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Decadal regime shifts in southern California's ichthyoplankton assemblage

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ABSTRACT: Marine ecosystems worldwide experience rapid, persistent reorganization of biological and physical characteristics, known as 'regime shifts.' Here we provide a multivariate analysis of the ichthyoplankton assemblage in southern California (USA) from 1951 to 2017 in both spring and summer. We found unequivocal support for compositional regime shifts in 1965 and 1976 across both seasons, and additional strong evidence for shifts in 1983 and 1990 in the spring assemblage. The 1965 regime shift was associated with increases from low to moderate abundance of several offshore taxa, as well as peaks in the abundance of *Sebastes* spp. The impacts of the 1976 regime shift have been widely documented elsewhere across the North Pacific; here we demonstrate that the 1976 regime shift in the southern Californian ichthyoplankton assemblage coincided with increases in a large group of taxa characteristic of southern and offshore environments. By contrast, shifts in 1983 and 1989 in the spring assemblage appear to have been driven by variations in just a few highly abundant taxa. Finally, despite speculation that there was a climate regime shift from a 'warm' to a 'cool' period in the late 1990s, we found no support for a shift in the larval fish assemblage during these years. Our analyses provide context for understanding the countervailing effects on fish of natural environmental variability from annual through multidecadal scales, with important implications for how marine assemblages will respond to secular, global changes in climate.

KEY WORDS: Ichthyoplankton · Larval ecology · Multivariate analysis · Regime shift · Southern California Bight

INTRODUCTION

Across decadal timescales or longer, marine ecosystems experience rapid, abrupt and persistent changes in structure and function, known as regime shifts (Möllmann et al. 2015). This concept first gained traction following the identification of large, step-like changes in over 100 biological and climate time series in the North Pacific during the mid-1970s and late 1980s (Ebbesmeyer et al. 1991, Hare & Mantua 2000). More recently, it has been suggested that regime shifts in the northern hemisphere throughout the 20th century occurred in a quasi-synchronous manner (McCall 1996, Möllmann & Diekmann 2012, Beaugrand et al. 2015, Powell & Xu 2015, Reid et al. 2016). Such changes in ecologically and commercially important species, or even entire species assemblages, are generally thought to represent nonlinear amplification of decadal climate variability, fishing pressure or some combination of natural and anthropogenic factors (Francis et al. 1998, Collie et al. 2004, Schwing et al. 2010, Litzow et al. 2014).

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However, in the absence of fully established mechanisms linking observations to theory, regime shifts have inspired controversy within the scientific literature; the term 'regime shift' itself carries different meanings in different contexts. For the purposes of marine management, such emphasis on the theoretical aspect of regime shifts can distract from progress in identifying abrupt ecological changes when and as they occur; as such, we follow a 'practical' definition of regime shifts proposed by Möllmann et al. (2015, p. 2), which defines regime shifts as

> dramatic, abrupt changes in the community structure that are persistent in time, encompassing multiple variables, and including key structural species—independently from the mechanisms causing them.

Understanding the extent to which these patterns have manifested across different systems in the past, and will continue to do so into the future, remains an important challenge for scientists and marine fisheries managers alike (Levin & Möllmann 2015).

One region that has been relatively well studied with respect to regime shifts is the North Pacific. It was here that the concept first gained traction in the ecological literature, after analysis of the leading principal components (PCs) of over 100 physical and biological time series revealed step-like changes in 1976 and 1989 (Ebbesmeyer et al. 1991, Hare & Mantua 2000). Of these 2 events, the 1976–1977 regime shift took place across a larger spatial extent throughout the North Pacific, from the Bering Sea to the southernmost portion of the California Current. Prominent physical features included intensification of the Aleutian Low Pressure System and increased sea surface temperatures in the coastal Northeast Pacific; biological changes involved increases in Alaskan salmon populations and decreases in the abundance and condition of most other groups studied, including Alaskan shrimp, west coast salmon, oysters and zooplankton (Ebbesmeyer et al. 1991, Miller et al. 1994, Hare & Mantua 2000, McGowan 2003). The 1989 event was less conspicuous among climate time series and spatially limited to the west coast; nonetheless, major decreases were observed in west coast groundfish and salmon populations, and increases in coastal pelagic species such as sardine and Pacific hake (Beamish et al. 1999, Hare & Mantua 2000, McFarlane et al. 2000).

Since the identification of the 1976 event, in which the Pacific Decadal Oscillation (PDO), one of the leading components of North Pacific climate variability, shifted from a negative ('cold') to a positive ('warm') phase, considerable attention has been paid to the utility of the PDO as a predictor of imminent biological regime shifts. Indeed, after the apparent reversal of the PDO to a 'cool' phase around 1998–1999, many speculated that an ecological regime shift would soon follow (McFarlane et al. 2000, Schwing & Moore 2000, Moser et al. 2001, Bograd & Lynn 2003, Peterson & Schwing 2003, Allen et al. 2006). However, later work would suggest that the 'negative run' of PDO values around 1998–2003 is better described as a transient event associated with the El Niño-Southern Oscillation (ENSO), rather than a true climate regime shift (Bond et al. 2003). Furthermore, the PDO was dominated by noise from 1989–2008, and projections of the North Pacific climate into the rest of the 21st century predict the increasing importance of anthropogenic warming over internal modes of variability (Bond et al. 2003, Overland & Wang 2007, Di Lorenzo et al. 2008, Bonfils & Santer 2011). This concept remains especially relevant as we gather data to evaluate the ecological importance of another potential climate regime shift in 2007–2008 (Litzow & Mueter 2014), followed by some of the most anomalously warm years in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) record in 2014–2016 (Leising 2015). The uncertainty surrounding the events after the late 1990s underscores the challenges of detecting discontinuities at the tail ends of time series; using traditional methods, most regime shifts are not detected until 10–20 yr after they have already occurred (Rodionov & Overland 2005). Without a complete understanding of the mechanisms linking ocean–atmosphere variability to biological regime shifts, any multi-year run of anomalously negative or positive values in a climate index such as the PDO might garner attention as a possible harbinger of an ecological catastrophe, even before sufficient data have been gathered to assess such a shift with statistical certainty. To date, few studies have used biological time series of sufficient length to evaluate whether a regime shift has indeed taken place in the North Pacific over the past 30 yr.

