

Influence of climate on the biodiversity and community structure of fishes in the southern California Current

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ABSTRACT: Previous studies have reported dramatic declines of midwater fishes in the southern California Current System (CCS) in response to reduced deepwater oxygen concentration, and many CCS endemics and cool-water affinity taxa have also declined since 1969. Here we show that these abundance changes are associated with changes in the diversity of the CCS fish community. Species richness was positively associated with periods of relatively high midwater oxygen concentration and with the warm phase of the Pacific Decadal Oscillation, the multivariate ENSO index, and warmer near-surface temperature. While the decline of CCS endemics and cool-water affinity taxa was not associated with a change in species richness, it significantly enhanced the evenness of the fish community by markedly reducing the abundance of dominant taxa. Community structure overall, however, changed relatively little: the rank order of the 15 most abundant taxa changed little between periods of high and low species richness and evenness. Overall, fish community structure in the CCS thus appears to have remained stable in recent decades, despite marked changes in abundance of entire suites of species and significant changes in several biological diversity indices. The increase in the Shannon-Wiener index of evenness associated with the marked decline of several dominant taxa in the CCS indicates that changes in simple diversity indices need to be interpreted cautiously: increased diversity cannot be equated with improved ecosystem functioning.

KEY WORDS: Species richness · Evenness · Northeast Pacific · Ichthyoplankton · Pacific Decadal Oscillation · ENSO · Warming

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INTRODUCTION

Scientific literature documenting the effects of climate change on marine biodiversity has grown in recent years (Halpern et al. 2008, Stuart-Smith et al. 2010, Doney et al. 2012). Much of this literature has focused on coastal habitats, such as coral reefs and the rocky intertidal, which are most accessible and often best-studied (Barry et al. 1995, Carpenter et al. 2008). For marine fishes, assessments of climate change impacts often depend on model projections of anticipated distribution changes (Cheung et al. 2009). In this paper, we examine changes in the

diversity of a broad range of coastal and oceanic fishes based on the multi-decadal ichthyoplankton time series maintained by the long-standing California Cooperative Oceanic Fisheries Investigations (CalCOFI) program.

The vast majority of marine teleost fish species are pelagic broadcast spawners, whose planktonic progeny can be effectively and quantitatively sampled with plankton nets during their very early life history. Because larval fish sampled in this manner are dominated by preflexion stage individuals, their abundance serves as a useful proxy for adult spawning stock biomass (Saville 1981, Moser et al. 2000, 2001,

Koslow et al. 2011). Ichthyoplankton time series thus provide a powerful tool to assess changes in fish communities, including both commercial and unexploited taxa, in relation to fishing, climate, and other potential factors.

The CalCOFI ichthyoplankton data set, which is based on reasonably consistent sampling methods since 1951, has provided the basis for a rich body of scientific work ranging from stock assessments, studies of seasonality and distribution, and community analyses to studies of the effects of fishing and climate. McClatchie (2014) provided a recent review of this extensive scientific literature. The present study builds, in particular, on a previous multivariate analysis of the abundance since 1951 of the commonly occurring taxa in this data set (Koslow et al. 2011, 2013). This analysis indicated that the time series exhibited 2 dominant temporal patterns or principal components (PCs). PC 1, which accounted for 20.5% of the variance, was dominated by a diverse assemblage of midwater fishes: 24 of 27 taxa with loadings ≥ 0.50 were mesopelagic fishes from 8 families (Table 1). The time series for PC 1 and annual mean oxygen concentration at 200–400 m depth in the CalCOFI region were closely correlated ($r = 0.75$, $p < 0.001$); the abundance of these mesopelagic taxa declined overall by ~63% during periods of reduced midwater oxygen concentration in the 1950s and since 1999 (Koslow et al. 2011). PC 1 was also significantly correlated with the multivariate ENSO index (MEI), Pacific Decadal Oscillation (PDO), the North Pacific Gyre Oscillation (NPGO), and annual mean temperature at 10 m and 200 m depth from the CalCOFI cruises.

PC 2, which accounted for 12.4% of the variance of the data set, was based on a decline since 1969 of mostly cool-water affinity fishes: of the 31 taxa with significant positive loadings (≥ 0.29), only 2 had warm-water (tropical or subtropical gyre) affinities, and all of the 7 taxa that loaded significantly negatively had warm-water affinities (Table 1). Six of the 7 most abundant taxa in the CalCOFI data set (Moser & Watson 2006) had loadings ≥ 0.50 on PC 2, indicating its importance for capturing a trend of major importance to the southern California Current fish community: Pacific sardine *Sardinops sagax*, which loaded negatively, and Pacific hake *Merluccius productus*, northern anchovy *Engraulis mordax*, rockfishes (*Sebastes* spp.), California smoothtongue *Leuroglossus stilbius*, and northern lampfish *Stenobrachius leucopsarus*, which all loaded positively. PC 2 declined markedly since 1969, reflecting a 72% decline in overall abundance of ichthyoplankton in

the data set (Koslow et al. 2013, 2015). PC 2 was closely correlated with a decline of similar magnitude of nearshore fishes ($r = 0.85$, $p < 0.01$), observed in an independent but complementary time series based on sampling power plant cooling-water intakes along the coast of southern California since 1972 (Miller & McGowan 2013, Koslow et al. 2015).

In view of the considerable changes in the abundance of key fish taxa and dominant ecological groups observed in recent decades in the southern California Current System (CCS), here we examined whether the diversity of fishes in this region may also have changed. We examined 2 components of ecological diversity, species richness and evenness (Pielou 1975, Magurran 2004), and in particular, whether these aspects of diversity appear to have been influenced by key indicators of a changing ocean environment or by the changing patterns of abundance in regional fish communities described above.

The CCS is characterized by pronounced decadal-scale variability—most notably, the PDO and NPGO (Mantua et al. 1997, di Lorenzo et al. 2008)—so it has not been possible to determine unequivocally whether recent ocean warming or declining midwater oxygen trends and their associated trends in regional fish communities are due to decadal-scale variability or secular climate change (McClatchie et al. 2010, Deutsch et al. 2014, Koslow et al. 2015). However, regardless of the underlying cause, the CalCOFI data set provides an exceptional opportunity to examine biodiversity changes in relation to large-scale physical and biological oceanographic changes. Furthermore, the CalCOFI ichthyoplankton time series is particularly well suited to such analysis: simple measures of species richness are sensitive to sampling effort (Gotelli & Colwell 2001), but the systematic CalCOFI ichthyoplankton sampling design has been carried out consistently over time, enabling us to avoid these potential biases.

