

# Impact of declining intermediate-water oxygen on deepwater fishes in the California Current

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**ABSTRACT:** Although declining oxygen concentration has been reported for the oxygen minimum zones (OMZs) of the tropical oceans and the North Pacific Ocean, consistent with model predictions of the effects of global warming, its ecological impacts are poorly understood. We report the apparent impact of declining oxygen on midwater fishes within the OMZ of the southern California Current (CC). Principal component analysis of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton time series from 1951 to 2008 indicates that the dominant temporal pattern (principal component 1 [PC1]) represents the marked decline of the region's mesopelagic fishes during periods of reduced oxygen. Of the 27 taxa with loadings > 0.5 on PC1, 24 were mesopelagic. PC1 was strongly correlated with intermediate-water oxygen concentrations ( $r = 0.75$ ,  $p < 0.05$ ), which were about 20% lower in the past decade and the 1950s than in the period from 1970 to 1995. The abundance of mesopelagic fishes represented by PC1 was reduced, on average, by 63% between periods of high and low oxygen concentrations. We hypothesize that the underlying mechanism is the shoaling of the hypoxic boundary layer during periods of reduced oxygen, which renders the mesopelagic fauna more vulnerable to visually orienting predators. The mesopelagic fish fauna provides a vital trophodynamic link between the marine plankton and many higher predators. The decline of deepwater fish populations has profound implications for commercial fisheries, marine food webs and marine conservation: climate models predict a 20 to 40% decline in global deepwater oxygen concentrations over the coming century.

**KEY WORDS:** Oxygen · Mesopelagic fishes · Oxygen-minimum zone · Climate change · California Current

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## INTRODUCTION

Global ocean climate models predict that oxygen levels in the deep ocean will decline by approximately 20 to 40% over the coming century. This is a result of projected increases in surface warming, which leads to enhanced vertical stratification of the upper mixed layer, which reduces ventilation of deeper waters (Sarmiento et al. 1998, Matear & Hirst 2003, Shaffer et al. 2009). Oxygen levels have already declined since the mid-twentieth century in the tropical oxygen minimum zones (OMZs) of the Indian, Pacific and Atlantic oceans and across the

North Pacific basin (Keeling & Garcia 2002, Whitney et al. 2007, Bograd et al. 2008, Stramma et al. 2008), although the trend has not been monotonic in the southern California Current (CC) (McClatchie et al. 2010). Northeast Pacific waters are naturally 'old', which has led to the formation of a distinct OMZ at mid-depths (200 to 1200 m) in the CC. Mean oxygen concentrations at 200 to 300 m are  $\sim 2.0 \text{ ml l}^{-1}$ , an approximate upper limit for hypoxia (Diaz & Rosenberg 2008), and decline to a minimum of  $< 0.5 \text{ ml O}_2 \text{ l}^{-1}$ , a level of severe hypoxia, at about 500 m (see Fig. 4 and 'Discussion'). Oxygen levels in the OMZ of the CC have declined substantially, approximately 20%

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since 1984 (Bograd et al. 2008), leading us to examine the impacts on deepwater fishes. Although there are reports of the effect of hypoxia and of hypoxic intrusions on various metazoan groups, particularly in the benthos (Levin 2003, Vaquer-Sunyer & Duarte 2008), the potential effect of long-term declining oxygen levels in the water column anticipated under most climate-change scenarios is poorly known. The greater motility of pelagic organisms has no doubt contributed to a belief that ecological effects in the water column will be mitigated, although habitat compression due to a shallow OMZ can significantly influence the foraging dynamics of pelagic fishes (Prince & Goodyear 2006).

The mesopelagic and continental slope demersal fishes, which are most vulnerable to reduced oxygen in the OMZ, represent a diverse fauna. Of the ~30 000 extant fish species, more than 10% live in the world's oceans below 200 m depth, and most of these are mesopelagic or inhabit the seafloor of the continental slope (Cohen 1970, Nelson 2006). In the ichthyoplankton data set from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program, mesopelagic fishes are the most diverse group, representing 38% of 586 ichthyoplankton taxa recorded (Moser & Watson 2006). Their abundance is second only to the coastal pelagic species and they comprise 20% of the total larvae. Globally, the biomass of mesopelagic fishes is estimated to be on the order of  $10^9$  t (cf. annual global marine fish landings of about  $10^8$  t) (Gjøsaeter & Kawaguchi 1980). As a major prey of various commercially exploited fishes (Bertrand et al. 2002, Potier et al. 2007), marine mammals (Pauly et al. 1998), squids (Kozlov 1995) and seabirds (Thompson et al. 1998), mesopelagic fishes represent a vital link in oceanic food webs worldwide. The fishes inhabiting the OMZ have evolved various adaptations to living in a low-oxygen environment, including reduced metabolism and enhanced gas exchange mechanisms, but they rely on aerobic metabolism, and the physiological burden of reduced oxygen levels is unclear (Childress & Seibel 1998). Of potentially greater importance, given the ability of fish to avoid hypoxic water, may be the contraction of their habitat as OMZs expand. This fauna is thus at potential risk, owing to reduced oxygen levels and expanding hypoxic regions globally. Paleo-oceanographic episodes of expanded OMZs, particularly in the late Cretaceous, Eocene and Miocene are believed to have contributed significantly to present patterns of biodiversity and biogeography of fishes at mid-ocean depths (White 1987).

The ichthyoplankton data set from the CalCOFI program allows us to investigate the potential effects

of climate variability and climate change on the diverse fish communities, both commercially exploited and unexploited, of the southern CC. The time series, which extends back to 1951, provides data on the quantitative abundance (no. fish  $m^{-2}$ ) of several hundred taxa from a range of habitats. Thus, although the depth range of adult mesopelagic fishes extends well beyond the sampling range of CalCOFI plankton tows, the larvae, particularly myctophids and bathylagids, are most concentrated within the depth range of CalCOFI samples (Ahlstrom 1959, Moser & Smith 1993, Moser & Watson 2006).