The Southern California Bight (SCB) is particularly well suited for such an assessment of long-term variability in a multi-species assemblage, thanks to the extensive sampling efforts of the CalCOFI program. Since 1951, CalCOFI has maintained one of the longest and most comprehensive ecosystem monitoring records in the world, with regular, quarterly sampling of key physical and biological variables from fixed stations. Overall, CalCOFI data provided a detailed account of the regional oceanographic changes that took place in concordance with the larger 1976 North Pacific regime shift event, most noticeably a general 'warming and freshening' of surface waters (Bograd & Lynn 2003). The 1976 event impacted biological populations across at least 4 trophic levels, including declines in overall abundance of fish larvae, coastal sciaenids, euphausiids and zooplankton; and increases in copepods (Roemmich & McGowan 1995, Moser et al. 2001, McGowan 2003). However, most of these studies were limited to comparisons of individual species' abundances between predesignated regime periods; to our knowledge, none have objectively examined natural breakpoints in assemblage structure. The speculative regime shift around the late 1990s in the North Pacific may explain recent biogeochemical changes to the source waters of the SCB, including declining oxygen and increased nitrogen and phosphate levels (Bograd et al. 2015). Thus far, evaluation of recent biological regime shifts is limited to the lowest levels of the food web: around 2000, the frequency of toxic *Pseudo-nitzschia* blooms increased (Sekula-Wood et al. 2011), and phytoplankton composition switched from mostly dinoflagellates to mostly diatoms (C. R. Anderson et al. 2006). The effects of these changes on higher trophic levels including zooplankton and ichthyoplankton remain understudied (Bograd et al. 2015).

Here, we used the CalCOFI larval fish time series to assess evidence for regime shifts in seasonal ichthyoplankton assemblage composition off southern California. We applied a unique multivariate approach to detect change points in a time series of abundance data for an assemblage of 35 taxa, taking advantage of a recently updated data curation methodology and improving upon previous analyses that examined changes in the abundance and distribution of individual taxa between pre-delineated regime periods (Moser et al. 2001, Rebstock 2002, Smith & Moser 2003, Hsieh et al. 2009, Miller & McGowan 2013, Koslow et al. 2015). Decadal variability in larval abundance is regarded as an appropriate indicator of long-term changes in adult spawning biomass, rather than short-term distributional shifts that are known to occur during El Niño or La Niña events (Moser et al. 2001, Ohman & Lavaniegos 2002, Hsieh et al. 2009). As such, characterizing the historic variation of the fish assemblage off southern California, with particular focus on the period after 1990, is an important step towards a better understanding and management of the state's living resources. The degree to which regime shifts have structured marine ecosystems over the past 3 decades will further inform our ability to contextualize potential future secular changes brought on by climate change.

MATERIALS AND METHODS

Data sources and curation

The CalCOFI program has regularly collected ichthyoplankton from over 700 species of fish at fixed locations from 1951 to the present (McClatchie 2013). The initial research design consisted of monthly cruises extending ~650 km offshore from the California–Oregon border to Baja California Sur, Mexico, and within the Sea of Cortez. The sampling frame was subsequently reduced to seasonal (4 times annually) cruises at 66 'core' stations off southern California, from just north of Point Conception to San Diego (Fig. 1). We analyzed ichthyoplankton time series from spring and summer samples, as these are more complete than either winter or fall.

We focused on ichthyoplankton collected from oblique plankton net tows. In all years, nets were lowered to a target depth and towed to the surface at a 45° angle at a constant speed. Samples were preserved in 5% formalin at sea, and ichthyoplankton were identified using microscopes in the laboratory. Most taxa were identified to the species level; however, some were only identified to genus or family. Specifically, croakers (Sciaenidae), bigscales (Melamphaidae), bristlemouths (Gonostomatidae), hatchetfishes (Sternoptychidae), wrasses (Labridae) and barracudina (Paralepididae) were identified to the family level; rockfishes (*Sebastes*), some lightfishes (*Vinciguerria*), sanddabs (*Citharichthys*), and 2 lanternfishes (*Nannobrachium* and *Diaphus*) were identified to genus. We standardized larval abundances by first dividing raw counts by the proportion of the sample that was sorted (most were 100% sorted, but in cases when zooplankton volumes were high, less than 100% was sorted) and then multiplying raw counts by a standard haul factor which accounts for differences in the volume of water filtered. Final abundances were in standard CalCOFI units of number of larvae per 10 m^2 surface area (Smith & Richardson 1977).

Sampling methodology changed twice between 1951 and the present (Thompson et al. 2017). From 1951–1969, oblique tows were conducted with ring nets that had a 1 m diameter opening and 550 µm mesh and were lowered to a depth of 140 m. In 1969, the depth was increased to 210 m and the net mesh size reduced to 505 µm. In 1978, the ring net was replaced with a bongo net where net diameters were 0.71 m. Analysis of the effects of the 1978 change indicated that bongo nets were significantly more effective than ring nets in capturing 4 taxa (*Cyclo-*

