

Dramatic declines in coastal and oceanic fish communities off California

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ABSTRACT: The California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton surveys and systematic sampling of southern California power plant cooling-water intakes (PPI) provide independent, complementary time series to assess fish communities off southern California from nearshore to oceanic environments. The PPI program has sampled the shallow nearshore fish community at 5 sites along the coast of southern California since 1972, while CalCOFI has sampled fish larvae along 6 transects at standard stations ranging from 35 m depth to more than 500 km offshore since 1951. Recently published analyses of these data sets led us to examine potential relationships between them. Although there was limited overlap in the taxa sampled by the 2 programs, key multivariate patterns were highly correlated between them. Both time series exhibited dramatic declines from the 1970s to the 2000s: 78 % for fishes entrapped by the power plants and 72 % for the overall abundance of larval fishes in the CalCOFI time series. These trends, which predominantly affected taxa with cool-water affinities, were shared by fishes across nearshore and oceanic habitats, and included several trophic guilds and many unfished or only lightly fished taxa. These declines were significantly correlated with declining zooplankton displacement volumes across the California Current System (CCS), which suggests the influence of large-scale climatic and oceanographic drivers. Over the past 4 decades, changing environmental conditions appear to have produced more losers than winners in the CCS.

KEY WORDS: Time series · Fish communities · Climate · California Current · Ichthyoplankton

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INTRODUCTION

It is now widely accepted that climate significantly influences marine fish populations across a wide range of time and space scales, from local to basin scale and from interannual variability to multi-decadal 'regime shifts' (Koslow 1984, Klyashtorin 1998, Hare & Mantua 2000, Beaugrand et al. 2015). Most studies, however, have focused on long-term change in commercially exploited species, although these represent only a small fraction of regional fish faunas. The abundance and variability of exploited populations are also generally influenced by fishing as well as environmental forcing (Hsieh et al. 2006). This focus on commercial fishes is largely due to the

paucity of time series for unexploited marine fishes (Koslow & Couture 2013, 2015). However, marine fishes are the most diverse vertebrates on Earth and are of immense ecological and even biogeochemical significance (Davison et al. 2013), as well as being critical to the economies, food supply and social fabric of many human populations. As science gains greater understanding of climatological variation, the response of broadly defined marine fish communities to natural internal climate variability is garnering increased interest, along with the potential influence of secular climate change. Owing to the potential difficulties of disentangling the impacts of environmental variability and commercial exploitation, a better understanding of climate impacts is

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likely obtained by examining time series of broadly defined fish communities as opposed to those for commercial fishes alone.

Off southern California, there are 2 complementary long-standing sampling programs for marine fishes that are entirely independent of commercial fishing. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has maintained an end-to-end ocean observation program since 1951, which includes monthly to quarterly sampling for larval fishes with plankton tows at core stations along 6 transects that extend from ~35 m depth inshore to >500 km offshore, and from the US–Mexico border to north of Point Conception (Fig. 1) (McClatchie 2014). Most fish larvae are captured at an early pre-flexion stage, and larval abundance provides an index of adult spawning stock biomass for a broad range of fishes in the California Current System (CCS) (Moser et al. 2001, Koslow et al. 2011). The dominant pattern, or principal component (PC), in this time series was based on the response of a suite of some 24 mesopelagic fishes to varying midwater oxygen concentrations and expansion/contraction of the oxygen minimum zone in the CCS (Koslow et al. 2011). PC 2 for the CalCOFI data involved many of the dominant regional taxa, including Pacific sardine, northern anchovy and Pacific hake, which have varied considerably in the CCS in recent decades (Chavez et al. 2003, Koslow et al. 2013). However, because relatively few CalCOFI stations are at bottom depths <100 m, it is uncertain how well the nearshore component of the regional fish community is represented in this time series.

