

RESEARCH ARTICLE

10.1002/2016JC011672

Key Points:

- Fish diversity was stable from 1985 to 1996 and 1999 to 2014 despite variable Pacific Equatorial Water
- Species evenness declined during the 1999 La Niña, but richness increased during 1997/1998 El Niño
- Species richness increased between 1985–1996 and 1999–2014 consistent with intrusion of warm water

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Citation:

McClatchie, S., A. R. Thompson, S. R. Alin, S. Siedlecki, W. Watson, and S. J. Bograd (2016), The influence of Pacific Equatorial Water on fish diversity in the southern California Current System, *J. Geophys. Res. Oceans*, 121, 6121–6136, doi:10.1002/2016JC011672.

Received 21 JAN 2016

Accepted 14 JUL 2016

Accepted article online 20 JUL 2016

Published online 20 AUG 2016

The influence of Pacific Equatorial Water on fish diversity in the southern California Current System

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Abstract The California Undercurrent transports Pacific Equatorial Water (PEW) into the Southern California Bight from the eastern tropical Pacific Ocean. PEW is characterized by higher temperatures and salinities, with lower pH, representing a source of potentially corrosive (aragonite, $\Omega < 1$) water to the region. We use ichthyoplankton assemblages near the cores of the California Current and the California Undercurrent to determine whether PEW influenced fish diversity. We use hydrographic data to characterize the interannual and seasonal variability of estimated pH and aragonite saturation with depth. Although there is substantial variability in PEW presence as measured by spice on the 26.25–26.75 isopycnal layer, as well as in pH and aragonite saturation, we found fish diversity to be stable over the decades 1985–1996 and 1999–2011. We detected significant difference in species structure during the 1998 La Niña period, due to reduced species evenness. Species richness due to rare species was higher during the 1997/1998 El Niño compared to the La Niña but the effect on species structure was undetectable. Lack of difference in the species abundance structure in the decade before and after the 1997/1999 ENSO event showed that the assemblage reverted to its former structure following the ENSO perturbation, indicating resilience. While the interdecadal species structure remained stable, the long tail of the distributions shows that species richness increased between the decades consistent with intrusion of warm water with more diverse assemblages into the southern California region.

1. Introduction

Some experimental studies [Cornwall and Hurd, 2015] and limited field studies indicate that ocean acidification may negatively affect fish physiology, survival, and diversity, either through sublethal effects, behavioral modification [Munday et al., 2010], or indirectly through changes in their habitat [Nagelkerken et al., 2015]. There are very few studies of acidification on fish in general because most work has focused on calcifying organisms. In the California Current system, water with aragonite saturation, $\Omega, < 1$ and $\text{pH} \approx 7.75$ is undersaturated with regards to a vulnerable mineral form of calcium carbonate called aragonite. Waters with this property are corrosive to the hard parts that organisms build out of aragonite and make it energetically unfavorable for those calcifying organisms to form shells, or otoliths, in these conditions. While most studies focused on calcifying organisms, some studies suggest that pH levels less than 7.4 [DePasquale et al., 2015] may be harmful to fish populations. As far as we are aware, there are virtually no studies on potential effects of acidification on fish diversity.

Field studies have several limitations regarding the interpretation of effects of acidification: there are few time series long enough to resolve multidecadal trends and the effects of acidification cannot be separated from the effects of temperature and oxygen because the variables are correlated [Alin et al., 2012]. Another problem for resolving the effects of acidification on fish diversity is that there are few surveys where fish species counts can be paired with physical variables. Further, potential effects on fish diversity cannot be directly attributed to acidification, and must be resolved as a multistressor effect which can best be described by changes in water mass properties. Here, we intend to make some progress in addressing the existing uncertainties regarding the impact of ocean acidification on marine fishes by examining changes in ichthyoplankton characteristics that are associated with naturally varying acidity.

Table 1. Characteristics of the Four Principal Water Masses in the California Current System^a

	Temperature	Salinity	Oxygen	Nutrients
Surface water masses (0–200 m)				
Pacific Subarctic	L	L	H	H
North Pacific Central	H	H	L	L
Coastal upwelled	L	H	L	H
Subsurface water masses (200–500)				
Pacific Equatorial	H	H	L	H

^aL = low, H = high [from Lynn and Simpson, 1987; Simpson, 1984].

There are two sources of relatively higher acidity water off southern and central California. Seasonal upwelling during the spring and summer brings lower pH waters onto the shelf, reaching depths of 40–120 m [Bograd *et al.*, 2015], and in some cases off Central California, reaching the surface [Feely *et al.*, 2008]. Coastal Upwelled Water originates from a mixture of

Pacific Subarctic and Pacific Equatorial Water (PEW). For upwelled water, it is the PEW component that brings low oxygen and low pH (≈ 7.61) [Meinvielle and Johnson, 2013] water to the mix. The second source of low pH water is advection of PEW from the south, primarily during the summer months [Nam *et al.*, 2015]. Coastal Upwelled Water and PEW have distinct oceanographic signatures, particularly in terms of temperature (Table 1). Upwelled waters are cool, saline, and oxygen poor, but relatively high in nutrients. PEW is warm, saline, oxygen poor, and is also relatively high in nutrients. While we cannot explicitly attribute changes in ichthyoplankton assemblages to acidification, we can quantify variation in mesopelagic larval assemblages, and relate the spatial and temporal variability of the ichthyoplankton to the interannual variability of PEW.

Hsieh *et al.* [2005] grouped ichthyoplankton off southern California into oceanic, coastal-oceanic, and coastal species as determined by a group of experts, using bottom depth and region of occurrence as the primary classification criteria. Oceanic ichthyoplankton assemblages, seaward of the slope, fluctuate with climatic variability more than either coastal-oceanic, or coastal species found over the continental shelf and slope [Moser *et al.*, 1987, 2001; Smith and Moser, 2003; Hsieh *et al.*, 2005; Koslow *et al.*, 2011; Thompson *et al.*, 2012; Koslow *et al.*, 2013]. Consequently, assemblages of oceanic ichthyoplankton are likely candidates to use in developing indices related to climate variability. Distinct assemblages of larvae of mesopelagic fish species (hereafter, mesopelagic larvae) are associated with warm water or cool water conditions. It should be noted that warm water conditions are not necessarily associated with periods of lower pH and greater concentration of PEW. During El Niño, for example, pH tends to be relatively high [Nam *et al.*, 2011]. Ichthyoplankton taxa at the northern edge of their range off southern California can be used as indicators of intrusions of PEW.

In general, diversity is greater in the warmer water masses and lower in cooler waters. Based on its temperature, increasing presence of PEW should lead to increased ichthyoplankton diversity, even though the acidity of PEW is higher. Species diversity is affected by both species richness (or the number of species) and species dominance (or evenness of the distribution of species abundances).

Cool water associated species tend to be resident off southern California and species richness of the resident assemblage should increase if species are added from the south due to intrusions and subsequent mixing with warm PEW. Species evenness would increase (i.e., species dominance would decrease) in this situation, and diversity would increase. One might expect similar patterns due to intrusions of warmer Pacific Central Water from offshore, namely increased species richness, increased evenness, and increased diversity if the offshore intrusions mix with resident species, or if the offshore assemblage displaces the resident assemblage.

Species richness would be expected to increase to an even greater degree if southern California species shift northwards and are displaced, rather than mixed with species from the warmer southern water. If entire assemblages are shifting north with the warming trend, and possibly with increased northward advection, southern species might displace cool water associated species. We should be clear that we refer to displacement of species and not displacement of water masses. The mechanisms would presumably include both movement of spawning fish and mortality of their offspring. Displacement of a water mass would seem unlikely off southern California where there is a complex dynamic between water masses.

El Niño conditions bring warmer water southern species into the southern California area [Lea and Rosenblatt, 2000] and should increase both species richness and evenness, the combination producing higher diversity. La

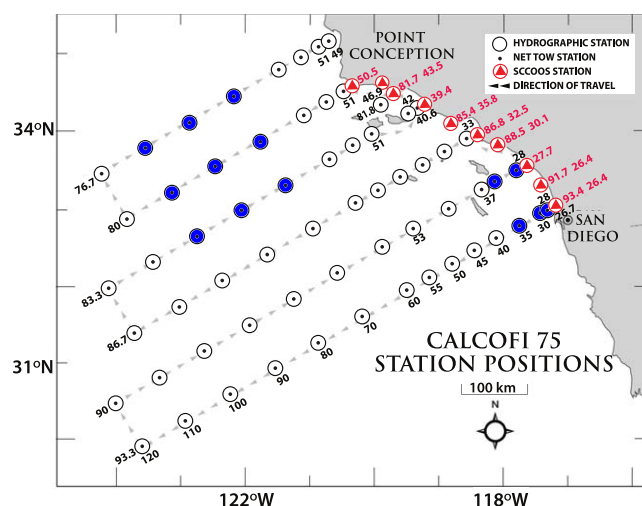


Figure 1. Map showing the “core” CalCOFI sampling domain off southern California comprising six lines or transects from San Diego to Avila Bay, now sampled quarterly. These stations have been sampled consistently since the beginning of the CalCOFI program except for the inshore stations (marked in red) that were added later as part of the Southern California Coastal Ocean Observing system (SCCOOS). Stations 93.3 30 and 80.0 80 and adjacent stations used in this study are colored blue.