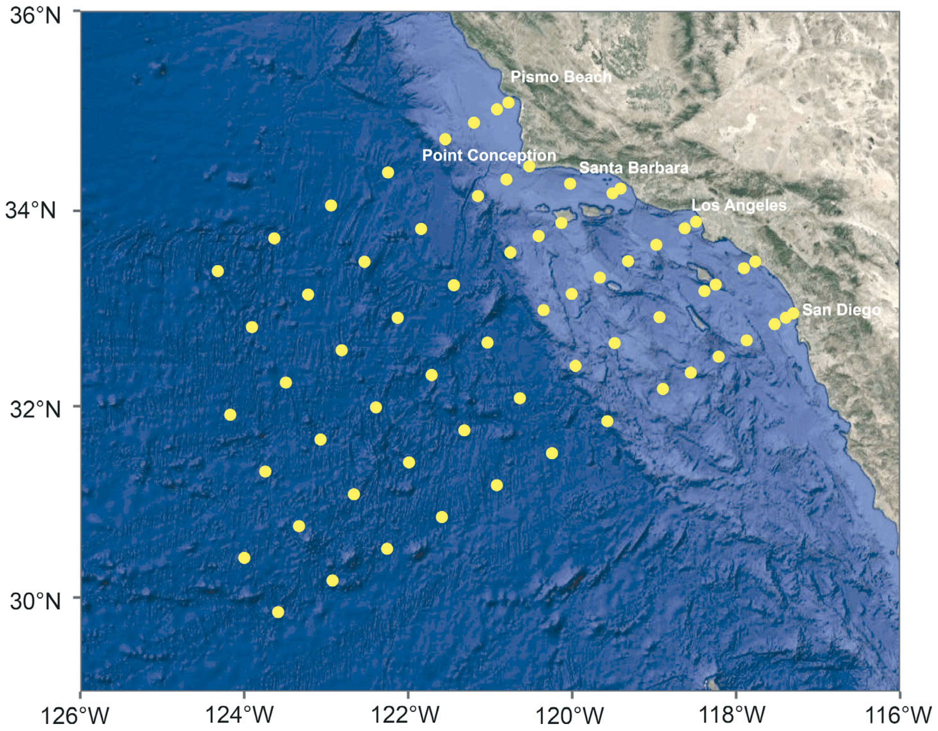


Fig. 1. Survey region showing the 66 core California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling stations (yellow dots)

thone spp., *Diogenichthys* spp., *Engraulis mordax* and *Vinciguerria* spp.), and we adjusted abundance estimates for these taxa between 1969 and 1978 as suggested by Thompson et al. (2017). Effects of the 1969 depth change on ichthyoplankton abundance estimates are unknown, but Ohman & Smith (1995) found that zooplankton abundances were directly comparable between 1951–1968 and 1969–1977 periods. Nevertheless, to determine if results were affected by the increased tow depth, we ran all analyses with the full suite of taxa and again excluding species with greater than 10% of larvae distributed below the upper 100 m of the water column (Ahlstrom 1959, Bowlin 2016).

All analyses and plots were made using R version 3.4.3 and associated package functions (R Core Team 2017). Because overall larval abundance is highest during spring, we restricted our analyses to taxa with at least 100 occurrences across all years for the spring assemblage (27 taxa in total), and 25 occurrences for the summer assemblage (35 taxa in total; Table 1). In total, 1 739 514 individual larvae were included in our analysis of the spring assemblage, and 680 010 individuals for the summer assemblage. Sampling frequency was reduced to triennial cruises between 1969 and 1983, accounting for 8 yr of missing data or 11% of years surveyed. As the analyses applied here for regime shift detection require complete time series, we performed linear interpolation to estimate abundances for the missing years using the 'zoo' package (Zeileis et al. 2018). Finally, all data were log-transformed ($\ln[x + 1]$) following Legendre & Gallagher (2001) and M. J. Anderson et al. (2006).

Regime shift detection

Regime shifts were detected with multivariate regression trees (MRTs), using the package 'rpart' (Therneau et al. 2018), with the default arguments for both respective functions. MRT is a form of chronological clustering which partitions a multivariate sequence into groups that minimize the within-group sum of squares; using time as the only explanatory variable enforces the constraint of temporal contiguity (Legendre & Legendre 2012, Morse et al. 2017, Perretti et al. 2017). Final partitions are determined by selecting the tree that minimizes the k-fold cross-validated prediction error (using the default setting of $k = 10$).

Following Perretti et al. (2017), we performed a sensitivity analysis to estimate the robustness of our regime shift years, as identified by the MRT analysis. We ran the same MRT algorithm on sample taxa

Table 1. Taxa included in the analysis. Group names are a composite of adult habitat and biogeographic affinities given by the expert classification system of Hsieh et al. (2005). SCB: Southern California Bight

Taxon	Group
Bathylagoides wesethi	Oceanic south
Ceratoscopelus townsendi	Oceanic south
Chauliodus macouni	Oceanic north
Chromis punctipinnis	Coastal SCB
Citharichthys spp.	Coastal cosmopolitan
Diaphus spp.	Oceanic cosmopolitan
Diogenichthys atlanticus	Oceanic cosmopolitan
Engraulis mordax	Coastal–oceanic cosmopolitan
Gobiidae	Coastal cosmopolitan
Gonostomatidae	Oceanic south
Hypsoblennius spp.	Coastal south
Icichthys lockingtoni	Coastal–oceanic north
Idiacanthus antrostomus	Oceanic north
Labridae	Coastal cosmopolitan
Leuroglossus stilbius	Coastal–oceanic north
Lipolagus ochotensis	Oceanic cosmopolitan
Melamphaidae	Oceanic cosmopolitan
Merluccius productus	Coastal–oceanic cosmopolitan
Nannobrachium spp.	Oceanic cosmopolitan
Paralabrax spp.	Coastal south
Paralepididae	Oceanic cosmopolitan
Protomyctophum crockeri	Oceanic cosmopolitan
Sardinops sagax	Coastal–oceanic cosmopolitan
Sciaenidae	Coastal south
Scomber japonicus	Coastal–oceanic cosmopolitan
Sebastes diploproa	Coastal south
Sebastes jordani	Coastal north
Sebastes spp.	Coastal
Sphyraena argentea	Coastal south
Stenobrachius leucopsarus	Oceanic north
Sternoptychidae	Oceanic cosmopolitan
Symbolophorus californiensis	Oceanic cosmopolitan
Tarletonbeania crenularis	Oceanic north
Tetragonurus cuvieri	Coastal–oceanic north
Trachurus symmetricus	Coastal–oceanic cosmopolitan
Triphoturus mexicanus	Oceanic south
Vinciguerria spp.	Oceanic south

ranging from 1 to the total number of taxa included in our original analysis (i.e. 27 for the spring and 35 for the summer). For a given sample size, the algorithm was applied to all possible combinations of taxa, with replacement, up to a maximum of 1000 combinations. The probability of detecting a regime shift in a single year is equal to the proportion of runs for which a regime shift was detected in that particular year, plus or minus 1 yr. We then performed a pairwise analysis of similarities (ANOSIM) using the package 'vegan' (Oksanen et al. 2018) to test for significant differences in compositional similarity between each regime period identified in the MRT analysis. To account for increasing probability of a Type I statistical error associated with multiple testing, we applied a Bonferroni adjustment to the threshold of significance; this lowered the p-value from 0.05 to 0.004.

