**RESEARCH ARTICLE**

**Key Points:**
- Changes in relative abundance and spatiotemporal metrics of warm- and cool-water mesopelagic ichthyoplankton differ strongly by species
- Relative abundance of warm-water mesopelagic ichthyoplankton show an increasing secular trend in the southern California Current System
- The most parsimonious explanation for the trend is increased presence of Pacific Equatorial Water in the inshore southern California region

**Supporting Information:**
- Supporting Information S1

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# Interannual and Secular Variability of Larvae of Mesopelagic and Forage Fishes in the Southern California Current System

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**Abstract** We used univariate and multivariate spatiotemporal delta models to quantify changes in the distribution of ichthyoplankton in the southern California Current System from 1951 to 2016. We focus on mesopelagic species, because they are most abundant, and on northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), and Pacific hake (*Merluccius productus*), because they are important commercial and forage fish species. Univariate models indicated that changes in the relative abundance, area occupied, center of gravity, and spatiotemporal variability of numerically dominant warm-water and cool-water-associated mesopelagic ichthyoplankton show strong species-specific differences. Multivariate models revealed that the warm-water-associated mesopelagic assemblage exhibits an increasing, nonmonotonic, secular trend of increasing relative abundance underlying interannual variability, suggesting a tropicalization of the southern California Current System. In contrast, the cool-water-associated mesopelagic assemblage shows mainly interannual variability, with little secular trend over the 65-year period. Correlation matrices of the modeled ichthyoplankton densities showed that the spatial distributions of northern anchovy and Pacific hake are highly correlated with cool-water mesopelagic ichthyoplankton, but Pacific sardine is spatially correlated with both warm- and cool-water-associated mesopelagic species. Declines of adult sardine, anchovy, and hake are occurring concurrently with tropicalization of the southern California Current System. The most parsimonious explanation for tropicalization of the ichthyoplankton is increased presence of Pacific Equatorial-influenced Water in the inshore southern California region.

**Plain Language Summary** We modeled the distribution of ichthyoplankton in the southern California Current System from 1951 to 2016. We focus on abundant mesopelagic species and on northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), and Pacific hake (*Merluccius productus*), because they are important commercial and forage fish species. Single species models indicated that changes in abundance, area, distribution center, and variability of the most abundant mesopelagic ichthyoplankton associated with warm and cool water show strong differences between the species. Models of species groups revealed that the warm-water mesopelagic larval fishes exhibit a long-term trend of increasing relative abundance underlying year-to-year variability, suggesting tropicalization of the southern California Current System. In contrast, the cool-water mesopelagic larvae show mainly year-to-year variability, with little long-term trend. Correlations between the modeled species showed that the spatial distributions of northern anchovy and Pacific hake are highly correlated with cool-water mesopelagic larvae, but Pacific sardine is correlated with both warm- and cool-water-associated mesopelagic species. The spatial variability of hake over time is highly positively correlated with cool-water mesopelagics and with northern anchovy, but sardine fluctuate independently of the mesopelagics and both anchovy and hake. Declines of adult sardine, anchovy, and hake are occurring concurrently with tropicalization of the southern California Current System. The simplest explanation for more tropical ichthyoplankton is increased presence of Pacific Equatorial-influenced Water in the inshore southern California region.

## 1. Introduction

Shifts in fish distributions under changing climate have been reported from many regions, where movements were found to be mainly poleward or across shelf into deeper water (Nye et al., 2009; Pinsky et al., 2013).

Distribution shifts are highly species-specific (Kleisner et al., 2017; Thorson et al., 2016). Some species do not move, and some species shift an order of magnitude further than others (Bell et al., 2015). Species distribution shifts are influenced by the presence or absence of barriers to movement and, in some cases, by fishing pressure (Bell et al., 2015). Although there have been considerable changes in the abundance of pelagic fishes off California, reported shifts in geographic distributions have been small (Hsieh et al., 2009), except for temporary shifts during extreme events such as some El Niños (Lea & Rosenblatt, 2000) and the recent North Pacific warm anomaly (Auth et al., 2017).

Spatiotemporal changes in ichthyoplankton assemblages can be a sensitive indicator of environmental change, and mesopelagic fishes are particularly sensitive to changes in water masses. The mesopelagic realm is usually defined as between depths of 200 and 1,000 m, while the epipelagic is shallower than 200 m. Mesopelagic fishes are the most abundant fish group off southern California (Moser & Ahlstrom, 1996a, 1996b). We focus on mesopelagic species, because they are most abundant, and on northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), and Pacific hake (*Merluccius productus*), because they are important commercial and forage fish species. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton (early life stage) data provide a consistent source of information on the distribution and abundance of mesopelagic and other forage ichthyoplankton off southern California since 1951 (McClatchie, 2013). Fish early life stages are typically constrained in space and time, compared to adult and subadult stages. This is in part due to wider physiological tolerance of environmental conditions and locomotion abilities of adult stages and in part to very specific habitat requirements during spawning and larval dispersal phases (Ciannelli et al., 2015). Therefore, to better understand how species will adapt to climate variability by changing their distribution, it is critical to consider not only adult but also early life stages.

It has been difficult to disentangle the effects of environmental variables on pelagic ichthyoplankton distribution and abundance, in part because multiple variables are correlated. Recent papers showed a 70% decline in species-aggregated abundance of ichthyoplankton off southern California, largely driven by declines in anchovy and hake, but the reasons for the observed decline remain elusive (Koslow et al., 2013, 2015). Changes in water masses provide a convenient aggregate environmental index for changes in variables such as temperature, salinity, nutrients, oxygen, and even, very approximately, for production (i.e., units of carbon volume$^{-1}$, aggregated over some time period, often a year).

Distinct groups of mesopelagic ichthyoplankton species are consistently associated with warm and cool waters off southern California, and we refer to these groups as warm- or cool-water assemblages (Hsieh et al., 2005; Moser et al., 1987; Table 1). Consequently, changes in the mesopelagic ichthyoplankton assemblages should be related to interannual and secular changes in the proportions of water masses in the CalCOFI region. In this paper we use secular trend as a shorter synonym for long-term, multidecadal, low frequency trend. Both the warm- and the cool-water assemblages are numerically dominated by single species. In general, the numerically dominant warm-water mesopelagics are *Vinciguerria* spp. ,mainly *V. lucetia*, in the offshore, and *Triphoturus mexicanus* in the inshore. The numerically dominant, cool-water-associated species offshore is *Stenobrachius leucopsarus*, but it is also widely distributed in the CalCOFI region. *Leuroglossus stilbius* is the numerically dominant cool-water species inshore (Table 1).

CalCOFI sampling that extended into Baja California from the 1950s to 1970s show that *V. lucetia* is often the most abundant species off central and southern Baja California (Moser et al., 2001). The Mexican lampfish, *Triphoturus mexicanus*, is common in the same waters as *V. lucetia* but tends to be found closer to shore off southern California (Moser et al., 2001). Similar to *V. lucetia*, *T. mexicanus* larvae are frequently numerically dominant off central and southern Baja California.

In contrast to *T. mexicanus* and *V. lucetia*, the distributions of northern lampfish, *Stenobrachius leucopsarus*, and California smoothtongue, *Leuroglossus stilbius*, extend northward of southern California (Moser, 1996). *S. leucopsarus* resides in the epipelagic and mesopelagic waters, and its biogeographic range runs south to northern Baja California, north to the Gulf of Alaska, and west to Japan (Moser et al., 2001). It is frequently the most common larva sampled off Oregon (Auth & Brodeur, 2006). *L. stilbius* live in epipelagic and mesopelagic waters and are found from Oregon to Baja California (Moser et al., 2001).

Forage fishes in the southern and central California Current System include mesopelagic fishes, Clupeiformes (Pacific sardine *Sardinops sagax*, northern anchovy *Engraulis mordax*, and Pacific herring *Clupea pallasi*), Perciformes (Pacific mackerel *Scomber japonicus* and jack mackerel *Trachurus symmetricus*), Gadiformes (Pacific

**Table 1**

*Ichthyoplankton Species From CalCOFI Surveys Off Southern California Categorized as Warm-Water or Cool-Water Associated Mesopelagic Assemblages, and Three Selected Forage Fish Species (Pacific Sardine, Northern Anchovy, and Pacific Hake)*

| Genus species | Common name | Subcategory |
|---|---|---|
| *Leuroglossus stilbius* | California smoothtongue | Cool-water inshore dominant |
| *Stenobrachius leucopsarus* | Northern lampfish | Cool-water offshore dominant |
| *Tarletonbeania crenularis* | Blue lanternfish | Cool water |
| *Lipolagus ochotensis* | Eared blacksmelt | Cool water |
| *Bathylagus pacificus* | Slender blacksmelt | Cool water |
| *Protomyctophum crockeri* | California flashlightfish | Cool water |
| *Triphoturus mexicanus* | Mexican lampfish | Warm-water inshore dominant |
| *Vinciguerria* spp. | Lightfishes | Warm-water offshore dominant |
| *Symbolophorus californiensis* | Bigfin lanternfish | Warm water |
| *Bathylagoides wesethi* | Snubnose blacksmelt | Warm water |
| *Ceratoscopelus townsendi* | Fangtooth lanternfish | Warm water |
| *Sardinops sagax* | Pacific sardine | Forage fish |
| *Engraulis mordax* | Northern anchovy | Forage fish |
| *Merluccius productus* | Pacific hake | Forage fish |

*Note.* Species listed as *dominant* are the most abundant species. Inshore and offshore are defined as inshore or offshore of CalCOFI station 60 (marked on Figure 1). CalCOFI = California Cooperative Oceanic Fisheries Investigations.

hake, *Merluccius productus*), and Osmeriformes (several species of smelts). Pacific sardine, Pacific hake, and anchovy are referred to as sardine, hake, and anchovy for the remainder of the text. Spatial correlations examined in this study, between mesopelagic ichthyoplankton and selected forage ichthyoplankton, provided insight into why forage species like anchovy and hake are not doing well off southern California, and this gives us a deeper insight into the reported fish declines off southern California.