The fish larvae in the CalCOFI samples are mostly very young, preflexion stage individuals with limited avoidance capability. Their abundance is generally considered to provide an index of adult spawning biomass, even though the effects of variable reproductive output, predation during the early life history and other factors are not accounted for (Moser 1996, Hsieh et al. 2005). For example, in the CalCOFI ichthyoplankton data set the abundances of northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* eggs and larvae, the key species for which formal stock assessments have been carried out, are highly correlated with assessments of their spawning stock biomass (Table 1). Moser et al. (2000, 2001) and Moser & Watson (1990) concluded that temporal patterns in the larval abundance of rockfishes *Sebastes* spp., various inshore species and California halibut *Paralichthys californicus* in the CalCOFI data set also reflected changes in the biomass of the adults.

The objective of the present study is to examine the dominant pattern in the CalCOFI ichthyoplankton

Table 1. Nonparametric correlations (Spearman's  $\rho$ ) between the average abundance (no.  $m^{-2}$ ) of eggs and larvae of northern anchovy and Pacific sardine from the CalCOFI ichthyoplankton data set and estimates of spawning stock biomass. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

|         | df | Anchovy                           |  | Sardine                          |
|---------|----|-----------------------------------|--|----------------------------------|
|         |    | Synthetic<br>biomass <sup>a</sup> | Egg production<br>biomass <sup>b</sup> | Stock<br>assessment <sup>c</sup> |
| Anchovy |    |                                   |  |                                  |
| Eggs    | 19 | 0.63***                           | 0.77***                                |                                  |
| Larvae  | 19 | 0.734***                          | 0.89***                                |                                  |
| Sardine |    |                                   |  |                                  |
| Eggs    | 24 |                                   |  | 0.50**                           |
| Larvae  | 24 |                                   |  | 0.73***                          |

<sup>a</sup>from Methot (1989)  
<sup>b</sup>from Jacobson et al. (1994)  
<sup>c</sup>from Hill et al. (2008)

time series and its relationships with environmental processes. As the basis for our study, we will use the physical and chemical data collected during CalCOFI surveys since 1951, as well as the ichthyoplankton time series, which provides fishery-independent, taxon-specific proxies for the abundance of a diverse assemblage of adult fishes. In particular, we examine the effects of declining oxygen levels on the fish fauna of the southern CC.

## MATERIALS AND METHODS

Our analysis is based on a subset of 51 CalCOFI stations that were consistently sampled from 1951 to the present and extended from San Diego to north of Point Conception, California, and from the coast (~50 m depth) to about 400 km offshore (ranging from ~250 to 550 km offshore, Fig. 1). Details of sample coverage by cruise are available from [www.calcofi.org/catlist/232-coverage.html](http://www.calcofi.org/catlist/232-coverage.html). Field sampling and lab processing protocols are described in Kramer et al. (1972) and Smith & Richardson (1977).

Sampling frequency ranged from monthly (mostly 1951 to 1960) to quarterly. This analysis was 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 at least 3 seasons. Only every third year was adequately sampled

between 1966 and 1984. The analysis was also carried out with annual means based on the mean values for all cruises conducted within the calendar year. The results were highly congruent with the correlation between the principal component 1 (PC1) time series equal to 0.95.

At each station, a suite of oceanographic variables, including temperature, salinity and oxygen, was measured at about 10 to 20 depths from the surface to approximately 10 m off the seafloor or to a maximum of 525 m depth, and a quantitative oblique plankton tow with a 505  $\mu\text{m}$  mesh net was carried out. A flowmeter mounted in the mouth of the net enabled water flow through the net to be estimated. All fish eggs and larvae were removed from the samples, identified to the lowest possible taxon and enumerated.

Since 1951, there have been 2 changes in zooplankton sampling worth noting. In 1969, the maximum depth of the net tows increased from about 140 to 210 m, and in 1977 the program switched from a 1.0 m diameter bridled ring net to an unbridled bongo net (McGowan & Brown 1966) with net diameters of 0.71 m. Differences in zooplankton displacement volume ( $\text{ml } 1000 \text{ m}^{-3}$ ) were observed between these nets (Ohman & Smith 1995). However, the larvae in the CalCOFI samples are predominantly small (preflexion stage) with limited avoidance ability (Moser & Watson 2006), and most are found in the upper 140 m of the water column although some extend deeper (Moser & Smith 1993). There is no evidence in our study of a break point in larval abundance in 1969 or 1977.

Additional climate indices used in the analyses were: (1) the annual average coastal upwelling based on wind-driven offshore Ekman transport off southern California ( $33^\circ \text{N}$ ,  $119^\circ \text{W}$ ), obtained from the Pacific Fisheries Environmental Laboratory (NOAA) at [www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data\\_download.html](http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html); (2) the Pacific Decadal Oscillation (PDO) (Mantua et al. 1997) from [www.atmos.washington.edu/~mantua/abst.PDO.html](http://www.atmos.washington.edu/~mantua/abst.PDO.html); (3) the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al. 2008) from [www.o3d.org/npgo](http://www.o3d.org/npgo); and (4) the Multivariate ENSO Index (MEI; ENSO: El Niño-Southern Oscillation) (Wolter & Timlin 1998) from [www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/table.html](http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/table.html).

A 38 kHz echo sounder (Simrad EK-60) was used during the January 2010 CalCOFI cruise to examine the vertical distribution to 750 m depth of acoustic backscattering over the survey area (Fig. 1). The acoustic backscattering was plotted in relation to oxygen concentration, which was measured at each sta-

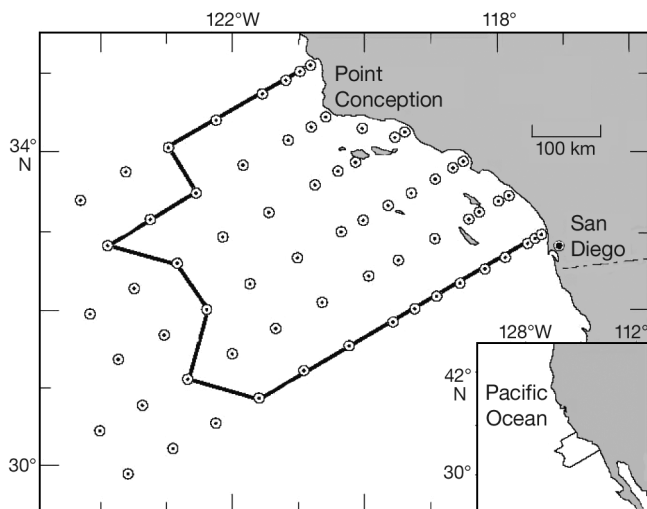


Fig. 1. The CalCOFI survey region off the coast of California showing the sampling stations. The core stations used in the current analysis are within the solid outline

tion from Niskin samples taken to 525 m depth and analyzed by means of a modified Winkler titration method (Carpenter 1965). The backscattering data, initially analyzed at 100 m intervals horizontally and 10 m vertically in units of nautical area backscattering (NASC,  $\text{m}^2$  nautical miles $^{-2}$ ), were normalized to the maximum value at each interval, averaged across the 6 transects and smoothed with a 2D boxcar filter.