Numerous studies have reported a poleward shift in species distributions in response to warming sea temperatures, but the impact on diversity has varied. In the North Sea, the shift into the region of more southerly species has led to an increase in species richness but a decline in mean fish size and commercial value (Hiddink & ter Hofstede 2008), whereas the kelp fish community off southern California has declined in both abundance and species richness (Holbrook et al. 1997). Diversity is often considered to be influenced by—and generally to decline in relation to—human disturbance, whether exploitation, pollution, eutrophication, or climate change (Magur-

Table 1. Taxa, their loadings (Load) on principal components (PC) 1 and 2, habitat, and biogeographic distribution, based on Koslow et al. (2011, 2013, 2015). The loadings are equivalent to the correlation between the taxa time series and the PC. Only taxa with loadings ≥ 0.29 are shown, the level at which correlation was nominally significant ($p < 0.05$) based on 29 degrees of freedom. Habitats: Epi, epipelagic; Meso, mesopelagic; Demersal. Biogeography codes are CC: California Current; TST: tropical/subtropical; B: boreal/sub-Arctic; TZ: transition zone; STG: subtropical gyre; Cosmo: cosmopolitan. Taxa at genus or family level with indeterminate biogeography are not classified

PC 1 Taxon	Load	Habitat	Biogeog	PC 2 Taxon	Load	Habitat	Biogeog
<i>Diogenichthys atlanticus</i>	0.86	Meso	STG CC	<i>Icichthys lockingtoni</i>	0.75	Epi	TZ CC
<i>Protomyctophum crockeri</i>	0.85	Meso	B TZ CC	<i>Sebastes paucispinis</i>	0.71	Demersal	B CC
<i>Ceratoscopus townsendi</i>	0.83	Meso	Cosmo	<i>Sebastes</i> spp.	0.70	Demersal	B CC
<i>Cyclothone</i> spp.	0.83	Meso		<i>Leuroglossus stilbius</i>	0.67	Meso	CC
<i>Nannobranchium</i> spp.	0.81	Meso		<i>Sebastes aurora</i>	0.63	Demersal	CC
Sternoptychidae	0.75	Meso		<i>Peprilus simillimus</i>	0.61	Epi	CC
<i>Stomias atriventer</i>	0.73	Meso	TST CC	<i>Engraulis mordax</i>	0.61	Epi	CC
<i>Symbolophorus californiensis</i>	0.73	Meso	TZ CC	<i>Merluccius productus</i>	0.56	BP	CC
<i>Chauliodus macouni</i>	0.71	Meso	B TZ CC	Sciaenidae	0.53	Demersal	
<i>Vinciguerria lucetia</i>	0.71	Meso	TST CC	<i>Pleuronichthys coenosus</i>	0.53	Demersal	B CC
Scopelarchidae	0.70	Meso		<i>Stenobranchius leucopsarus</i>	0.53	Meso	B TZ CC
<i>Bathylagoides wesethi</i>	0.69	Meso	CC	Myctophidae	0.52	Meso	
<i>Bathylagus pacificus</i>	0.68	Meso	B CC	<i>Melamphaes</i> spp.	0.51	Meso	
<i>Scomber japonicus</i>	0.68	Epi	CC	<i>Sebastolobus</i> spp.	0.50	Demersal	
Paralepididae	0.67	Meso		Labridae	0.47	Demersal	
<i>Microstoma</i> spp.	0.67	Meso	B TZ CC	<i>Pleuronichthys decurrens</i>	0.46	Demersal	B CC
<i>Argentina sialis</i>	0.65	Meso	CC	<i>Sebastes jordani</i>	0.46	Demersal	CC
<i>Lipolagus ochotensis</i>	0.64	Meso	B TZ CC	<i>Sebastes goodei</i>	0.46	Demersal	B CC
<i>Hygophum reinhardtii</i>	0.61	Meso	STG CC	<i>Tarletonbeania crenularis</i>	0.44	Meso	B TZ CC
<i>Idiacanthus antrostomus</i>	0.57	Meso	Cosmo	<i>Cololabis saira</i>	0.43	Epi	B TZ CC STG
Gobiidae	0.57	Demersal		<i>Glyptocephalus zachirus</i>	0.38	Demersal	B CC
<i>Myctophum nitidulum</i>	0.55	Meso	TST	<i>Pleuronichthys verticalis</i>	0.34	Demersal	CC TST
<i>Triphoturus mexicanus</i>	0.54	Meso	TST CC	<i>Diaphus</i> spp.	0.34	Meso	TZ CC
<i>Aristostomias scintillans</i>	0.53	Meso	B CC	<i>Diogenichthys atlanticus</i>	0.34	Meso	TST STG CC
Myctophidae	0.52	Meso		Trachipteridae	0.33	Meso	
<i>Citharichthys</i> spp.	0.50	Demersal		<i>Parophrys vetulus</i>	0.31	Demersal	B CC
<i>Notolychnus valdiviae</i>	0.50	Meso	TST CC STG	<i>Scorpaenichthys marmoratus</i>	0.30	Demersal	B CC
<i>Paralabrax</i> spp.	0.49	Demersal		Gobiidae	0.30	Demersal	
<i>Melamphaes</i> spp.	0.47	Meso		<i>Trachurus symmetricus</i>	0.29	Epi	Cosmo
<i>Scopelogadus bispinosus</i>	0.47	Meso	TST CC STG	<i>Chauliodus macouni</i>	0.29	Meso	B TZ CC
Labridae	0.47	Demersal		<i>Bathylagus pacificus</i>	0.29	Meso	B CC
<i>Pleuronichthys verticalis</i>	0.46	Demersal	CC TST	<i>Idiacanthus antrostomus</i>	-0.32	Meso	Cosmo
<i>Paralichthys californicus</i>	0.45	Demersal	CC TST	<i>Ceratoscopus townsendi</i>	-0.34	Meso	Cosmo
<i>Poromitra</i> spp.	0.44	Meso		Agonidae	-0.35	Demersal	
<i>Notoscopelus resplendens</i>	0.44	Meso	TST CC STG	<i>Myctophum nitidulum</i>	-0.38	Meso	TST STG
Cottidae	0.44	Demersal		<i>Vinciguerria lucetia</i>	-0.48	Meso	TST CC
<i>Zaniolepis</i> spp.	0.44	Demersal		<i>Hygophum reinhardtii</i>	-0.48	Meso	STG CC
Sciaenidae	0.43	Demersal		<i>Sardinops sagax</i>	-0.75	Epi	CC
<i>Hypsoblennius</i> spp.	0.42	Demersal					
<i>Glyptocephalus zachirus</i>	0.40	Demersal	B CC				
<i>Tactostoma macropus</i>	0.40	Meso	TZ CC				
<i>Microstomus pacificus</i>	0.39	Demersal	B CC				
<i>Hippoglossina stomata</i>	0.38	Demersal	TST CC				
<i>Sebastes</i> spp.	0.37	Demersal	B CC				
<i>Peprilus simillimus</i>	0.35	Epi	CC				
<i>Sphyræna argentea</i>	0.34	Epi	CC				
<i>Nansenia candida</i>	0.31	Meso	TZ CC				
Atherinopsidae	0.30	Epi					
<i>Engraulis mordax</i>	0.30	Epi	CC				
<i>Cololabis saira</i>	-0.43	Epi	B TZ CC STG				
<i>Sebastes diploproa</i>	-0.45	Demersal	B CC				
<i>Sebastes goodei</i>	-0.48	Demersal	B CC				

ran 2004). Although human impacts on the fish community of the CCS remain uncertain, previous studies (Koslow et al. 2011, 2013, 2015) clearly indicate that this community has not been at a stable equilibrium over recent decades; how, then, has declining fish abundance related to changes in the oxygen minimum zone (OMZ) and warming affected the diversity of the fish community of the CCS?