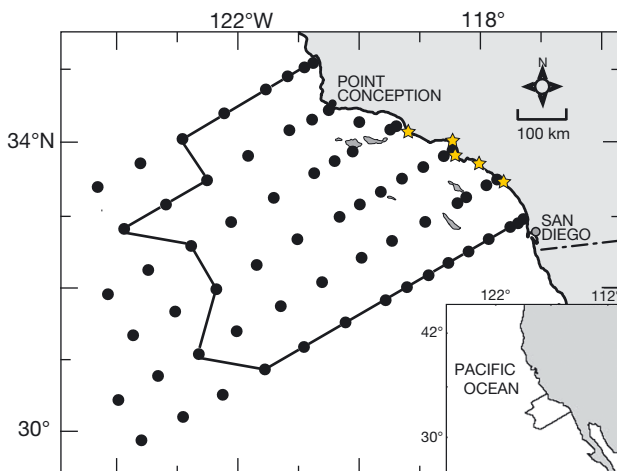


Fig. 1. Survey region showing the 66 CalCOFI sampling stations (●) and the 5 power plant intake (PPI) sites (★). The solid outline encloses the consistently sampled core stations included in the PCA

Juvenile and adult fishes entrapped by coastal power plant cooling-water intakes (PPI) are monitored at 5 sites along the coast of southern California, providing a time series of the region's nearshore fish community (Fig. 1). PC analysis (PCA) of this time series indicated a dramatic decline (78%) in fish abundance since 1972, as well as latitudinal shifts in fish assemblages (Miller & McGowan 2013). The correlation of the dominant multivariate pattern of change with warming regional ocean temperature suggested that changing ocean conditions were likely responsible.

Both the CalCOFI and PPI time series indicate that fish communities in the CCS are responding to changing environmental conditions—dissolved oxygen and temperature—but each program samples only a portion of the CCS, leaving open the question of how pervasive these patterns actually are. Oceanic fishes (e.g. mesopelagic and other offshore species) are not sampled by PPIs. Conversely, some nearshore fishes, such as surfperches (Embiotocidae) and various croakers (Sciaenidae), are unsampled or undersampled by CalCOFI. In this paper, we compared these 2 time series to examine the coherence of temporal patterns for fish assemblages across the southern CCS.

METHODS

The starting points for our study were the time series described in Koslow et al. (2011, 2013, 2014) and Miller & McGowan (2013), and the reader is directed there for details of the underlying sampling methodologies. Briefly, however, the CalCOFI time series is based on the annual mean abundance of larval fish sorted from oblique bongo-net tows from the surface to ~210 m depth at 51 consistently sampled core stations (Fig. 1). Larval fish are identified and enumerated to the lowest possible taxon. Taxa were included in the analysis only if present in at least half the years of the time series, such that 86 taxa were included. PCA of the CalCOFI data set was based on the correlation matrix of log-transformed mean annual abundances.

The PPI data set was derived from periodic sampling of fishes entrapped in the cooling-water intake of 5 southern California power plants (Fig. 1). The intakes ranged from 289 to 960 m offshore and were mostly at ~10 m depth, with one at 27.5 m depth. No changes in the power plant cooling-water systems occurred during this period, and the data were standardized to account for changes in the total volume of

water circulated by each power plant over time. The PCA for the PPI data set was based on the variance-covariance matrix.

We chose to focus on biological variables. An independent index directly relatable to observed fish abundances was the mean annual zooplankton displacement volume from the CalCOFI plankton tows measured after gelatinous zooplankton >5 cm were removed (Smith & Richardson 1977). Small zooplankton displacement volume provides an index of food available to plankton-feeding fishes, which includes juvenile and adult forms of many species represented in the 2 time series and the larvae sampled in the CalCOFI series. The annual means were log-transformed prior to analysis.

The variables in our study were autocorrelated, which can inflate estimates of the effective degrees of freedom. Following Pyper & Peterman (1998), we estimated the number of effective degrees of freedom (N^*) based on Chelton (1984):

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N} \sum_1^j \rho_{xx}(j) \rho_{yy}(j)$$

where N is the number of data points in the original time series and ρ is the autocorrelation of variable x or y at lags 1 to j , with a maximum lag of $j = 10$.

