



(2006) argued that the likely mechanism was the availability of suitable forage for early life stages, as high transport years tended to be associated with greater abundance of northern copepod species known to be both larger and to contain greater lipid reserves than southern species (consistent with Keister et al. 2011; Peterson et al. 2014). Ralston et al. (2013) similarly suggested that this mechanism was likely to be related to foraging for central California rockfish, as well as advection towards (or away from) optimal habitat for early life history stages. Further, Ralston et al. (2015) compared an index of epipelagic forage community structure with large-scale, regional, and in situ oceanographic variables and found significant relationships among isopycnal depth, upwelling indices, and forage community structure, and especially with sea level height in winter, highlighting the importance of transport conditions on the CCE food web.

The biogeochemical properties of the source waters are also important. Oxygen has long been known to define habitat suitability, particularly depth distribution, for rockfish and other groundfish in the CCE (Vetter and Lynn 1997; Keller et al. 2010; McClatchie et al. 2010), and rockfish are thought to be particularly vulnerable to the impacts of low oxygen during the spawning season, due to the increased metabolic demands associated with gestation, which may be associated with 60% to 100% greater oxygen demands than nongestating individuals (Boehlert et al. 1991; Hopkins et al. 1995). Recently hatched larvae are highly vulnerable to low oxygen levels, as ongoing studies suggest that mortality rates increase substantially at oxygen levels below 2.8 mg·L<sup>-1</sup> (N. Kashef, D. Stafford, and S. Sogard, unpublished data). Although average oxygen levels in most benthic adult rockfish habitats are well above that level (Gilly et al. 2013; Keller et al. 2015), short-term variability in oxygen to lower levels during the reproductive season could potentially result in impacts on reproductive output and success as a result of physiological processes associated with the reproductive ecology of rockfish (Hopkins et al. 1995). Our results show that subarctic water mass (PSUW) concentrations between high and low rockfish recruitment years can decline up to 20% (Fig. 6). Since PSUW has a much higher preformed dissolved oxygen content than PEW (6.4 versus 1.3 mL·L<sup>-1</sup>; Fig. 6), a greater fraction of PSUW within the CCE should supply gestating, spawning, and larval rockfish with an environment higher in DO (see figure 10 in Meinvielle and Johnson 2013). Although it is unlikely that environmental impacts on spawning females through oxygen concentrations alone drive the highly variable recruitment observed in these populations, it is likely that year class strength is a function of the cumulative impacts of multiple environmental factors operating on both the physiology of gestating and spawning females of these primitively viviparous species as well, as that influences the density-independent survival rates of early and late stage larvae (Houde 2008).

### Ecosystem and management implications

Understanding the factors that drive variable recruitment in marine fish populations and disentangling such factors from underlying productivity functions (e.g., stock–recruitment relationships) is critical for estimation of population productivity in stock assessments (Beverton and Holt 1957; Conn et al. 2010; Mangel et al. 2013). Along the US west coast, rockfish are perceived as particularly challenging for stock assessment and management, due to the combined characteristics of slow growth, late maturity, high longevity, and extreme recruitment variability (Clark 2002; Berkeley et al. 2004; Thorson et al. 2013). Our results on source water variability and ocean climate dynamics during the recent LMH of 2014–2016 improve the understanding of environmental drivers of recruitment variability for these populations. Accounting for these relationships will help to better understand the near-term drivers of such variability in stock assessment and the longer-term implications of climate-driven changes in transport

and upwelling dynamics as related to ecosystem functioning throughout the CCE.