Quantitative ichthyoplankton abundance estimates (no. ind.  $\text{m}^{-2}$  over the survey region) were derived for each taxon from the counts combined with estimates of the water filtered for each sample and the tow depth. Approximately 400 taxa are currently identified and enumerated within the CalCOFI region (Moser 1996), of which 86 taxa from 36 families were chosen for this analysis based on their consistent identification and enumeration since 1951 and occurrence in at least half the years. The annual mean abundances of fish eggs and larvae were log transformed to normalize the variance. (The eggs were identified to species and included in the analysis for 3 species: northern anchovy, Pacific sardine and Pacific saury *Cololabis saira*.) We used SPSS 18 ([www.spss.com/](http://www.spss.com/)) to carry out a principal component analysis (PCA) based on the correlation matrix, which normalizes the data by the mean and SD for each taxon (Legendre & Legendre 1998). This prevented the analysis from being biased toward the more abundant and variable taxa. Correlation coefficients are sensitive to the presence of dual zeroes; hence, we decided to use annual means over the survey grid and restrict the analysis to taxa present in most years.

The resulting correlation matrix was indeterminate because there were more variables than degrees of freedom, so the PCA was repeated on a reduced data set of 41 taxa, almost all of which were identified to the species level and occurred in almost all years.

Correlation analysis of time series is complicated by nonstationarity and autocorrelation. Significant trends (nonstationarity) shared between time series are a major source of spurious correlations and can also bias autocorrelation analysis (Diggle 1990). Autocorrelation reduces the effective number of independent data points (or degrees of freedom), leading to inflated estimates of significance, if uncorrected. To correct for these sources of uncertainty, correlations were carried out on detrended time series of dependent and independent variables. In the case of significant autocorrelations, significance levels of results were corrected following Pyper & Peterman (1998) by adjusting the number of independent data points ( $N^*$ ):

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N} \sum_{j=1} \rho_{XX}(j) \rho_{YY}(j) \quad (1)$$

where  $N$  is the sample size and  $\rho_{XX}(j)$  and  $\rho_{YY}(j)$  are the autocorrelations of time series  $X$  and  $Y$  at lag  $j$ . When initially examining patterns in the data sets, we use the term 'nominal' to indicate significance levels based on the uncorrected number of data points in the time series.

We also removed the trends and autocorrelation in the time series by first-differencing to examine correlations at high-frequency (i.e. interannual) time scales (Jenkins & Watts 1968, Diggle 1990). In the first-differenced time series, the value of each data point at time ( $t$ ) is based on its value in the original time series at time ( $t$ ) minus its value at time ( $t - 1$ ). The period of intermittent CalCOFI surveys (1967 to 1983) was removed from the first-differenced time-series analysis.

Nonparametric Spearman's  $\rho$  correlation analyses based on rank orders of abundance were carried out for several analyses; results were generally quite similar to results based on parametric correlation analyses.

We calculated the relative light ( $I$ ) available due to a change in depth ( $d$ ) of the hypoxic boundary layer as  $I = \exp(kd)$ , where  $k$  is the light extinction coefficient.

## RESULTS

The results of the PCAs on the full (86 taxa) and reduced (41 taxa) CalCOFI ichthyoplankton data sets were highly congruent in their output for PC1. PC1 accounted for 20.5% of the variance of the full data set and 28.7% of the variance of the reduced data set. However, the reduced data set also had reduced variability. However, the correlation of the PC1 time series from the 2 analyses was 0.97, indicating the output for PC1 was highly robust, being based on similar loadings for the major taxa. We present here the PCA based on the full data set, since our objective is to examine as broadly as possible the taxa contributing to the dominant pattern in the ichthyoplankton time series. Further PCs accounted for a rapidly diminishing proportion of the variance in both PCAs. In the PCA based on 86 taxa, PC2 accounted for 12.4% and PC3 for 6.8%. (A more comprehensive treatment of the PCA will be the subject of a subsequent paper.)

Fully 49 of the 86 taxa nominally loaded significantly and positively on PC1 with factor loadings  $\geq 0.29$  (Table 2). These loadings are equivalent to



Table 2. Taxa that contributed significantly to principal component 1 (PC1) with their loadings on PC1, equivalent to their correlation with the PC1 time series, and their habitat affinity. For loadings (or correlations,  $r$ )  $> 0.29$  (or  $< -0.29$ ),  $p < 0.05$  for  $df = 44$ . Differenced (Diff.): correlations for first-differenced time series;  $O_2$  correlation (correl.) Spearman's  $\rho$  correlation of taxa time series with mean  $O_2$  concentration at 200 to 400 m. \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