We examined the fish community time series for potential regime shifts using cumulative sum (cusum) plots of PC 1 (PPI) and PC 2 (CalCOFI), which were transformed to their standardized residuals (the difference of each value from the overall mean, divided by the standard deviation) if not already expressed as standardized residuals (Breaker 2007). We tested the potential breakpoints indicated by cusum plots using the sequential t -test analysis of regime shifts (STARS) method (Rodionov 2004). Our data exhibited significant autocorrelation, so we interpreted the results of these analyses with caution (Rudnick & Davis 2003).

RESULTS

The first question we addressed was the comparability of the dominant PCs derived from the independent PPI and CalCOFI time series. PC 1 extracted from the CalCOFI data set, hereafter referred to as PC 1 (CalCOFI) and described more fully in Koslow et al. (2011), was dominated by a broad suite of mesopelagic fishes. Mesopelagic fishes are the most species-rich assemblage in the CalCOFI data set (Moser & Watson 2006). Of 27 taxa with loadings ≥ 0.50 on PC 1 (CalCOFI), 24 were mesopelagic taxa from 8 families. (The loading is equivalent to the correlation

of the original variable and PC time series.) PC 1 (CalCOFI) was most closely linked to variation in midwater (200 to 400 m) oxygen concentrations ($r = 0.75$, $p < 0.05$); all 24 mesopelagic taxa loading highly on this PC responded coherently (i.e. with the same sign) to changes in oxygen concentration. However, midwater fishes are not sampled by the power plant intakes and variation in midwater oxygen concentration is unrelated to nearshore ecology, so it is not surprising that PC 1 (CalCOFI) was not significantly correlated with PC 1 of the PPI time series, hereafter referred to as PC 1 (PPI), ($r = 0.29$, $df = 27$, $p > 0.10$). It is not considered further in this study.

PC 2 (CalCOFI) explained 12.4% of the variance of the time series, with 6 of the 7 most abundant taxa in the CalCOFI ichthyoplankton data set loading highly (loadings ≥ 0.5) on it: northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, Pacific hake *Merluccius productus*, rockfishes (bocaccio *Sebastes paucispinis*, aurora rockfish *S. aurora*, and unidentified rockfishes *Sebastes* spp.), and 2 midwater fishes, northern lampfish *Stenobranchius leucopsarus* and California smoothtongue *Leuroglossus stilbius* (Koslow et al. 2013). In all, 15 taxa loaded highly on PC 2 (CalCOFI) (Table 1). This is a notably diverse assemblage, which includes epipelagic schooling plankton feeders (northern anchovy and Pacific sardine), several non-schooling plankton feeders living in the water column (the medusafish *Icichthys lockingtoni* and Pacific pompano *Peprilus simillimus*), the Pacific hake (a meso- and epipelagic predator), several mesopelagic planktivores (the northern lampfish, California smoothtongue, *Melamphaes* spp. and Myctophidae), the benthic C-O sole *Pleuronichthys coenosus*, and several benthopelagic rockfishes and the thornyheads *Sebastobus* spp. However, many of these taxa are linked insofar as their larvae tend to co-occur in CalCOFI samples, an assemblage that Moser et al. (1987) termed the 'northern' complex, whose taxa have predominantly cool-water (sub-Arctic or transition zone) affinities. Of the 15 taxa loading highly on PC 2 (CalCOFI), 14 have declined since the 1970s; only Pacific sardine have increased and loaded oppositely onto the PC (Table 1).

PC 1 (PPI) explained 44% of the variance in the PPI data set (Miller & McGowan 2013) and was highly correlated with PC 2 (CalCOFI) ($r = 0.85$, $N^* = 10$, $p < 0.01$) (Fig. 2). A total of 15 taxa had loadings ≥ 0.50 on PC 1 (PPI), with 10 taxa loading positively and 5 loading negatively. Interestingly, despite the strong correlation between these 2 PC time series, they held few taxa in common, only 5 of the 15 taxa that loaded