Through use of a coupled ocean modeling and observational framework, we developed a deeper understanding of source water variability as a driver of abundance of juvenile rockfish 3 to 4 months after parturition. Current stock assessment models for many adult rockfish incorporate abundance data of these life history stages in their recruitment estimates. Prior to our study, coastal sea level and the associated transport strength were reliable indicators of juvenile rockfish abundance (Ralston et al. 2013). Yet, coastal sea level failed to persist as a strong indicator during the LMH of 2014–2016, coinciding with unanticipated high abundance of juvenile rockfish despite high relative sea level. The relationships quantified in this study based on subsurface conditions persisted through the recent anomalous events and was superior retrospectively. These findings hold promise to reduce uncertainty in our stock assessments and associated harvest limits (Stige et al. 2013; Stachura et al. 2014) and for monitoring ecosystem conditions. Prior to recruitment to the fishery, juvenile rockfish are a critical forage fish for predators (e.g., seabirds, sea lions, and salmon), and their availability corresponds closely with predator diets (McClatchie et al. 2016b; Wells et al. 2017; Daly et al. 2017; Warzybok et al. 2018). Our findings on source water variability and presumed transport anomalies are likely useful for quantifying the environmental determinants of juvenile rockfish availability and, more notably, variability in the trophic structure of the ecosystem.

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### References

- Auad, G., Roemmich, D., and Gilson, J. 2011. The California Current System in relation to the Northeast Pacific Ocean circulation. *Prog. Oceanogr.* **91**: 576–592. doi:10.1016/j.pcean.2011.09.004.
- Bakun, A. 1973. Coastal upwelling indices, West Coast of North America, 1946–71. NOAA Tech. Rep. NMFS SSRF-671.
- Bakun, A., Black, B.A., Bograd, S.J., Garcia-Reyes, M., Miller, A.J., Rykaczewski, R.R., and Sydeman, W.J. 2015. Anticipated effects of climate change on coastal upwelling ecosystems. *Curr. Clim. Change Rep.* **1**: 85–93. doi:10.1007/s40641-015-0008-4.
- Beamish, R.J. 1993. Climate and exceptional fish production off the west coast of North America. *Can. J. Fish. Aquat. Sci.* **50**(10): 2270–2291. doi:10.1139/f93-252.
- Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, **29**: 23–32. doi:10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2.
- Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. HMSO, London. Republished by Chapman and Hall, 1993.
- Boehlert, G.W., Kusakari, M., and Yamada, J. 1991. Oxygen consumption of gestating female *Sebastes schlegelii*: estimating the reproductive costs of livebearing. In *Rockfishes of the genus Sebastes: their reproduction and early life history. Developments in environmental biology of fishes*. Vol. 11. Edited by G.W. Boehlert and J. Yamada. Springer, Dordrecht. doi:10.1007/978-94-011-3792-8\_9.
- Bograd, S.J., Buil, M.P., Di Lorenzo, E., Castro, C.G., Schroeder, I.D., Goericke, R., Anderson, C.R., Benitez-Nelson, C., and Whitney, F.A. 2015. Changes in source waters to the Southern California Bight. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **112**: 42–52. doi:10.1016/j.dsr2.2014.04.009.
- Bond, N.A., Cronin, M.F., Freeland, H., and Mantua, N. 2015. Causes and impacts

- of the 2014 warm anomaly in the NE Pacific. *Geophys. Res. Lett.* **42**: 3414–3420. doi:10.1002/2015GL063306.
- Checkley, D.M., and Barth, J.A. 2009. Patterns and processes in the California Current System. *Prog. Oceanogr.* **83**: 49–64. doi:10.1016/j.pocean.2009.07.028.
- Chelton, D.B., Bernal, P.A., and McGowan, J.A. 1982. Large-scale interannual physical and biological interaction in the California Current. *J. Mar. Res.* **40**: 1095–1125.
- Clark, W.G. 2002. F 35% revisited ten years later. *N. Am. J. Fish. Manage.* **22**: 251–257. doi:10.1577/1548-8675(2002)022<0251:FRTYL>2.0.CO;2.
- Colebrook, J.M. 1977. Annual fluctuations in biomass of taxonomic groups of zooplankton in the Californian Current, 1955–1959. *Fish. Bull.* **75**: 357–368.
- Collins, C.A., Pennington, J.T., Castro, C.G., Rago, T.A., and Chavez, F.P. 2003. The California Current system off Monterey, California: physical and biological coupling. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **50**(14–16): 2389–2404. doi:10.1016/S0967-0645(03)00134-6.