Multivariate abundance trends

To help determine which taxa drove regime shifts, we employed several multivariate analyses that investigated species-specific changes in assemblage structure over the CalCOFI sampling period. To visualize temporal variability among individual taxa, we first calculated *z*-scores for individual taxa. Next, we created heatmaps of abundance anomalies where columns were years and rows taxa using the package 'gplots' (Warnes et al. 2016). The heatmaps were coupled with dendrograms created using Euclidian distance matrices and hierarchical clustering (method = 'complete') that evaluated which species varied together through time. We added vertical lines on the heatplots to identify years when MRT and sensitivity analyses detected regime shifts.

Finally, we performed nonmetric multidimensional scaling (NMDS) using the package 'vegan' (Oksanen et al. 2018) on the assemblage data to evaluate (1) how well the years in the CalCOFI sampling period separated from each other (based on their assemblage composition) in comparison to the results of the MRT analysis and (2) to further reveal compositional changes through time by overlaying the respective loadings of each NMDS axis on individual species. NMDS plots were made using ggplot2 (Wickham et al. 2016) with the color of species names corresponding to adult habitat affinity and biographical distribution as defined by (Hsieh et al. 2005) (Table 1).

RESULTS

Regime shift detection

MRT clustering detected change points in 1965, 1976, 1983, 1990 and 2001 for the spring assemblage, and in 1965, 1976 and 1999 for the summer assemblage. For the spring assemblage, 1976 was identified as the primary breakpoint, followed by 1964 and 1982, then 1990 and finally 2001. While all 5 change points were supported by our initial constraint, which was to prune the tree at the number of splits which minimized the cross-validated error, subsequent sensitivity analysis of candidate regime years showed little support for a 2003 change point. There was a near-0% probability of detecting a change point in

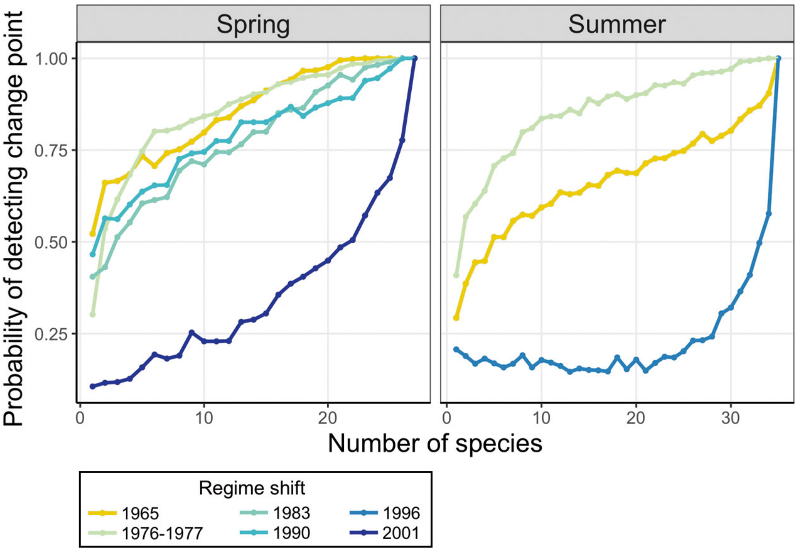


Fig. 2. Sensitivity analysis showing change point probability accumulation curves for bootstrapped sub-samples of the spring and summer CalCOFI larval fish assemblages

2001 using a single taxon from the spring assemblage, as indicated by the leftmost point on the probability accumulation curve for this year (Fig. 2). By comparison, all other candidate regime years identified by the initial MRT analysis were detected in 30–50 % of individual taxa. As the number of taxa included in the analysis increased, support for the 1976 change point was the highest, displaying a 75 % detection rate for random samples of 5 taxa. Change points in 1965, 1990 and 1983 also displayed similarly strong support using random samples less than half the size of the complete assemblage. Support for the 2001 change point stayed comparatively low until nearly all taxa were included in the analysis, suggesting this was an artifact of the clustering algorithm itself rather than a biological regime shift.

For the summer assemblage, the initial MRT analysis identified change points in 1965, 1976 and 1996. The sensitivity analysis for the summer assemblage did not follow the hierarchy of the regression tree splits, but rather displayed similar trends to the spring sensitivity analysis. The probability curves for the 1976 and 1996 change points in the summer assemblage displayed trends nearly identical to those for the 1976 and 2001 change points in the spring assemblage (Fig. 2). Support for the 1965 change point was qualitatively lower for subsets of the summer assemblage than for the spring assemblage.

Finally, pairwise ANOSIM revealed significant pairwise dissimilarities between all regime periods ($p \leq 0.004$), with the exception of the 1983–1989 and 1990–2017 regime periods in the spring assemblage (Table 2).