Several hypotheses present themselves in framing this study. Although various mesopelagic taxa are adapted to life at low oxygen concentrations, the biomass and diversity of macrobenthos, zooplankton, and fishes are generally reduced in the core of the OMZ, a permanent feature associated with the mesopelagic waters of productive eastern boundary currents (Childress & Seibel 1998, Helly & Levin 2004). It is therefore generally predicted that an expanded OMZ will lead to reduced species diversity (Seibel 2011). Since the 1980s, oxygen concentrations at midwater depths in the CCS have declined by ~20%, and the OMZ itself has shoaled by up to 90 m in the CalCOFI sampling area (Bograd et al. 2008, McClatchie et al. 2010). Given these major changes, it is of interest to examine whether this has resulted in reduced diversity and a transition toward a community adapted to the more extreme low-oxygen conditions observed off southern Baja California (Mexico) and the eastern tropical Pacific. Our first hypothesis, therefore, has 2 parts: that reduced oxygen concentration at midwater depths will lead to reduced diversity, and that reduced oxygen will lead to a replacement of a midwater fauna with cool-water affinities with fishes from lower latitudes that are presumably better adapted to an expanded OMZ.

A second set of hypotheses is related to the declining abundance of the region's cool-water affinity assemblage (Barry et al. 1995, Miller & McGowan 2013, Koslow et al. 2013, 2014, 2015). Are cool-water taxa being replaced by taxa with warmer-water affinities, and if so, is this assemblage more or less diverse than the cool-water taxa? In the northern CCS where periodic warming leads to replacement of a cool-water by a warm-water zooplankton assemblage, the cool-water assemblage is notably larger and associated with enhanced juvenile salmon survival, but it is reduced in species richness (Peterson 2009).

MATERIALS AND METHODS

The study is based on the annual abundance of larval fish sampled at 51 stations that were consistently sampled on 4 seasonal CalCOFI cruises per year

from 1969 to 2011, the last year for which data were available at the start of analysis. The stations extend from San Diego to north of Pt. Conception and from the coast (~50 m depth) to about 400 km offshore (range from ~250 to 550 km offshore; Fig. 1). The samples are from quantitative oblique zooplankton net tows with 505 μm mesh that collect ichthyoplankton from approximately 210 m to the surface. CalCOFI used a 1 m diameter bridled ring net until 1977 and a 0.71 m diameter unbridled bongo net subsequently. A flowmeter was used to estimate the volume of water filtered. All fish eggs and larvae were sorted from the samples in the laboratory, identified to the lowest taxonomic level possible, and enumerated. The taxonomic resolution from 1969 to the present is consistent, which is the reason for starting our time series with that year; taxonomic resolution is coarser from previous cruises, with more taxa resolved only to the genus or family level. Further details of the field sampling and laboratory protocols may be found in Kramer et al. (1972), Smith & Richardson (1977), and McClatchie (2014).

Sampling frequency was quarterly. However, fish spawning is seasonal, so only annual mean abundance data were considered useful. Our analyses were based on annual means derived from seasonal means to minimize bias when sampling frequency was greater during a particular season. January and February were combined as winter; March through May as spring; June through August as summer; and September through December as fall. Years were removed from the analysis if sampling did not cover

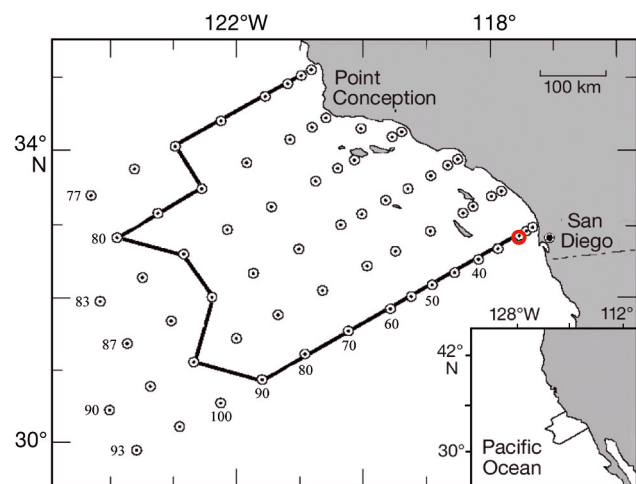


Fig. 1. Core California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling stations off the coast of southern California, USA. The stations within the area demarcated with a solid line were most consistently sampled throughout the time series and were used in this study. Spiciness was defined at Station 30 on line 93 (circled in red)

all 4 seasons, since decreased seasonal coverage significantly influenced species richness. All years were adequately sampled with full seasonal coverage since 1984 but only 3 years prior (1969, 1972, and 1975).

Following Magurran (2004), α diversity is considered to have 2 primary dimensions, species (or taxon) richness and evenness. We used the abundance data for 233 larval fish taxa from 1969–2011 to examine changes in the following measures of biodiversity: species richness (S), which is the total number of taxa present in a given year, and the Shannon-Wiener index (H'), a measure of both diversity and evenness:

$$H' = -\sum_i p_i \log(p_i) \quad (1)$$

where p is the proportion of species i in the annual sample.

In addition to S and H' , which are most commonly used in biodiversity studies, we examined several additional indices of richness and evenness: Margalef's species richness index (d), Pielou's measure of evenness (J'), and Simpson's evenness index ($1 - \lambda$):

$$d = (S - 1) / \log(N) \quad (2)$$

$$J' = H' / H'_{\max} \quad (3)$$

where $H'_{\max} = \ln(S)$, and $\lambda = \sum_i p_i^2$.

For our data set, the correlation (r) of species richness (S) with Margalef's richness index (d) was 0.91, so we only used S in our study. The correlation of the Shannon-Wiener index (H') with the Pielou and Simpson evenness indices was 0.99 and 0.96, respectively, indicating that H' is primarily an index of community evenness, so only H' was used further in our study. S and H' were not significantly correlated in our data set ($r = 0.17$, $p > 0.10$), indicating they were measures of different aspects of community diversity.

Over 90% of larvae were identified to species, and the remainder to genus or family, based on Moser (1996). All fishes identified to species were classified by their adult habitat (epipelagic, mesopelagic or bathypelagic, benthic, and demersal and benthopelagic) and by biogeographic distribution (boreal, transition zone, CC, tropical/subtropical, subtropical gyre, cosmopolitan, or some combination of these), following Hsieh et al. (2005) and Moser (1996). Cool-water affinity taxa were defined as having boreal and/or transition zone distributions, potentially extending into the CalCOFI region; warm-water affinity taxa were defined as those found in tropical/subtropical waters, as well as potentially in the CC. Taxa defined as having cosmopolitan distributions were

found in both cool and warm waters, and taxa classified as CC were restricted primarily to the CC region. These classifications were used to examine which components of the California fish community changed in abundance.

We then examined correlations of S and H' with local and large-scale environmental factors: sea surface (10 m) temperature (T_{10}), midwater (200–400 m) oxygen concentration, and spiciness, which were all based on the annual averages from the quarterly CalCOFI cruises, with data obtained at the same core stations that comprised the ichthyoplankton data set. Spiciness (non-dimensional) is a state variable that is most sensitive to isopycnal thermohaline variations, and whose value increases with increasing temperature and salinity. Spiciness at Stn 30 on line 93 of the CalCOFI grid (Fig. 1) along the isopycnal $\sigma_\theta = 26.5 \text{ kg m}^{-3}$ was used as a proxy for the influence of the poleward-flowing California Undercurrent (CUC), which transports relatively warm, high-salinity water from the equatorial Pacific, with high spiciness indicating strong influence of the CUC (Bograd et al. 2015). Spiciness was computed according to Flament (2002). Seasonal mean temperature, salinity, density, and oxygen concentration were computed from the values at the core CalCOFI stations from each seasonal cruise obtained from the CalCOFI database at www.calcofi.org/data/ctd.html, and annual means were computed as the mean of the cruise means.