Table 1. Taxa with loadings ≥ 0.5 , dominating PC 1 from the power plant intake (PPI) data set and PC 2 from the CalCOFI data set. The taxa in common between the 2 data sets are in **bold**. The CalCOFI PCA was carried out based on the correlation matrix, so the maximum loadings (equivalent to the correlation between the variable and the PC time series) lie between 1.0 and -1.0 ; the PPI PCA was carried out on the covariance matrix and the loadings are not so constrained

Taxa PC 1 (PPI)	PC 1 (PPI) loadings	Taxa PC 2 (CalCOFI)	PC 2 (CalCOFI) loadings
<i>Anchoa compressa</i> : Deepbody anchovy	1	<i>Icichthys lockingtoni</i> : Medusafish	0.75
<i>Atherinopsis californiensis</i> : Jacksmelt	-0.53	<i>Sebastes paucispinis</i> : Bocaccio	0.71
<i>Cymatogaster aggregata</i> : Shiner perch	1.83	<i>Sebastes</i> spp.: Rockfishes	0.7
<i>Embiotoca jacksoni</i> : Black perch	1.73	<i>Leuroglossus stilbius</i> : California smoothtongue	0.67
<i>Engraulis mordax</i>: Northern anchovy	0.8	<i>Sebastes aurora</i> : Aurora rockfish	0.63
<i>Genyonemus lineatus</i>: White croaker	1.84	<i>Peprilus simillimus</i>: Pacific pompano	0.61
<i>Hyperprosopon argenteum</i> : Walleye surfperch	1.93	<i>Engraulis mordax</i>: Northern anchovy	0.61
<i>Paralabrax clathratus</i> : Kelp bass	0.99	<i>Merluccius productus</i> : Pacific hake	0.56
<i>Peprilus simillimus</i>: Pacific pompano	1.79	<i>Sciaenidae</i>: Croakers	0.53
<i>Phanerodon furcatus</i> : White surfperch	2	<i>Pleuronichthys coenosus</i> : C-O sole	0.53
<i>Sardinops sagax</i>: Pacific sardine	-0.65	<i>Stenobranchius leucopsarus</i> : Northern lampfish	0.53
<i>Scomber japonicus</i> : Pacific mackerel	-0.57	Myctophidae: Lanternfishes	0.52
<i>Seriplus politus</i>: Queenfish	1.4	<i>Melamphaes</i> spp.: Bigscale fishes	0.51
<i>Trachurus symmetricus</i> : Jack mackerel	-0.59	<i>Sebastolobus</i> spp.: Thornyheads	0.5
<i>Haemulon californiensis</i> : Salema	-0.89	<i>Sardinops sagax</i>: Pacific sardine	-0.75

highly on each PC: northern anchovy, Pacific sardine, Pacific pompano, and the croakers, white croaker *Genyonemus lineatus* and queenfish *Seriplus politus* (Table 1). Most of the taxa that loaded most highly on PC 2 (CalCOFI) are distributed too far offshore to be sampled by the power plant intakes, such as the thornyheads, Pacific hake and various mesopelagic taxa; and, conversely, most taxa that dominated PC 1 (PPI) either do not have pelagic larvae (the viviparous surfperches [Embiotocidae]) or have restricted nearshore distributions, such as deepbody anchovy *Anchoa compressa*, jacksmelt

Atherinopsis californiensis, kelp bass *Paralabrax clathratus* and salema *Haemulon californiensis*. Thus, the highly correlated pattern observed in these 2 PCs was shared across a broader range of fishes in the California Current from nearshore to oceanic waters than was represented in either data set alone.

Both PC 1 (PPI) and PC 2 (CalCOFI) exhibited a strong decline from about 1970 to 2010. The abundance of nearshore fishes based on the overall PPI entrapment rate declined 78% from 1972 to 2010 (Miller & McGowan 2013), while ichthyoplankton taxa that loaded highly on PC 2 (CalCOFI) declined 76% with Pacific sardine included and 83% without Pacific sardine. (Pacific sardine was the only taxon loading highly on PC 2 that increased over this period.) As noted, many of the most abundant taxa in the CCS loaded highly on PC 2 (CalCOFI), and the decline in PC 2 (CalCOFI) reflects the overall decline in the abundance of larval fish in the CalCOFI time series of 72% between the decades of 1972 to 1981 and 2002 to 2011 (Fig. 3). Much of this decline can be attributed to the decline of northern anchovy and Pacific hake, the 2 most abundant larval fishes in the CalCOFI data set. However, overall larval fish abundance over this time period declined 31% even with these 2 species removed.