Although the southern California region experiences complex mixing of water masses (Bograd et al., 2001; Bograd & Lynn, 2003; Lynn & Simpson, 1987), the source water properties for Pacific Subarctic Water (PSA), Pacific Equatorial Water (PEW), and North Pacific Central Water (NPCW) are clearly expressed on isopycnals at known locations (Bograd et al., 2015). In this study, we relate the spatiotemporal variability of mesopelagic and forage ichthyoplankton assemblages to changing proportions of three source water masses of the southern California Current System. Modeling changes in ichthyoplankton assemblages over 65 years using a spatiotemporal delta model (Thorson et al., 2015, 2016) led us to hypothesize that increasing proportion of PEW is associated with a tropicalization of the mesopelagic ichthyoplankton assemblage (i.e., an increase in the relative abundance of warm-water species). We tested this hypothesis by quantifying secular changes in water mass proportions using optimal multiparameter analysis (Poole & Tomczak, 1999; Tomczak & Large, 1989), based on mixing of source waters on isopycnals at locations where their properties are most clearly expressed Bograd et al. (2015). We related temporal changes in the proportions of water masses to modeled trends in larval mesopelagic and forage fish assemblages. Part of our goal was to understand how long-term, secular changes in ichthyoplankton assemblages relate to secular changes in water masses in the southern California Current System. As far as we are aware, it has not been demonstrated that long-term changes in the proportions of water masses can explain observed changes in the distribution of pelagic fish larvae and by inference the distribution of spawning pelagic fish. Furthermore, by using spatial statistics, we have demonstrated how the spatial patterns of ichthyoplankton have changed over more than six decades off southern California, which is an advance on spatially aggregated analyses.

## 2. Methods

### 2.1. Sampling Domain

The CalCOFI program currently samples on a quarterly basis; for the spring season (March-April-May) examined in this study, the program samples 113 stations (Figure 1) taking a suite of hydrographic profiles and fixed-depth bottle samples from 5- to 500-m depths. In this study, inshore and offshore are defined as inshore or offshore of CalCOFI station 60 (marked on Figure 1). Off southern California, station 60 roughly corresponds to the outer shelf edge at the Santa Rosa Ridge, although water much deeper than shelf depth (200 m)
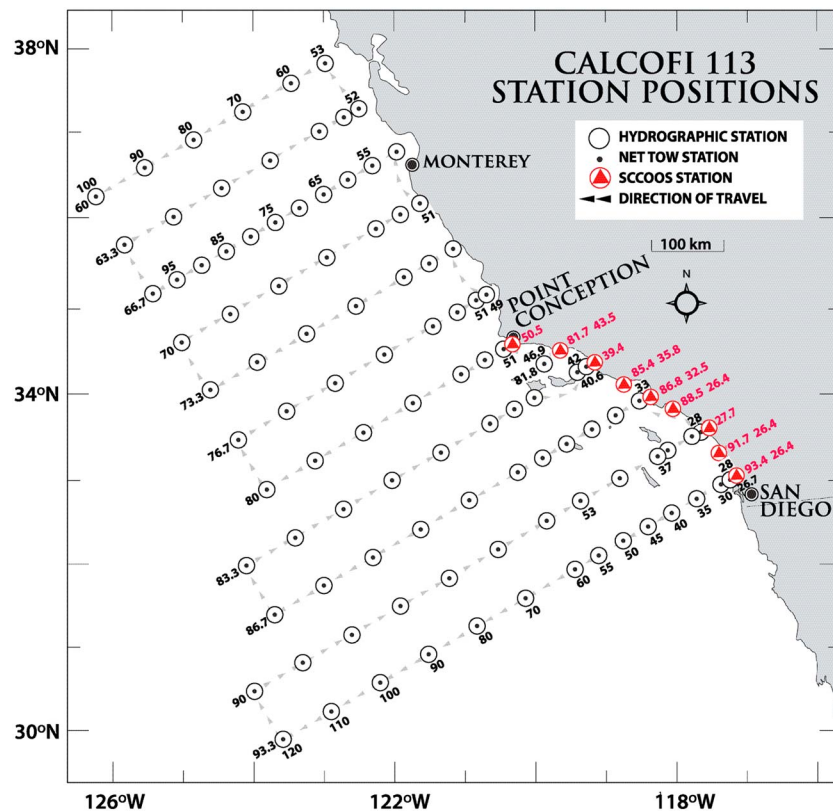
**Figure 1.** Map showing the current CalCOFI sampling domain in spring (March-April-May) off southern California comprising 11 lines or transects from San Diego to San Francisco. The six southern lines stations have been sampled consistently since regular CalCOFI surveys began in 1951, except for the inshore stations (marked in red) that were added in 2005 as part of the Southern California Coastal Ocean Observing system (SCCOOS). Station numbers referred to in the text are marked along the southernmost line. CalCOFI = The California Cooperative Oceanic Fisheries Investigations.

also occurs inshore of the Santa Rosa Ridge (Figure 1). 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 National Atmospheric and Oceanic Administration Environmental Research Division Data Access Program on the Internet at http://upwell.pfeg.noaa.gov/erddap/index.html. A detailed summary of the CalCOFI program is provided by McClatchie (2013).

### 2.2. Ichthyoplankton Data Consistency

CalCOFI collects ichthyoplankton at each station (Figure 1) using oblique, vertical, and surface plankton tows. The commonest sampling interval in the CalCOFI series is quarterly, but this study utilized only spring data (March-April-May). We neglected the within season variation in the interests of retaining the most complete time series. CalCOFI sampling was remarkably consistent from 1951 to 1968 and from 1984 to 2016. However, the intervening 14-year period (1969–1983) was only sampled triennially, creating considerable data gaps. Larval fish time series (larvae $(10 \text{ m})^{-2}$) used in this study were obtained from counts of larvae in oblique Cal-COFI net tow samples at stations in Figure 1), excluding offshore stations seaward of station 120 (marked on Figure 1). Samples were collected and processed using standard CalCOFI methods for oblique tow deployment and sample processing (documented in Kramer et al., 1972; Smith & Richardson, 1977). Fish larvae were identified to the lowest possible taxon, usually species, by the National Atmospheric and Oceanic Administration Southwest Fisheries Science Center ichthyoplankton laboratory. There are important caveats to be considered during analysis of CalCOFI ichthyoplankton data, including changes in gear type and deployment, avoidance behavior, relationship between larvae and spawning adults, and taxonomic resolution. These considerations are detailed in the supporting information S1.

### 2.3. Statistical Methods

We examined the spatiotemporal variability of combined mesopelagic and forage fish ichthyoplankton (Table 1) using the statistical methods in the VAST package (Thorson & Barnett, 2017) of the R statistical lan-

guage (Ihaka & Gentleman, 1996; R Core Team, 2017). We then repeated the analysis for individual species, focusing on the four numerically dominant mesopelagic species of the warm- and cool-water-associated groups in both the inshore and offshore (Table 1). The proportion of the assemblages occupied by numerically dominant species varies by year, location, and species, ranging from ≈10% to 90%, but, in most cases, is higher than ≈40% (McClatchie et al., 2016).

We use VAST because it estimates one or more unobserved spatial factors that represent dominant patterns in the dynamics of the ichthyoplankton community. Each factor is orthogonal to all other factors, and factors collectively represent the aggregate impact of environmental variables and intrinsic dynamics that drive spatial and temporal variation in species density for multiple species. We attribute observed covariation in spatial dynamics among species to similar or different responses to these spatial factors, and VAST estimates covariation while accounting for the noisy and zero-inflated data that are typical of biological sampling designs.

We estimate variation in population density, $d(s, c, t)$, for each species, $c$, sampling location, $s$, and year, $t$. To do so, we apply a multivariate spatiotemporal delta model that includes two spatiotemporal predictors (see supporting information S1 for statistical details of the method). This model-based approach to estimating distribution shift can account for differences in the spatial distribution of sampling, unlike conventional sample-based estimators (Thorson et al., 2016). To inspect model results, we interpret loadings matrices and spatial/spatiotemporal factors after applying a principal component analysis rotation (see Thorson et al., 2016, for details). This rotation ensures that the first factor (which we call the dominant factor) explains the greatest possible proportion of spatial or spatiotemporal variance, the second factor explains the most possible after accounting for the first, and so forth.

Fitting across the spatial and temporal gaps in the data is designed to produce accurate trends in distribution centers and areas occupied, where uncertainty is reflected in wider confidence intervals (Thorson & Barnett, 2017). It is not intended to produce accurate spatial maps in areas where there are no data, because we do not include covariates that could otherwise be used to extrapolate larval densities within unsampled areas. The CalCOFI survey time series includes very significant changes in area sampled (Figure S1), and we have masked areas where spatial maps of the model fits would be unreliable (see Figure 2, e.g.). Years with no surveys, when CalCOFI surveys were reduced to triennial (see Figure 2), were excluded from the analysis.