S and H' were also examined in relation to an index of upwelling (W) based on a spatially explicit estimate of environmental variability derived from a 31 yr (1980–2010) CCS reanalysis using a Regional Ocean Modeling System (ROMS) with 4-dimensional variational data assimilation, which is described in detail by Neveu et al. (2016). We used model output in the southern/central CCS sector (30–38°N, 116–126°W) to provide spatially resolved estimates of upwelling. Annual means were computed for each grid point (with a resolution of 0.1° of longitude and latitude) as the mean of the monthly means for the months of April to September, corresponding to the main upwelling season, from 1980 to 2010. The ROMS-based first empirical orthogonal function (EOF 1) index of regional upwelling was first analyzed by Jacox et al. (2014). Upwelling in the region exhibits a spatially heterogeneous pattern, with an increasing trend near the coast, which is dominant, and a declining trend offshore (Jacox et al. 2014, Siegelman-Charbit et al. unpubl.). The sign of EOFs is arbitrary, and the sign of W is set here to reflect the dominant increasing trend in regional upwelling.

The following large-scale oceanographic variables were used: the PDO (Mantua et al. 1997; <http://research.jisao.washington.edu/pdo/PDO.latest.txt>); the NPGO (Di Lorenzo et al. 2008; www.o3d.org/npgo), and the MEI (Wolter & Timlin 1998; www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/table.html).

We also examined potential changes in biodiversity related to dominant patterns of variability in the abundance of dominant fish assemblages in the CCE, based on the previously published PCA of the CalCOFI ichthyoplankton time series discussed above: PC 1, primarily the variation in abundance of mid-water fishes (Koslow et al. 2011), and PC 2, which follows variation in the abundance of predominantly cool-water affinity fishes (Koslow et al. 2011, 2015).

RESULTS

The 233 fish taxa recorded in the core CalCOFI study area from 1969–2011 were dominated by benthic and mesopelagic taxa (102 and 90, respectively), with considerably fewer epipelagic and benthopelagic taxa (25 and 10, respectively). There were 77 cool-water taxa, whose distributions extended into the transition zone or boreal (subarctic) regions (i.e. the Gulf of Alaska and Bering Sea), 85 warm-water taxa, with distributions extending into tropical/sub-tropical waters, and 41 taxa primarily restricted to the CC. There were relatively few offshore (subtropical gyre) (7) and cosmopolitan taxa (22). The numbers of cool-water and warm-water affinity taxa in the data set are roughly comparable, consistent with the general characterization of the southern CC as an ecotone or region of mixing of these 2 faunas. However, the fishes endemic to the CCS include many of the dominant taxa and those of commercial importance, such as the mackerels, Pacific sardine, northern anchovy, Pacific hake, and rockfishes. The biogeography of the zooplankton differs significantly, with the dominant taxa generally having broader distributions (Moser & Watson 2006; cf. Brinton 1962, McGowan 1971).

Examining relationships of species richness (S) across habitats, richness was significantly correlated among mesopelagic, epipelagic, and benthic fishes, but species richness for benthopelagic fishes was not correlated with richness for any other habitat (Table 2A). This may be because there were relatively few benthopelagic species in the data set, with little variability: all but 2 years had between 4 and 7 benthopelagic taxa present.

In relation to biogeographic distribution, species richness in the time series was significantly corre-

Table 2. Pearson correlations of annual fish species richness time series (A) across habitats, 1969–2011, and (B) in relation to biogeographic distribution; ns: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. All correlations had 29 df. Cold-water: boreal and transition zone, overlapping into California Current (CC); CC endemic: restricted to CC; warm-water: tropical/subtropical, overlapping with CC

(A)	Epipelagic	Benthic	Benthopelagic	
Mesopelagic	0.55**	0.44*	0.18 ns	
Epipelagic		0.48**	0.24 ns	
Benthic			0.20 ns	
(B)	CC endemic	Warm-water	Sub-tropical gyre	Cosmopolitan
Cold-water	0.15 ns	0.09 ns	0.17 ns	0.01 ns
CC endemic		0.53**	0.43**	0.65***
Warm-water			0.47**	0.52**
Subtropical gyre				0.52**

lated among CC, cosmopolitan, and warm-water taxa, indicating that species richness varied coherently among these groups. However, species richness for cool-water affinity fishes was not significantly correlated with S for fishes with any other distribution (Table 2B). Variability in S within each biogeographic group was significantly correlated with overall species richness, but the correlation between S overall and with the cool-water affinity taxa was considerably weaker than the correlation for other biogeographic groupings. These patterns indicate that interannual variability in species richness in the southern CC has been influenced predominantly by coherent changes in the contribution of CC endemic and warm-water taxa from the south and offshore, changes that have operated largely independently of the contribution of cool-water affinity taxa.

Species diversity showed divergent relationships with the dominant patterns of abundance across the fish community, PC 1 and PC 2. Species richness was closely correlated with PC 1 ($r = 0.82$, $p < 0.001$, $df = 29$) but uncorrelated with PC 2, whereas the Shannon-Wiener index of evenness was significantly correlated with PC 2 but not PC 1 (Table 3, Fig. 2A). This suggests that the changes in abundance characterized by PC 1 are closely associated with changes in species richness in the southern CC since 1969, whereas PC 2 is associated with changes of dominance and evenness in the fish community.

PC 1 was most heavily dominated by mesopelagic fish taxa, but demersal and epipelagic fishes also contributed significantly to the pattern (Table 1).

Table 3. Pearson correlations of time series of annual species richness (*S*) and the Shannon-Wiener index (*H'*) with PC 1 and PC 2 of the CalCOFI ichthyoplankton time series, 1969–2011 (Koslow et al. 2011, 2015), and with ocean time series: annual mean oxygen concentration at 200–400 m depth (Deep O_2) and temperature at 10 m depth (T_{10}) from CalCOFI cruises, the Regional Ocean Modeling System-based estimate of the upwelling flux (*W*), the multivariate ENSO index (MEI), the Pacific Decadal Oscillation (PDO), and North Pacific Gyre Oscillation (NPGO); ns: not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. All correlations had 29 df

	PC 1	PC 2	Deep O_2	T_{10}	<i>W</i>	MEI	PDO	NPGO
<i>S</i>	0.82***	-0.07 ns	0.50**	0.39*	-0.42*	0.47*	0.44*	-0.48**
<i>H'</i>	-0.21 ns	-0.55**	-0.20 ns	0.39*	0.59**	-0.03 ns	-0.11 ns	0.01 ns

Overall, species richness and PC 1 were most highly correlated with the species richness of mesopelagic fishes ($r = 0.86$ and $r = 0.81$, $p < 0.001$, $df = 29$), but were also significantly correlated with the number of benthic and epipelagic species (Table 4). This web of inter-correlations, along with the correlations of species richness among mesopelagic, epipelagic, and benthic groups (Table 2A), suggests that species richness across ocean habitats is responding to broad patterns of ocean forcing.