2013 for an overview of the CalCOFI program]. Although the CalCOFI sampling protocol does not adequately capture high-frequency variability [e.g., Nam *et al.*, 2011, 2015], its long-time series spanning multiple climate regimes allows for the detection of interannual variability in water mass properties and ichthyoplankton community structure [McClatchie, 2013; McClatchie *et al.*, 2014].

Oceanography off southern California is complex because there are distinct subregions nearshore influenced by the California Undercurrent, offshore influenced by the California Current, far offshore at the edge of the central gyre, in addition to the more productive, windier region bordering central California and the oligotrophic water to the south of the Ensenada Front along the U.S.-Mexican border. This subregional complexity, combined with mixing and displacement of assemblages makes it difficult to interpret patterns and trends in diversity if the core CalCOFI sampling domain is averaged or treated as a single assemblage.

Based on patterns in sea surface temperature and wind stress [Mendelssohn and Schwing, 2002], ocean color [Thomas and Strub, 2001] or zooplankton species [Bernal, 1979], the core sampling domain of CalCOFI (Figure 1) spans an inshore and offshore subregion, and borders two more subregions to the north and south. The waters off southern California exhibit complex oceanographic patterns with considerable mixing of different source waters. To test for influence of PEW, we examined two time series (1951–2014) from CalCOFI stations that represent the California Undercurrent and California Current off southern California. The $\sigma_t = 26.25\text{--}26.75 \text{ kg m}^{-3}$ isopycnal layer at the nearshore continental slope CalCOFI station 93.3 30 off San Diego has properties representative of the core of the California Undercurrent [Bograd *et al.*, 2015] and PEW. The 25.8 kg m^{-3} isopycnal at station 80.0 80 offshore from Point Conception has properties of Pacific Subarctic Water in the core of the California Current [Bograd *et al.*, 2015].

Spice as defined by Flament [2002] measured on the $\sigma_t = 26.25\text{--}26.75$ density surface at CalCOFI station 93.3 30 provides a useful measure of PEW presence [Bograd *et al.*, 2015], where increasing spice reflects either higher temperatures or higher salinities [Huyer *et al.*, 1998]. We began by testing for long-term trend in spice anomalies on the $26.25\text{--}26.75$ isopycnal layer at the nearshore CU slope station, 93.3 30. We also looked for change points in mean spice that might separate periods with differing ichthyoplankton assemblages. We compared ichthyoplankton time series over decadal periods defined by the spice data. We examined the proportions of warm and cool water associated species to answer our first question: Have the mesopelagic species dominants changed off southern California? We then examined the entire

Niña conditions, in contrast, are associated with greater offshore transport [Song *et al.*, 2012] and cooler conditions that would decrease diversity. The relative effects of El Niño and La Niña on ichthyoplankton diversity are currently unknown.

In this study, we hypothesize that presence of PEW increased ichthyoplankton species dominance and species richness, and thereby increased fish diversity off southern California. Our analyses use the California Cooperative Oceanic Fisheries Investigations (CalCOFI) hydrographic and ichthyoplankton data set collected since 1951. The CalCOFI data are ideal for testing this hypothesis because ichthyoplankton data are collected at the same locations as physical profiles, methods are rigorously standardized and calibrated, larval fish are counted and consistently identified to species, and effort is quantified [see McClatchie,

ichthyoplankton community to address two more questions: first, is there any evidence that species abundance patterns have changed? Second, is there any evidence for an increase in diversity that might be related to presence of PEW off southern California?

2. Methods

2.1. Sampling Domain

The CalCOFI program currently samples 75 hydrographic stations (Figure 1) on a quarterly basis taking a suite of hydrographic profiles and fixed-depth bottle samples from 5 to 500 m depths. Data collection and quality control for physical and chemical data are detailed in cruise reports posted on CalCOFI web pages (www.calcofi.org). Final data are served through the NOAA Environmental Research Division Data Access Program (ERDDAP) on the Internet at <http://coastwatch.pfeg.noaa.gov/erddap/index.html>. A detailed summary of the CalCOFI program is provided by McClatchie [2013]. In this study, we focus on a nearshore continental slope station (CalCOFI line 93.3 station 30, hereafter 93.3 30) and an offshore station (80.0 80) for the physical and chemical analyses, and included their adjacent stations for the ichthyoplankton analyses (Figure 1). We use spice [Flament, 2002; Bograd et al., 2015; Nam et al., 2015] on an isopycnal surface as an indicator of the California Undercurrent.

2.2. Spice, pH, and Aragonite Saturation State

Spice at CalCOFI station 93.3 30 was estimated from temperature and salinity on the 26.25–26.75 kg m⁻³ isopycnal layer. We excluded around 1% of the data at depths ≤100 m, since changes in spice at shallower depths may result from surface warming rather than influence of PEW. Eighty-two percent of spice values on the 26.25–26.75 kg m⁻³ isopycnal layer were deeper than 175 m and 77% were between 175 and 300 m. We found no relationship between spice and depth, indicating that changes in spice were more likely to reflect changes in water masses than changes in depth.

Spice has a strong seasonal signal and is higher in the summer off southern California [Nam et al., 2015]. We calculated the climatology for years 1984–2014, taking the averages for each month when the station was sampled, and subtracted the climatology from the spice time series to produce a deseasonalized anomaly time series. The sampling was approximately quarterly so the deseasonalization was based on an approximately quarterly climatology rather than a strictly monthly climatology. We used the Pettitt test for change point detection [Pettitt, 1979] to determine if there were breakpoints in the deseasonalized spice anomaly series that we could use to objectively separate time intervals over which to compare ichthyoplankton assemblages.

We estimated pH (pH^{est}) and aragonite saturation state values (Ω_{arag}^{est}) for CalCOFI time-series observations at stations 80.0 80 and 93.3 30 using empirical relationships from Alin et al. [2012]. For pH and Ω_{arag} proxy variables, we used oxygen and temperature data collected during CTD casts on CalCOFI cruises conducted between January 1984 and April 2014. Error of the resulting estimates should be on the order of ±0.03 for pH^{est} and 0.06 for Ω_{arag}^{est} between 1997 and 2014 [Alin et al., 2012]. However, error on estimates should progressively increase farther back in time, as the empirical relationships are based on a calibration data set collected in 2007 [Alin et al., 2012]. Carbon samples and water masses represented in the calibration data set thus contained more anthropogenic CO₂ than their counterparts from earlier CalCOFI surveys would have (e.g., 1984–1996). As a result, our calculations represent underestimates of pH and Ω_{arag} for 1984–1996 due to the higher anthropogenic CO₂ burden in more recent waters and in the calibration data set. Our estimates of change in pH and Ω_{arag} thus represent a lower bound for actual change between the 1985–1996 and 1999–2011 decadal periods.

2.3. Ichthyoplankton Data Consistency

CalCOFI collects ichthyoplankton at each station (Figure 1) using oblique, vertical, and surface plankton tows. The most common sampling interval in the CalCOFI series is quarterly. CalCOFI sampling at stations 80.0 80 and 93.3 30 was remarkably consistent from 1951 to 1968, and from 1984 to the present. However, the intervening 14 year period (1969–1983) was only sampled triennially, creating considerable data gaps. Larval fish time series ($larvae (10 m)^{-2}$) used in this study were obtained from counts of larvae in oblique CalCOFI net tow samples at stations 80.0 80 and 93.3 30 and adjacent stations (see below, and Figure 1). The years 2012, 2013, and 2014 were available only for stations 80.0 80 and 93.3 30, and 2015 samples were

unprocessed, due to processing backlogs limiting most of our analyses to end in 2011. Samples were collected and processed using standard CalCOFI methods for oblique tow deployment and sample processing (documented in *Kramer et al.* [1972]; *Smith and Richardson* [1977]).

During the CalCOFI time series, maximum net tow depth (140–210 m) and net mesh type (silk to nylon) were changed in 1969, and ring nets were abandoned in favor of bongo nets in 1978 [McClatchie, 2013]. Intercalibration of the gear types addressed zooplankton volume [Ohman and Smith, 1995] and copepod densities [Rebstock, 2002]. Ichthyoplankton catches by ring nets and bongo nets were compared for commercial species (sardine, anchovy, hake, jack mackerel, and Pacific mackerel) in the 1980s, but the data are only just being published at the time of writing. Larger anchovy larvae avoided the ring net more readily than the bongo net [Hewitt, 1980]. The general consistency in catch rates between net types can likely be extended to other species of fish larvae.

