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Epipelagic and mesopelagic fishes in the southern California Current System: Ecological interactions and oceanographic influences on their abundance

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ABSTRACT

We use zooplankton and ichthyoplankton data from the ~60-year CalCOFI time series to examine relationships of mesopelagic (*i.e.* midwater) fishes in the California Current System with midwater predators, potential competitors (epipelagic planktivorous fishes) and zooplankton prey, within the context of local and basin-scale oceanography. Equilibrium-based near-steady state models and the "wasp-waist" paradigm for eastern boundary currents predict tightly-coupled trophic interactions, with negative correlations between the abundance of planktivorous competitors and between dominant planktivores and their prey. Testing these hypotheses with the CalCOFI time series, we found them to be generally invalid. Potential competitors within the mesopelagic community (planktivorous vertical migrators (VMs) and non-migrators (NMs)) were highly positively correlated, as were these groups with the mesopelagic piscivores (*e.g.* dragonfishes) that prey on them. In addition, the abundance of VMs was mostly positively correlated with that of epipelagic planktivores, such as anchovy, mackerels and hake. The VMs and epipelagic planktivores were negatively correlated with key potential planktonic prey groups, indicating a lack of bottom-up forcing. However, neither do these negative correlations appear to signify top-down forcing, since they seem to be mediated through correlations with key environmental drivers, such as the Pacific Decadal Oscillation (PDO), sea surface temperature, and the relative strength of the California Current. We suggest that the web of correlations linking key meso- and epipelagic planktivores, their predators and prey is mediated through common links with basin-scale oceanographic drivers, such as the PDO and ENSO cycles. Thus, the abundance of mesopelagic fishes in the California Current is closely tied to variation in the oxygen minimum zone, whose dynamics have been linked to the PDO. The PDO and other drivers are also linked to the transport of the California Current System, which influences the abundance of many dominant taxa off southern California that have broad biogeographic distributions linked to water masses that extend to the north (Transition Zone/sub-Arctic faunas) or the south (tropical/subtropical faunas).

1. Introduction

Mesopelagic (aka midwater) fishes have been largely neglected in models of pelagic food web dynamics for productive marine ecosystems. The 'wasp-waist' paradigm, for example, posits that eastern boundary current ecosystems are unstable because only a few species, such as sardine and anchovy, dominate the key mid-trophic level that transfers energy between the zooplankton and higher trophic levels. As a result, their variability is thought to control the abundance of their zooplankton prey from the top down and of their predators from the bottom up (Cury et al., 2000). However, diverse and abundant assemblages of midwater fishes also reside within these ecosystems, a significant proportion of which conduct diel vertical migrations to feed on the zooplankton in epipelagic waters. Mesopelagic fishes are generally not considered in this paradigm, presumably because their abundance and ecological impact are not considered significant relative to the epipelagic schooling planktivores. For example, a recent Atlantis model for the northern California Current was parameterized such that the biomass of deep vertical migrators was about 10% that of the small epipelagic planktivorous fishes (Horne et al., 2010). These biomass estimates for midwater fishes were derived from Pearcy and Laurs' (1966) studies of the midwater fauna carried out off Oregon using an Isaacs–Kidd midwater trawl (IKMT) with a 6 square-foot mouth opening.

In recent years, biomass estimates for midwater fishes have been revised upward by about an order of magnitude, based on the use of acoustics in combination with trawl sampling (Koslow et al., 1997). There is evidence that midwater fishes avoid small trawls en masse (Kaartvedt et al., 2012) and escape through the meshes of large trawls. Davison (2011) estimated that the biomass of midwater fishes in the California Current averaged 24.0 g wet weight/m^2, based on comparison of IKMT and Matsuda–Oozeki–Hu trawl (MOHT) tows with multi-frequency acoustic sampling, compared with Pearcy and Laurs' (1966)

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estimate of 3.6 g/m^2. Davison's (2011) estimate is comparable with the estimate of Field et al. (2006) for the biomass of 'forage fish,' *i.e.* small epipelagic planktivorous fishes, in the northern California Current: 27.1 g/m^2. However, the Field et al. estimate was based on the coastal region out to a depth of 1280 m, typically 20–80 km from shore, where these forage fishes are most concentrated. In fact, the California Current extends about 385 km offshore. If we consider the entirety of the California Current, which extends 2000 km from 30°–48° N latitude, the total mesopelagic fish biomass is ~24 million tonnes, compared with ~1.7 million tonnes for the combined biomass of sardine and anchovy in the region (Hill et al., 2009; Jacobson et al., 1994). Clearly, the trophic impact of mesopelagic fishes cannot be disregarded in considering the interactions between the zooplankton and their predators in the California Current System as a whole.