Multivariate abundance trends

Many taxa experienced similar responses to one another following the different regime periods. In the spring assemblage, hierarchical cluster analysis revealed 3 groupings of taxa displaying qualitatively similar abundance patterns (Fig. 3a), many of which shared adult habitat affinity characteristics, according to the group classification system of Hsieh et al. (2005) (Table 1). From 1951–1965, standardized abundance was lowest in the first cluster grouping, composed of mostly southern-distributed and/or offshore taxa, and highest in the second cluster grouping, composed of mostly northern-distributed and/or coastal taxa. Following the 1965 change point, abundance anomalies in these 2 assemblage clusters converged to intermediate levels, although northern-distributed taxa tended to remain slightly higher in the spring until 1976. Abundances also increased for certain individual taxa from the third cluster,

Table 2. Results of pairwise analysis of similarities (ANOSIM) between different regime periods, as identified by multivariate regression tree analysis. Lower diagonal represents values of the ANOSIM R statistic ranging from −1 to 1, where an R value of 0 represents completely random grouping. Upper diagonal represents p-values for the significance (**bold**; $p < 0.05$) of the observed pairwise R

Spring	1951–1963	1964–1975	1976–1982	1983–1989	1990–2017
1951–1963		**<0.001**	**0.007**	**<0.001**	**<0.001**
1964–1975	0.22		**<0.001**	**<0.001**	**<0.001**
1976–1982	0.35	0.43		**<0.001**	**0.005**
1983–1989	0.58	0.70	0.73		**0.047**
1990–2017	0.58	0.60	0.32	0.221	

Summer	1951–1963	1964–1975	1976–2014
1951–1963		**<0.001**	**<0.001**
1964–1975	0.27		**<0.001**
1976–2014	0.72	0.48	

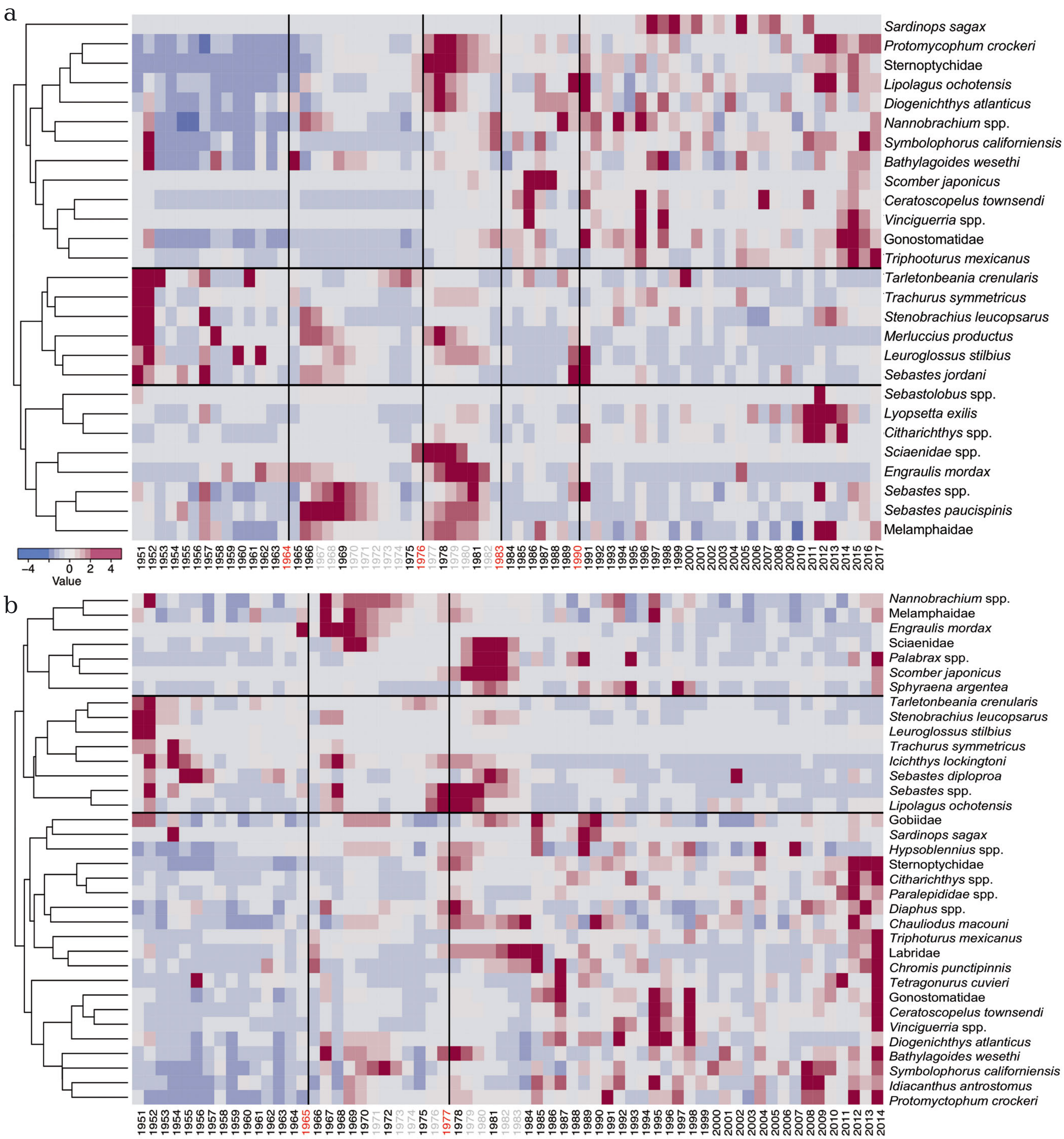


Fig. 3. Heatmaps depicting *z*-scores of raw abundances of the (a) spring and (b) summer assemblages, with years as columns and taxa as rows. Horizontal black lines represent groups of taxa whose variance through time is most similar, ordered according to a hierarchical clustering algorithm. Vertical black lines, and red font, represent regime shift years according to multivariate regression tree analysis. Years where linear interpolation was performed are shown in grey font

especially *Sebastes* spp. (coastal/coastal north), Melamphaeidae (oceanic cosmopolitan) and *Engraulis mordax* (coastal–oceanic cosmopolitan). The compositional changes following the 1976 change point are qualitatively most obvious, with the strongest increases in abundance among offshore taxa from the first cluster grouping. For the third cluster grouping, increases in abundance during the 1976–1983 period do not appear to have lasted beyond the 1983 change point. At this time, declines in northern taxa from the second cluster grouping are more apparent. Increases in the abundance of southern offshore taxa in the first cluster grouping appear to dominate overall variability in the larval fish assemblage after the 1983 change point. There are no widespread compositional changes that appear to separate the 1983–1990 regime period from the 1990–2017 regime period in the spring assemblage, besides perhaps the major increase in *Sardinops sagax* abundance after 1990.