- Conn, P.B., Williams, E.H., and Shertzer, K.W. 2010. When can we reliably estimate the productivity of fish stocks? *Can. J. Fish. Aquat. Sci.* **67**(3): 511–523. doi:10.1139/F09-194.
- Cury, P.M., Shin, Y.J., Planque, B., Durant, J.M., Fromentin, J.M., Kramer-Schadt, S., Stenseth, N.C., Travers, M., and Grimm, V. 2008. Ecosystem oceanography for global change in fisheries. *Trends Ecol. Evol.* **23**: 338–346. doi:10.1016/j.tree.2008.02.005. PMID:18436333.
- Cury, P.M., Fromentin, J.-M., Figuet, S., and Bonhommeau, S. 2014. Resolving Hjort's Dilemma: How is recruitment related to spawning stock biomass in marine fish? *Oceanography*, **27**(4): 42–47. doi:10.5670/oceanog.2014.85.
- Daly, E.A., Brodeur, R.D., and Auth, T.D. 2017. Anomalous ocean conditions in 2015: impacts on spring Chinook salmon and their prey field. *Mar. Ecol. Prog. Ser.* **566**: 169–182. doi:10.3354/meps12021.
- Davis, R.E., Ohman, M.D., Rudnick, D.L., Sherman, J.T., and Hodges, B. 2008. Glider surveillance of physics and biology in the southern California Current system. *Limnol. Oceanogr.* **53**: 2151–2168. doi:10.4319/lo.2008.53.5\_part\_2.2151.
- Di Lorenzo, E., and Mantua, N.J. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nat. Clim. Change*, **6**: 1042–1047. doi:10.1038/nclimate3082.
- Di Lorenzo, E., Schneider, N., Cobb, K.M., Franks, P.J.S., Chhak, K., Miller, A.J., McWilliams, J.C., Bograd, S.J., Arango, H., Curchitser, E., Powell, T.M., and Riviere, P. 2008. North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophys. Res. Lett.* **35**: L08607. doi:10.1029/2007GL032838.
- Fiedler, P.C., and Mantua, N.J. 2017. How are warm and cool years in the California Current related to ENSO? *J. Geophys. Res. Oceans*, **122**: 5936–5951. doi:10.1002/2017JCO13094.
- Flament, P. 2002. A state variable for characterizing water masses and their diffusive stability: spiciness. *Prog. Oceanogr.* **54**: 493–501. doi:10.1016/S0079-6611(02)00065-4.
- Freeland, H.J., Gatién, G., Huyer, A., and Smith, R.L. 2003. Cold halocline in the northern California Current: an invasion of subarctic water. *Geophys. Res. Lett.* **30**(3): 1141. doi:10.1029/2002GL016663.
- Gilly, W.F., Beman, J.M., Litvin, S.Y., and Robison, B.H. 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annu. Rev. Mar. Sci.* **5**: 393–420. doi:10.1146/annurev-marine-120710-100849.
- Grantham, B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., Lubchenco, J., and Menge, B.A. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature*, **429**: 749–754. doi:10.1038/nature02605. PMID:15201908.
- Hare, J.A., Morrison, W.E., Nelson, M.W., Stachura, M.M., Teeters, E.J., Griffis, R.B., Alexander, M.A., Scott, J.D., Alade, L., Bell, R.J., Chute, A.S., Curtis, K.L., Curtis, T.H., Kircheis, D., Kocik, J.F., Lucey, S.M., McCandless, C.T., Milke, L.M., Richardson, D.E., Robillard, E., Walsh, H.J., McManus, M.C., Marancik, K.E., and Griswold, C.A. 2016. A vulnerability assessment of fish and invertebrates to climate change on the northeast U.S. continental shelf. *PLoS ONE*, **11**(2): e0146756. doi:10.1371/journal.pone.0146756. PMID:26839967.
- Hickey, B., MacFadyen, A., Cochlan, W., Kudela, R., Bruland, K., and Trick, C. 2006. Evolution of chemical, biological and physical water properties in the northern California current in 2005: remote or local wind forcing? *Geophys. Res. Lett.* **33**: L22S02. doi:10.1029/2006GL026782.