### 2.4. Water Mass Analysis

The dominant water types contributing to upper-ocean conditions in the CalCOFI domain are PSA, PEW, and NPCW (Sverdrup & Fleming, 1941). A plausible hypothesis to explain the spatial and temporal trends in ichthyoplankton is that they are driven by changes in the proportion of water masses. We calculated the fractional contribution of these water masses over time using a Python-adapted version of the optimal multiparameter analysis method developed by Karstensen and Tomczak (Tomczak, 1981; Tomczak & Large, 1989). The CalCOFI data are ideal for this purpose because they are derived from a consistent, quality-controlled set of profiles measuring multiple properties from the same oceanographic stations over time. We calculated the percentages of water influenced by PSA, NPCW, and PEW using CalCOFI data for each spring from 1950 to 2016.

Water mass property ranges (Table 2) were determined by linearly regressing salinity and oxygen against potential temperature at the CalCOFI stations and isopycnals identified by Bograd et al. (2015) as exhibiting representative signatures of influence by the three major water masses: station 80.80 on the $\sigma_\theta = 25.8$ kg/m$^3$ isopycnal (PSA-influenced) and stations 93.30 (PEW-influenced) and 93.110 (NPCW-influenced) on the $\sigma_\theta = 26.5$ kg/m$^3$ isopycnal (see Figure 1 for station locations). Linear regressions were calculated using data restricted to within $\pm 0.3$ kg/m$^3$ of the respective isopycnals.

We further limited the number of CalCOFI data considered based on maximum temporal expression of each water type: all spring-time (March–May) values for PSA and NPCW and spring samples collected during the 1997–1998 El Niño event for PEW. We used potential temperature, salinity, oxygen, and mass conservation to solve the system of equations and estimate water mass percentages. Given the number of determining parameters (four), our solution is limited to three water masses. We therefore solved the system of equations for the average of the upper and lower bounds of all three water type definitions. We calculated time series showing the average percentage of the upper ocean (0–400 db) influenced by each water mass and qualitatively compared the observed trends for each water mass with trends in the ichthyoplankton assemblages.
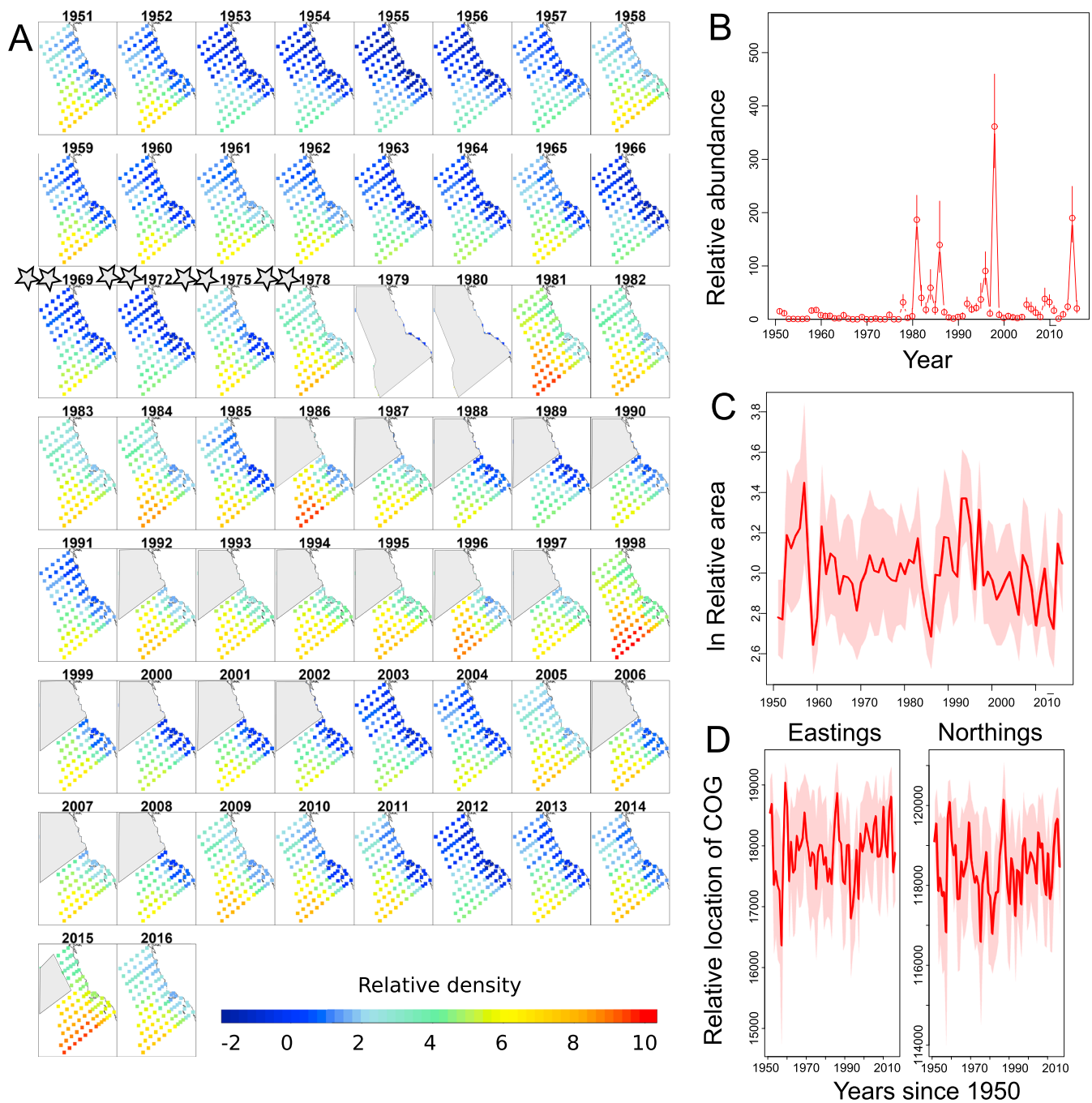
**Figure 2.** Time series of spring season larval distribution of *Vinciguerria* spp. from 1951 to 2016. (a) Modeled spatiotemporal distribution of *Vinciguerria* spp. density. Areas where data are too sparse to model accurately or years where only sardine, anchovy, and hake were counted are masked. Stars indicate missing survey years when surveys were triennial. (b) Relative index of abundance from 1951 to 2016. (c) Relative area occupied on a $log_e$ scale from 1951 to 2016. Shading denotes standard error of the estimates. (d) Relative spatial position of spawning distribution center of gravity (COG). Larger easting values are further east, larger northing values are further north. Units are relative.

## 3. Results

### 3.1. Univariate Analysis: Taxon-Specific Response to Climate Variability

The inshore numerically dominant mesopelagic species show stronger secular trends over 1951–2016 than the offshore species. Inshore, over the 65-year time series, the warm-water dominant species is increasingly abundant, and the cool-water dominant is less abundant (Table 3). None of the four classifications (warm or cool offshore and warm or cool inshore) show evidence of decadal shifts. The warm-water mesopelagic

**Table 2**
*Property Endpoints of Water Mass Definitions: Potential Temperature, Salinity, Oxygen, Phosphate, and Silicate*

| Water type | Potential temperature (°C) | Salinity (ml/ L) | Oxygen | Phosphate ($\mu$mol/L) | Silicate ($\mu$mol/L) |
|---|---|---|---|---|---|
| Lower PSA | 8.87 | 33.59 | 3.58 | 1.72 | 23.20 |
| Upper PSA | 11.91 | 33.46 | 5.44 | 0.90 | 6.91 |
| Lower PEW | 7.66 | 34.32 | 0.70 | 2.86 | 55.10 |
| Upper PEW | 10.26 | 34.07 | 2.39 | 2.00 | 25.98 |
| Lower NPCW | 6.25 | 34.13 | 1.21 | 2.81 | 63.11 |
| Upper NPCW | 9.37 | 33.92 | 3.66 | 1.65 | 20.78 |

*Note.* PSA = Pacific Subarctic Water; PEW = Pacific Equatorial Water; NPCW = North Pacific Central Water.

dominant species show more interannual variability than the cool-water dominants in both the inshore and the offshore CalCOFI regions. Interannual variability was the most obvious feature of the spawning center of gravity time series. Maximum zonal interannual variability of spawning center of gravity was about six times greater than meridional variability. There were no monotonic shifts in the center of gravity of spawning, either to the north or offshore. It was not uncommon for interannual range in centroid position to encompass more than half, and sometimes the full range, of observed variability within periods as short as 5 years (Table 3)

Among the numerically dominant mesopelagic ichthyoplankton, the offshore species (*Vinciguerria* spp. and *S. leucopsarus*) show less secular trend in density, area occupied, and center of gravity than the inshore species (*T. mexicanus* and *L. stilbius*). Neither of the offshore dominants (*Vinciguerria* spp. or *S. leucopsarus*) shows any evidence of decadal trends or shifts over the period 1951–2016. However, *Vinciguerria* spp. shows notable increases of abundance during strong El Niños, so interannual variability dominates fluctuations of this warm-water species. In the inshore, the warm-water mesopelagic dominant *T. mexicanus* has increased its density over the secular time scale. *T. mexicanus* has also increased its density in the offshore. In contrast to this inshore warm-water dominant species, the cool-water inshore dominant *L. stilbius* decreased its density in the inshore. The inshore warm-water *T. mexicanus* exhibits some of the interannual variability shown by the offshore warm-water *Vinciguerria* spp., but the pattern is less extreme (Table 3).

Larval distributions of spawning mesopelagic fish in the CalCOFI survey area show taxon-specific responses to climate variability, even within the warm- or cool-water-associated functional groups (defined in Table 1). To illustrate these differences, in the remainder of this section, we present detailed single species analyses for the four numerically dominant warm- and cool-water-associated species of the offshore and inshore areas (defined in section 3.1).