Fish larvae were identified to the lowest possible taxon, usually species, by the National Atmospheric and Oceanic Administration (NOAA) Southwest Fisheries Science Center (SWFSC) ichthyoplankton laboratory. Prior to analysis, data extracted from the CalCOFI database were prepared by removing cephalopod paralarvae, unidentified Myctophidae, and unidentified and damaged larval fish categories. The taxonomic resolution for all species in the CalCOFI ichthyoplankton time series has been progressively extended further back in time by reidentifying larvae, and is currently consistent for all species back to 1965.

As discussed above, the sampling changes from ring nets to bongo nets in 1978 were unlikely to bias our results. The taxonomic resolution was consistent back to 1965, but sampling gaps from 1969–1983 degraded the temporal resolution and could introduce seasonal bias into analyses. Consequently, although we include years prior to 1985 for reference in figures of larval abundance, we focus on the 1985–2011 time interval.

2.4. Diversity Analyses

A simple way to examine changes in species diversity is to compare the species abundance distributions ranked in descending order of abundance. The ranked species abundance curves provide both a measure of the sampled species richness (the width of the distribution) and a measure of species dominance or evenness (the shape of the curve). Maximum evenness will give a totally flat curve. A steeper curve indicates more dominance or less evenness. This method is nonparametric in that it does not assume that the species abundance pattern conforms to any particular distribution.

Uncorrected species abundance proportions are generally positively biased due to a combination of undetected species and inadequate sample size [Chao et al., 2015]. Without correction, estimates of the number of species will be less than the true species richness [Chao et al., 2015]. Ichthyoplankton sample size was increased by including immediately adjacent stations around station 80.0 80 and 93.3 30 (Figure 1). For station 80.0 80, the adjacent stations were stations 70 and 90 on line 80, stations 70, 80, and 90 on line 76.7, and stations 70, 80, and 90 on line 83.3. For station 93.3 30, the adjacent stations were stations 28 and 35 on line 93.3, and stations 28 and 35 on line 90.0. There are no transect lines to the south of line 93.3.

As a result of the uneven distribution of CalCOFI stations, the spatial extent of regions used to increase sample size was different (Figure 1). To determine whether any bias was introduced by differing spatial extent, we compared the distribution of species abundances obtained from station 80.0 80 with the distribution obtained from this station and its eight nearest stations. We found no difference in the distributions for the period 1985–1995 or 1999–2014 (Two sample Kolmogorov-Smirnov tests, $p = 0.69$ and 0.91 , respectively). This indicates that there was no bias introduced by the regional extent of the sample areas.

We then corrected species abundances using the Jade package [Hsieh and Chao, 2014] and used rank/abundance plots [Whittaker, 1965] to compare the distribution of species in the ichthyoplankton assemblages in the regions around the offshore California Current station (CC) and the nearshore slope California Undercurrent station (CU) during 1985–1996 and 1999–2011 (decades prior to and after the extreme 1997/1999 ENSO event).

We compared the bias-corrected empirical distributions for both decadal time periods (1985–1996 and 1999–2011) and for the strong 1997/1999 ENSO event around each location (CC and CU, Figure 1). The comparison of decadal and ENSO periods was restricted to September through April to minimize seasonal bias, since the 1997 El Niño spanned July 1997 to April 1998 off southern California, while the La Niña lasted

from May 1998 to December 1998. Ichthyoplankton exhibit strong seasonality which could lead to bias if the seasons compared are not consistent as possible. We did not attempt to correct for any changes in the phenology of spawning in this study. We tested differences between the decadal distributions, between the El Niño and La Niña distributions, and between the decadal and the ENSO distributions using Kolmogorov-Smirnov tests.

2.5. Species Composition and Multivariate Analyses

We evaluated how assemblage composition varied before (1985–1996) and after (1999–2011) the 1997/1999 ENSO event in the CU and CC regions. We chose the 1997/1999 ENSO event because it is the most extreme ENSO in the CalCOFI time series. To visualize variability in species composition among years, we created two-way dendrograms for the CU and CC regions in each season. We included in the analysis only species with at least 25 individuals 10 m^{-2} and we log-transformed (\ln) ichthyoplankton densities. We constructed two-way dendrograms based on Euclidian distances and complete linkages to evaluate similarity among years and similarity among species. Heat maps of ichthyoplankton densities were used to summarize the groupings obtained. We then used redundancy analysis (RDA) on Hellinger-transformed densities to test if assemblages differed significantly among periods, accounting for multiple testing using sequential Bonferroni adjustment. Following significance testing, we examined the dendrograms to determine which, if any, species drove differences among periods and whether species found during the 1997/1999 ENSO event stood out from the other periods.

3. Results

3.1. Pacific Equatorial Water Presence, Spice, pH, and Aragonite Saturation

Spice on the 26.25–26.75 isopycnal layer at CalCOFI station 93.3 30 shows a climatological seasonal signal [Nam *et al.*, 2015] with higher values from May to August. One change point in the differenced spice anomaly time series was detected in the third quarter of 1995 ($p = 0.0015$, Pettitt test) [Pettitt, 1979] (Figure 2). The change in mean spice on the 26.25–26.75 isopycnal layer at CalCOFI station 93.3 30 was significantly higher after the change point, changing fastest during the 1997/1999 ENSO event (Figure 2). Considerable noise remaining in the deseasonalized spice anomaly could be due to interannual variability in mesoscale eddy activity [Huyer *et al.*, 1998]. Increased change in the mean spice anomaly after the change point at CalCOFI station 93.3 30 suggests greater presence of PEW after 1995. Based on these results, we compared ichthyoplankton diversity before and after the change point in the spice time series (1985–1996 versus 1999–2011).

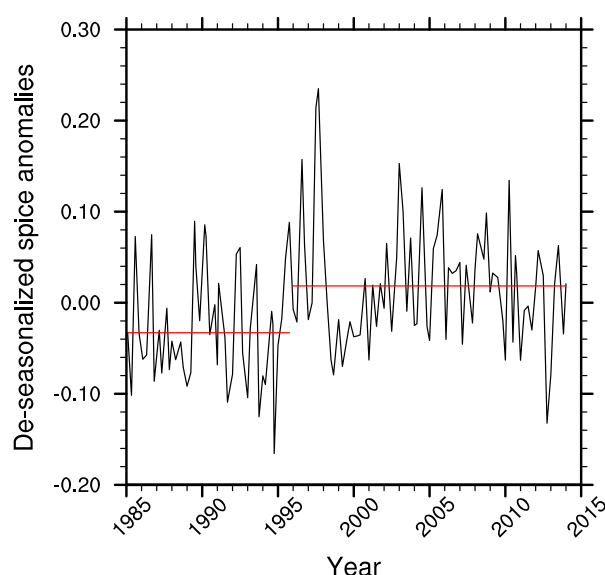


Figure 2. Deseasonalized anomalies of spice at CalCOFI station 93.3 30 on the 26.25–26.75 isopycnal layer for 1985–2014. Red lines show average spice for two periods distinguished using Pettitt's test for change point detection [Pettitt, 1979]. The break point is third quarter of 1995.

Estimated pH and Ω_{arag} values showed strong seasonal variability between 15 and 500 m water depth at both stations between 1984 and 2014 (Figure 3). At the offshore station (CC), the overall maximum and minimum values for pH^{est} were 8.09 and 7.51, while overall Ω_{arag}^{est} maximum and minimum values were 2.84 and 0.56. Between 1985–1996 and 1999–2011, average Ω_{arag}^{est} and pH^{est} between 15 and 100 m depth fell by 0.22 and 0.04 (representing a 9% increase in acidity), respectively. In the upper water column, Ω_{arag}^{est} values ≥ 2.0 occurred 62% of the time with a maximum water depth of 103 m, and pH^{est} values ≥ 8.0 occurred 68% of the time in the same depth range during the 1985–1996 interval (Table 2). Over the 1999–2011 interval, the maximum depth of the same Ω_{arag}^{est} and pH^{est} values was 18 m shallower, and the respective frequencies of these conditions in the upper water column had fallen to