- Hilborn, R., Stewart, I.J., Branch, T.A., and Jensen, O.P. 2012. Defining trade-offs among conservation, profitability, and food security in the California current bottom-trawl fishery. *Conserv. Biol.* **26**: 257–268. doi:10.1111/j.1523-1739.2011.01800.x. PMID:22443131.
- Hopkins, T.E., Eldridge, M.B., and Cech, J.J. 1995. Metabolic costs of viviparity in yellowtail rockfish, *Sebastes flavidus*. *Environ. Biol. Fishes*, **43**(1): 77–84. doi:10.1007/BF00001819.
- Houde, E.D. 2008. Emerging from Hjort's shadow. *J. Northw. Atl. Fish. Sci.* **41**: 53–70. doi:10.2960/J.v41.m634.
- Huff, D.D., Lindley, S.T., Wells, B.K., and Chai, F. 2012. Green sturgeon distribution in the Pacific Ocean estimated from modeled oceanographic features and migration behavior. *PLoS ONE*, **7**(9): e45852. doi:10.1371/journal.pone.0045852. PMID:23029274.
- Huyer, A., Barth, J.A., Kosro, P.M., Shearman, R.K., and Smith, R.L. 1998. Upper-ocean water mass characteristics of the California current, Summer 1993. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **45**(8): 1411–1442. doi:10.1016/S0967-0645(98)80002-7.
- Ingleby, B., and Huddleston, M. 2007. Quality control of ocean temperature and salinity profiles — historical and real-time data. *Journal Marine Syst.* **65**: 158–175. doi:10.1016/j.jmarsys.2005.11.019.
- Jacox, M., Hazen, E.L., and Bograd, S.J. 2016. Optimal environmental conditions and anomalous ecosystem responses in the California Current. *Sci. Rep.* **6**: 27612. doi:10.1038/srep27612.
- Keister, J.E., Di Lorenzo, E., Morgan, C.A., Combes, V., and Peterson, W.T. 2011. Zooplankton species composition is linked to ocean transport in the Northern California Current. *Glob. Change Biol.* **17**(7): 2498–2511. doi:10.1111/j.1365-2486.2010.02383.x.
- Keller, A.A., Simon, V.H., Chan, F., Wakefield, W.W., Clarke, M.E., Barth, J.A., Kamikawa, D.J., and Fruh, E.L. 2010. Demersal fish and invertebrate biomass in relation to an offshore hypoxic zone along the U.S. West Coast. *Fish. Oceanogr.* **19**(1): 76–87. doi:10.1111/j.1365-2419.2009.00529.x.
- Keller, A., Wallace, J.R., Horness, B.H., Hamel, O.S., and Stewart, I.J. 2012. Variations in eastern North Pacific demersal fish biomass based on the U.S. west coast groundfish bottom trawl survey (2003–2010). *Fish. Bull.* **110**: 205–222.
- Keller, A.A., Ciannelli, L., Wakefield, W.W., Simon, V., Barth, J.A., and Pierce, S.D. 2015. Occurrence of demersal fishes in relation to near-bottom oxygen levels within the California Current large marine ecosystem. *Fish. Oceanogr.* **24**: 162–176. doi:10.1111/fog.12100.
- King, J.R., Agostini, V.N., Harvey, C.J., McFarlane, G.A., Foreman, M.G.G., Overland, J.E., Di Lorenzo, E., Bond, N.A., and Aydin, K.Y. 2011. Climate forcing and the California Current ecosystem. *ICES J. Mar. Sci.* **68**: 1199–1216. doi:10.1093/icesjms/fsr009.
- Laidig, T.E., Chess, J.R., and Howard, D.F. 2007. Relationship between abundance of juvenile rockfishes (*Sebastes* spp.) and environmental variables documented off northern California and potential mechanisms for the covariation. *Fish. Bull.* **105**: 39–48.