Species richness was significantly correlated with deepwater oxygen concentration ($r = 0.50$, $p < 0.01$, $df = 26$), along with average annual temperature at 10 m depth from CalCOFI cruises, the regional upwelling flux (*W*), the MEI, PDO, and NPGO (Fig. 2B, Table 3). These ocean variables were also significantly correlated with PC 1, the dominant pattern of changing fish abundance (Koslow et al. 2011). It is notable that the sign of the correlations of species richness with near-surface temperature, upwelling, MEI, PDO, and NPGO consistently indicates that species richness responds positively to relatively poor productivity conditions: the warm phase of the PDO, reduced coastal upwelling conditions, El Niño (rather than La Niña) events, and the relatively unproductive phase of the NPGO (di Lorenzo et al.

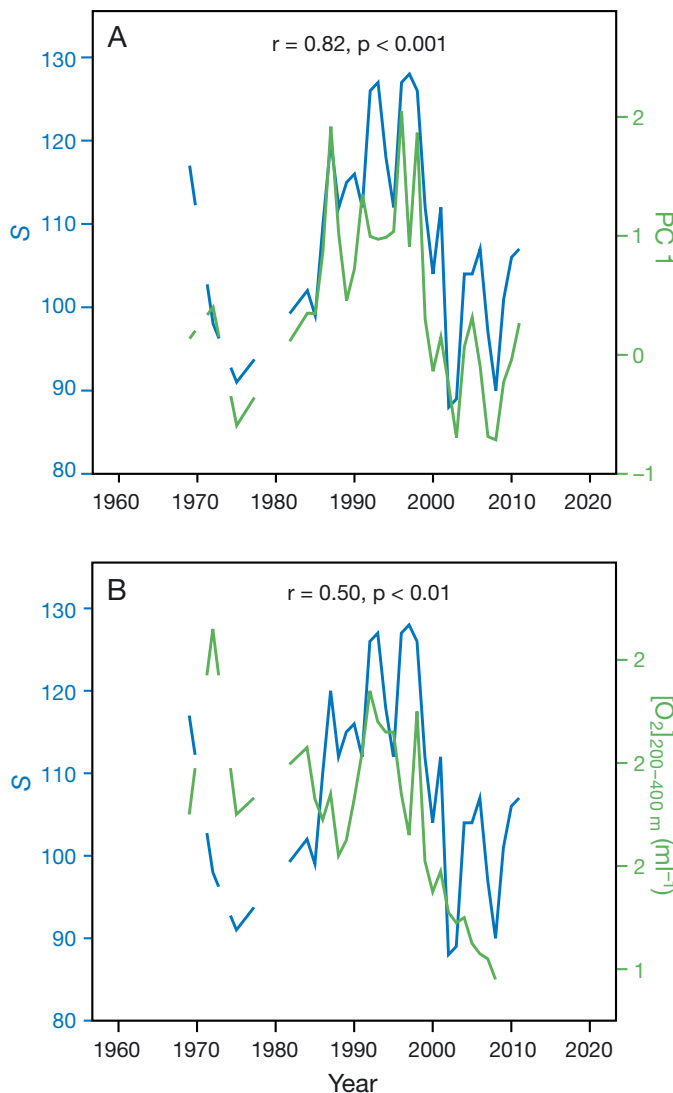


Fig. 2. Time series of species richness (*S*) and (A) the first principal component (PC 1) for the abundance of CalCOFI larval fishes, dominated by 24 mesopelagic fish taxa (Koslow et al. 2011), and (B) annual mean oxygen concentration at 200–400 m depth from CalCOFI cruises (Koslow et al. 2011)

Table 4. Pearson correlations of time series of the annual number of mesopelagic, epipelagic, benthic, and benthopelagic species with species richness (*S*), the Shannon-Wiener index (*H'*), PCs 1 and 2, and ocean time series for oxygen concentration at 200–400 m depth ($[O_2]_{200-400m}$), temperature at 10 m depth (T_{10}), the regional upwelling flux (*W*), the multivariate ENSO index (MEI), the Pacific decadal oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO); ns: not significant, ms: marginally significant ($0.05 < p < 0.10$), * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. All correlations had 29 df

	Meso-pelagic	Epi-pelagic	Benthic	Benthopelagic
<i>S</i>	0.86***	0.74***	0.79***	0.36*
<i>H'</i>	0.051 ns	-0.01 ns	-0.054 ns	0.08 ns
PC 1	0.81***	0.58**	0.55**	0.20 ns
PC 2	-0.29 ns	-0.01 ns	0.10 ns	0.29 ns
$[O_2]_{200-400m}$	0.52**	0.28 ns	0.31 ns	0.16 ns
T_{10}	0.41*	0.24 ns	0.29 ns	0.05 ns
<i>W</i>	-0.41*	-0.35 ms	-0.21 ns	-0.27 ns
MEI	0.51**	0.22 ns	0.32 ns	0.10 ns
PDO	0.49**	0.22 ns	0.20 ns	0.34 ms
NPGO	-0.31 ns	-0.22 ns	-0.48*	-0.36 ms

Table 5. Pearson correlations of time series for species richness (*S*) of species assemblages grouped by biogeographic distribution in relation to overall *S*, patterns of abundance (PC 1, PC 2), and ocean time series: annual mean oxygen concentration at 200–400 m depth (Deep O₂) and temperature at 10 m depth (*T*₁₀) from CalCOFI cruises, the regional upwelling flux (*W*), multivariate ENSO index (MEI), Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), and spiciness index. CC: California Current; warm-water: tropical/sub-tropical; STG: subtropical gyre; cold-water: taxa with boreal and/or transition zone distributions; ns: not significant, ms: marginally significant (0.05 < *p* < 0.10), **p* < 0.05, ***p* < 0.01, ****p* < 0.001

	<i>S</i>	PC1	PC2	[O ₂] _{200-400m}	MEI	PDO	NPGO	<i>T</i> ₁₀	<i>W</i>	Spiciness
Warm meso	0.84***	0.79***	-0.19 ns	0.62***	0.42*	0.43*	-0.33 ms	0.36 ms	-0.46*	-0.16 ns
Cool meso	0.15 ns	0.22 ns	-0.29 ns	-0.22 ns	0.34 ms	0.39*	0.12 ns	0.32 ms	-0.01 ns	0.18 ns
Cold-water	0.35*	0.17 ns	0.21 ns	0.06 ns	0.20 ns	-0.08 ns	-0.09 ns	-0.05 ns	0.16 ns	0.05 ns
CC	0.75***	0.54**	-0.02 ns	0.27 ns	0.31 ns	0.22 ns	-0.38*	0.27 ns	-0.23 ns	0.05 ns
Warm-water	0.90***	0.80***	-0.04 ns	0.54**	0.41*	0.51**	-0.50**	0.42*	-0.55**	-0.16 ns
STG	0.63***	0.51**	-0.39*	0.30 ns	0.24 ns	0.21 ns	-0.06 ns	0.33 ms	-0.20 ns	0.08 ns
Cosmopolitan	0.71***	0.66***	-0.28 ns	0.24 ns	0.46*	0.54**	-0.28 ns	0.36 ms	-0.32 ns	0.25 ns

2008). However, the correlations of species richness with warm, relatively unproductive ocean conditions seem to be driven primarily by the mesopelagic group, the only community that is significantly correlated consistently with these conditions (Table 4). Among the mesopelagic group, only the sub-group with warm-water affinities is significantly linked with these ocean variables (Table 5). In fact, examining how species richness is influenced by ocean drivers across groups with different biogeographic distributions, warm-water affinity fishes generally appear to exhibit enhanced species richness in relation to variables linked with warm conditions, rather than the species richness of cool-water affinity fishes appearing to decline (Table 5). However, none of these groups of taxa was significantly correlated with spiciness, a measure of the influence of relatively warm, high-salinity water entering the SCB from the CUC (Table 5). In general, there were significant inter-related trends in species richness among CC endemic and warm-water affinity (tropical/sub-tropical and subtropical gyre) assemblages, but not among assemblages with cool-water affinities or between the cool-water and CC endemic assemblages (Table 2B, Fig. 3).