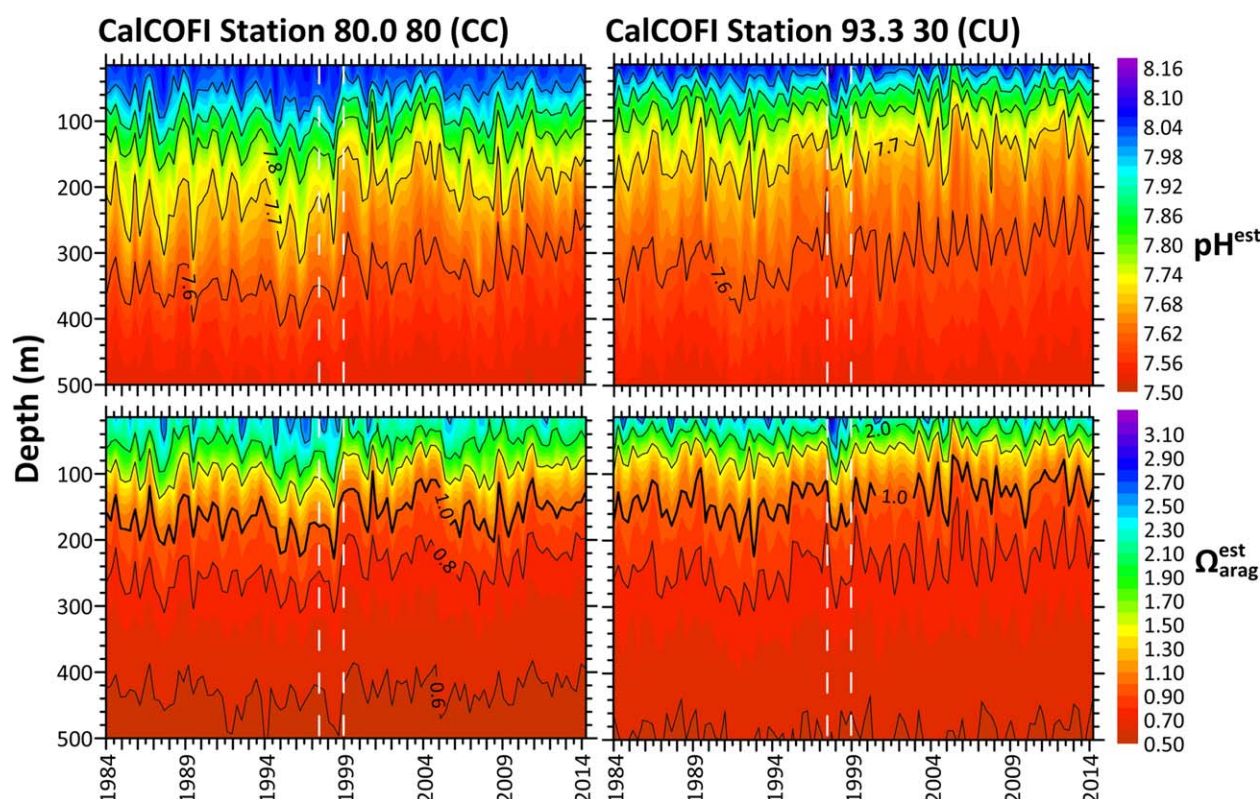


Figure 3. Estimated pH (top: pH^{est}) and aragonite saturation state (bottom: Ω_{arag}^{est}) time series for CalCOFI stations 80.0 80 (left: California Current) and 93.3 30 (right: California Undercurrent). Isolines for pH^{est} are spaced at 0.1 unit intervals, and for Ω_{arag}^{est} every 0.2 units below the aragonite saturation threshold ($\Omega_{arag}^{est} = 1.0$, bold black line) and every 0.5 units above the threshold. The time series starts with the first cruise in 1984 (January) and includes all quarterly CalCOFI cruises until April 2014. Major ticks represent January of each year and minor ticks July. White-dashed lines denote the extreme 1997/1999 ENSO period.

49% and 59%. The aragonite saturation horizon ($\Omega = 1$, ASH, which is the depth at which aragonite has a saturation state of 1.0, i.e., neither supersaturated nor undersaturated) oscillated seasonally. Organisms below the ASH depth experience corrosive conditions. The ASH varied from as deep as 228 m up to as shallow 85 m at CC, and on average was found at 146 ± 30 m deep.

Conditions at the slope station (CU) contrasted with those at the offshore station (CC) in a number of ways. As with the offshore station, the minimum values of Ω_{arag}^{est} and pH^{est} did not change over any time interval examined, suggesting undetectable influence of anthropogenic CO_2 or water mass change toward the 500 m depth limit, but the maximum values for both parameters were higher at the nearshore station than offshore for all time intervals considered (Table 2). However, the gradient of biogeochemical conditions was steeper at the slope, with the maximum depths of $\Omega_{arag}^{est} \geq 2.0$, $pH^{est} \geq 8.0$, and the average ASH being substantially shallower at the slope than offshore (Table 2). Between 1984–1996 and 1999–2011, average ASH depth shoaled by 18 m, and average 15–100 m Ω_{arag}^{est} and pH^{est} declined by 0.20 and 0.05 (11% increase in acidity), respectively. Finally, the frequencies of the high Ω_{arag}^{est} and pH^{est} conditions declined even more steeply at the slope site, but this is to some extent an artifact of the way these metrics were calculated (Table 2). However, we can say that the high Ω_{arag}^{est} and pH^{est} values occurred over a more contracted depth range and less often overall. Finally, the uppermost reach of the ASH depth was 35 m shallower at the slope station (CU) compared to the offshore station (CC).

3.2. Temporal Trends in Warm and Cool Water Mesopelagic Ichthyoplankton Assemblages

Distinct groups of mesopelagic fish species are consistently associated with warm and cool waters off southern California and we refer to these groups as warm or cool water assemblages (Table 3). The warm water assemblage is made up of Mexican lampfish (*Triphoturus mexicanus*), lightfishes (mainly *Vinciguerria lucetia*), snubnose blacksmelt (*Bathylagoides wesethi*), Diogenes lanternfish (*Diogenichthys laternatus*), fangtooth lanternfish (*Ceratoscopelus townsendi*), and bigfin lanternfish (*Symbolophorus californiensis*). Species associated with cooler water

Table 2. Estimated Aragonite Saturation State, pH Statistics, and Changes Between the 1985–1996 and 1999–2001 Periods^a

Parameter	Station	1985–1996	1999–2011	1984–2014	$\Delta_{(1999-2001)-(1985-1996)}$
Average ASH depth (m, \pm SD)	80.0 80 (CC)	169 \pm 34	143 \pm 32	155 \pm 35	26
	93.0 30 (CU)	141 \pm 32	123 \pm 34	135 \pm 34	18
ASH depth range (m)	80.0 80 (CC)	98–250	84–229	84–267	n.a.
	93.0 30 (CU)	71–250	50–201	50–250	n.a.
Total Ω_{arag}^{est} range (15–500 m depth)	80.0 80 (CC)	0.56–2.84	0.56–2.68	0.56–2.84	n.a.
	93.0 30 (CU)	0.58–2.96	0.58–2.91	0.57–3.14	n.a.
Total pH^{est} range (15–500 m depth)	80.0 80 (CC)	7.51–8.09	7.51–8.08	7.51–8.09	n.a.
	93.0 30 (CU)	7.52–8.15	7.52–8.12	7.52–8.15	n.a.
Ω_{arag}^{est} average (15–100 m depth)	80.0 80 (CC)	2.08 \pm 0.4	1.86 \pm 0.4	1.97 \pm 0.4	0.22
	93.0 30 (CU)	1.77 \pm 0.5	1.57 \pm 0.5	1.72 \pm 0.5	0.20
pH^{est} average (15–100 m depth)	80.0 80 (CC)	8.00 \pm 0.1	7.96 \pm 0.1	7.98 \pm 0.1	0.04
	93.0 30 (CU)	7.93 \pm 0.1	7.88 \pm 0.1	7.91 \pm 0.1	0.05
Maximum depth of $\Omega_{arag}^{est} \geq 2.0$	80.0 80 (CC)	103	85	103	18
	93.0 30 (CU)	61	60	84	0
Frequency of $\Omega_{arag}^{est} \geq 2.0$ (15 m to max depth above)	80.0 80 (CC)	62%	49%	52%	13%
	93.0 30 (CU)	61%	39%	40%	22%
Maximum depth of $pH^{est} \geq 8.0$	80.0 80 (CC)	103	85	103	18
	93.0 30 (CU)	60	60	75	0
Frequency of $pH^{est} \geq 8.0$ (15 m to max depth above)	80.0 80 (CC)	68%	59%	59%	9%
	93.0 30 (CU)	61%	38%	40%	23%

^aASH = aragonite saturation horizon, Ω_{arag}^{est} = estimated aragonite saturation state, pH^{est} = estimated pH, and n.a. = not available.

are northern lampfish (*Stenobrachius leucopsarus*), California smoothtongue (*Leuroglossus stilbius*), eared black-smelt (*Lipolagus ochotensis*), blue lanternfish (*Tarletonbeania crenularis*), and California flashlightfish (*Protomyctophum crockeri*) (Table 3). Both the warm water and the cool water assemblages are numerically dominated by single species. This is common in species distributions which are generally highly left skewed because few species are numerically abundant while many species are rare. The warm water mesopelagic assemblage at the offshore CC station is dominated by *Vinciguerria lucetia* until 2000 (Figure 4a), and by *Triphoturus mexicanus* at the slope CU station (Figure 4a). In contrast, the cool water mesopelagic assemblage is dominated by *Stenobrachius leucopsarus* at CC (Figure 4b) and by *Leuroglossus stilbius* at CU (Figure 4b).