The decline of fishes in the PPI and CalCOFI time series was significantly correlated with log-transformed zooplankton displacement volume, which also declined dramatically during this period:

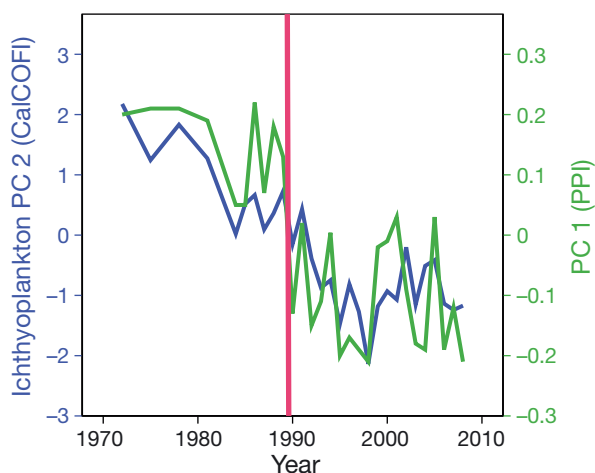


Fig. 2. Time series for PC 1 (PPI) and PC 2 (CalCOFI). The red line indicates an apparent regime shift in 1989 to 1990

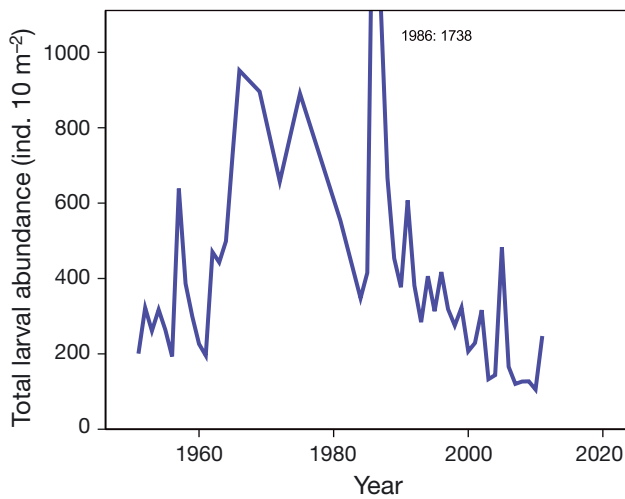


Fig. 3. Time series of total larval fish abundance (ind. 10 m^{-2}) from the CalCOFI data set

$R_{PC1(PPI)} = 0.66$ ($N^* = 9$), $p < 0.05$; $R_{PC2(CalCOFI)} = 0.71$ ($N^* = 14$), $p < 0.01$ (Fig. 4).

The PC 2 (CalCOFI) and PC 1 (PPI) time series both displayed a significant shift ca. 1989 to 1990, declining markedly at this time (Fig. 2). Plots of the cusum of the standardized residuals for both time series show breaks at this point (Fig. 5). STARS indicated that the declines in PC 1 (PPI) and PC 2 (CalCOFI) between 1989 and 1990 represented community shifts to a period of decreased abundance. A t -test based on the mean and standard deviation from 1972 to 1989 indicated that a shift of 0.042 standardized units in PC 1 (PPI) and of 0.69 units in PC 2 (CalCOFI) would be significant at $p < 0.05$; the subsequent declines were 0.26 and 0.88 units, respectively.