Mesopelagic fishes are highly diverse, with the greatest species richness of any ecological group in the ichthyoplankton collection of the California Cooperative Oceanic Fisheries Investigations (CalCOFI): 38% of the 586 taxa identified (Moser and Watson, 2006). Remarkably, much of this diverse assemblage appears to respond coherently to environmental forcing. Koslow et al. (2011) reported that the dominant pattern in the CalCOFI ichthyoplankton time series (or first principal component (PC)) was almost wholly dominated by mesopelagic fishes, including migrators and non-migrators, planktivores and piscivores across 8 taxonomic families. The abundance of this group declined 63% between a period of high abundance corresponding to a period of high midwater oxygen levels extending from about 1970 to 1995, relative to the 1950s and the 2000s.

The dominant midwater fishes are zooplanktivores: of the 11 midwater species that are among the 20 most abundant taxa in the CalCOFI ichthyoplankton time series, all are zooplanktivores (Table 11.1 in Moser and Watson, 2006). How does the marine ecosystem respond to dramatic decadal-scale change in the biomass of mesopelagic zooplanktivores? Potentially, such perturbations of the marine food web enable us to probe fundamental issues related to the structure and dynamics of marine ecosystems.

One key question is whether marine ecosystem dynamics conform sufficiently to the underlying steady state, near-equilibrium assumptions of most ecosystem models to allow them to predict, even qualitatively, the potential impacts of perturbations. Near-equilibrium conditions are an implicit assumption of mass balance, Ecopath, and qualitative models (Christensen and Walters, 2004; Dambacher et al., 2003; Field et al., 2006; Polovina, 1984; Steele, 1974), as well as of more dynamic ecosystem models, such as Nemuro or Atlantis (Fulton et al., 2011; Megrey et al., 2007). Given this assumption, significant change in one component of a trophic level, such as the mesopelagic planktivores, should be reflected in the biomass of its predators, competitors, and prey. Thus, the wasp-waist paradigm predicts that significant change in the biomass of planktivores will lead to opposite top-down impacts on prey populations and positively-correlated changes in predator populations. A steady state model predicts that, all else being equal, a shift in one major group of planktivores, such as the mesopelagic planktivores, will be compensated by change in the opposite direction by key competitors (*e.g.* epipelagic planktivores).

The dynamics of relatively simple aquatic ecosystems, such as small, high-latitude lakes, are consistent with the predictions of near-equilibrium ecosystem models (Dodson, 1979; Gliwicz and Prejs, 1977). However, the evidence from open-ocean systems has been equivocal (Frank et al., 2005; Koslow, 1983). Unfortunately, there are relatively few ocean time series of sufficient length and breadth to test whether ocean ecosystems are sufficiently near steady state for their dynamics to conform, even qualitatively, to the predictions of models that assume such conditions. This question is of considerable importance, given the increasing use of such models to predict the potential impacts of fishing, climate change, and other perturbations. If the predictions of such models are not supported even qualitatively — that is, if even the direction of change cannot be predicted — their utility falls into serious question, and other means of prediction or analysis must be sought.

Given the open nature of ocean systems, the applicability of near-equilibrium models cannot be assumed. Eastern boundary systems, such as the California Current System, are characterized by significant advection from the north (the main flow of the current) and the south (the Inshore Countercurrent and undercurrent), with mixing from the subtropical gyre offshore as well (Checkley and Barth, 2009; Hickey, 1998). Within the California Current System, many of the dominant species of copepods, euphausiids, and midwater fishes have extensive distributions across the North Pacific (Brinton, 1962; McGowan, 1971; Moser and Watson, 2006), such that the relative influence of local *in situ versus* large-scale advective processes in regulating abundance remains an open question (Roessler and Chelton, 1987).

We propose to examine this question using the CalCOFI time series. Koslow et al. (2011) reported a coherent response by some 24 mesopelagic taxa to decadal changes in mid-depth oxygen concentrations, resulting in a factor of ~2.7 difference in the apparent spawning biomass of these taxa between the periods 1951–1965 and 2000–2008 relative to 1966–1999. What were the responses of their epipelagic competitors and zooplankton prey to these changes? Are these responses consistent qualitatively with the predictions of simple steady-state ecosystem models?