| Taxon                               | Loading | Habitat              | Diff.<br>r | $O_2$<br>correl. |
|-------------------------------------|---------|----------------------|------------|------------------|
| <i>Diogenichthys atlanticus</i>     | 0.86    | Mesopelagic          | 0.53***    | 0.71***          |
| <i>Protomyctophum crockeri</i>      | 0.85    | Mesopelagic          | 0.35*      | 0.59***          |
| <i>Ceratoscopelus townsendi</i>     | 0.83    | Mesopelagic          | 0.50***    | 0.71***          |
| <i>Cyclothone</i> spp.              | 0.83    | Mesopelagic          | 0.44**     | 0.79***          |
| <i>Nannobranchium</i> spp.          | 0.81    | Mesopelagic          | 0.32*      | 0.76***          |
| Sternoptychidae                     | 0.75    | Mesopelagic          | 0.54***    | 0.70***          |
| <i>Stomias atriventer</i>           | 0.73    | Mesopelagic          | 0.61***    | 0.52***          |
| <i>Symbolophorus californiensis</i> | 0.73    | Mesopelagic          | 0.33*      | 0.53***          |
| <i>Chauliodus macouni</i>           | 0.71    | Mesopelagic          | 0.04       | 0.60***          |
| <i>Vinciguerria lucetia</i>         | 0.71    | Mesopelagic          | 0.44**     | 0.55***          |
| Scopelarchidae                      | 0.70    | Mesopelagic          | 0.38**     | 0.55***          |
| <i>Bathylagoides wesethi</i>        | 0.69    | Mesopelagic          | 0.44**     | 0.54***          |
| <i>Bathylagus pacificus</i>         | 0.68    | Mesopelagic          | 0.13       | 0.74***          |
| <i>Scomber japonicus</i>            | 0.68    | Epipelagic           |            |                  |
| Paralepididae                       | 0.67    | Mesopelagic          | 0.23       | 0.57***          |
| <i>Microstoma</i> sp.               | 0.67    | Mesopelagic          | 0.43**     | 0.48***          |
| <i>Argentina sialis</i>             | 0.65    | Mesopelagic          | 0.40**     | 0.53***          |
| <i>Lipolagus ochotensis</i>         | 0.64    | Mesopelagic          | 0.33*      | 0.48***          |
| <i>Hygophum reinhardtii</i>         | 0.61    | Mesopelagic          | 0.45**     | 0.57***          |
| <i>Idiacanthus antrostomus</i>      | 0.57    | Mesopelagic          | -0.29*     | 0.47**           |
| Gobiidae                            | 0.57    | Demersal nearshore   |            |                  |
| <i>Myctophum nitidulum</i>          | 0.55    | Mesopelagic          | 0.59***    | 0.50***          |
| <i>Triphoturus mexicanus</i>        | 0.54    | Mesopelagic          | 0.49***    | 0.50***          |
| <i>Aristostomias scintillans</i>    | 0.53    | Mesopelagic          | 0.50**     | 0.52***          |
| Myctophidae                         | 0.52    | Mesopelagic          | 0.39**     | 0.56***          |
| <i>Citharichthys</i> spp.           | 0.50    | Demersal shelf       |            |                  |
| <i>Notolychnus valdiviae</i>        | 0.50    | Mesopelagic          | 0.44**     | 0.59***          |
| <i>Paralabrax</i> spp.              | 0.49    | Demersal nearshore   |            |                  |
| <i>Melamphaes</i> spp.              | 0.47    | Mesopelagic          | 0.28       | 0.39**           |
| <i>Scopelogadus mizolepis</i>       | 0.47    | Mesopelagic          | 0.02       | 0.54***          |
| <i>bispinosus</i>                   |         |                      |            |                  |
| Labridae                            | 0.47    | Demersal nearshore   |            |                  |
| <i>Pleuronichthys verticalis</i>    | 0.46    | Demersal shelf       | 0.15       | 0.50***          |
| <i>Paralichthys californicus</i>    | 0.45    | Demersal shelf       | 0.42**     | 0.39**           |
| <i>Poromitra</i> spp.               | 0.44    | Mesopelagic          | 0.30*      | 0.25*            |
| <i>Notoscopelus resplendens</i>     | 0.44    | Mesopelagic          | 0.45**     | 0.49***          |
| Cottidae                            | 0.44    | Demersal nearshore   |            |                  |
| <i>Zaniolepis</i> spp.              | 0.44    | Demersal shelf       | 0.08       | 0.33*            |
| Sciaenidae                          | 0.43    | Demersal inner shelf |            |                  |
| <i>Hypsoblennius</i> spp.           | 0.42    | Demersal nearshore   |            |                  |
| <i>Glyptocephalus zachirus</i>      | 0.40    | Demersal shelf/slope | 0.04       | 0.27*            |
| <i>Tactostoma macropus</i>          | 0.40    | Mesopelagic          | 0.41**     | 0.07             |
| <i>Microstomus pacificus</i>        | 0.39    | Demersal shelf/slope | 0.22       | 0.32**           |
| <i>Hippoglossina stomata</i>        | 0.38    | Demersal shelf       | 0.03       | 0.26*            |
| <i>Sebastes</i> spp.                | 0.37    | Demersal shelf       | 0.27       | 0.34*            |
| <i>Peprilus simillimus</i>          | 0.35    | Pelagic              |            |                  |
| <i>Sphyræna argentea</i>            | 0.34    | Epipelagic           |            |                  |
| <i>Nansenia candida</i>             | 0.31    | Mesopelagic          | 0.29       | 0.08             |
| Atherinopsidae                      | 0.30    | Epipelagic           |            |                  |
| <i>Engraulis mordax</i> eggs        | 0.30    | Epipelagic           |            |                  |
| <i>Cololabis saira</i> eggs         | -0.43   | Epipelagic           |            |                  |
| <i>Sebastes diploproa</i>           | -0.45   | Demersal shelf/slope | 0.10       | -0.27*           |
| <i>Sebastes goodei</i>              | -0.48   | Demersal shelf/slope | -0.09      | -0.41**          |

the correlation of the individual time series with the PC1 time series ( $r \geq 0.29$ ,  $df = 44$ ,  $p < 0.05$ ). Only 3 taxa loaded significantly negatively on PC1. Of the 27 taxa with factor loadings on PC1  $\geq 0.5$ , 24 were mesopelagic fishes from 8 families: Myctophidae, Gonostomatidae, Sternoptychidae, Stomiidae, Phosichthyidae, Scopelarchidae, Argentinidae and Microstomatidae. Of the remaining 22 taxa that nominally loaded significantly on PC1, 6 were mesopelagic and 8 were demersal fishes of the shelf and slope.

Time series of the abundance of 4 common taxa from 4 families that loaded highly on PC1 are shown in Fig. 2: *Cyclothone* spp. (Gonostomatidae; cosmopolitan), *Vinciguerria lucetia* (Phosichthyidae; tropical/subtropical, both hemispheres), *Diogenichthys atlanticus* (Myctophidae; cosmopolitan) and *Bathylagoides wesethi* (Microstomatidae, cold water). Although these (and other taxa that loaded highly on PC1) have varied biogeographic distributions, all share a common abundance pattern displayed by the PC1 time series (Fig. 3), characterized by relatively low abundance in the 1950s and in the past decade, with elevated abundance in the 1980s and 1990s.