Warm and cool assemblages exhibited different trends at the California Current station (CC, offshore) and the California Undercurrent station (CU, nearshore continental slope) (Figures 4). The dominant signal for both warm and cool assemblages at CC was the extreme 1997/1999 ENSO event. Changes in larval abundance associated with this event were a factor of two larger than for any other event in the 1951–2011 time series (not shown here).

The response of the fish assemblages to the 1997/1999 ENSO was much stronger at the offshore CC station (Figures 4a and 4c) than at the slope station, CU (Figures 4b and 4d). Both warm and cool ichthyoplankton

Table 3. Ichthyoplankton Species From CalCOFI Surveys Off Southern California Categorized as Warm or Cool-Water Associated Mesopelagic Assemblages^a

Genus Species	Common Name	Subcategory
<i>Leuroglossus stilbius</i>	California smoothtongue	Cool-water
<i>Lipolagus ochotensis</i>	Eared blacksmelt	Cool-water
<i>Protomyctophum crockeri</i>	California flashlightfish	Cool-water
<i>Stenobrachius leucopsarus</i>	Northern lampfish	Cool-water
<i>Tarletonbeania crenularis</i>	Blue lanternfish	Cool-water
<i>Vinciguerria</i> spp.	Lightfishes	Warm-water
<i>Triphoturus mexicanus</i>	Mexican lampfish	Warm-water
<i>Symbolophorus californiensis</i>	Bigfin lanternfish	Warm-water
<i>Bathylagoides wesethi</i>	Snubnose blacksmelt	Warm-water
<i>Ceratoscopelus townsendi</i>	Fangtooth lanternfish	Warm-water
<i>Diogenichthys laternatus</i>	Diogenes lanternfish	Warm-water

^a*Vinciguerria* spp. includes the much more common *Vinciguerria lucetia* and *V. poweriae* which also is found offshore.

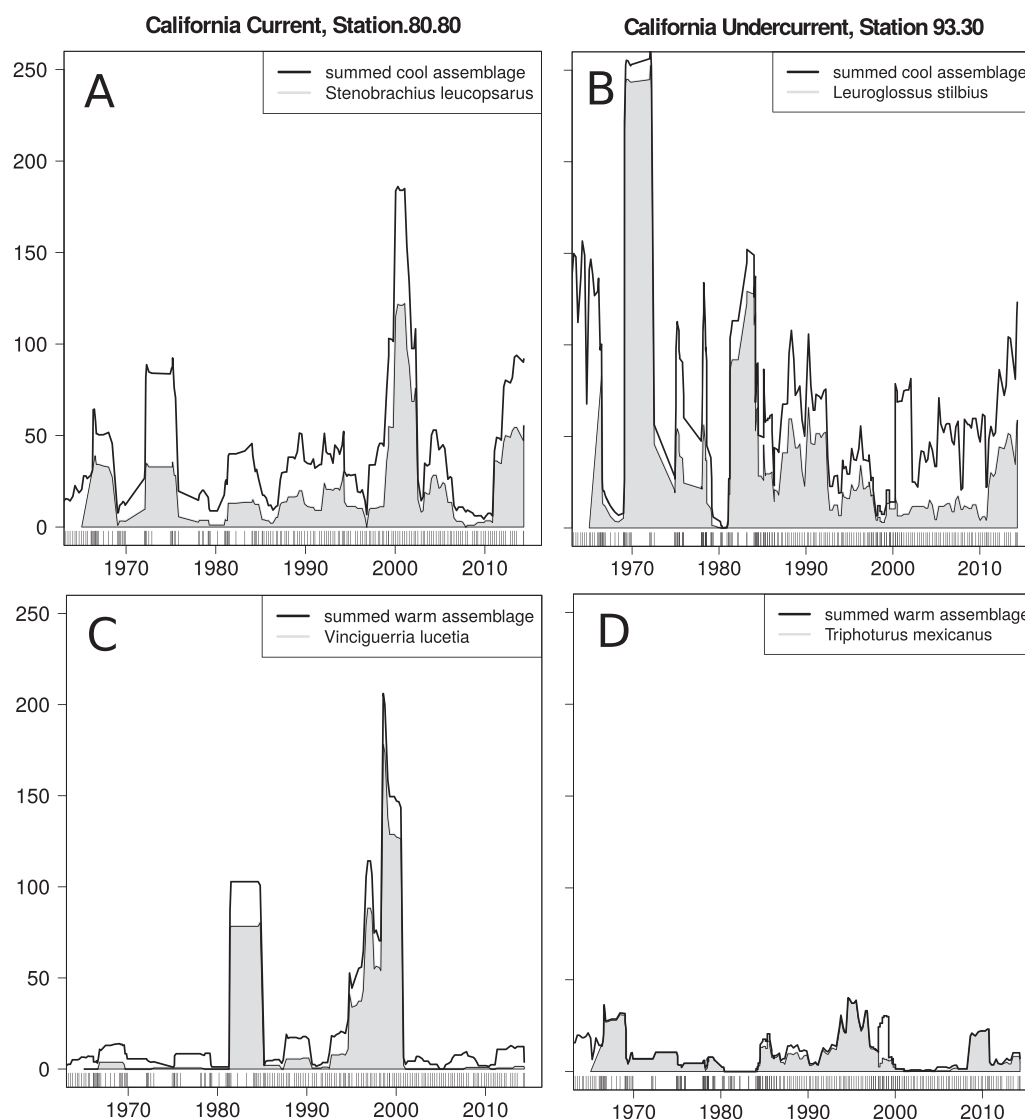


Figure 4. Time series of cool water associated (a and b) and warm water associated (c and d) mesopelagic ichthyoplankton assemblage densities (larvae 10 m^{-2}) from 1965 to 2014 at (left column) CC and (right column) CU. The numerically dominant species at each location (gray fill) is overlaid on total assemblage densities to illustrate differing species dominance in the assemblages. 2012–2014 data were available for only stations 80.0 80 and 93.3 30 at the time of writing.

assemblages at CU showed a very limited response to the large 1997/1999 ENSO event, which was very different to the strong offshore response. The cool water assemblage at CC peaked most dramatically during the 1998 La Niña, and then decayed to previous abundance levels over the following two years (Figure 4a). The warm water assemblage at CC increased in abundance during the 1982/1983 ENSO and then peaked again during the 1997/1998 El Niño, declining precipitously after the subsequent 1998 La Niña (Figure 4c).

In contrast, the cool water assemblage at CU fluctuated widely with indications of declining abundance of the numerically dominant species from 1987 to 2010, but failed to show much response to the 1997/1999 ENSO (Figure 4b). The warm water assemblage at CU exhibited the lowest temporal variability in larval abundance over the time series, with little response to the 1997/1999 ENSO event (Figure 4d).

3.3. Changes in Mesopelagic Ichthyoplankton Species Dominance

The relative proportions of species in warm and cool assemblages might be expected to vary over time on decadal scales with presence of PEW off southern California (section 3.1, Figure 2). Alternatively, the interannual perturbation forced by the strong 1997/1999 ENSO event might change species dominance in the