The spatiotemporal distribution of *Vinciguerria* spp. (offshore warm water) density (Figure 2a) does not show a secular trend, and its index of abundance is dominated by outbursts associated with El Niños (Figure 2b). There is no trend in the spawning area occupied by *Vinciguerria* spp. from 1951 to 1991 within the CalCOFI domain, but a decline in area occupied was evident after about 1990 (Figure 2c). The reduced spawning area occupied

**Table 3**
*Summary of the Trends in Relative Abundance (RA), Center of Gravity (COG), and Area Occupied (AO) by the Numerically Dominant, Warm-, and Cool-Water-Associated Mesopelagic Larvae at Secular, Decadal, and Interannual Time Scales*

| Time scale | Assemblage | Inshore | Offshore |
|---|---|---|---|
| Secular | Warm-water | Stronger trend in RA, COG, and AO | Weaker trend in RA, COG, and AO |
| | | Increasing RA | |
| | | No monotonic trends in COG | |
| | Cool-water | Decreasing RA | |
| | | No monotonic trends in COG | |
| Decadal | Warm-water | No trend in RA, COG, and AO | No trend |
| | Cool-water | No trend | No trend |
| Interannual | Warm-water | Less extreme RA peaks during El Niño | Extreme RA peaks during El Niño |
| | | Highly variable COG | Highly variable COG |
| | Cool-water | Less variable COG | Less variable COG |

by *Vinciguerria* spp. after 1990 was associated with a trend to a more inshore, northern spawning center of gravity (Figure 2d). As explained in the last paragraph of section 3.3, it is important to bear in mind that data gaps increase the uncertainty, as reflected in wider confidence intervals, around trends in distribution centers and areas occupied.

Unlike *Vinciguerria* spp. (offshore warm water), *T. mexicanus* (inshore warm water) does show a secular trend toward higher density in the southwest of the CalCOFI domain (Figure 3a). Outbursts of *T. mexicanus* are spatiotemporally correlated with with outbursts of *Vinciguerria* spp. (see section 3.4 and cf. Figure 3b with Figure 2b). There is evidence of an increase in abundance of *T. mexicanus* larvae since about 1978 (Figure 3b). The relative area occupied by *T. mexicanus* spawning in the CalCOFI domain increased until about 1990 but subsequently decreased and became more variable (Figure 3c). The period when area occupied expanded was associated with a trend toward a more offshore, southern spawning center of gravity (Figure 3d). The post-1990 decline in spawning area occupied was associated with a more inshore, northern spawning center of gravity, as was the case for *Vinciguerria* spp.

*S. leucopsarus* (offshore cool water) shows the most variable distribution of the four numerically dominant mesopelagics (Figure 4). There is no clear evidence of any trend in larval density nor in the index of relative abundance (Figures 4a and 4b). The spawning area occupied in the CalCOFI domain is variable around a relatively constant mean (Figure 4c), and there is no consistent temporal trend in the center of gravity of spawning (Figure 4a and 4d).

In contrast, the spatiotemporal maps for *L. stilbius* (inshore cool water) show a secular trend of declining density in the inshore from 1951 to 2016 (Figure 5a). The relative index of larval abundance, while variable, shows a clear decline over the time series (Figure 5b). The spawning area occupied follows the trends in larval abundance, decreasing for four decades, then increasing over a decade, before decreasing again in more recent years (Figures 5c and 5d). Declining spawning area of this cool-water species was associated with an offshore, southward shift in spawning center of gravity, which is the opposite pattern observed for the warm-water species *Vinciguerria* spp. and *T. mexicanus*.

### 3.2. Multivariate Analysis: Spatial Correlations Between Mesopelagic Species

The species within the groups classified as warm- or cool-water associated based on taxonomic knowledge are shown, in what follows, to be highly spatially correlated, indicating overlapping spawning habit. The species correlations derived from the modeling support the functional groupings of warm- and cool-water-associated species in Table 1. In contrast to the high positive spatial correlations within the warm- and cool-water-associated mesopelagic ichthyoplankton groups, the correlations between these groups reflect the spatial separation of their spawning habitats. Warm- and cool-water species dominants are poorly spatially correlated. The inshore warm-water dominant *T. mexicanus* has very low spatial correlations with both the inshore and offshore cool-water dominants, *L. stilbius* ($r = 0.21$) and *S. leucopsarus* ($r = 0.15$; Figure 6a and Table 1). The offshore warm-water dominant *Vinciguerria* spp. has a low spatial correlation with both the inshore and offshore cool-water dominants, *L. stilbius* ($r = 0.27$) and *S. leucopsarus* ($r = 0.27$).

Spatial correlations provide a measure of how fish spawning habitats overlap. Spatiotemporal correlations indicate whether species show similar (correlated) or different (uncorrelated) responses to shared environmental conditions. Spatial correlations provide insight into the robustness of warm- and cool-water mesopelagic fish associations derived from taxonomic knowledge (see Table 1).

More detailed correlations between species are given in the remainder of this section. The inshore cool-water dominant *L. stilbius* has a spatial distribution that has strong positive correlation with the offshore cool-water dominant *S. leucopsarus* ($r = 0.93$), as well as with other cool-water mesopelagics; *Tarletonbeania crenularis* ($r = 0.78$), *Lipolagus ochotensis* ($r = 0.80$), and *Bathylagus pacificus* ($r = 0.75$; Figure 6a and Table 1). The offshore cool-water dominant *S. leucopsarus* also shows high positive correlations with other cool-water species *L. ochotensis* (0.82), *T. crenularis* (0.87), and *B. pacificus* (0.84; Figure 6a and Table 1).