For the summer assemblage, the 3 cluster groupings show more obvious differences in abundance between the regime periods (Fig. 3b). The first cluster is composed of several coastal and coastal–oceanic cosmopolitan taxa whose abundances were lowest prior to the 1965 change point, peaked from 1965 to 1983, and maintained lower abundance through the end of the sampling period in 2014. The 1965 change point appears to have been driven by large increases in this first group. The second and third clusters appear to respond more prominently to the 1976 change point, with taxa from the second cluster (mostly coastal and/or northern-distributed) maintaining low abundance throughout the sampling period, and taxa from the third cluster (mostly offshore and southern distributed) experiencing a near-unilateral increase, similar to the first cluster grouping for the spring assemblage.

The trend of increasing abundance of southern oceanic species apparent in both heatmaps is reinforced by the results of both of the NMDS analyses. Ordination of the spring assemblage in the NMDS plot (Fig. 4a) reveals the strongest separation of regime periods before and after the 1976–1977 regime shift, with latter years moving closer to an offshore, southern composition. The summer assemblage follows the same apparent pattern, with strongest separation of regime periods before and after the 1976 change point, and a long-term trend towards offshore southern assemblage composition (Fig. 4b). NMDS is theoretically aligned with ANOSIM in that both methods are based on the rank order of dissimilarity values; as such, it is important to note the high degree of spatial overlap (implying greater compositional similarity) between the convex polygons encompassing the 1983–1989 and 1990–2017 regime periods in the spring assemblage, which was the only non-significant pairwise result of the ANOSIM (Table 2).

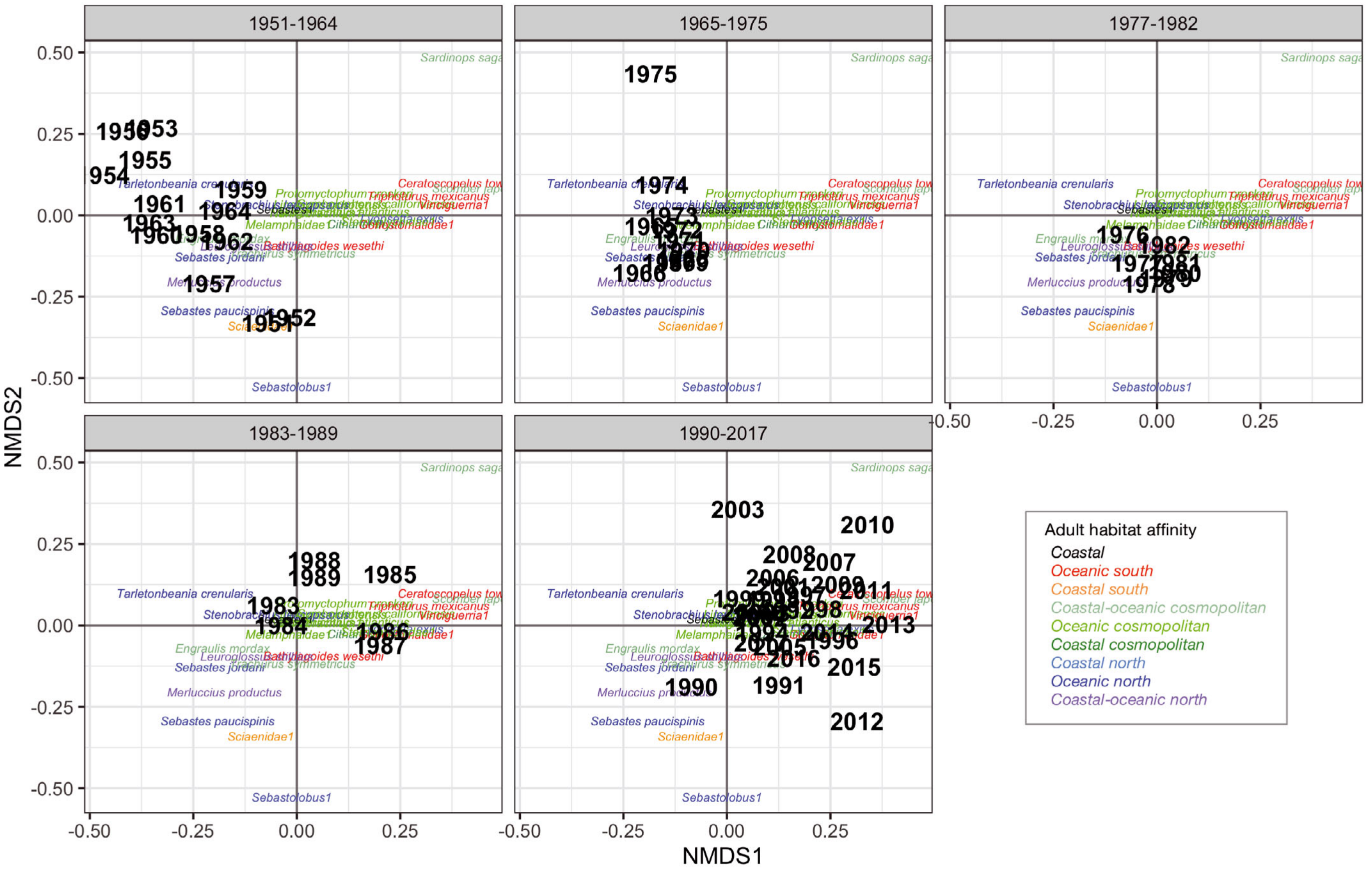
The 1969 change in sampling depth did not appear to affect our results. All regime breakpoints and supporting analyses were qualitatively identical when analyses were restricted to include only taxa whose larvae primarily reside in the upper 100 m of the water column (see Tables S1 & S2 and Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m607p071_supp.pdf).