2. Methods

We base our time series for the relative abundance of fish populations in the California Current System on their annual mean larval abundance in the CalCOFI ichthyoplankton data set. The annual means are estimated from the mean of their seasonal means within the core CalCOFI sampling area (Fig. 1) (see Koslow et al., 2011 for details of the analytical methods). The use of larval abundance as an index of adult spawning biomass may be traced back to Hensen and Apstein (1897) (Hewitt, 1985). This approach has been validated for many fish stocks, based on comparison of larval abundances with other estimates of stock abundance, such as from formal stock assessment, *e.g.* for northern anchovy (*Engraulis mordax*) (Hewitt, 1985), Pacific sardine (*Sardinops sagax*) (Koslow et al., 2011), rockfishes (*Sebastes* spp.), California halibut and several nearshore fishes (Moser and Watson, 1990; Moser et al., 2000, 2001). While larval indices assume reasonably constant larval mortality and adult fecundity, they do not require ancillary data on such parameters, so their lack of precision may be compensated by the greater length and availability of these time series.

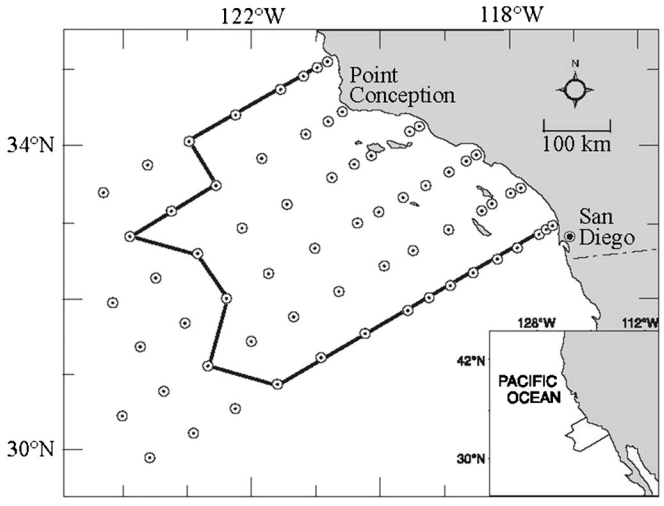

Fig. 1. The core CalCOFI survey area. The stations used in the study are within the solid outline.

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We also created several aggregate abundance indices to examine the potential interactions of particular trophic levels and ecological groups, based on the sum of the log-transformed larval abundances of mesopelagic vertical migrators, non-migratory planktivores, and non-migratory piscivorous fishes. Table 1 lists the species comprising these groups. An epipelagic planktivore index was based on the summed log-transformed abundance of the larvae of northern anchovy, Pacific sardine, Pacific saury (*Cololabis saira*), Pacific mackerel (*Scomber japonicus*) and horse mackerel (*Trachurus symmetricus*). An index for the total abundance of upper water column planktivores was computed as the sum of migratory and epipelagic planktivores. Log-transformed abundances were used to normalize the variance and moderate the influence of the most abundant taxa.

We examined potential associations of planktivore abundance with the abundance of their planktonic prey, using the CalCOFI time series for the abundance of total calanoid copepods (Lavaniegos and Ohman, 2007), zooplankton displacement volume, and the abundance of three key euphausiid species, *Euphausia pacifica*, *Thysanoessa spinifera*, and *Nematoscelis difficilis* (Brinton and Townsend, 2003, updated). To reduce the dimensionality of the zooplankton variables, a principal component (PC) analysis was carried out on their log-transformed values. The PCA was carried out with SPSS and was based on the correlation matrix, which normalizes the data by the mean and SD for each taxon, thereby limiting bias toward the more abundant and variable taxa (Legendre and Legendre, 2012).

Local physical variables, such as annual mean oxygen concentration at 200–400 m and temperature at 200 m and 10 m, were derived from the means of these variables averaged over the same CalCOFI stations and cruises as the ichthyoplankton. Our upwelling index was based on the annual average for coastal upwelling at 33°N lat 119° W long obtained from the Pacific Fisheries Environmental Laboratory (NOAA): http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html. A time series of sea level off San Francisco, a proxy for the low-frequency advection of the California Current (Chelton et al., 1982), was obtained from the University of Hawaii Sea Level Center (http://uhslc.soest.hawaii.edu/). Monthly mean sea levels were computed from the daily averages and annual means computed as the mean of the monthly means. The sea level time series had a strong linear trend, which was removed prior to analysis by extracting the residuals from a linear regression of sea level with year.

We also obtained indices of large-scale oceanographic processes: the Pacific Decadal Oscillation (PDO) (Mantua et al. (1997): http://www.atmos.washington.edu/~mantua/abst.PDO.html), the North Pacific Gyre Oscillation (NPGO) (Di Lorenzo et al., 2008: http://www.o3d.org/npgo), and the Multivariate ENSO Index (MEI) (Wolter and Timlin, 1998): http://www.esrl.noaa.gov/psd/enso/mei/table.html.