The inshore warm-water dominant *T. mexicanus* is highly positively spatially correlated with the offshore warm-water dominant *Vinciguerria* spp. ($r = 0.91$) and with the other warm-water mesopelagics; *Symbolophorus californiensis* ($r = 0.78$), *Ceratoscopelus townsendi* ($r = 0.82$), and *Bathylagoides wesethi* ($r = 0.84$; Figure 6a and Table 1). The offshore warm-water dominant *Vinciguerria* spp. is highly spatially correlated with *S. californiensis* ($r = 0.96$), *B. wesethi* ($r = 0.98$), and *C. townsendi* (0.97; Figure 6a).
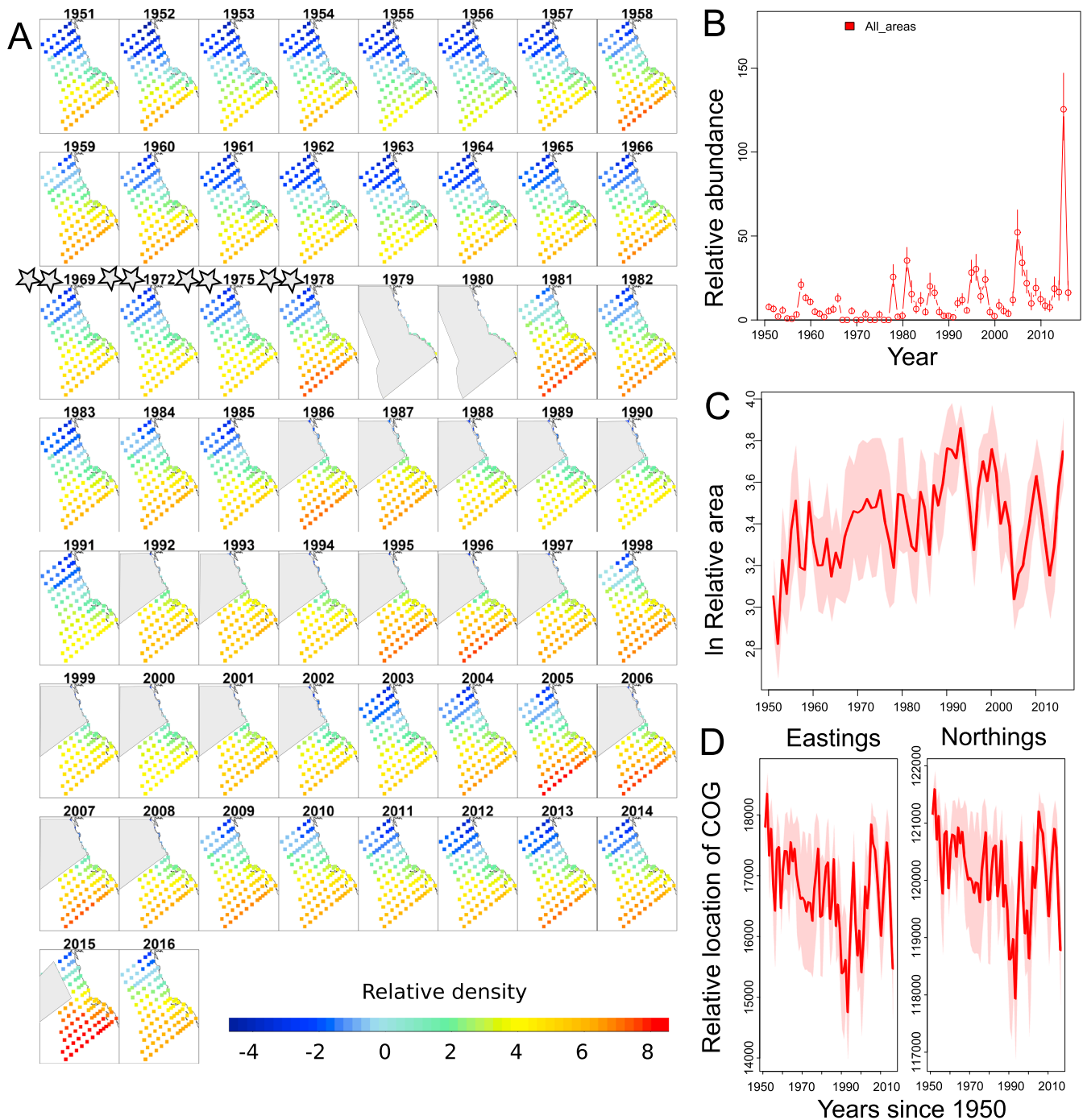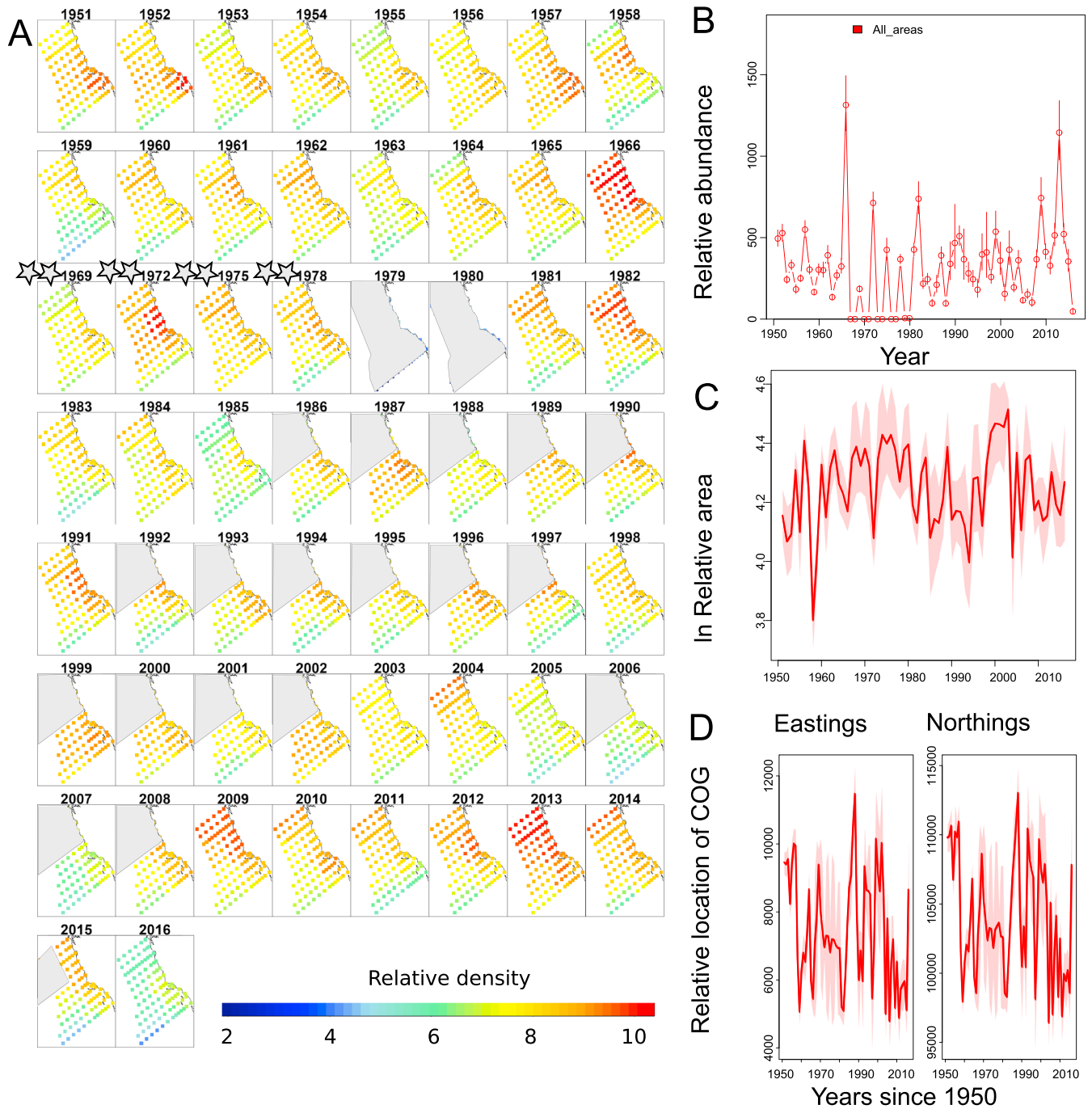
**Figure 3.** Time series of spring season larval distribution of *Triphoturus mexicanus* from 1951 to 2016. (a) Modeled spatiotemporal distribution of *T. mexicanus* density. Areas where data are too sparse to model accurately or years where only sardine, anchovy, and hake were counted are masked. Stars indicate missing survey years when surveys were triennial. (b) Relative index of abundance from 1951 to 2016. (c) Relative area occupied from 1951 to 2016. Shading denotes standard error of the estimates. (d) Relative spatial position of spawning distribution center of gravity (COG). Larger easting values are further east, larger northing values are further north. Units are relative.

**Figure 4.** Time series of spring season larval distribution of *Stenobrachius leucopsarus* from 1951 to 2016. (a) Modeled spatiotemporal distribution of *S. leucopsarus* density. Areas where data are too sparse to model accurately or years where only sardine, anchovy, and hake were counted are masked. Stars indicate missing survey years when surveys were triennial. (b) Relative index of abundance from 1951 to 2016. (c) Relative area occupied from 1951 to 2016. Shading denotes standard error of the estimates. (d) Relative spatial position of spawning distribution center of gravity (COG). Larger easting values are further east, larger northing values are further north. Units are relative.

### 3.3. Spatial Correlations Between Forage Fish and Mesopelagic Ichthyoplankton

Spatial correlations between forage fish and mesopelagic ichthyoplankton show that the spawning habitats of sardine, hake, and anchovy overlap with members of the cool-water mesopelagic ichthyoplankton assemblage.
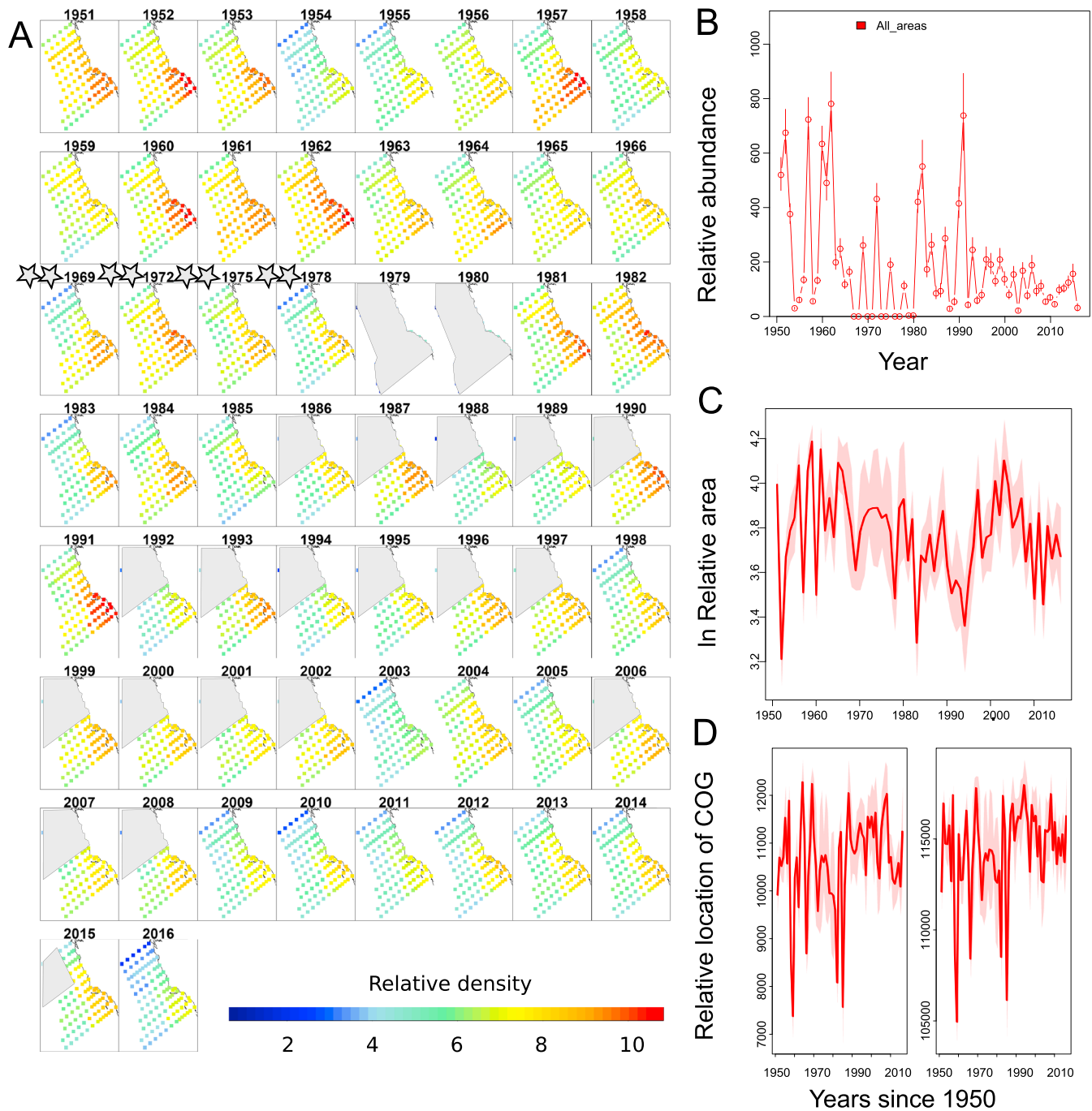
**Figure 5.** Time series of spring season larval distribution of *Leuroglossus stilbius* from 1951 to 2016. (a) Modeled spatiotemporal distribution of *L. stilbius* density. Areas where data are too sparse to model accurately or years where only sardine, anchovy, and hake were counted are masked. Stars indicate missing survey years when surveys were triennial. (b) Relative index of abundance from 1951 to 2016. (c) Relative area occupied from 1951 to 2016. Shading denotes standard error of the estimates. (d) Relative spatial position of spawning distribution center of gravity (COG). Larger easting values are further east, larger northing values are further north. Units are relative.