DISCUSSION

Our work provides evidence for multiple regime shifts in the composition of southern California's spring and summer fish assemblage since 1951, augmenting our existing understanding of multi-decadal biological variability in this region. Both seasonal assemblages exhibited regime shifts in 1965 and 1976; we also found evidence for regime shifts in the spring assemblage in 1983 and 1990. Sensitivity analysis of the change point years detected by the MRT clustering algorithm indicates that these shifts were prevalent across a broad portion of the assemblage, rather than driven by a single or several taxa. Insofar as the CalCOFI ichthyoplankton includes a range of taxa in both coastal and pelagic environments, and serves as an appropriate indicator of adult biomass (Moser & Watson 1990, Gunderson 1993, Moser et al. 2000, Hsieh et al. 2005), we believe these results qualify as evidence for regime shifts in community composition that affected ecologically and commercially important species. Finally, our failure to detect similar shifts during the period from the late 1990s to the present dampens previous speculations that a 'cold period' that commenced in 1999 in the SCB had dramatic impacts on the region's fish community.

To our knowledge, this is the first time that a 1965 change point has been observed in the CalCOFI ichthyoplankton assemblage. Prominent changes during this time include increases from low to moderate abundance for several offshore taxa across both seasons, namely Melamphaeidae, Sternoptychidae, *Nannobrachium*, *Diogenichthys atlanticus, Lipolagus ochotensis* and *Protomyctophum crockeri*. *Engraulis mordax* also demonstrates strong increases around this time, although this shift is visible prior to the 1965 regime shift for the spring assemblage (Fig. 3a). In the spring assemblage, several species of rockfish also exhibit strong increases during the 1965–1976 period, namely *Sebastes paucispinis* and other *Sebastes* spp. (unidentified rockfish larvae). Moser et al. (2000) documented a peak in the abundance of rockfish larvae in the CalCOFI sampling region around the mid- to late 1960s, prior to the 1976 shift into a 'cool' period. A 1965 regime shift

a) Spring



b) Summer

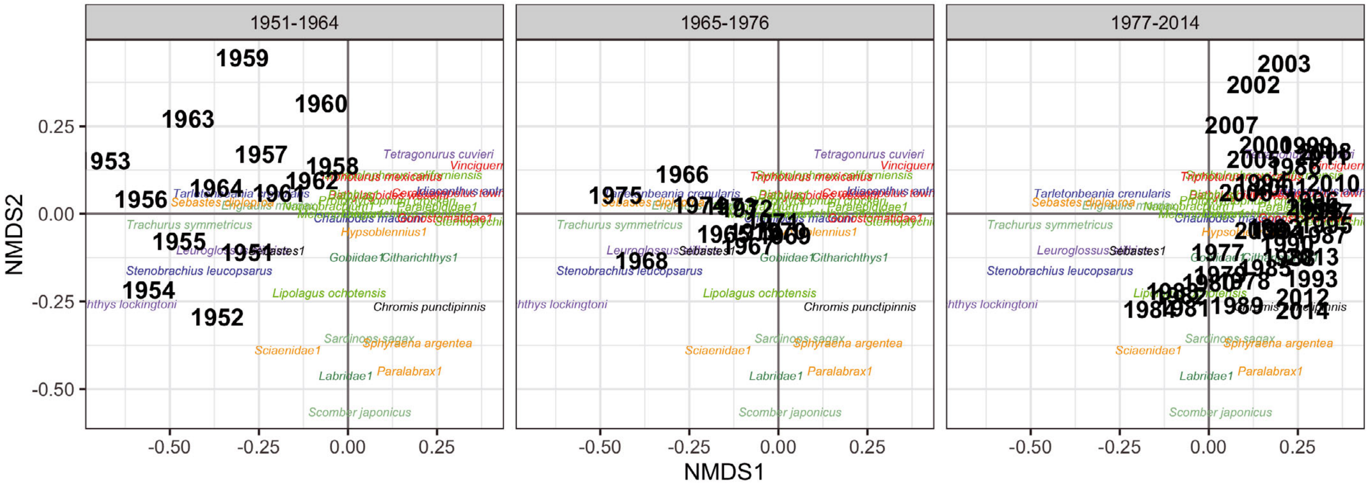


Fig. 4. Nonmetric multidimensional scaling (NMDS) plots for each identified regime period within the (a) spring and (b) summer CalCOFI larval fish assemblages. Group names are a composite of adult habitat and biogeographic affinities given by the expert classification system in Hsieh et al. (2005)

was also detected in California's commercial pelagic fisheries landings, although the exact abundance trends characterizing this shift were not described in detail (Powell & Xu 2012). Rebstock (2002) also detected a change point in the late 1960s in the CalCOFI zooplankton record, but attributed this to a change in the CalCOFI sampling depth. We believe that the sampling change did not affect our results for several reasons. First, the change in sampling methodology did not take place until 1969 (Thompson et al. 2017), whereas we detected a regime shift in 1965. Second, our analyses of the spring and summer assemblages excluding taxa distributed below the top 100 m of the water column (Ahlstrom 1966, Bowlin 2016) found equally strong evidence for a 1965 regime shift in both seasons (see Fig. S1 in the Supplement).

We were particularly interested in determining whether a biological regime shift took place in the waters off southern California during the late 1990s, following speculation that a multi-year stretch of negative PDO values starting in 1998 marked the start of a 'cold regime' in the North Pacific (Bograd et al. 2000, McFarlane et al. 2000, Peterson & Schwing 2003, Zwolinski & Demer 2012). Indeed, while the water column biogeochemistry and phytoplankton assemblage composition of the SCB appear to have undergone abrupt changes during this period (Sekula-Wood et al. 2011, Bograd et al. 2015), we found no evidence for such a regime shift in the ichthyoplankton assemblage. Rather, the assemblage structure that began in the mid- to late 1980s for the spring assemblage, and in the 1970s for the summer assemblage, appears to have continued through the end of the CalCOFI sampling period. Our combined multivariate approach emphasizes a long-term trend since 1976 towards a more southern, offshore assemblage composition in this region. These 'warm offshore' taxa separate well as clusters in the heatmaps and NMDS plots for both seasons.