- Leising, A.W., Schroeder, I.D., Bograd, S.J., Abell, J., Durazo, R., Gaxiola-Castro, G., Bjorkstedt, E.P., Field, J., Sakuma, K., Robertson, R.R., Goericke, R., Peterson, W.T., Brodeur, R., Barceló, C., Auth, T.D., Daly, E.A., Suryan, R.M., Gladics, A.J., Porquez, J.M., McClatchie, S., Weber, E.D., Watson, W., Santora, J.A., Sydeman, W.J., Melin, S.R., Chavez, F.P., Golightly, R.T., Schneider, S.R., Fisher, J., Morgan, C., Bradley, R., and Warybok, P. 2015. State of the California Current 2014–15: impacts of the warm-water “blob”. *CalCOFI Rep.* **56**: 31–68.
- Locarnini, R.A., Mishonov, A.V., Antonov, J.I., Boyer, T.P., and Garcia, H.E. 2010. *World Ocean Atlas 2009. Volume 1: Temperature* [online]. Edited by S. Levitus. NOAA Atlas NESDIS 68, US Government Printing Office, Washington, D.C. Available from [ftp://ftp.nodc.noaa.gov/pub/WOA09/DOC/wao09\\_vol1\\_text.pdf](ftp://ftp.nodc.noaa.gov/pub/WOA09/DOC/wao09_vol1_text.pdf).
- Lynn, R.J., and Simpson, J.J. 1987. The California Current System: the seasonal variability of its physical characteristics. *J. Geophys. Res.* **92**(C12): 12947–12966. doi:10.1029/JC092iC12p12947.
- Mangel, M., MacCall, A.D., Brodziak, J., Dick, E.J., Forrest, R.E., Pourzand, R., and Ralston, S. 2013. A perspective on steepness, reference points, and stock assessment. *Can. J. Fish. Aquat. Sci.* **70**(6): 930–940. doi:10.1139/cjfas-2012-0372.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., and Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteor. Soc.* **78**: 1069–1079. doi:10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2.
- McCabe, R.M., Hickey, B.M., Kudela, R.M., Lefebvre, K.A., Adams, N.G., Bill, B.D., Gulland, F.M.D., Thomson, R.E., Cochlan, W.P., and Trainer, V.L. 2016. An unprecedented coastwide toxic algal bloom linked to anomalous ocean conditions. *Geophys. Res. Lett.* **43**: 10366–10376. doi:10.1002/2016GL070023. PMID:27917011.
- McClatchie, S., Goericke, R., Cosgrove, R., Auad, G., and Vetter, R. 2010. Oxygen in the Southern California Bight: multidecadal trends and implications for demersal fisheries. *Geophys. Res. Lett.* **37**: L19602. doi:10.1029/2010GL044497.
- McClatchie, S., Thompson, A.R., Alin, S.R., Siedlecki, S., Watson, W., and Bograd, S.J. 2016a. The influence of Pacific Equatorial Water on fish diversity in the southern California Current System. *J. Geophys. Res. Oceans*, **121**(8): 6121–6136. doi:10.1002/2016JC011672.
- McClatchie, S., Goericke, R., Leising, A., Auth, T.D., Bjorkstedt, E., Robertson, R.R., Brodeur, R.D., DU, X., Daly, E.A., Morgan, C.A., Chavez, F.P., Debich, A.J., Hildebrand, J., Field, J.C., Sakuma, K.M., Jacox, M.G., Kahru, M., Kudela, R., Anderson, C., Lavaniegas, B.E., Gomes-Valdes, J., Jimenez-Rosenberg, S.P.A., McCabe, R., Melin, S.R., Ohman, M.D., Sala, L.M., Peterson, B., Fisher, J., Schroeder, I.D., Bograd, S.J., Hazen, E.L., Schneider, S.R., Golightly, R.T., Suryan, R.M., Gladics, A.J., Lored, S., Porquez, J.M., Thompson, A.R., Weber, E.D., Watson, W., Trainer, V., Warzybok, P., Bradley, R., and Jahncke, J. 2016b. State of the California Current 2015–16: Comparisons with the 1997–98 El Niño. *CalCOFI Rep.* **57**: 5–61.