The time series were often nonstationary and autocorrelated. Significant trend (nonstationarity) shared between time series is a major source of spurious correlations and can bias autocorrelation analysis (Diggle, 1990). Autocorrelation reduces the effective number of independent data points (or degrees of freedom), leading to inflated estimates of significance. To correct for these issues, we followed the protocols set out in Koslow et al. (2013). Briefly, we initially tested whether there were significant trends in the time series based on significant correlations with Year. When present, the trend was removed by replacing the original time series with the residuals from the linear regression of the original time series with Year. Correlation analysis was re-run on the residual time series, and where the correlations remained significant based on the nominal degrees of freedom, the number of independent data points (N*) was estimated to assess statistical significance, following Pyper and Peterman (1998):

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

where N is the number of data points in the original time series, and ρ_{XX} (j) and ρ_{YY} (j) are the autocorrelations of time series X and Y at lag j. The expression was evaluated for lags of 1 to 10 years. 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.

Table 1
The species from the CalCOFI ichthyoplankton time series comprising the aggregate mesopelagic diel migratory and non-migratory planktivores and the mesopelagic piscivores. Species with warm-water (W) and cool-water (C) affinities are indicated.

Vertical migrators	Non-migrators	Mesopelagic piscivores
Leuroglossus stilbius	*Bathylagus pacificus* (C)	*Chauliodus macouni* (C)
Bathylagoides wesethi	*Melamphaes* spp.	*Idiacanthus antrostomus* (W)
Ceratoscopelus townsendi (W)	*Microstoma microstoma* (C)	*Stomias atriventer* (W)
Diaphus theta (C)	*Poromitra* spp.	
Diogenichthys atlanticus (W)	*Protomyctophum crockeri* (C)	
Diogenichthys spp.	*Cyclothone* spp.	
Hygophum reinhardtii (W)	*Scopelogadus bispinosus* (W)	
Lipolagus ochotensis (C)	Sternoptychidae	
Myctophum nitidulum (W)		
Nannobrachium spp. (C)		
Notolychnus valdiviae (W)		
Notoscopelus resplendens (W)		
Stenobrachius leucopsarus (C)		
Symbolophorus californiensis (C)		
Tarletonbeania crenularis (C)		
Triphoturus mexicanus (W)		
Vinciguerria lucetia (W)		

3. Results

The time series for the detrended abundance of mesopelagic migratory and non-migratory plankton-feeding fishes and their mesopelagic piscivorous predators were highly correlated with one another, correlations ranging between 0.76 and 0.87. All were strongly correlated with changes in midwater oxygen concentration, with correlations between 0.68 and 0.77 (Fig. 2, Table 2). Scatterplots indicate that the relationships between mesopelagic fish abundance and oxygen concentration were somewhat nonlinear, with steeper rates of decline at low oxygen concentrations ($\leq$1.5 ml O_2/l) and declining rates of increase at relatively high oxygen concentrations (Fig. 3).

The abundance of these mesopelagic fish assemblages was also generally significantly positively correlated with the abundance of dominant epipelagic planktivores in the California Current: northern anchovy (*E. mordax*), jack mackerel (*T. symmetricus*), and Pacific mackerel (*S. japonicus*), as well as with Pacific hake (*Merluccius productus*). We included hake in these comparisons because although they are often considered piscivorous, Pacific hake preys predominantly on krill when young, becoming increasingly piscivorous with age (Field et al., 2006). There were no significant correlations with the abundance of sardine (Table 3).

The abundance of epi- and mesopelagic planktivores was next examined in relation to local, regional, and large-scale ocean climate indices. In addition to strong correlations with deepwater oxygen concentration, the mesopelagic assemblages were consistently, though more weakly, positively correlated with sea level along the coast, indicative of weak flow of the California Current, and the MEI, indicative of El Niño conditions (Table 4), which is also associated with a weak California Current. Also consistent with this pattern, the mesopelagic planktivores were positively correlated with the warm phase of the PDO and negatively correlated with the NPGO, indicative of low-nutrient, low-chlorophyll conditions. The diel migratory mesopelagic fish assemblage was also negatively correlated with upwelling conditions along the coast (Table 4). The epipelagic planktivores, except for Pacific sardine, were also positively correlated with the warm phase of the PDO, and Pacific hake and jack mackerel abundance was negatively