Our findings mesh well with documented changes to the physical oceanography of this region following the 1976 regime shift, including decreased salinity, increased stratification and weakened upwelling, as well as a documented shoreward advance of offshore mesopelagic fishes into the primary CalCOFI sampling domain (Bograd & Lynn 2003, Hsieh et al. 2009). Smith & Moser (2003) also documented declines in overall fish larvae and egg abundance following the 1976 regime shift, but similar to Hsieh et al. (2009), these changes were examined between pre-defined regime periods. This trend towards a more southern and offshore assemblage composition continued through the end of the 1990s and into the present, with little evidence to suggest that the larval fish assemblage has reverted to a 'cool' assemblage or otherwise shifted in its composition throughout the late 1990s or early 2000s. Analysis of the CalCOFI record on a smaller temporal scale, from 1985–2015, confirms our findings of long-term stability in overall assemblage structure during this period, despite a step-wise increase in the presence of more acidic and spicy Pacific Equatorial Water after 1995; rather, taxonomic richness has steadily increased, and ichthyoplankton assemblage structure exhibited short-term changes after El Niño events followed by subsequent recovery (McClatchie et al. 2016).

In the spring assemblage, when overall species abundance is higher, we also detected change points in 1983 and 1989. Qualitatively, both periods separate well on the NMDS plot for the spring assemblage (Fig. 4a), but both are superimposed by the general pattern of the 1976–2014 period, which clusters towards southern and offshore assemblage composition. Although the 1983 shift has also been detected in southern California's coastal assemblage (Miller & McGowan 2013), here we interpret our results with caution, as high abundances in the years around 1978 and 1981 could be inflated due to linear interpolation. The apparent 1989 change point in the spring assemblage aligns with several accounts of a 1989 regime shift from across the North Pacific (Hare & Mantua 2000, deYoung et al. 2008) and across the northern hemisphere (Beaugrand et al. 2015). However, this was the only change point that did not yield significant differences between periods, according to the results of the ANOSIM. It is also less clear from our analysis which taxa or group(s) of taxa are the principal drivers of this shift in the spring assemblage; *Sardinops sagax* increased over the course of this period, but not until well into the 1990s. Nevertheless, Koslow et al. (2015) found evidence for a 1989 regime shift in the second principal component (PC2) of the CalCOFI ichthyoplankton record. Along with Miller & McGowan (2013), Koslow et al. (2015) described broad declines across multiple levels of the southern California fish assemblage since 1989. This particular analysis used annual mean abundances across all seasons, so it is not surprising that the year-round CalCOFI PC2 represented a significantly larger portion of northern-affiliated taxa than was captured by our approach, which focused exclusively on the spring and summer assemblages.

While we see our multivariate approach and application of updated data curation methodology as a major improvement in the use of the full CalCOFI ichthyoplankton record for the purposes of detecting regime shifts, we recognize the limitations of our work and approach. A recognized shortcoming of the regime shift literature is the failure to formally test for both abrupt and gradual change (Litzow & Mueter 2014). While our study provides ample evidence that southern California's larval fish assemblage did not experience a regime shift during the late 1990s to early 2000s, as was previously speculated, we recommend that future work using the CalCOFI record also assess the importance of gradual change, especially given that secular warming will likely play a primary role in shaping the North Pacific throughout the rest of the 21st century (Di Lorenzo et al. 2008, Bonfils & Santer 2011). Indeed, both seasonal heatmaps display gradual accumulation of southern offshore species after the 1976 regime shift (Fig. 4). Another limitation posed by the CalCOFI ichthyoplankton record is the missing data throughout the 1970s. Although we did our best to minimize the effects of linear interpolation on the results of our MRT analysis, we have more confidence in our assessment of long-term trends in community composition than we do in the exact year of each regime shift during the 1970s and 1980s. Finally, changes in abundance in the SCB might obscure geographical variation outside of the CalCOFI sampling period. Whether the prominence of the southern offshore assemblage since the 1970s reflects a population increase or simply a shift in the northern range boundary of southern-distributed taxa remains a question for future studies that combine CalCOFI data with surveys further north and south of the SCB, such as data from the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) program in Baja California Sur (Bautista-Romero et al. 2018).

Recent analysis of 11 marine systems across the northern hemisphere, including the CalCOFI zooplankton record, detected near-synchronous regime shifts in the mid-1970s and the late 1980s (Beaugrand et al. 2015). The 1976 shift was only detected in Pacific systems, and this shift appears to have the most putative impact on southern California's larval fish assemblage. The shift in the late 1980s was more coherent across the entire northern hemisphere, and we have shown that changes in the 1980s remain important for at least the spring assemblage. Beaugrand et al. (2015) also suggested that a semi-synchronous regime shift occurred during the late 1990s; however, none of the datasets from the Pacific Ocean exhibited change points during this time (including eastern and western Pacific Rim salmon, CalCOFI zooplankton and western Pacific zooplankton), a result which aligns with our findings of stability in the ichthyoplankton assemblage over the past 30 yr. Nonetheless, regime shifts have continued to structure systems across the North Atlantic through at least the beginning of the 21st century, with recent observed shifts in zooplankton (Morse et al. 2017) and fish recruitment (Perretti et al. 2017) in the western North Atlantic. Clearly, while historically synchronous regime shift patterns may have provided some insight into global teleconnections between different patterns of decadal climate variability, such as the PDO and the Atlantic Multidecadal Oscillation, a detailed, system-specific approach is warranted.

Regime shifts have structured biological communities in the SCB and across the North Pacific as a whole, for at least as long as the duration of existing time series data, and perhaps as far back as the Little Ice Age (Skrivanek & Hendy 2015). However, as anthropogenic climate change contributes to secular warming across the globe, scientists must evaluate its potential impacts on biological populations that are adapted to modes of internal climate variability, especially in dynamic boundary current regions such as the SCB. Since the 1970s and 1980s, southern California's larval fish assemblage has become steadily dominated by taxa previously limited to southern and offshore water masses, with no apparent signs of reversal. It is clear that future management and study of California's marine resources must account for the large and often countervailing impacts of climate variability across multiple timescales.

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