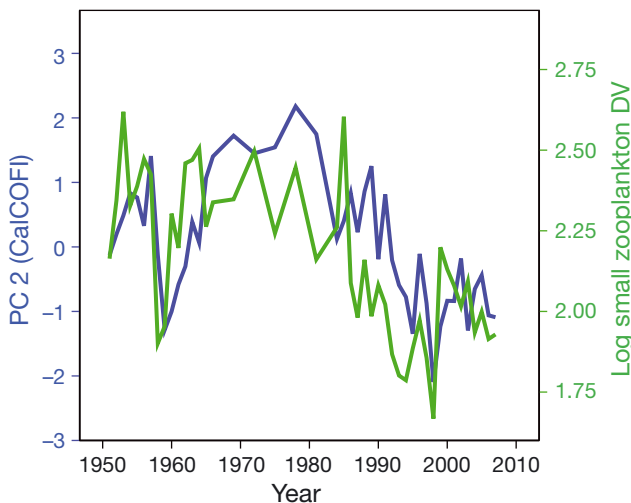


Fig. 4. Time series for PC 2 (CalCOFI) and the log-transformed displacement volume (DV) of zooplankton from CalCOFI zooplankton tows ($r = 0.71$, $p < 0.05$)

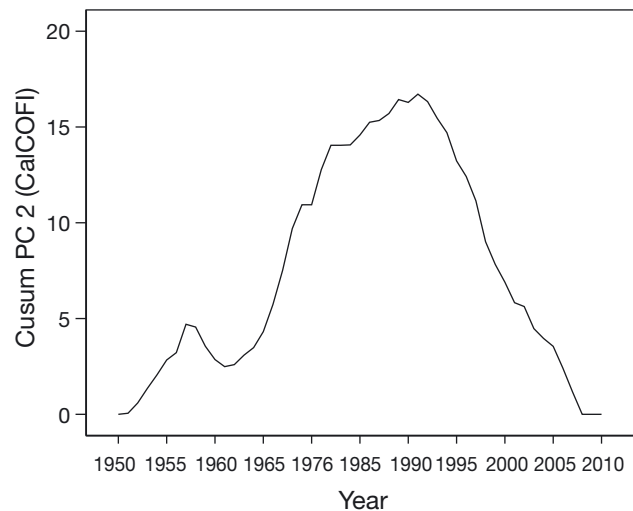
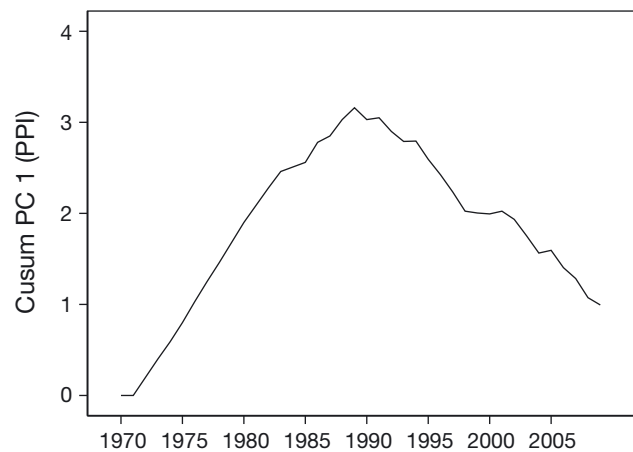


Fig. 5. Time series for the cumulative sum (cusum) of the standardized residuals (Z) of the PC 1 (PPI) and PC 2 (CalCOFI) time series. The PC 2 (CalCOFI) time series is based on a PCA of the correlation matrix, so it is already expressed in units of standardized residuals

DISCUSSION

The broad decline of fishes from nearshore to offshore habitats across the southern CCS from the 1970s to 2010 indicates profound change in the region's ecology. The decline includes epi- and mesopelagic taxa, planktivores, benthic feeders and piscivores, and both exploited and unexploited species. Of the 7 most common taxa in the CalCOFI ichthyoplankton data set, 6 loaded highly on PC 2 (CalCOFI), and all but Pacific sardine declined markedly over the period.

Several factors point to large-scale environmental forcing as the key factor driving this change. First, many taxa sharing this trend are unfished or only lightly fished, such as most surfperches, sciaenids

and mesopelagic fishes. Thus, although fishing may have contributed to the decline of certain taxa, it cannot explain the decline of many others. Generally, fish populations in the CCS are presently assessed to be sustainably exploited (Worm et al. 2009). It is also worth noting that although southern California is a highly developed coastal region, many of the taxa are predominantly distributed offshore but share the same trend as more coastal taxa.