However, 21 of the 24 mesopelagic species with loadings  $\geq 0.5$  were significantly correlated with the PC1 time series after first-differencing, indicating significant correlations at interannual time scales as well as based on low-frequency trends (Table 2). Most mesopelagic and shelf/slope demersal taxa with weaker but nominally significant loadings on PC1 (loadings  $< 0.50$  and  $> 0.29$ ) were not significantly correlated with PC1 after the time series were first-differenced. PC1 thus appears to represent primarily the coherent response of a broad suite of mesopelagic fishes to some large-scale environmental forcing.

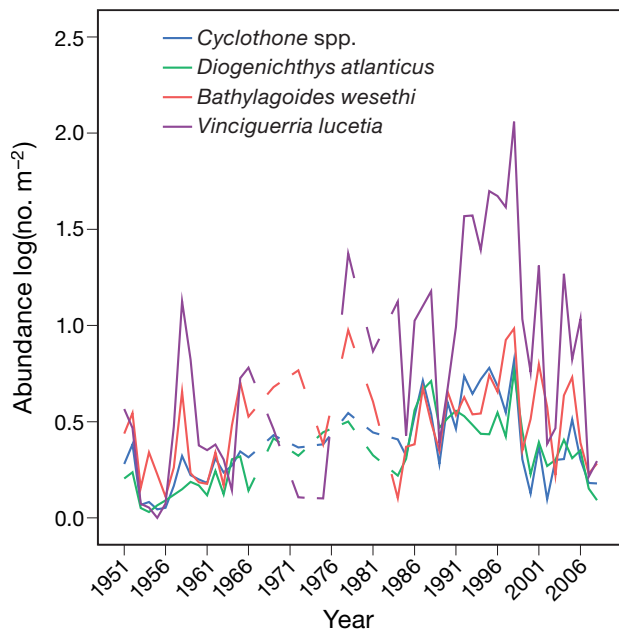


Fig. 2. Time series of 4 commonly occurring midwater taxa with various biogeographic distributions that loaded highly on principal component 1 (PC1): *Cyclothone* spp. (Gonostomatidae; cosmopolitan), *Vinciguerria lucetia* (Phosichthyidae; tropical/subtropical, both hemispheres), *Diogenichthys atlanticus* (Myctophidae; cosmopolitan) and *Bathylagoides wesethi* (Microstomatidae; coldwater)

The PC1 time series displayed a significant positive temporal trend, as did the PDO, sea surface temperature (SST), and temperature at 200 m. The linear trend was removed from the time series before further analysis, by using the residual time series (see 'Materials and methods'). Oxygen concentration at midwater depths, the MEI, NPGO, and upwelling time series showed no significant temporal trend.

The PC1 time series was significantly correlated with several large-scale indices of climate variability

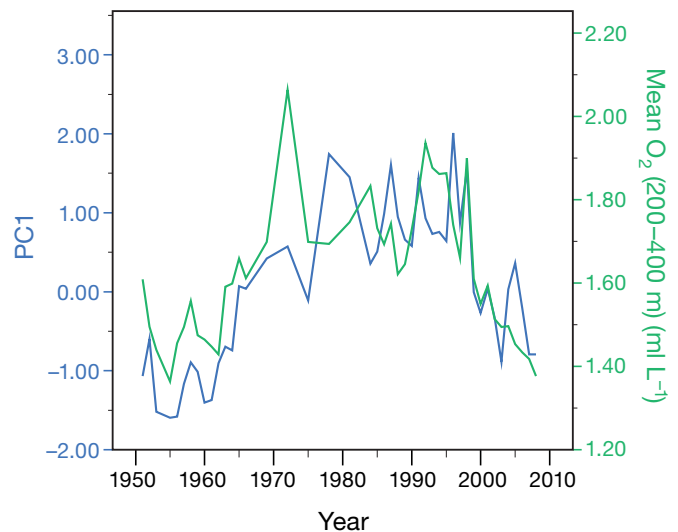


Fig. 3. Time series of principal component 1 (PC1) and mean oxygen concentrations at 200 to 400 m depth in the CalCOFI survey area, 1951 to 2008

and local environmental variables (Table 3). Before detrending the time series, PC1 was significantly correlated with the mean annual oxygen concentration at 200 to 400 m depth, the temperature at 200 m and at the sea surface, and the PDO and MEI. After detrending, the correlations with temperature at 200 m and the sea surface were no longer significant, indicating that the initial correlations were based primarily on the shared temporal trend. However, a significant correlation of PC1 with the NPGO emerged after detrending, indicating that the lack of a shared trend had previously masked the correlation. The correlation with midwater (200 to 400 m) oxygen concentration remained strongest ( $r = 0.75$ ). The correlations with midwater oxygen and the 3 large-scale climate indices (PDO, NPGO and MEI) all remained

Table 3. Pearson correlations of principal component 1 (PC1) with mean annual oxygen concentration at 200 to 400 m depth, the Pacific Decadal Oscillation (PDO), Multivariate ENSO Index (MEI), North Pacific Gyre Oscillation (NPGO), sea surface temperature (SST), temperature anomalies ( $T$ ) at 200 m depth, and mean upwelling at 33° N, 119° W. Correlations are shown before and after detrending PC1, PDO, SST and  $T$  (200 m) with 2-tailed significance levels based on the nominal time series length ( $n = 46$ ), the adjusted significance levels based on the estimated number of independent data points ( $N^*$ ) and the first-differenced correlations and significance. Significance levels: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ ; ns: not significant

|  | O <sub>2</sub> (200–400 m) | PDO     | MEI     | NPGO    | SST     | $T$ (200 m) | Upwelling |
|--|----------------------------|---------|---------|---------|---------|-------------|-----------|
| PC1                                      |                            |         |         |         |         |             |           |
| Pearson correlation (without detrending) | 0.75***                    | 0.56*** | 0.47*** | -0.23   | 0.45**  | 0.44**      | -0.25     |
| Detrended                                | 0.74***                    | 0.45**  | 0.40**  | -0.41** | 0.17    | 0.22        | -0.17     |
| $N^*$ and significance                   | 14**                       | 35**    | 38*     | 30*     | ns      | ns          | ns        |
| Differenced correlation                  | 0.35*                      | 0.05 ns | 0.21    | -0.36*  | 0.04 ns | 0.25        | -0.36*    |

significant after applying a correction for autocorrelation to the effective number of independent data points ( $N^*$ ) (Table 3). Midwater oxygen concentration was also significantly correlated individually with all but 2 of the 39 mesopelagic and demersal shelf and slope taxa that loaded significantly on PC1 (Table 2).