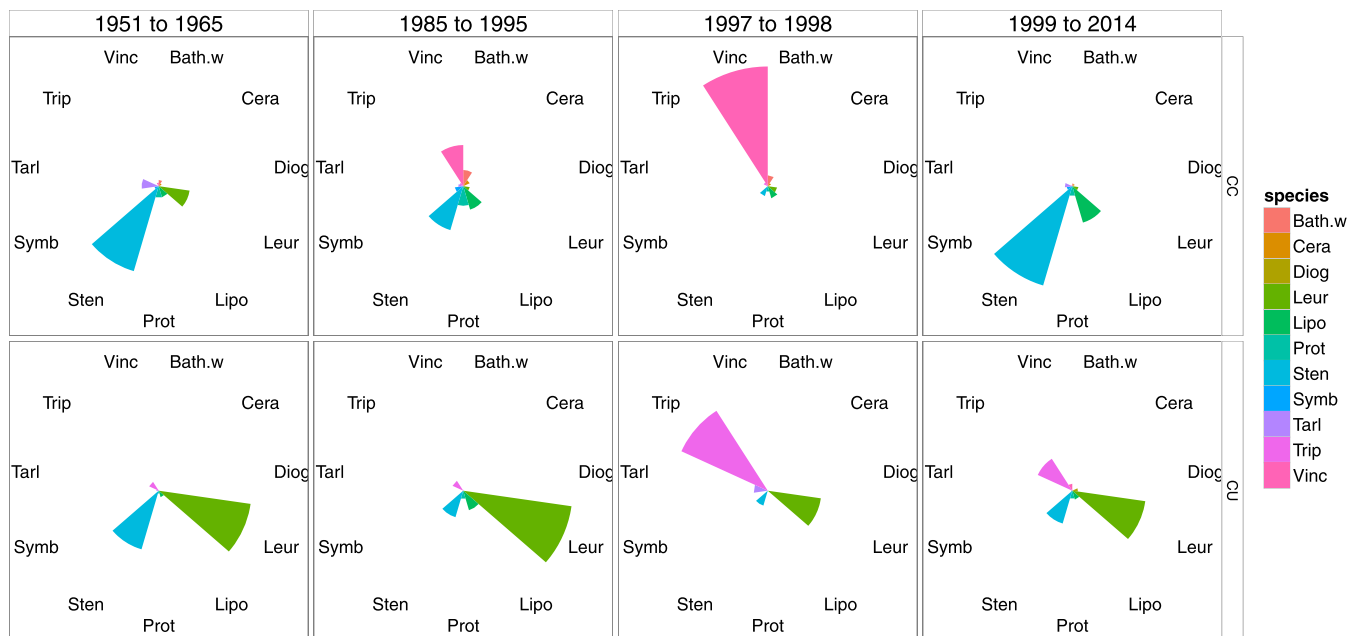


Figure 5. Proportional dominance of ichthyoplankton species in Table 3 at representative California Current (CalCOFI station 80.0 80, CC, top row) and California Undercurrent (station 93.3 30, CU, bottom row) locations during 1951 through 1965, 1985–1996, 1997–1998, and 1999–2014. Data were excluded for the period 1969–1984 when surveys were triennial rather than quarterly. Species codes are: Leur = *Leuroglossus stilbius*, Lipo = *Lipolagus ochotensis*, Prot = *Protomycophum crockeri*, Sten = *Stenobranchius leucopsarus*, Tarl = *Tarletonbeania crenularis*, Vinc = *Vinciguerria lucetia*, Trip = *Triphoturus mexicanus*, Symb = *Symbolophorus californiensis*, Bath.w = *Bathylagoides wesethi*, Cera = *Ceratoscopelus townsendi*, and Diog = *Diogenichthys laternatus* (see Table 3).

assemblages either permanently or temporarily, depending on how resilient the assemblages are. A return of perturbed assemblages to their condition prior to the perturbation could be interpreted as evidence of resilience.

Species dominance in the warm and cool water associated mesopelagic fish assemblages is different at CC and CU. At CC on average from 1965–2014, five species make up 80–85% of the assemblage. Species dominance is stronger at CU where only three species make up 83–85% of the assemblage. The cool water associated northern lampfish (*Stenobranchius leucopsarus*) constitutes the highest proportion of the assemblage at the California Current (CC) station (Figure 5) whereas the cool water California smoothtongue (*Leuroglossus stilbius*) is dominant at the California Undercurrent (CU) station. These species retain their dominance of the assemblages at both locations over the entire time series (Figure 5), indicating that the pattern of dominance is relatively stable on decadal scales. However, there was a notable shift in dominance at both CC and CU due to the 1997/1999 ENSO perturbation. At both the offshore and the nearshore slope stations, a warm water species assumed temporary dominance, but the temporarily dominant species differed between locations. At the offshore location (CC), the lightfishes (*Vinciguerria lucetia*) dominated the assemblage temporarily, while at the slope location (CU) the Mexican lampfish (*Triphoturus mexicanus*) assumed dominance during the 1997/1998 El Niño (Figure 5). In both cases, the assemblages returned to their condition prior to the 1997/1999 ENSO event, indicating that the assemblages were resilient to the strong ENSO perturbation.

3.4. Changes in Ichthyoplankton Assemblage Structure and Diversity

Based on species abundance patterns, we found no difference between diversity in the two decadal periods (1985–1996 and 1999–2011) at either the California Undercurrent (CU) or the California Current (CC) station (Kolmogorov-Smirnov test, $p > 0.05$, Figure 6). In contrast, diversity during the 1998 La Niña period was significantly lower than diversity in both the previous decade ($D=0.48$, $p=0.006$) and the subsequent decade ($D=0.40$, $p=0.037$) near the CC location. Diversity was also lower during La Niña, but not El Niño, compared to both the previous decade ($D=0.40$, $p=0.037$) and the subsequent decade ($D=0.44$, $p=0.016$) near the CU location.

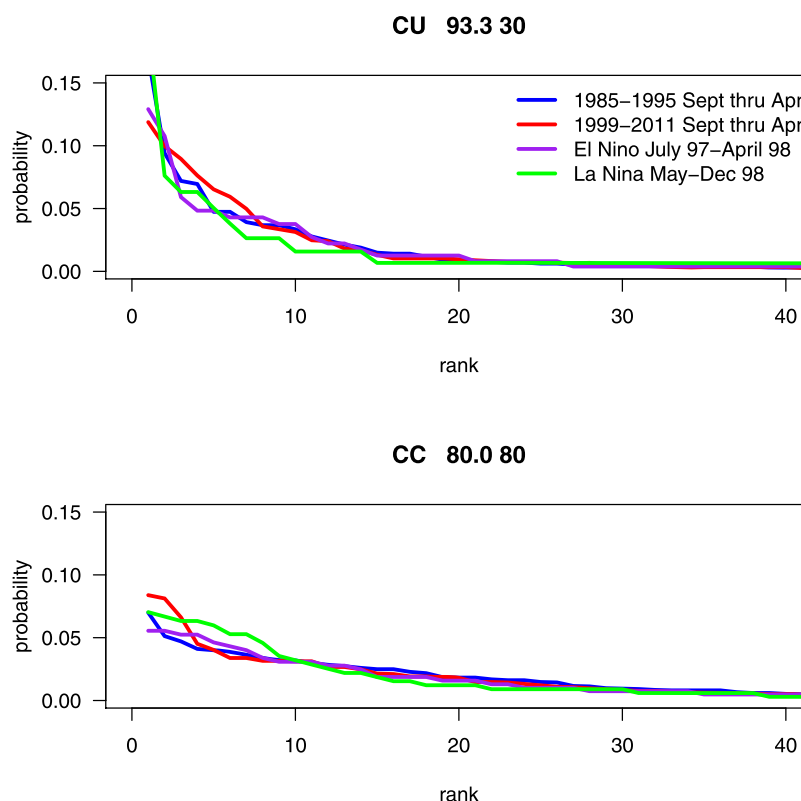


Figure 6. Species rank/abundance plots for the ichthyoplankton assemblage in three time periods (1985–1996, 1997–1998, and 1999–2011) at (a) CalCOFI station 93.3 30 and associated stations and (b) station 80.0 80 and associated stations (see Figure 1). Data were restricted to September through April to avoid seasonal bias when comparing to the ENSO events.

The fact that we were able to detect lower diversity during a strong La Niña, but were not able to detect higher diversity during a strong El Niño (Figure 6) suggests that species differences occurring during El Niño are primarily due to rare species occurrences. This would affect the tail of the ranked species abundance distribution, which would be harder to detect using a KS-test. This is illustrated by comparing species richness between the 1997/1998 El Niño and the 1998 La Niña (Table 4). Species richness was higher offshore (CC) than on the slope (CU), and at both locations, species richness was higher during the el Niño. There were

128 species present during the El Niño compared to 87 species during the La Niña at CC. There were 84 species during El Niño but 69 species present during the La Niña at CU. This comparison clearly illustrates the long tail of the El Niño ranked species abundance distributions.

Species evenness increased during the La Niña near CC. This appears to be due to an increase in the abundance of the 3–8th ranked species (Figure 6b). El Niño had little effect on evenness near CC. In contrast, evenness decreased on the slope near CU during El Niño and decreased further during La Niña. The species abundance shift during El Niño at CU occurred over the same 3–8th

Table 4. Sampled and Predicted Total Species Richness in the Decade Before (1985–1996), During the 1997/99 ENSO Event, and in the Following Decade (1999–2011) Based on the California Current Station (CC), the California Undercurrent Station (CU) and Associated Stations (Figure 1)^a

	Detected Species	Undetected Species	Predicted Species Richness
CC and associated stations			
1985–1996	111	14	125
1997/1998 El Niño	74	54	128
1998 La Niña	59	28	87
1999–2011	129	30	159
CU and associated stations			
1985–1996	91	23	114
1997/1998 El Niño	47	37	84
1998 La Niña	33	36	69
1999–2011	96	58	154

^aSpecies richness is calculated using the number of species sampled (i.e., detected) corrected for the number of undetected species.

ranked species as for the offshore assemblage, but during La Niña a wider range of species (3–13th ranked species) changed relative abundance (Figure 6a).