As noted above, PC 2 was significantly correlated with the Shannon-Wiener index, a measure of evenness in the community (Fig. 4A). Thirty-nine taxa contributed significantly to PC 2, which displayed a strong declining trend in abundance from 1969 to the present. Ten of the 11 most abundant taxa in the ichthyoplankton data set loaded significantly on PC 2 (Moser & Watson 2006), and 8 of these shared this declining trend, such that overall larval fish abundance in the CalCOFI data set declined 72% over this period (Koslow et al. 2015). A plot of cumulative dominance based on the rank-order of abundance of

taxa during years of high PC 2 (1969, 1978, 1981) and low PC 2 (1995, 1998, 2003) clearly shows the shift to a community less dominated by a few highly abundant taxa (Fig. 5). The Shannon-Wiener index was significantly correlated with near-surface temperature (Fig. 4B, Table 4), reflecting that this marked decline in abundance, which increased community evenness, predominantly affected fishes with CC endemic or cool-water affinity distributions (Table 1). Although there were many more taxa that declined

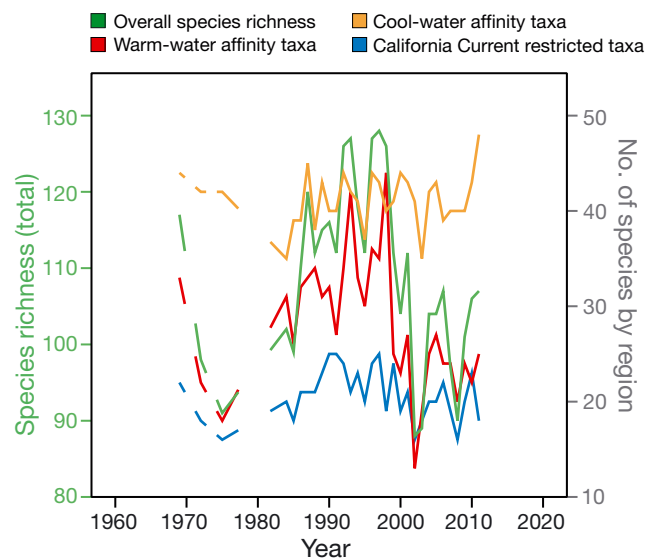


Fig. 3. Time series for overall species richness (green, left axis) and (right axis) the number of warm-water affinity (red), cool-water affinity (orange), and California Current restricted (blue) taxa from the CalCOFI time series. Warm-water affinity taxa have tropical/subtropical distributions potentially in combination with California Current distributions, and cool-water affinity taxa have boreal (sub-Arctic) and/or transition zone distributions potentially in combination with being found in the California Current

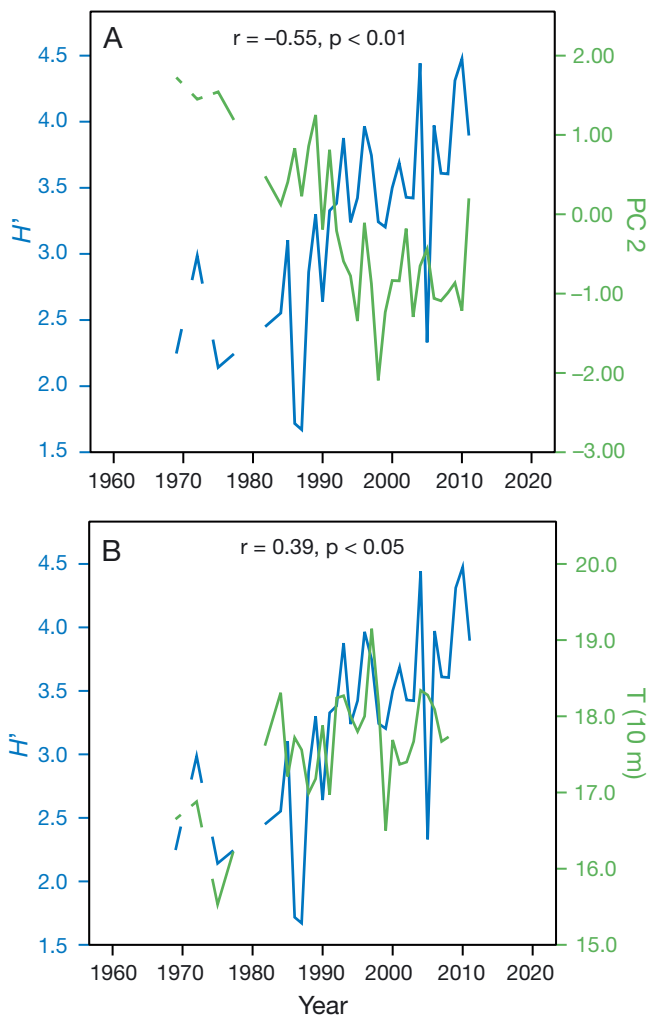


Fig. 4. Time series of the Shannon-Wiener index (H'), a measure of evenness for the CalCOFI ichthyoplankton time series, in relation to (A) PC 2 for the time series of ichthyoplankton abundance, and (B) the annual mean temperature at 10 m depth from the CalCOFI cruises

than increased as part of this pattern (Table 1), those that increased mostly had warm-water affinities, including Pacific sardine, which has previously been noted to respond oppositely to the northern anchovy in the CCS (Chavez et al. 2003) (Table 1). During this period of increased evenness, Pacific sardine replaced northern anchovy as the most abundant taxon in the data set, and several other taxa with warm-water affinities, including the myctophid *Triphoturus mexicanus* and the phosichthyid *Vinciguerria luce-tia*, increased in abundance and in their rank order of abundance within the community (Table 6). However, PC 2 was not associated with a decline in species richness. The Shannon-Wiener index was significantly correlated with the regional upwelling flux

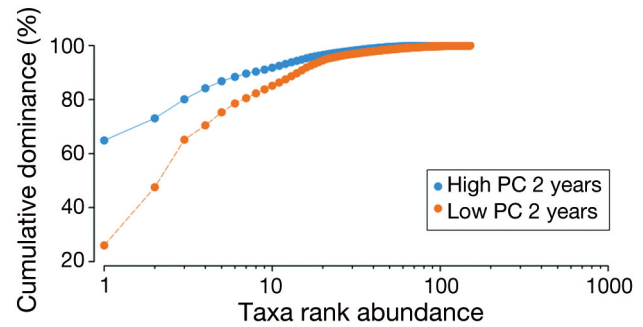


Fig. 5. Cumulative dominance based on rank-order abundance between years when the Shannon-Wiener index (H') was high (>3.5 : 2004, 2006–2011; shown in blue) and when it was low (<3.5 : 1969–1992; orange)

(W) (Table 3), but this correlation, as well as the correlation with temperature at 10 m (T_{10}), was based on the long-term trends in the variables. Neither correlation was significant with the detrended variables of W or T_{10} .