To examine whether the time series were correlated at interannual time scales as well as based on low-frequency trends, the analysis was re-examined after the time series were first-differenced. The correlation with midwater oxygen concentration remained significant, along with the correlation with the NPGO. There was also a significant correlation with local upwelling (Table 3).

We also examined the relative contribution of these environmental variables to explaining the PC1 time series using stepwise regression analysis (Table 4). Only the mean oxygen at 200 to 400 m depth and the PDO entered a stepwise regression significantly. The standardized regression coefficient ( $\beta$ ), which indicates the relative influence of the variables in the regression, was almost twice as large for midwater oxygen as for the PDO.

The time series for PC1 indicates 2 periods of low abundance in the first and last decades (1951 to 1960 and 1999 to 2008) of the time series and a period of relatively high abundance from 1966 to 1999. The PC1 time series closely follows trends in mean oxygen concentration at 200 to 400 m (the midwater depths at which oxygen was consistently sampled during the CalCOFI cruises) estimated over the core stations from the CalCOFI surveys ( $r = 0.75$ ) (Fig. 3). The larval abundances of the 24 mesopelagic taxa with loadings on PC1  $\geq 0.5$  were, on average, 63.3% (a factor of 2.7) lower during the periods of reduced oxygen concentrations (1950s and post-1999) than during the period of relatively higher intermediate-water oxygen concentrations (1966 to 1999). The 37

mesopelagic and shelf and slope demersal taxa with loadings on PC1  $> 0.29$  declined 62.7% between these periods of high and low midwater oxygen concentration. The 2 rockfishes, *Sebastes diploproa* and *S. goodei*, that loaded significantly negatively on PC1 were a factor of 1.7 higher during the periods of reduced oxygen concentration.

## DISCUSSION

Much of the variability in the time series was at low frequencies and associated with variables predicted to vary with long-term climate change, such as deep-water oxygen content and temperature at the sea surface and at depth. We therefore examined whether PC1 might reflect a long-term phenological shift in the midwater community. However, there was no clear biogeographic pattern in the distribution of these taxa: 7 had predominantly coldwater (northerly) affinities, 8 had warmwater (southerly) affinities and 8 had a broad, approximately cosmopolitan distribution; one taxon was mostly restricted to the CC (Table 5). This generalized distribution indicates that the pattern was unlikely to be the result of changes in currents or water masses or a shift related to water temperatures that might favor either a northerly or southerly fauna.

The deep ocean is often assumed to be highly stable on interannual to interdecadal time scales, and most research on the influence of climate on the fish population dynamics of the California Current ecosystem has focused on individual commercially exploited species, such as northern anchovy and Pacific sardine (Checkley et al. 2009). This may be a consequence of our limited knowledge of the OMZ and the midwater habitat (Robison 2009), as well as a tendency to focus on species-by-species interactions with the environment rather than to consider the

Table 4. Results of stepwise regression analysis. Potential independent variables are: mean  $O_2$  (200 to 400 m), Pacific Decadal Oscillation (PDO), temperature at 400 m, Multivariate ENSO Index (MEI). Probability to enter is  $p < 0.05$ . Only the mean  $O_2$  (200 to 400 m) and PDO entered the regression significantly. Abbreviations as in Table 1

| Model                  | Unstandardized coefficients |       | Standardized coefficients<br>Beta | $t$    | $p$   | $R^2$ |
|------------------------|-----------------------------|-------|-----------------------------------|--------|-------|-------|
|                        | B                           | SE    |                                   |        |       |       |
| 1 (Constant)           | -7.181                      | 0.983 |                                   | -7.303 | 0.000 | 0.548 |
| Mean $O_2$ (200–400 m) | 4.435                       | 0.602 | 0.747                             | 7.371  | 0.000 |       |
| 2 (Constant)           | -5.944                      | 0.965 |                                   | -6.160 | 0.000 | 0.648 |
| Mean $O_2$ (200–400 m) | 3.686                       | 0.589 | 0.621                             | 6.253  | 0.000 |       |
| PDO                    | 0.376                       | 0.115 | 0.325                             | 3.276  | 0.002 |       |

Table 5. The vertical and biogeographic distribution of mesopelagic fishes with loadings of 0.50 or greater on PC1. Classification is from Hsieh et al. (2009)

| Taxon                               | PC1 loading | Vertical distribution | Biogeography       |
|-------------------------------------|-------------|-----------------------|--------------------|
| <i>Diogenichthys atlanticus</i>     | 0.86        | Mesopelagic           | Warm               |
| <i>Protomyctophum crockeri</i>      | 0.85        | Migrator              | Cold               |
| <i>Ceratoscopelus townsendi</i>     | 0.83        | Migrator              | Broad              |
| <i>Cyclothone</i> spp.              | 0.83        | Migrator              | Warm               |
| <i>Nannobranchium</i> spp.          | 0.81        | Migrator              | Broad              |
| Sternoptychidae                     | 0.75        | Mesopelagic           | Broad              |
| <i>Stomias atriventer</i>           | 0.73        | Mesopelagic           | Warm               |
| <i>Symbolophorus californiensis</i> | 0.73        | Mesopelagic           | Cold               |
| <i>Chauliodus macouni</i>           | 0.71        | Mesopelagic           | Cold               |
| <i>Vinciguerria lucetia</i>         | 0.71        | Migrator              | Warm               |
| Scopelarchidae                      | 0.70        | Mesopelagic           | Broad              |
| <i>Bathylagoides wesethi</i>        | 0.69        | Mesopelagic           | Cold               |
| <i>Bathylagus pacificus</i>         | 0.68        | Mesopelagic           | Cold               |
| Paralepididae                       | 0.67        | Mesopelagic           | Broad              |
| <i>Microstoma</i> sp.               | 0.67        | Mesopelagic           | Cold               |
| <i>Argentina sialis</i>             | 0.65        | Mesopelagic           | California Current |
| <i>Lipolagus ochotensis</i>         | 0.64        | Mesopelagic           | Cold               |
| <i>Hygophum reinhardtii</i>         | 0.61        | Migrator              | Warm               |
| <i>Idiacanthus antrostomus</i>      | 0.57        | Mesopelagic           | Warm               |
| <i>Myctophum nitidulum</i>          | 0.55        | Migrator              | Broad              |
| <i>Triphoturus mexicanus</i>        | 0.54        | Migrator              | Warm               |
| <i>Aristostomias scintillans</i>    | 0.53        | Mesopelagic           | Cold               |
| Myctophidae                         | 0.52        |                       | Broad              |
| <i>Notolychnus valdiviae</i>        | 0.50        | Migrator              | Broad              |