Lack of difference in the species abundance structure in the decade before and after the 1997/1999 ENSO event showed that the assemblage reverted to its former structure following the ENSO perturbation, indicating resilience. While the species pattern has remained stable, the long tail of the distributions shows that species richness increased between the decades at both CC and CU. The total number of species at CC (and associated stations) rose from 125 to 159 species, while at CU the number of species rose from 114 to 154 species (Table 4).

3.5. Changes in Ichthyoplankton Species Composition

Ichthyoplankton species composition differed significantly in the decades before and after the 1997/1999 ENSO event near the offshore (CC) and slope (CU) stations in both winter and spring (Table 5). The decadal differences are strongest in winter (Figures 7a and 7c). Differences in species composition between the decades were driven primarily by changes in the abundance of four species: northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*), Pacific sardine (*Sardinops sagax*), and a cool water mesopelagic dominant named California smoohtongue (*L. stilbius*). Removing these four species from the analysis eliminated significant differences between the decades. With the exception of sardine, these four species were less abundant in later years (Figure 7). During more recent years, especially in the offshore (CC) during spring, a cool water myctophid called California flashlightfish (*P. crockeri*), as well as jack mackerel (*Trachurus symmetricus*) and sardine (only up to 2006) became more abundant (Figure 7).

In contrast to the decadal comparison, where species differed most in winter, ichthyoplankton species changes during the 1997/1998 El Niño manifested most clearly in the summer and fall seasons (Table 5), despite the fact that El Niño reaches its peak in the northern hemisphere winter. For example, in summer 1998, near the end of the extreme El Niño, the offshore (CC) ichthyoplankton assemblage included high densities of the midwater, subtropical mesopelagics such as lightfishes (*Vinciguerria lucetia*) and snubnose blacksmelt (*B. wesethi*) (Table 3). During the same summer, the slope (CU) assemblage was characterized by high densities of lightfishes and bigfin lanternfish (*S. californiensis*). In the fall of 1998, right at the end of the extreme El Niño, the ichthyoplankton assemblage on the slope (CU) included high densities of southern species such as chub mackerel (*Scomber japonicus*) and California barracuda (*S. argentea*). All of these occurrences suggest advection of southern ichthyoplankton species into the southern California region during the extreme 1997/1998 El Niño and perhaps more favorable spawning conditions for southern fish if they were already present. However, the resilient species abundance patterns indicating stable evenness and species richness shows that the advection of southern species had no lasting effect on community structure.

Table 5. Redundancy Analysis Results Evaluating Potential Differences in Assemblage Composition in Years Before (1985–1996) and After (1999–2011) the 1997/1999 ENSO Event

	adj. R^2	p -Value RDA	If Significant, Which Species Are Important Drivers?	Does El Niño Stand Out?
CC Stations				
Winter	0.44	0.005	Fewer <i>E. mordax</i> , <i>L. stilbius</i> and <i>M. productus</i> in later years	No
Spring	0.35	0.005	More <i>P. crockeri</i> , <i>S. sagax</i> , and <i>T. symmetricus</i> in later years	No
Summer	0.05	0.036		More <i>V. lucetia</i> and <i>B. wesethi</i>
Fall	0.01	0.3		No
CU stations				
Winter	0.18	0.005	Fewer <i>E. mordax</i> , <i>M. productus</i> , and <i>S. sagax</i> in later years	More <i>V. lucetia</i> and <i>D. atlanticus</i>
Spring	0.16	0.01	Fewer <i>E. mordax</i> , <i>L. stilbius</i> , and <i>M. productus</i> in later years	No
Summer	0.03	0.05		More <i>V. lucetia</i> and <i>S. californiensis</i>
Fall	0.06	0.05		More <i>S. japonicus</i> and <i>S. argentea</i>

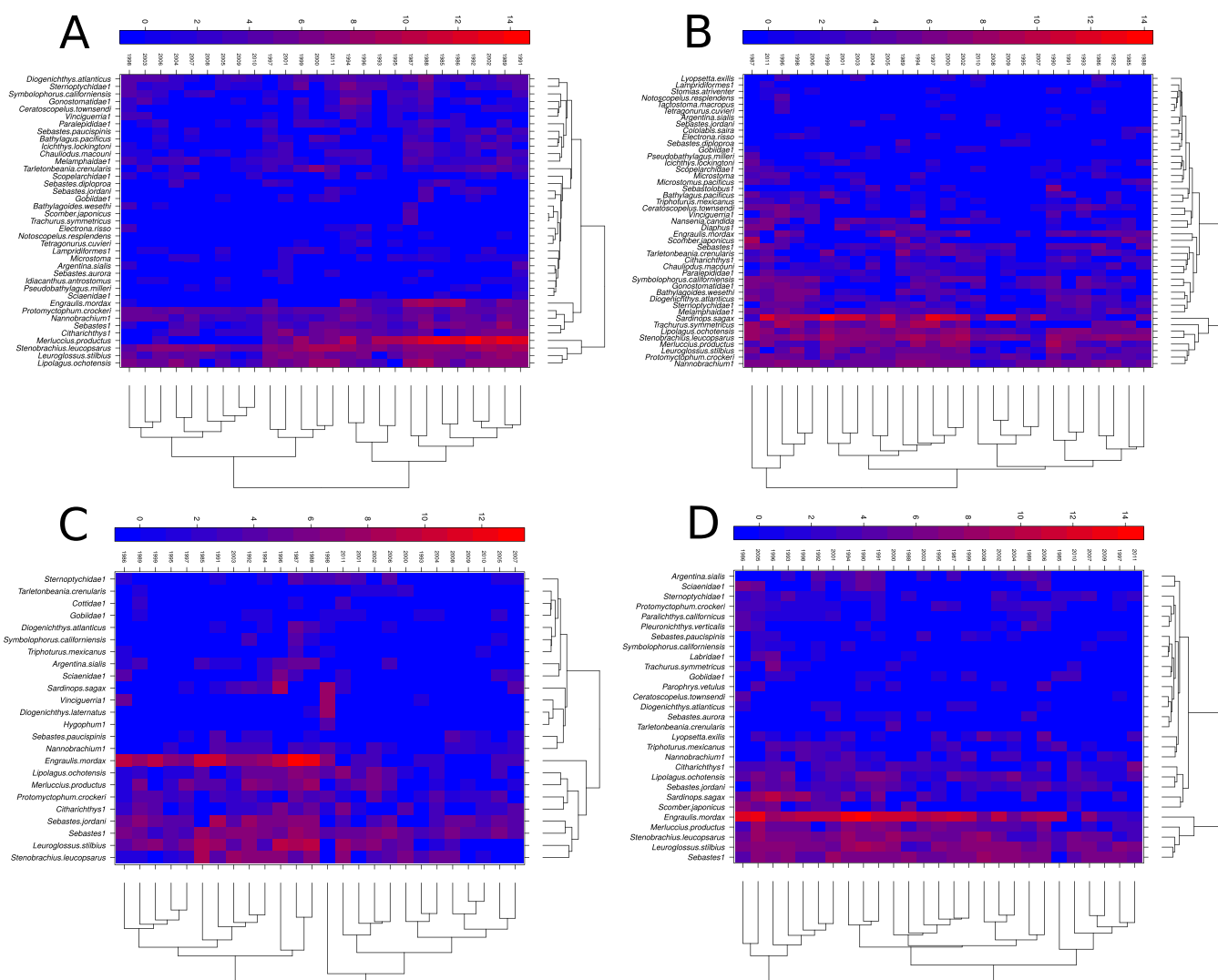


Figure 7. Ichthyoplankton species composition clustered by species and year to show temporal changes in the assemblage from 1985 to 2011 (a) at the offshore CalCOFI station 80.0 80 (CC) and adjacent stations in winter, and (b) at the same stations as (a) in spring, (c) at the slope CalCOFI station 93.3 30 (CU) and adjacent stations in winter, and (d) at the same stations as (c) in spring.

4. Discussion

Ichthyoplankton analyzed in this study were collected with nets deployed to a depth of 210 m. Since 77% of spic values on the $26.25\text{--}26.75\text{ kg m}^{-3}$ isopycnal layer were between 175 and 300 m depth, much of the PEW may lie below the ichthyoplankton sampling range. However, mesopelagic fish constitute the largest proportion of species in the CalCOFI samples, and adults tend to live deeper than their larvae, although there are species-specific differences in the vertical distribution of life stages (Bowlin, 2016). Based on the deeper distribution of adults, we assume that the habitat of these fishes extends into PEW off southern California.