Although substantial changes were observed since 1969 in the abundance of various taxa and in species richness and the Shannon-Wiener index (H'), the species composition and community structure overall remained stable throughout this period. Although some changes are noted above in the rank order of abundance of the dominant fish taxa between periods of low and high H' ($H' < 3.5$: 1969–1992, cf. $H' > 3.5$: 2004, 2006–2011), the Spearman ρ correlation for the rank of abundance between these periods for the 15 most abundant taxa was 0.82 ($p < 0.001$, $df = 13$). The rank order of abundance for the dominant 15 taxa between periods of low and high species richness ($S < 110$ species yr^{-1} : 2000, 2002–2011, cf. $S > 110$ species yr^{-1} : 1987–1999) was even more invariant: Spearman's $\rho = 0.88$ ($p < 0.001$, $df = 13$; Table 6). Indeed, the same 15 taxa were most abundant during the periods of low and high species richness. The increase in species richness during the period of high S occurred entirely among uncommon species: the most abundant species to occur in the high S but not in the low S period, *Sebastes melanostomus*, occurred in only 2 tows, viz. 1 in 1989 and 1 in 1997. However, there was a clear pattern in the biogeographic distribution of these taxa: of 33 taxa that occurred only in the high S years and whose biogeographic distribution could be assessed, 23 were warm-water taxa and only 6 were cool-water taxa, although overall the numbers of warm- and cool-water affinity taxa occurring throughout the time series were roughly equal. The 6 cool-water taxa that occurred in only high S years were inshore species

Table 6. Rank order of abundance and mean abundance (numbers of larvae 10 m^{-2} for the 15 most abundant taxa) during years of low H' (<3.5 ; 1969–1992) and high H' (>3.5 ; 2004, 2006–2011) and of low S (<110 species yr^{-1}) and high S (>110 species yr^{-1})

Taxon, low S	Abund.	Taxon, low H'	Abund.	Taxon, high H'	Abund.	Taxon, high S	Abund.
<i>Engraulis mordax</i>	27 312	<i>Engraulis mordax</i>	63 541	<i>Sardinops sagax</i>	8873	<i>Engraulis mordax</i>	40 344
<i>Merluccius productus</i>	7418	<i>Merluccius productus</i>	29 363	<i>Engraulis mordax</i>	4633	<i>Merluccius productus</i>	15 457
<i>Sardinops sagax</i>	5689	<i>Leuroglossus stilbius</i>	7857	<i>Sebastes</i> spp.	4530	<i>Sardinops sagax</i>	8980
<i>Sebastes</i> spp.	5598	<i>Sebastes</i> spp.	7422	<i>Merluccius productus</i>	3669	<i>Vinciguerria lucetia</i>	6059
<i>Leuroglossus stilbius</i>	4066	<i>Stenobranchius leucopsarus</i>	4083	<i>Leuroglossus stilbius</i>	3413	<i>Leuroglossus stilbius</i>	5637
<i>Stenobranchius leucopsarus</i>	3528	<i>Lipolagus ochotensis</i>	1787	<i>Vinciguerria lucetia</i>	3066	<i>Sebastes</i> spp.	5616
<i>Lipolagus ochotensis</i>	1419	<i>Sardinops sagax</i>	1630	<i>Stenobranchius leucopsarus</i>	2864	<i>Stenobranchius leucopsarus</i>	4201
<i>Vinciguerria lucetia</i>	1114	<i>Vinciguerria lucetia</i>	1570	<i>Citharichthys sordidus</i>	1049	<i>Lipolagus ochotensis</i>	1615
<i>Citharichthys stigmaleus</i>	782	<i>Sebastes jordani</i>	1283	<i>Lipolagus ochotensis</i>	978	<i>Sebastes jordani</i>	1451
<i>Protomyctophum crockeri</i>	707	<i>Genyonemus lineatus</i>	1021	<i>Citharichthys stigmaleus</i>	920	<i>Triphoturus mexicanus</i>	912
<i>Sebastes jordani</i>	625	<i>Citharichthys stigmaleus</i>	893	<i>Protomyctophum crockeri</i>	764	<i>Citharichthys sordidus</i>	911
<i>Citharichthys sordidus</i>	563	<i>Protomyctophum crockeri</i>	833	<i>Triphoturus mexicanus</i>	699	<i>Citharichthys stigmaleus</i>	907
<i>Triphoturus mexicanus</i>	536	<i>Nannobranchium ritteri</i>	752	<i>Trachurus symmetricus</i>	647	<i>Nannobranchium ritteri</i>	897
<i>Trachurus symmetricus</i>	508	<i>Triphoturus mexicanus</i>	646	<i>Sebastes jordani</i>	559	<i>Protomyctophum crockeri</i>	846
<i>Nannobranchium ritteri</i>	504	<i>Scomber japonicus</i>	585	<i>Bathylagus wesethi</i>	504	<i>Trachurus symmetricus</i>	836

endemic to the CCS region. The influx of new species is thus significantly dominated by warm-water affinity taxa ($\chi^2 = 8.37$, $p < 0.01$). This is consistent with the correlation between species richness and warm, relatively unproductive conditions: warm near-surface temperature, reduced coastal upwelling, the warm phase of the PDO, and the El Niño phase of the MEI. There was no clear pattern in the habitat preference of newly occurring taxa, with approximately equal numbers of benthic/benthopelagic and mesopelagic taxa (14 and 13, respectively, occurring during warm conditions).

DISCUSSION

We initially identified 2 sets of hypotheses related to potential changes in diversity of the CCS fish community over recent decades. We hypothesized, first, that the diversity of midwater fishes would decline in response to intensification of the OMZ off southern California (Koslow et al. 2011) and that midwater fishes with cool-water affinities would be replaced by a fauna with warm-water affinities and presumably better adapted to a shallower, more intense OMZ. We hypothesized, second, that diversity would be significantly influenced by the decline in abundance of a largely CCS endemic and cool-water affinity assemblage that comprises most of the dominant taxa in the region (Koslow et al. 2013, 2015).

We found partial support for our first set of hypotheses. Species richness declined significantly during periods of lower midwater oxygen availability. However, this was not due to the replacement of the resident fauna with a more depauperate fauna better adapted to low-oxygen conditions. Rather, species richness is influenced as much by temperature as deepwater oxygen concentration, and these ocean variables are themselves correlated, with periods of higher oxygen concentration associated with the warm phase of the PDO and El Niño conditions. The enhanced species richness observed during periods of higher deepwater oxygen concentrations is derived from an apparent influx of taxa with warm-water affinities. Thus the decline in species richness during periods of low oxygen concentration is primarily due to the loss of taxa with warm-water rather than cool-water affinities; the numbers of cool-water affinity fish taxa did not vary significantly between these periods.