Hake is the most highly spatially correlated with the cool-water-associated offshore dominant *S. leucopsarus* (0.95), as well as with *T. crenularis* (*r* = 0.89), *B. pacificus* (*r* = 0.87), and *L. ochotensis* (*r* = 0.88), which are all cool-water mesopelagics (Table 1). Hake is also highly spatially correlated with sardine (*r* = 0.90; Figure 6a).

Sardine is the most positively spatially correlated with the offshore cool-water dominant *S. leucopsarus* (*r* = 0.79) and the inshore cool-water dominant *L. stilbius* (*r* = 0.76). Although sardine are quite well spatially correlated (*r* = 0.71) with other cool-water mesopelagics (*T. crenularis*, *B. pacificus*, and *L. ochotensis* [*r* = 0.67]),
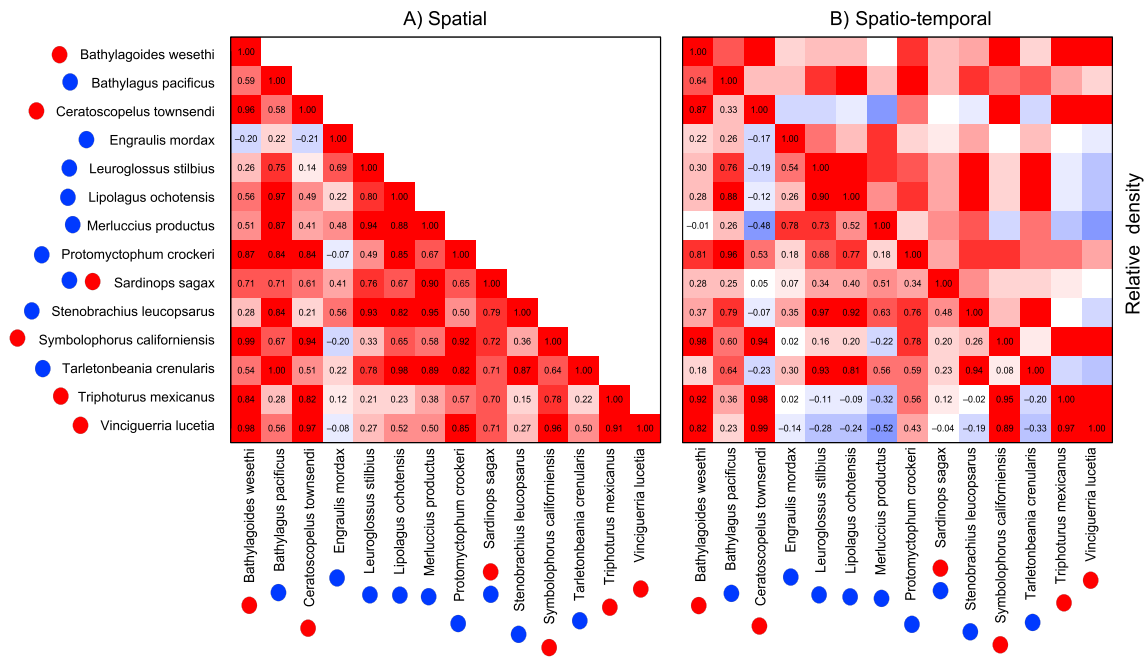
**Figure 6.** Spatial and spatiotemporal correlations between mesopelagic and forage fish ichthyoplankton. (a) Spatial correlation for ichthyoplankton relative densities. (b) Spatiotemporal correlation for ichthyoplankton relative densities. Red squares denote positive correlations; blue square denote negative correlations. Colored dots next to species names indicate warm- (red) or cool-water (blue) associated species. Sardine is marked with both red and blue circles to indicate correlations with both warm- and cool-water species.

they are also equally well-correlated with warm-water species (*S. californiensis* [*r* = 0.72], *T. mexicanus* [*r* = 0.70], and *Vinciguerria* spp. [*r* = 0.71]; Figure 6a). This likely reflects the broad range of conditions in which sardine can spawn (Zwolinski et al., 2011).

Anchovy is moderately positively spatially correlated only with the inshore cool-water dominant *L. stilbius* (*r* = 0.69). Anchovy are not highly spatially correlated with either sardine (*r* = 0.41) or with hake (*r* = 0.48), indicating that their spawning habitats do not greatly overlap, but this is already well known.

### 3.4. Spatiotemporal Correlations Between Species

Spatiotemporal correlations indicate which species fluctuate together over time and space under shared environmental conditions. It is interesting to note that sardine do not show any spatiotemporal correlations higher than 0.51 (Figure 6b). In other words, sardine seem to fluctuate in time and space with little relationship to either anchovy or hake or to the mesopelagic species in Table 1. In contrast, anchovy and hake fluctuate together with a spatiotemporal correlation of 0.78 (Figure 6b). Anchovy do not fluctuate with either warm or cool mesopelagics (all spatiotemporal correlations are <0.54). Hake fluctuations are moderately correlated with the offshore cool-water dominant mesopelagic *L. stilbius* (*r* = 0.73).

The other high spatiotemporal correlations reflect fluctuations of the warm- or cool-associated species assemblages. The inshore cool-water dominant *L. stilbius* fluctuates coherently with the offshore cool-water dominant *S. leucopsarus* (*r* = 0.97), as well as with other cool-water mesopelagics; *T. crenularis* (*r* = 0.93) and *L. ochotensis* (*r* = 0.90; Figure 6b). The inshore warm-water dominant *T. mexicanus* fluctuates with the offshore warm-water dominant *Vinciguerria* spp. (*r* = 0.97) and with other members of the warm-water assemblage; *B. wesethi* (*r* = 0.92), *C. townsendi* (*r* > = 0.98) and *S. californiensis* (*r* > = 0.95; Figure 6b).

### 3.5. Spatiotemporal Variability Maps

The spatiotemporal model fitted five spatial factors to the ichthyoplankton density surfaces for the 11 mesopelagic and 3 forage fish species in Table 1. The first two factors were visualized on a map to show spatiotemporal variability of the species groups that load onto each factor. Loadings on the first two factors explained 43% and 35% of the variance (Figure 7). The first factor loads positively and most strongly (>0.5) on warm-water mesopelagic species, except for *B. pacificus* which is thought to be associated with cool water, but loads with the warm-water mesopelagics in this study (Figure 7). The second factor loads positively
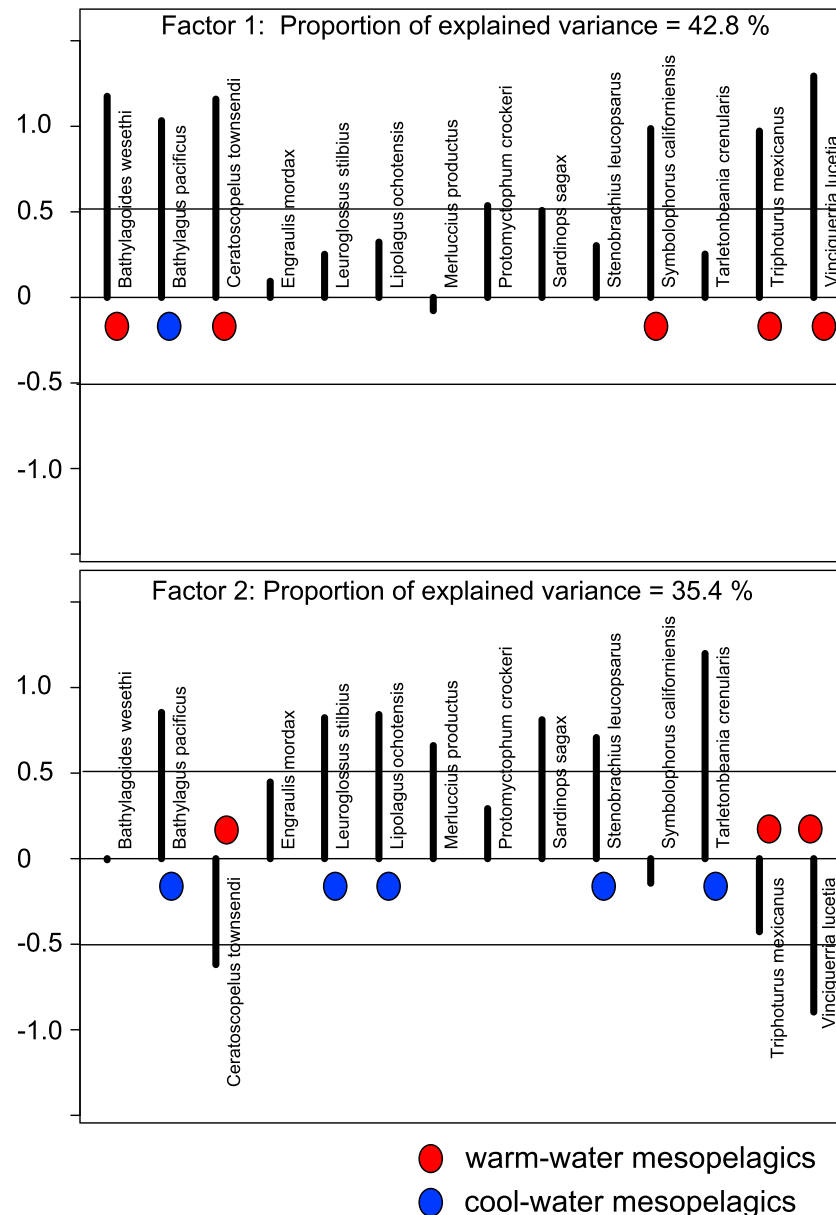
**Figure 7.** Factor loadings on spatiotemporal variability of ichthyoplankton relative density (see Figure 8). Mesopelagic species with loadings >0.5 or < −0.5 are marked with dots; red (for warm-water associated) or blue (cool-water associated). Pacific hake, Pacific sardine, and northern anchovy load positively on factor 2 with cool-water mesopelagic species.