Bongo net sampling extended below the aragonite saturation horizon (ASH), which is the depth below which organisms experience corrosive conditions. Overall the ASH varied from 84 to 267 m at CC, and the average depth shoaled by 26 m between 1985–1996 and 1999–2011 (Table 2). The average ASH depth at CU shoaled by 18 m between the earlier and later study windows. At CU, the ASH reached 50 m at its shallowest expression, and average ASH depth was 20–28 m shallower than at CC in each interval. Further, we find that the shoaling of the ASH and lower pH waters associated with the California Undercurrent appears to have occurred between the 1985–1996 and 1999–2011 intervals (Figure 8), rather than in a more gradual linear fashion through time as suggested by the analyses of Feely *et al.* [2012] and Meinville and Johnson

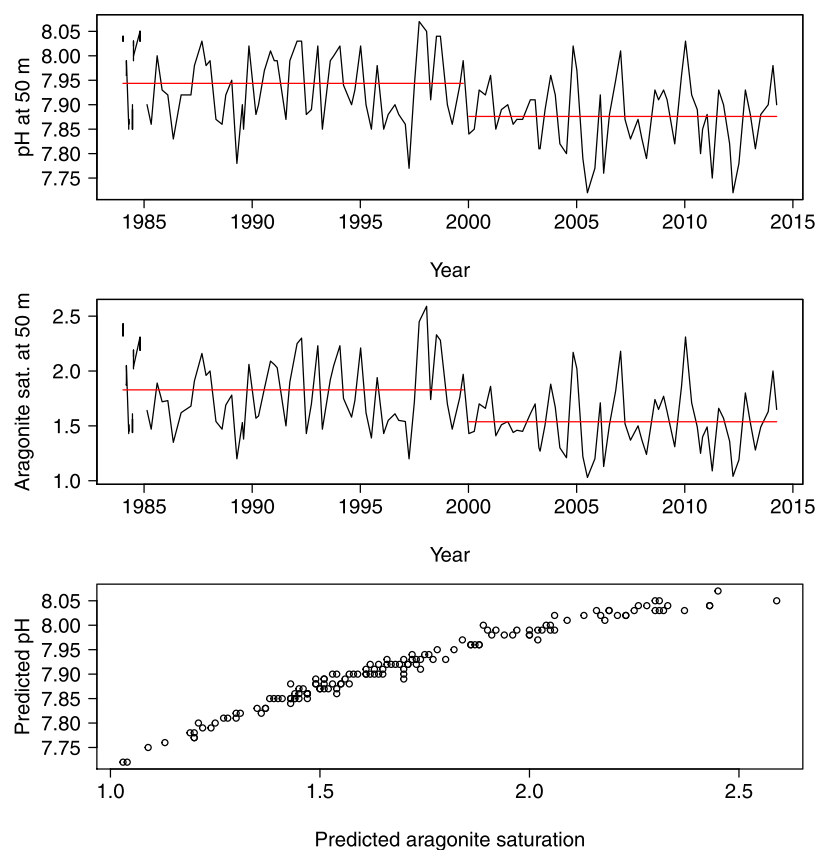


Figure 8. Time series of pH and aragonite saturation at 50 m depth at CalCOFI station 93.3 30 for 1985–2014. Red lines show averages for two periods distinguished using Pettitt’s test for change point detection [Pettitt, 1979]. The break point is second quarter of 1999.

[2013]. Based on decadal open-ocean surveys, *Feely et al.* [2012] estimated a 100 m shoaling of the ASH between 1994 and 2004 in the eastern subtropical Pacific west of the continental shelf, and an average ASH shoaling within the California Current of $>5 \text{ m yr}^{-1}$. The more temporally resolved data set analyzed here indicates both that the overall shoaling in the CU and CC regions was less than previously estimated and may have occurred in a discrete shift rather than a steady trend as suggested by the change point analysis. Thus, it is clear that ichthyoplankton assemblages were exposed, not just to the effects of PEW, but to substantially more corrosive conditions in the upper water column over a protracted period of time.

Some experimental studies suggest that the corrosive conditions to calcifying organisms are not yet at levels that are harmful to fish. Levels of pH around 7.4 have been shown to impact survivability of estuarine fish [DePasquale et al., 2015], and the estimated record here never fell below 7.5. DePasquale et al. [2015] suggest that estuarine fish exposed to pH values less than 7.4 from the time they are in eggs through early larval stages significantly decreases survival. The CalCOFI region is projected to experience those conditions by the end of the 21st century [Gruber et al., 2012], or sooner, as this region experiences high variability, and as such will experience these conditions as part of that variability [Hauri et al., 2013; Takeshita et al., 2015]. Applying linear extrapolation of observed changes in pH of 0.04 over 32 years (1980–2012) [Meinvielle and Johnson, 2013], the threshold of 7.4 will be experienced in the CalCOFI region within the next 20 years, which is conservative because it depends on the empirical algorithm [Alin et al., 2012] that does not take increasing anthropogenic carbon into account. While the ichthyoplankton assemblages studied here are not found to respond to changes in corrosivity observed from 1985 to 2011, a response may still be elicited in the future.

We also assume that the perturbation of ichthyoplankton diversity that we measured due to the 1997/1999 ENSO event and the resilience of the assemblage structure (and associated diversity) that we measured in the ichthyoplankton is representative of the adults. It is generally assumed that the abundance of ichthyoplankton is correlated with the spawning stock biomass of the adults in the same year, because this has

been found to be true in virtually every case where the relationship has been tested [Moser and Watson, 1990; Ralston *et al.*, 2003]. Nevertheless, the relationship is variable and it has not been tested in any mesopelagic species, primarily because there are no estimates of mesopelagic fish biomass to test it with. Consequently we cannot state with certainty that resilience in the larval assemblage represents resilience in the adult assemblage, but it is likely that it does.

Our results do not indicate replacement of cool water by warm water-associated mesopelagic species from 1985 to 2011, despite a warming trend off southern California. The decadal trends in fish species were less consistent (Table 5) than we would expect if a simple displacement of ichthyoplankton assemblages was occurring. We conclude that the dominant forcing on changes in the ichthyoplankton assemblages is intrusion and subsequent mixing of water masses. This mechanism is consistent with the strong seasonality that we observed, with the effects that were observed during the extreme 1997/1999 ENSO event, and with stable patterns of diversity, presumably maintained by mixing of water masses. The decadal increase in species richness at both locations is consistent with intrusion of warm water masses with more diverse ichthyoplankton assemblages.

Our analyses show that the fish assemblages are resilient over the last 30 years (1985–2011) despite the occasional extreme ENSO event that causes significant perturbation in the structure and diversity of assemblages. This does not mean that the fish assemblages have not changed, nor does it mean that they will not change in the future as low pH events become more common [Hauri *et al.*, 2013; Takeshita *et al.*, 2015]. While the assemblage structure and diversity has been stable over 30 years, we see changes in the proportional dominance of species from 1985 to 2011, particularly at the offshore California Current station in winter and spring seasons. Stable diversity of the ichthyoplankton assemblage initially seems to be inconsistent with fish declines off southern California [Koslow *et al.*, 2013, 2015]. Koslow *et al.* [2015] reported 72% declines in the abundance of cool water associated fish species since the 1997/1999 ENSO event, based on an EOF analysis of 27 species from all of the consistently sampled CalCOFI stations. We also noted a decline in the abundances of oceanic species, but found that differences in the assemblages in the decades before and after the 1997/1999 ENSO event were driven by only four abundant species (anchovy, hake, sardine, and the dominant offshore cool water mesopelagic species, *Leuroglossus stilbius*). Declines in a few abundant species are not incompatible with stable diversity because diversity is determined by the skewed distribution of the broader assemblage of over 400 species.

We conclude that the southern California ichthyoplankton assemblage is resilient, despite some changes in species composition manifested in the offshore regions. We would argue that the major stressor of the ichthyoplankton assemblage at this time is extreme ENSO events operating at the interannual scale, rather than decadal-scale climate trends in acidification and its correlated variables.

Acknowledgments

Funding was provided by the National Oceanic and Atmospheric Administration (NOAA) California Cooperative Oceanic Fisheries Investigations (CalCOFI) and Fisheries and The Environment (FATE) programs, by a grant from the NOAA Ocean Acidification program, and by the Pacific Marine Environmental Laboratory. This is NOAA PMEL contribution number 4407. We are grateful to Toby Garfield and Richard Feely for sharing their insights on our analyses, and to Paul Fiedler for an internal NOAA review. We thank two anonymous reviewers whose comments improved our manuscript. Data used are publicly available through NOAA ERDDAP in the CalCOFI program data tables (<http://coastwatch.pfeg.noaa.gov/erddap/index.html>).

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