Second, the timing of the most marked decline (1989 to 1990) coincides with a regime shift that has been identified for a range of physical and biological variables along the west coast of North America from the Aleutian Low pressure index and sea surface temperature to a wide range of fishery and other biological time series (Hare & Mantua 2000, Breaker 2007, deYoung et al. 2008). The 1989 regime shift was characterized predominantly by declines in fishery productivity based on a review of 100 fishery and climate time series from Alaska to California (Hare & Mantua 2000).

The decline in both nearshore and offshore fishes predominantly affected taxa with cool-water, more northerly affinities. Miller & McGowan (2013) showed that the changes in the nearshore fish community since 1972 have led to a northerly shift in their mean latitudinal range, and Koslow et al. (2013) pointed out that the dominant species in PC 2 (CalCOFI) were characterized as a northerly assemblage with predominantly sub-Arctic and transition zone distributions as described by Moser et al. (1987). The southern CCS is an ecotone, where fish faunas with northerly and tropical/sub-tropical affinities converge (Briggs 1974, Horn & Allen 1978, Moser & Watson 2006). Physical mechanisms behind this dramatic decline in fish abundance in the southern CCS was not a subject of our study, but prior studies suggest it may be related to 2 mechanisms: (1) a general warming associated with decreased transport of the California Current leading to a decline in taxa with cool-water affinities, which are generally the most abundant fishes in the region; and (2) a decline in productivity, also associated with decreased transport of the California Current and associated with a decline in zooplankton (Roemmich & McGowan 1995), leading to a bottom-up decline in fish abundance. Further mechanistic studies are needed to elucidate these patterns.

The marked decline of the cool-water fauna in the southern CCS in relation to a general warming trend might imply that this fauna is being replaced by a warm-water fauna. Thus, Miller & McGowan

(2013) reported a southerly trend in the mean distribution of nearshore fishes from 1972 to 2010, and Barry et al. (1995) reported a general replacement of northerly with southerly affinity species in the rocky intertidal. Koslow et al. (2014) reported that mesopelagic fishes with warm-water affinities were positively correlated with sea surface temperature, sea level at San Francisco (i.e. weak transport of the California Current), the multivariate El Niño–Southern Oscillation index and the warm phase of the Pacific Decadal Oscillation. However, mesopelagic fishes with both cool- and warm-water affinities have decreased since 1999: the strong decline in midwater oxygen concentration apparently trumped the effect of other environmental variables.

It would be premature to firmly link the decline of fishes across the southern CCS to particular environmental mechanisms or to assess the relative roles of climate variability and climate change in driving these changes. There is still considerable uncertainty over the extent to which the long-term warming of the CCS and of the northeast Pacific generally since the beginning of the twentieth century can be attributed to secular global warming or to decadal scale variability in atmospheric circulation (Johnstone & Mantua 2014).

However, despite these uncertainties, several aspects of our study bear reiteration. First, the fish fauna of the southern CCS has persistently declined from nearshore to oceanic waters for approximately 4 decades with no sign of reversal, although there have been several apparent regime shifts in the North Pacific since the early 1970s, i.e. 1976 to 1977, 1989 to 1990 and 1999 to 2000 (Breaker 2007). Furthermore, the decline is observed predominantly in fishes with cool-water affinities in both the nearshore PPI and more offshore CalCOFI time series, with initial declines deepening after the 1989 to 1990 regime shift. Finally, one of the most striking aspects of this study is the strong coherence between these 2 independent time series and the nearshore and offshore fish communities that they represent. Cool-water marine ecosystems are generally more productive than warm-water ecosystems, and it is apparent that changing ocean conditions have produced far more losers than winners across a range of fish communities in the southern CCS over the past 40 yr. Without the CalCOFI and PPI time series, such dramatic changes would likely not have been possible to document, as they are not observed so clearly in the commercial fishery data (Worm et al. 2009, Koslow & Davison 2015).

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