- Meinville, M., and Johnson, G.C. 2013. Decadal water-property trends in the California Undercurrent, with implications for ocean acidification. *J. Geophys. Res. Oceans*, **118**: 6687–6703. doi:10.1002/2013JC009299.
- Miller, R.R., Field, J.C., Santora, J.A., Schroeder, I.D., Huff, D.D., Key, M., Pearson, D.E., and MacCall, A.D. 2014. A spatially distinct history of the development of California groundfish fisheries. *PLoS ONE*, **9**(6): e99758. doi:10.1371/journal.pone.0099758. PMID:24967973.
- Moore, A.M., Arango, H.G., Broquet, G., Edwards, C., Veneziani, M., Powell, B.,



- Foley, D., Doyle, J.D., Costa, D., and Robinson, P. 2011. The Regional Ocean Modeling System (ROMS) 4-dimensional variational data assimilation systems Part II — performance and application to the California Current System. *Prog. Oceanogr.* **91**(1): 50–73. doi:10.1016/j.pocean.2011.05.003.
- Mueter, F.J., Boldt, J.L., Megrey, B.A., and Peterman, R.M. 2007. Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts. *Can. J. Fish. Aquat. Sci.* **64**(6): 911–927. doi:10.1139/f07-069.
- Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* **56**(12): 2404–2419. doi:10.1139/f99-201.
- Neveu, E., Moore, A.M., Edwards, C.A., Fiechter, J., Drake, P., Crawford, W.J., Jacox, M.G., and Nuss, E. 2016. An historical analysis of the California Current circulation using ROMS 4D-Var: System configuration and diagnostics. *Ocean Model.* **99**: 133–151. doi:10.1016/j.ocemod.2015.11.012.
- Parrish, R.H., Nelson, C.S., and Bakun, A. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.* **1**: 175–203.
- Parrish, R.H., Schwing, F.B., and Mendelssohn, R. 2000. Mid-latitude wind stress: the energy source for climatic shifts in the North Pacific Ocean. *Fish. Oceanogr.* **9**: 224–238. doi:10.1046/j.1365-2419.2000.00136.x.
- Pepin, P. 2016. Reconsidering the impossible — linking environmental drivers to growth, mortality, and recruitment of fish. *Can. J. Fish. Aquat. Sci.* **73**(2): 205–215. doi:10.1139/cjfas-2015-0091.
- Petersen, C.H., Drake, P.T., Edwards, C.A., and Ralston, S. 2010. A numerical study of inferred rockfish (*Sebastes* spp.) larval dispersal along the central California coast. *Fish. Oceanogr.* **19**(1): 21–41. doi:10.1111/j.1365-2419.2009.00526.x.
- Peterson, W.T., Fisher, J.L., Peterson, J.O., Morgan, C.A., Burke, B.J., and Fresh, K.L. 2014. Applied fisheries oceanography: ecosystem indicators of ocean conditions inform fisheries management in the California Current. *Oceanography*, **27**(4): 80–89. doi:10.5670/oceanog.2014.88.
- Pozo Buil, M., and Di Lorenzo, E. 2017. Decadal dynamics and predictability of oxygen and subsurface tracers in the California Current System. *Geophys. Res. Lett.* **44**(9): 4204–4213. doi:10.1002/2017GL072931.
- Ralston, S., and Howard, D.F. 1995. On the development of year class strength and cohort variability in two northern California rockfishes. *Fish. Bull.* **93**: 710–720.
- Ralston, S., Sakuma, K.M., and Field, J.C. 2013. Interannual variation in pelagic juvenile rockfish (*Sebastes* spp.) abundance — going with the flow. *Fish. Oceanogr.* **22**: 288–308. doi:10.1111/fog.12022.
- Ralston, S., Field, J.C., and Sakuma, K.M. 2015. Long-term variation in a central California pelagic forage assemblage. *J. Mar. Syst.* **146**: 26–37. doi:10.1016/j.jmarsys.2014.06.013.