potential community-wide impacts of large-scale environmental change. Hsieh et al. (2009) examined trends in the abundance of 34 of the region's mesopelagic species, but restricted their analysis to the period from 1951 to 1998, thereby excluding the marked decline in these populations over the past decade. They noted the influence of the PDO and warming on these populations, but did not examine relationships with oxygen content at midwater depths. While Hsieh et al. (2009) noted similar trends in most of these species (excluding the past decade), they did not examine the broader community-wide pattern. Our multivariate analysis highlights the coherent response of the region's mesopelagic fishes, and to a lesser extent its shelf and slope demersal fishes, to decadal-scale trends in intermediate-water oxygen concentration since 1951, as well as correlations with the primary regional ocean climate indices: the MEI, PDO and NPGO.

We suggest that the apparent response of a broad assemblage of deepwater fishes in the southern CC, a decline of >60%, indicates the potential sensitivity of the deepwater fish fauna to climate-induced changes in intermediate-water oxygen levels, particularly in those regions of the world's oceans with

well-developed OMZs. What is the likely mechanism (or mechanisms) underlying this relationship? We examine here a range of hypotheses.

The ~20% decline in midwater oxygen content led to a shoaling of oxygen isolines within the OMZ of the southern CC of up to 90 m (Bograd et al. 2008, McClatchie et al. 2010). This could potentially influence the midwater fauna through several mechanisms. It could have direct physiological effects on the fauna. It could potentially affect the abundance of their forage or shrink their foraging habitat. It could potentially affect their spawning habitat or habitat during their early life history. And it could influence their availability to predators.

Hypoxia has often been directly linked to mortality of marine life (Chan et al. 2008, Diaz & Rosenberg 2008, Vaquer-Sunyer & Duarte 2008). However, we believe it unlikely that the decline in mesopelagic fish abundance is the result of a direct physiological effect of declining oxygen levels. The hypoxic boundary layer (HBL) in the CC is at several hundred meters depth and its shoaling has been on the order of tens of meters on interannual to decadal time scales. Mesopelagic fishes can readily adjust their vertical position on this scale.

Nor is it likely that the decline in midwater fishes is due to compression of their foraging habitat. Nine of the fishes with loadings of 0.5 or greater on PC1 are vertical migrators that feed in well-oxygenated, near-surface waters; 14 of the fishes are non-migrators (Table 5). The foraging habitat of the migratory fishes would not be affected by declining midwater oxygen levels, and it is unclear whether an expanding midwater hypoxic zone would prove favorable or unfavorable to fishes adapted to permanently residing within it.

It is also unlikely that the decline of midwater fishes is due to an influence of oxygen levels on spawning or larval habitat, since these species spawn predominantly within the upper 200 m, and their larvae remain within well-oxygenated epipelagic waters (Ahlstrom 1959, Moser & Smith 1993).

We suggest that enhanced vulnerability to predators due to a shoaling hypoxic boundary layer may be responsible for the strong correlation between mid-



water oxygen content and the abundance of midwater fishes. During CalCOFI cruises, the mesopelagic micronekton is concentrated in a deep-scattering layer (DSL) within the HBL, where oxygen concentrations are  $\sim 0.5$  to  $1.5$   $\text{ml O}_2 \text{ l}^{-1}$  (Vaquer-Sunyer & Duarte 2008). This is currently at depths of  $\sim 350$  to  $450$  m, just above the region of severe hypoxia (Fig. 4). Acoustic backscattering of a fauna unable to penetrate hypoxic waters delineates the HBL in the southern CC, much as backscattering from Peruvian anchoveta *Engraulis ringens* marks the shallower HBL at 50 to 100 m depth off Peru (Bertrand et al. 2010). The aggregation of the mesopelagic micronekton within the HBL in the CC suggests that this fauna descends as deeply as possible to avoid visually orienting predators, while avoiding the effects of hypoxia. Off southern California, we did not observe deeper DSLs, in marked contrast to well-oxygenated regions of the world ocean, such as the South Pacific and North Atlantic oceans, where DSLs of mesopelagic fishes and other micronekton are regularly found at depths of 500 to 1000 m (Chapman & Marshall 1966, Williams & Koslow 1997).

Because light declines exponentially with depth, shoaling of the HBL—and of the fauna within the DSL—significantly increases vulnerability of those fauna to predators that orient visually. Studies in the tropical Atlantic and Pacific oceans have now docu-

mented how various predators that feed at midwater depths enhance their foraging in regions where the OMZ aggregates and traps their prey (Prince & Goodyear 2006, Nasby-Lucas et al. 2009). Off southern California, the depth of the HBL has shoaled as much as 90 m and, on average, has shoaled 41 m between 1984 and 2006 (Bograd et al. 2008). Assuming a light extinction coefficient appropriate for clear oceanic water ( $k = 0.022$ ), the light available for predators feeding within the HBL has increased by a factor of 2.5 over this period, assuming a shoaling of 41 m, and by a factor of 7.2 if the DSL has shoaled 90 m. A shoaling HBL, by forcing the DSL into shallower, better-lit waters, clearly enhances vulnerability of its fauna to visually orienting predators.