most strongly (>0.5) on the cool-water mesopelagic species while loading negatively on the warm-water mesopelagics, including the dominant warm-water species, *Triphoturus mexicanus* and *Vinciguerria lucetia* (Figure 7 and Table 1). All of the forage fish species load positively and more strongly on factor 2, along with the cool-water mesopelagics (Figure 7).

Spatiotemporal maps of the first factor indicate a nonmonotonic, secular trend. Relative density of species loading on factor 1 increased with time from 1951 to 2016, but the increase was the largest in the 1970s and 1980s, thereafter declining somewhat but remaining higher than densities in the 1950s and 1960s (Figure 8). The long-term trend occurred over the whole CalCOFI survey area rather than being limited to inshore waters or the immediate region of the Southern California Bight. Species loading most strongly on factor 1 are the warm-water mesopelagics *B. wesethi*, *C. townsendi*, *S. californensis*, *T. mexicanus*, and *Vinciguerria* spp., as well as the cool-water mesopelagic *B. pacificus* (Figure 7).
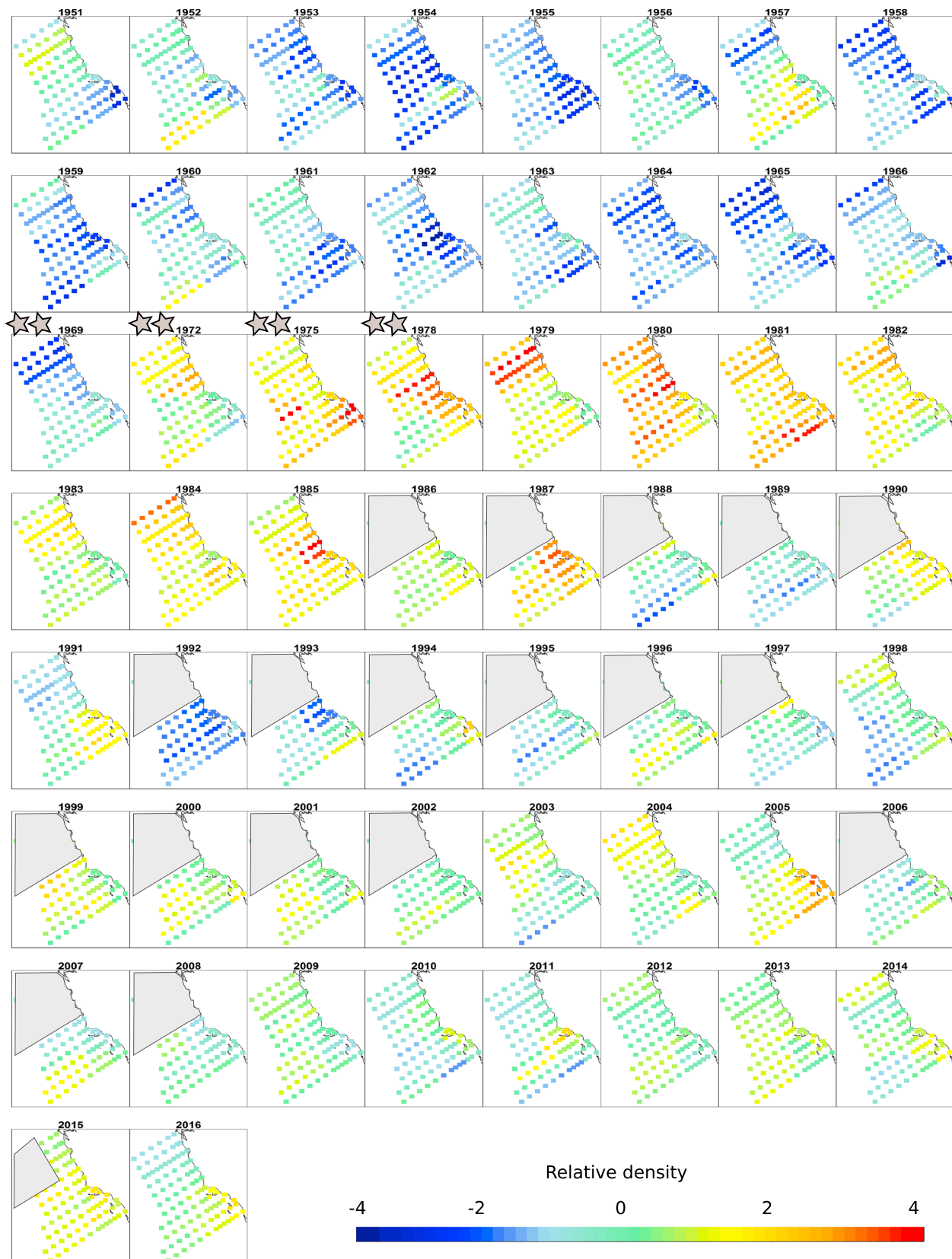
**Figure 8.** Spatiotemporal variability of loading factor 1 (see Figure 7) for ichthyoplankton relative density. Areas where data are too sparse to model accurately or years where only sardine, anchovy, and hake were counted are masked. Stars indicate missing survey years when surveys were triennial.

The spatial-temporal maps of factor 2 (not shown) differ from those for factor 1 (Figure 8) in showing more interannual variability. Changes in the relative density persist for as little as 1 year (1956, 1972, 1980, and 1981) to as long as 3–5 years (1960–1964, 1967–1971, 1995–1997, and 2009–2011), where longer persistence often seems to be ended by El Niño years.

In summary, the warm-water mesopelagic assemblage exhibits an increasing, nonmonotonic, secular trend in relative density overlaid on interannual variability from 1951 to 2016, suggesting a *tropicalization* of the California Current System off southern and central California. Individual warm-water species like *Vinciguer-ria* spp. and *T. mexicanus* also show increasing frequency of spikes in abundance over time, suggesting that warm events are becoming more frequent (Figures 2b and 3b). In contrast, the cool-water mesopelagic assemblage shows interannual variability, with a degree of persistence ranging from ≈1 to 3–5 years, without much secular trend. Anchovy and hake exhibit spatiotemporal variability more similar to the cool-water than the warm-water-associated mesopelagic ichthyoplankton, but sardine fluctuate independently.

### 3.6. Trends in Water Masses

Next we examine the spatial and temporal variability in the percentages of water masses from 1950 to 2016, with the goal of elucidating possible drivers for the observed tropicalization of the ichthyoplankton assemblage. The underlying rationale is that increased relative density of warm-water species, which we refer to as tropicalization, should initially arise by introduction of these species in water originating either to the south or offshore of southern California. Persistence of these species will presumably depend upon suitably warm conditions that could arise when a higher percentage of subtropical water is present off southern California.

The most notable secular trends in water masses are an increase in the percentage of warm, saline Pacific Equatorial-influenced Water (PEW-influenced) inshore and off the shelf on the southern CalCOFI transect (Figure 9; CalCOFI stations 30 and 90, respectively, on line 93.3, see Figure 1 for station and line locations).

The increase in PEW-influenced water was notable inshore in the Southern California Bight (CalCOFI station 30), which has the highest percentage of PEW-influenced water (Figure 9). PEW-influenced water also increased off the shelf, at station 90 (Figure 9). At both locations, the increase in PEW-influenced water occurred after the mid-1990s.

Least secular change in PEW-influenced water was seen offshore, at station 120, where the percentage of PEW-influenced water was low (Figure 9). At this offshore location (CalCOFI station 120; see Figure 1), where the percentage of Pacific Subarctic-influenced Water (PSAW-influenced) was the highest (Figure 9), we detected a very weak secular trend toward lower percentages of PSAW-influenced water. These secular trends, of notably increasing subtropical water inshore and off the shelf and possibly decreasing subarctic water far offshore, were weaker further north (CalCOFI line 80; see Figure 1), due to higher interannual variability (Figure 9).

In contrast to the observed changes in subtropical PEW-influenced water, the proportion of warm North Pacific Central-influenced Water (NPCW-influenced) off southern California decreased inshore on the southern CalCOFI transect (CalCOFI station 30 line 93.3; Figure 9). This suggests that the offshore influence of the central gyre has decreased after the mid-1990s, concurrently with the increase in PEW-influenced water. This analysis suggests that the southern boundary of the CalCOFI region (Figure 1) is experiencing increasing subtropical influence inshore and that this influence is derived from the south rather than from offshore. The rate of change has not been constant and appeared to be greatest over the period 1990–1998 (Figure 9).