- Reid, J.L., Jr. 1962. On circulation, phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific Ocean. *Limnol. Oceanogr.* **7**: 287–306. doi:10.4319/lo.1962.7.3.0287.
- Reilly, C.A., Echeverria, T.W., and Ralston, S.V. 1992. Interannual variation and overlap in the diets of pelagic juvenile rockfish (Genus: *Sebastes*) off central California. *Fish. Bull.* **90**: 505–515.
- Roesler, C.S., and Chelton, D.B. 1987. Zooplankton variability in the California Current, 1957–1982. *CalCOFI Rep.* **28**: 59–96.
- Rose, K.A., Fiechter, J., Curchitser, E.N., Hedstrom, K., Bernal, M., Creekmore, S., Haynie, A., Ito, S.I., Lluch-Cota, S., Megrey, B.A., and Edwards, C.A. 2015. Demonstration of a fully-coupled end-to-end model for small pelagic fish using sardine and anchovy in the California Current. *Prog. Oceanogr.* **138**: 348–380. doi:10.1016/j.pocean.2015.01.012.
- Ross, J.R., and Larson, R.J. 2003. Influence of water column stratification on the depth distributions of pelagic juvenile rockfishes off central California. *CalCOFI Rep.* **44**: 65–75.
- Sakuma, K.M., Field, J.C., Mantua, N.J., Ralston, S., Marinovic, B.B., and Carrion, C.N. 2016. Anomalous epipelagic micronekton assemblage patterns in the neritic waters of the California Current in spring 2015 during a period of extreme ocean conditions. *CalCOFI Rep.* **57**: 163–183.
- Santora, J.A., Schroeder, I.D., Field, J.C., Wells, B.K., and Sydeman, W.J. 2014. Spatio-temporal dynamics of ocean conditions and forage taxa reveals regional structuring of predator–prey relationships. *Ecol. Appl.* **24**: 1730–1747. doi:10.1890/13-1605.1. PMID:29210234.
- Santora, J.A., Hazen, E.L., Schroeder, I.D., Bograd, S.J., Sakuma, K.M., and Field, J.C. 2017a. Impacts of ocean climate variability on biodiversity of pelagic forage species in an upwelling ecosystem. *Mar. Ecol. Prog. Ser.* **580**: 205–220. doi:10.3354/meps12278.
- Santora, J.A., Sydeman, W.J., Schroeder, I.D., Field, J.C., Miller, R.R., and Wells, B.K. 2017b. Persistence of trophic hotspots and relation to human impacts within an upwelling marine ecosystem. *Ecol. Appl.* **27**: 560–574.
- Schirripa, M.J., and Colbert, J.J. 2006. Interannual changes in sablefish (*Anoplopoma fimbria*) recruitment in relation to oceanographic conditions within the California current system. *Fish. Oceanogr.* **15**: 25–36. doi:10.1111/j.1365-2419.2005.00352.x.
- Schroeder, I.D., Santora, J.A., Moore, A.M., Edwards, C.A., Fiechter, J., Hazen, E.L., Bograd, S.J., Field, J.C., and Wells, B.K. 2014. Application of a data-assimilative regional ocean modeling system for assessing California Current System ocean conditions, krill, and juvenile rockfish interannual variability. *Geophys. Res. Lett.* **41**: 5942–5950. doi:10.1002/2014GL061045.
- Schwing, F.B., O'Farrell, M., Steger, J.M., and Baltz, K. 1996. Coastal upwelling indices, West Coast of North America, 1946–1995. NOAA Tech. Memo., NOAA-TM-NMFS-SWFSC-231.
- Stachura, M.M., Essington, T.E., Mantua, N.J., Hollowed, A.B., Haltuch, M.A., Spencer, P.D., and Branch, T.A. 2014. Linking Northeast Pacific recruitment synchrony to environmental variability. *Fish. Oceanogr.* **23**: 389–408. doi:10.1111/fog.12066.