There is thus to date no evidence to support the hypothesis that warm-water affinity mesopelagic taxa, which might be better adapted to the shallow,

more extreme OMZ conditions that extend from southern Baja California into the Eastern Tropical Pacific, are replacing the cool-water affinity and CC endemic mesopelagic fishes during periods of reduced oxygen conditions. Higher midwater oxygen concentrations in the CalCOFI survey area were correlated with relatively warm conditions. A preponderance of the 50 taxa (benthic and epipelagic as well as mesopelagic fishes) that were only recorded when oxygen concentrations and PC 1 were relatively high (1969–1998, cf. 1999–2011) had warm-water affinities, including 23 warm-water taxa and 3 cool-water taxa. Of the mesopelagic fishes that were present only in years of high midwater oxygen concentration, 11 had tropical/subtropical distributions and 3 had boreal or transition zone distributions. This did not, however, differ significantly from the proportion of warm-water versus cool-water mesopelagics in the data set as a whole ($\chi^2 = 1.83$, ns). There was thus no influx of warm-water affinity taxa into the region during periods of low oxygen concentration; indeed, the trend was the opposite, such that a preponderance of the taxa that were no longer found in the region during these periods had warm-water affinities. We therefore reject our second hypothesis, that declining midwater oxygen concentrations would be associated with an influx of a more southerly fauna. Rather, the influx (or efflux) of a warm-water affinity fauna into (or out of) the southern California region seemed influenced primarily by temperature.

The substantial changes in the abundance and diversity of predominantly mesopelagic fishes comprising PC 1 appear to be wholly related to changes in the ocean environment rather than to fishing, since these fishes are not subject to commercial fisheries.

Although PC 1 captures a pattern that affected a substantial proportion of the taxa in the time series, the Shannon-Wiener index, primarily a measure of community evenness, did not vary significantly in relation to it. This is because this index is primarily influenced by changes in relative dominance, and the taxa most influencing PC 1 were not the most dominant. PC 2, however, affected most of the dominant taxa. Therefore, PC 2 had a significant impact on community evenness and hence on the Shannon-Wiener index through the dramatic reduction in the abundance of the most abundant taxa. All of the 6 most abundant taxa loaded significantly on PC 2, and the top 3 (northern anchovy, Pacific hake, and California smoothtongue) declined between 57 and 88% between low H' and high H' periods. However, there were no significant changes in species richness between these periods.

Although the dominant patterns of change in the abundance of fishes in the CCS are reflected in changes in key indices of biodiversity (S and H'), community structure as reflected in the rank order of the most abundant taxa varied little between periods of relatively high and low species richness or evenness. The warm-water affinity taxa newly recorded in the CalCOFI dataset during the period of enhanced species richness have thus far remained relatively uncommon. Whether these taxa are harbingers of greater changes to come is unknown; climate change is today at a very early stage. However, our current ability to observe such subtle changes points to the value of identifying and enumerating as many taxa as possible from plankton samples, so sensitive biodiversity and multivariate analyses can be applied. It should be noted that a similar underlying resilience in fish community structure has been reported even in regions, such as Tasmania, where long-term warming trends in ocean temperature have been more pronounced, leading to a significant influx of a warmer-water fauna (Stuart-Smith et al. 2010).

There is a growing interest in the effects of climate change on the diversity and structure of marine fish populations and communities (Cheung et al. 2009, Doney et al. 2012). Not unexpectedly, marine fish populations have been reported to mostly shift or extend their distributions poleward in response to ocean warming (Hiddink & ter Hofstede 2008, Last et al. 2011), but this response is not uniform, with some species shifting their depth distribution to remain within their temperature preference (Dulvy et al. 2008, Mueter & Litzow 2008). Although zooplankton communities may dramatically shift their distribution in relation to temperature (Beaugrand et al. 2002) or hydrographic conditions (Peterson 2009), fish populations with cold-water affinities in regions such as the Gulf of Maine have been reported to largely maintain their distribution but decline in abundance in response to rising temperature (Nye et al. 2009). Many of the dominant fishes of the CCS appear to have responded similarly. Although it is unclear whether the decline of some taxa with broad sub-Arctic or transition zone distributions, such as the northern lampfish, have declined throughout their range or only shifted their distribution poleward in response to warming, certain cool-water affinity CC endemics, such as the northern anchovy, have declined drastically in recent decades (MacCall et al. 2016).

We have emphasized the potential influence of climate and ocean conditions on biodiversity rather

than fishing, despite the preponderance of declining trends in abundance. This is because PC 1 was dominated by mesopelagic taxa, none of which is commercially exploited. Furthermore, although 10 of the 11 most abundant ichthyoplankton taxa off southern California loaded significantly on PC 2, two are warm-water affinity species (Panama lightfish *Vinciguerria lucetia* and Pacific sardine) that displayed an increasing trend, and the remainder have predominantly cool-water affinities but half are either unexploited or only lightly fished: northern anchovy, northern lampfish, shortbelly rockfish *Sebastes jordani*, and California smoothtongue. Fishery exploitation rates in the CC have generally declined since the 1980s and the fisheries are generally believed to be well managed (Worm et al. 2009). Fishing therefore seems unlikely as a dominant factor driving observed changes in abundance and diversity in this region.

Changes in the various diversity indices appear to be sensitive measures of ecosystem status and are therefore potential indicators that may be included in management and ecosystem assessments. However, their interpretation is not always straightforward. Although the massive decline in mesopelagic and other species abundances, apparently in response to declining oxygen concentrations and other factors, was reflected in a decline in the community's species richness, the decline of many of the region's dominant taxa led to an apparent increase in diversity as expressed in the Shannon-Wiener index, because it is primarily a measure of evenness. Productive marine ecosystems are often naturally dominated by a few taxa, such as northern anchovy and Pacific hake; their collapse is by no means desirable, although certain diversity indices may be thereby enhanced. Similar findings have been reported for the North Sea, where species richness has increased in recent years at the expense of fishery potential as cool-water affinity fishes with high commercial value were increasingly replaced by a more diverse but less commercially valuable assemblage of warm-water fishes (Hiddink & ter Hofstede 2008). Simple diversity indices must therefore be used and interpreted with caution.

Although there has not been a significant re-ordering of the dominant taxa in the CCE over the study period (1969–2011), the region has experienced significant change in community structure based on a dramatic unidirectional decline in the community's ecological dominants, leading to a more evenly distributed community. This unidirectional trend is striking and resists full understanding, given that the region's oceanography (e.g. patterns of near-surface temperature, upwelling, and other variables) has

been dominated to date by the decadal-scale variability of the PDO and NPGO rather than secular change. However, the dominant community trends are correlated with rising ocean temperatures and declining midwater oxygen concentrations, which are both predicted to become increasingly dominated by secular climate change (Helm et al. 2011, Rykaczewski et al. 2015). The long-term trajectory for the productivity of the CCE remains an active area of investigation, potentially influenced by long-term changes in upwelling, stratification, the strength of the CC, and the nutrient content of CCE source waters (Rykaczewski et al. 2015). However, the continued decline of the dominant fish taxa of the CCE could potentially have profound consequences for regional marine fisheries and apex predators, several of which have experienced reproductive failure in recent years in response to declining forage fish resources (McClatchie et al. 2016).

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