Our hypothesis that enhanced vulnerability of the fish to predators may be responsible for the strong correlation between midwater oxygen content and the abundance of midwater fishes is supported by the inverse correlation of several predators with the trends exhibited by their mesopelagic prey. Of the 3 taxa that loaded significantly inversely on PC1, 2 were *Sebastes* species, *S. goodei* and *S. diploproa*, which prey on krill and midwater fishes (Brodeur & Pearcy 1984, Love et al. 2002). *S. diploproa* is one of the few *Sebastes* species whose depth range extends to the HBL (Vetter & Lynn 1997, Love et al. 2002). Species of *Sebastes* have been observed to aggre-

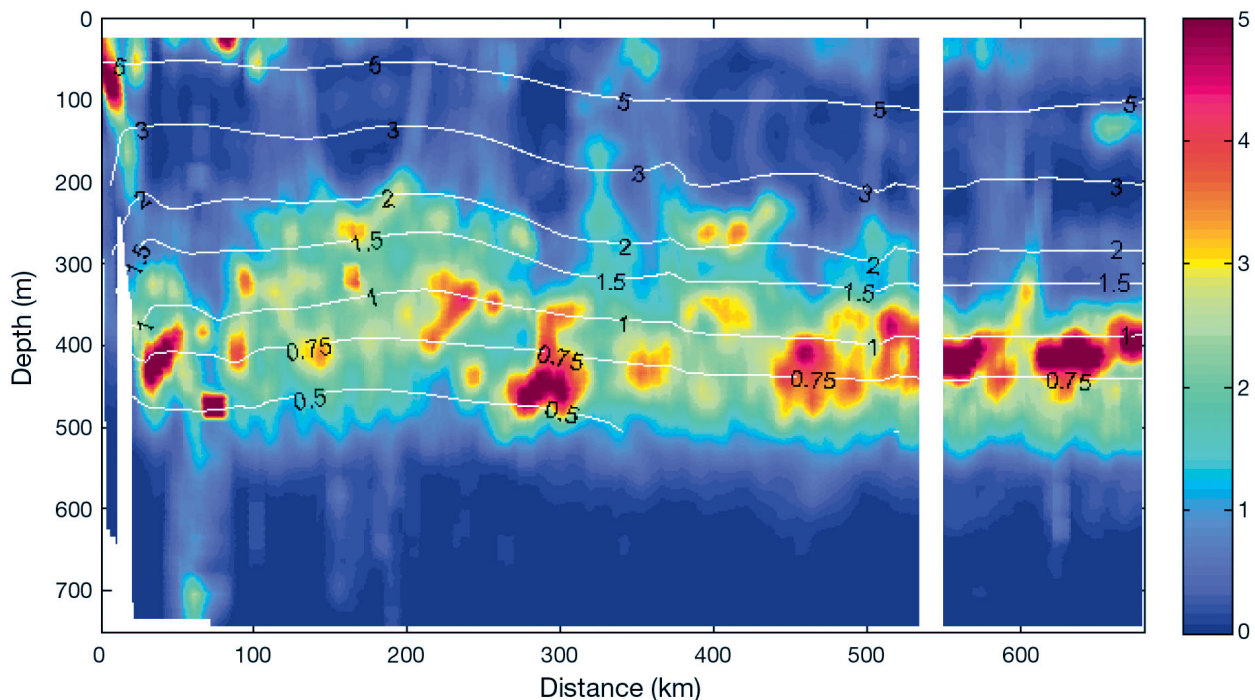


Fig. 4. Color contours of the distribution of the daytime acoustic backscattering from the January 2009 CalCOFI cruise in relation to distance offshore and depth, showing isolines of oxygen concentration ( $\text{ml O}_2 \text{ l}^{-1}$ ). The acoustic backscattering, normalized to the maximum at each sampling interval, and oxygen data are averaged over the 6 CalCOFI transects shown in Fig. 1

gate on banks and seamounts to intercept and prey upon vertical migrators unable to descend to their preferred daytime depth (Isaacs & Schwartzlose 1965). We hypothesize that species of *Sebastes*, no doubt along with other predators on the micronekton of DSLs, such as various marine mammals, squids, tunas and other open-water predatory fishes (Pinkas et al. 1971, Pauly et al. 1998, Bertrand et al. 2002, Whitehead et al. 2003, Potier et al. 2007), make use of a shoaling HBL in a similar way. It may appear counterintuitive that a predator would increase in abundance during a period when its prey is in decline. However, the decline in mesopelagic prey abundance during periods of a shoaling HBL may be more than matched by their increased availability if they remain during the day at shallower depths where ambient light conditions are significantly enhanced.

Reduced oxygen levels have been observed within the OMZ of the tropical Atlantic, Pacific and Indian oceans, as well as in the waters off Japan, the subarctic Pacific and the CC (Andreev & Kusakabe 2001, Ono et al. 2001, Emerson et al. 2004, Whitney et al. 2007, Bograd et al. 2008, Stramma et al. 2008, McClatchie et al. 2010). Although localized hypoxia has been reported on the continental shelf in the northern CC in apparent response to enhanced upwelling (Chan et al. 2008), there is no significant relationship between upwelling in the southern CC (33° N, 119° W) and the CalCOFI deepwater oxygen time series. However, upwelling was significantly correlated with PC1 at interannual time scales, that is, after detrending. In general, however, the fluctuations in mid-water oxygen levels in the CC appear to be linked to basin-scale, if not global, climate processes.

Climate models predict a 20 to 40% decline in deepwater oxygen content over the coming centuries owing to global warming, which will lead to expansion of OMZs and reduced oxygenation within them (Bopp et al. 2002, Matear & Hirst 2003, Oschlies et al. 2008). Our results suggest that such reductions in intermediate-water oxygen levels could precipitate a profound response across a broad range of taxonomic families and ecological groups that inhabit intermediate-water depths, particularly within the global ocean OMZs.

The causes of the observed decline in intermediate-water oxygen levels in the southern CC are not well understood. The increasing trend in oxygen levels in the 1960s indicates that the 60 yr pattern cannot be entirely attributed to global warming, but the cause of the decline since the 1990s remains unclear as well. The oxygen content at intermediate water depths in the CC is influenced by advection into the

region of subarctic, subtropical and tropical water masses (Lynn & Simpson 1987), as well as by biological production and community metabolism within the CC region itself. Warming, increased stratification and decreased oxygen levels at depth are widely observed in the source waters of the CC across the north Pacific Ocean (Andreev & Kusakabe 2001, Ono et al. 2001, Emerson et al. 2004, Whitney et al. 2007, Stramma et al. 2008). Although the precise contributions of various water types and mechanisms to declining oxygen levels remain unclear, it is apparent that these changes are widespread in the North Pacific and other oceans. The sharp decline of the midwater fish fauna, some of the major consumers of marine zooplankton production and key prey to a wide range of piscivorous fishes, squids, seabirds and marine mammals, could have major impacts on marine fisheries, marine conservation and the structure of marine food webs.

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