- Stige, L.C., Hunsicker, M.E., Bailey, K.M., Yaragina, N.A., and Hunt, G.L., Jr. 2013. Predicting fish recruitment from juvenile abundance and environmental indices. *Mar. Ecol. Prog. Ser.* **480**: 245–261. doi:10.3354/meps10246.
- Sydeman, W.J., Thompson, S.A., Field, J.C., Peterson, W.T., Tanasichuk, R.W., Freeland, H.J., Bograd, S.J., and Rykaczewski, R.R. 2011. Does positioning of the North Pacific Current affect downstream ecosystem productivity? *Geophys. Res. Lett.* **38**: L12606. doi:10.1029/2011GL047212.
- Szoboszlai, A.I., Thayer, J.A., Wood, S.A., Sydeman, W.J., and Koehn, L.E. 2015. Forage species in predator diets: synthesis of data from the California Current. *Ecol. Inform.* **29**: 45–56. doi:10.1016/j.ecoinf.2015.07.003.
- Szuwalski, C.S., Vert-Pre, K.A., Punt, A.E., Branch, T.A., and Hilborn, R. 2015. Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish. Fish.* **16**: 633–648. doi:10.1111/faf.12083.
- Thayer, J.A., Field, J.C., and Sydeman, W.J. 2014. Changes in California Chinook salmon diet over the past 50 years: relevance to the recent population crash. *Mar. Ecol. Prog. Ser.* **498**: 249–261. doi:10.3354/meps10608.
- Thomson, R.E., and Krassovski, M.V. 2010. Poleward reach of the California Undercurrent extension. *J. Geophys. Res. Oceans*, **115**: C09027. doi:10.1029/2010JC006280.
- Thorson, J.T., Stewart, I.J., Taylor, I.G., and Punt, A.E. 2013. Using a recruitment-linked multispecies stock assessment model to estimate common trends in recruitment for US West Coast groundfishes. *Mar. Ecol. Prog. Ser.* **483**: 245–256. doi:10.3354/meps10295.
- Todd, R.E., Rudnick, D.L., Mazloff, M.R., Cornuelle, B.D., and Davis, R.E. 2012. Thermohaline structure in the California Current System: Observations and modeling of spice variance. *J. Geophys. Res. Oceans*, **117**: C02008. doi:10.1029/2011JC007589.
- Veneziani, M., Edwards, C.A., Doyle, J.D., and Foley, D. 2009. A central California coastal ocean modeling study: 1. Forward model and the influence of realistic versus climatological forcing. *J. Geophys. Res. Oceans*, **114**: C04015. doi:10.1029/2008JC004774.
- Vetter, R., and Lynn, E. 1997. Bathymetric demography, enzyme activity patterns, and bioenergetics of deep-living scorpaenid fishes (genera *Sebastes* and *Sebastolobus*): paradigms revisited. *Mar. Ecol. Prog. Ser.* **155**: 173–188. doi:10.3354/meps155173.
- Warzybok, P., Santora, J.A., Ainley, D.G., Bradley, R.W., Field, J.C., Capitolo, P.J., Carle, R.D., Elliott, M., Beck, J.N., McChesney, G.J., Hester, M.M., and Jahncke, J. 2018. Prey switching and consumption by seabirds in the central California Current upwelling ecosystem: Implications for forage fish management. *J. Mar. Syst.* **185**: 25–39.
- Wells, B.K., Santora, J.A., Henderson, M.J., Warzybok, P., Jahncke, J., Bradley, R.W., Huff, D.D., Schroeder, I.D., Nelson, P., Field, J.C., and Ainley, D.G. 2017. Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. *J. Mar. Syst.* **174**: 54–63. doi:10.1016/j.jmarsys.2017.05.008.
- Williams, E.H., and Ralston, S. 2002. Distribution and co-occurrence of rockfishes (family: Sebastidae) over trawlable shelf and slope habitats of California and southern Oregon. *U.S. Fish. Bull.* **100**: 836–855.
- Wolter, K., and Timlin, M.S. 1998. Measuring the strength of ENSO events: how does 1997/98 rank? *Weather*, **53**: 315–324. doi:10.1002/j.1477-8696.1998.tb06408.x.