## 4. Discussion

In this study we found that the first and second modes of the multivariate assemblage explain a high proportion (78%) of the total spatiotemporal variance. The species that load most heavily on the first mode of variability are primarily warm-water associated and have a secular trend in abundance, while those that load on the second mode of variability are cold-water associated and show an interannual pattern of abundance. We chose not to relate these trends to climate indices which are proxies for a suite of forcing variables. In this paper we took the approach of relating the trends we see directly to a postulated forcing. We believe that this is more instructive than relating the changes to proxy variables where the actual forcings are not directly examined.

Multivariate spatiotemporal analysis detected a long-term increasing but nonmonotonic, secular trend in the density of the warm-water mesopelagic assemblage over the whole CalCOFI survey area (peaks in the 1970s
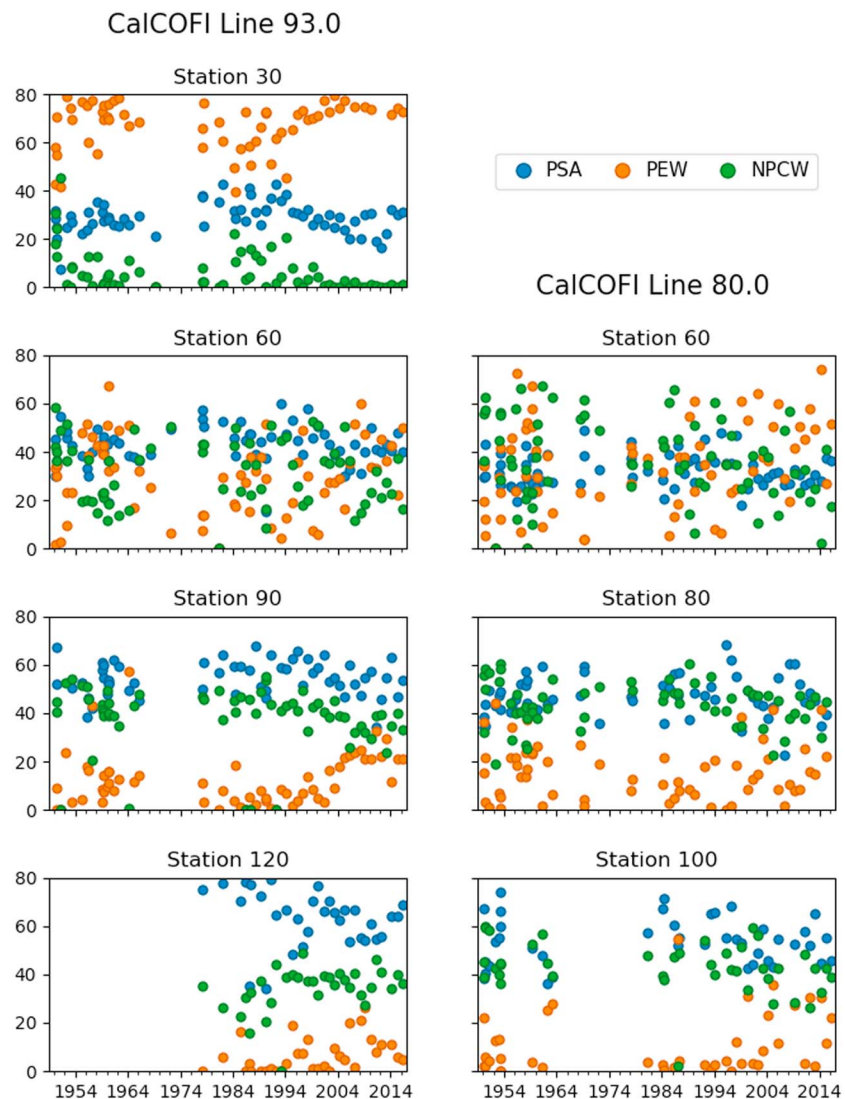
**Figure 9.** Optimal multiparameter water mass analysis showing time series of percentage of three water masses (Pacific Subarctic-influenced Water [PSA], Pacific Equatorial-influenced Water [PEW] and North Pacific Central-influenced Water [NPCW]) at four stations on CalCOFI line 93.3 and three stations on line 80.0 over 10–400 db during spring (March to May; see Figure 1 for line and station locations).

through 1987 and then intermediate values thereafter). It is not easy to determine whether this trend is sensitive to other parts of the signal because *sensitivity* could be defined multiple ways. Spatial dynamic factor analysis visualizes axes of covariation in a way that is similar to principal component analysis and empirical orthogonal function approaches (but which accounts for noisy sampling data and spatial correlations and therefore is more applicable here), that is, each factor is orthogonal to the others. Due to the constraint that factors are orthogonal, a change in one factor will drive changes in other factors as well. However, the dominant factor (factor 1 in Figure 8) is least sensitive to the inclusion of other factors, because it is defined as representing the main axis of variation.

The fact that the changes were not restricted to the inshore, or to the immediate region of the Southern California Bight, and instead extended well into the offshore, suggests possible involvement of both PEW- and NPCW-influenced waters. Both water masses would bring warm-water species into the CalCOFI domain, during some of the El Niños that affect the northeast Pacific. However, we detected a decrease in the percentage of NPCW-influenced water inshore, while the percentage of PEW-influenced water is increasing inshore along the southern CalCOFI area. Considerable mixing occurs in the southern California region, so we also expect to see the influence of PEW-influenced water offshore. This suggests that tropicalization may be driven

by increasing PEW-influenced water inshore combined with mixing of this water across the wider CalCOFI domain. Pelagic fish most likely move with the water masses they live in, affecting where they spawn as a result, but greater presence of PEW-influenced water might also favor larval survival locally, which could increase larval abundance and enhance the observed tropicalization.

Unlike other studies that have examined long time series of species distributions (e.g., Nye et al., 2009; Pinsky et al., 2013), we did not find a strong poleward or offshore shift of species distribution over time. Thorson et al. (2016) also failed to detect strong poleward movement, and we believe that along the U.S. West Coast, Pinsky et al. (2013) confounded a southward shift in the average location of sampling during the triennial bottom trawl survey with a southward shift in distribution for sampled species. Several factors may contribute to a lack of major distribution shifts. First, during spawning, hake and sardine are in a spatially constrained phase of their life cycle (Ciannelli et al., 2015), although this is not true for mesopelagic fishes. Other studies that have documented poleward shifts in distribution have examined adults during the nonspawning season that are more likely to exhibit plastic responses to climate variability. Second, it is possible that the area examined does not allow us to detect secular changes in larval distribution. For example, larval sardine (Auth et al., 2017) and juvenile hake (Phillips et al., 2007) have both increased in abundance off Oregon and Washington, suggesting the existence of uncommonly sampled and therefore poorly known, spawning habitats outside of our sampling area. Lastly, the California Current may simply not have experienced the same type of temperature change as observed for example on the Northeast shelf of the United States. Since 1982, the North Sea, Newfoundland, and Labrador Sea experienced a greater temperature changes than the California Current System (Belkin, 2009), and these are the areas where poleward distribution shifts were first detected (e.g., Perry et al., 2005). We note that pelagic fish species also show more variable distributions than bottom-associated species (Thorson et al., 2016).

Tropical/subtropical species that reach southern California tend to have northern range limits off southern or south central California in or near the current CalCOFI domain (Moser, 1996). For example, larval ranges for *Vinciguerria* and *Triphoturus* both extend to San Francisco, but abundance and frequency of occurrence drop off very rapidly north of Point Conception (see Figure 1). Boreal species mainly have southern range limits off central California or farther north and generally do not occur off southern California. On the other hand, cool-water species that occur off southern Califonia tend to range south to at least central Baja, so the current CalCOFI area is not as close to their southern range limits (Moser, 1996). For example, *Leuroglossus* larvae range to southern Baja but start dropping off south of central Baja, and *Stenobrachius* range to central Baja but start dropping off at the transition between northern and central Baja. Since changes are likely to be most visible near range limits, the species we expect to see changes in are the tropical/subtropical ones. This was in fact what we found in this study.

The secular increase of PEW in the southern California region is co-occurring with larger scale changes of atmospheric and ocean-atmosphere interactions in the Equatorial and North Pacific since the late 1980s. Specifically, since the late 1980s, there is an increasing occurrence of Central Pacific El Niño (Yeh et al., 2009), which, through extra-tropical atmospheric connections, has a strong influence on atmospheric and ocean variability in the midlatitudes (Di Lorenzo et al., 2010). While it is premature to attribute the secular changes of PEW off southern California to these larger scale ocean-atmospheric changes, it is worth noting the co-occurrence and continuing to monitor their evolution over time.

Our study demonstrates a tropicalization of the ichthyoplankton assemblages off southern California that appears to be associated with changes in proportions of the southern subtropical water mass, particularly in the inshore. While this is consistent with what might be expected as the climate warms, the response of the ichthyoplankton assemblage is complex, with many species-specific differences. Our results do not fit tidily into the developing paradigm of northward or offshore shifts of species distributions with climate change. To the contrary, our results suggest long-term trends are overlayed upon large interannual variability that is correlated among species and, at least for the dominant warm-water-associated mesopelagic ichthyoplankton, likely driven by extreme El Niño-Southern Oscillation events. The changes that we observed likely reflect both advection and changes in the spawning distribution of adults. It may be that the paradigm of poleward or offshore distribution shifts may need to be modified in the California Current System to take account of the pulsing of warm events and subsequent persistence of these effects in the ichthyoplankton assemblages.

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