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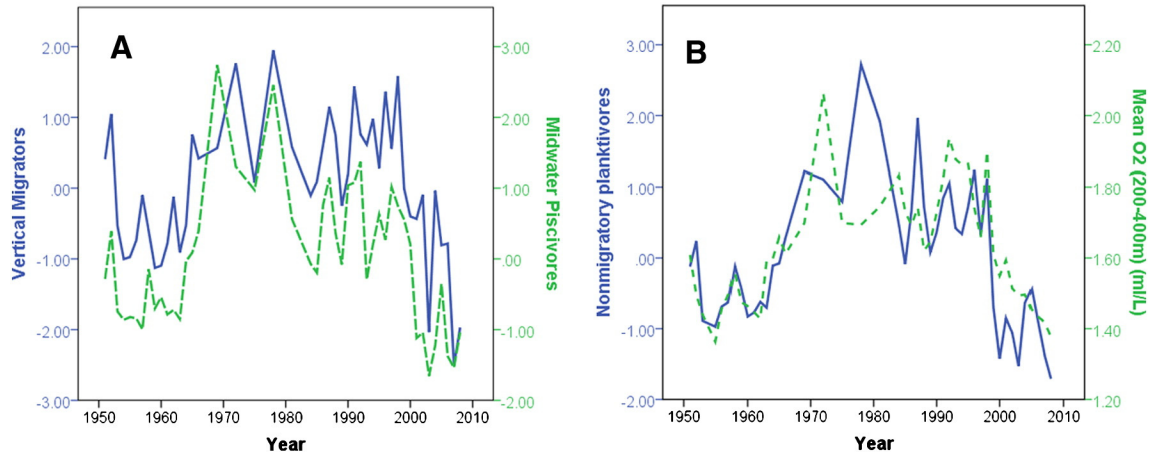

Fig. 2. A) Detrended time series for mesopelagic vertical migrators (planktivores) (dashed line) and piscivorous fishes (solid line) in the southern California Current. B) Time series of mean annual oxygen concentration at 200–400 m (dashed line) and detrended nonmigratory planktivorous fishes. Fish abundances based on larval abundances from CalCOFI ichthyoplankton time series. A color version of the figure is available online.

correlated with the NPGO. Jack mackerel abundance was significantly correlated with sea level, indicating a positive association with weak advection of the California Current. There was a weak association between the abundance of the two mackerel species and El Niño conditions (Table 4). All correlations indicated that planktivores abundance was associated with a suite of ocean conditions indicative of low-productivity conditions. Pacific sardine abundance was not significantly correlated with any of the oceanographic variables analyzed.

We examined whether relations between these taxa and the environment might be enhanced at lags of 1–3 years in the environmental time series. This would be expected if spawning stock size and larval production in a given year is significantly related to larval survival due to favorable conditions in previous years. However, the correlations generally diminished with lags, except for the correlation between midwater fishes and the NPGO, which peaked at a lag of 1 year at levels of $r = -0.41$ to -0.58.

Although the mesopelagic groups contained roughly equal numbers of taxa with warm- and cool-water affinities, we examined whether the correlations with weak advection of the California Current and warm-water conditions (El Niño and the warm phase of the PDO) might predominantly influence taxa with southerly warm-water affinities. We therefore summed the mean annual log-transformed larval abundances of mesopelagic species with predominantly warm- or cool-water affinities and examined relationships of these biogeographic assemblages with the oceanographic indices. Both warm- and cool-water affinity mesopelagic fishes were strongly correlated with changes in deepwater oxygen concentration, but their abundances were not significantly correlated with each other after detrending and correcting for autocorrelation (Table 5). The mesopelagic fauna with warm-water affinities exhibited significant correlations with weak flow of the California Current, El Niño conditions, warm SST, and the warm phase of the PDO. The correlation with coastal sea level was particularly strong, suggesting that the component of the mesopelagic fauna with a predominantly tropical/subtropical distribution is enhanced in the Southern California Bight when flows of the undercurrent and Davidson Countercurrent are particularly strong. The mesopelagic fauna with northerly cool-water displayed no significant correlations with any of these variables (Table 5).

Table 2
Correlations between the detrended abundance of diel migratory planktivores, non-migratory planktivores, mesopelagic piscivores, and mean annual oxygen concentration at 200–400 m depth in the CalCOFI area, 1951–2008. Degrees of freedom corrected for autocorrelation shown in parentheses with significance level: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

	Vertical migrators	Non-migratory planktivores	Mesopelagic piscivores
Non-migratory planktivores	0.87*** (13)		
Mesopelagic piscivores	0.77*** (14)	0.84*** (11)	
Midwater O_2	0.71** (14)	0.77** (11)	0.68* (11)

We next examined whether the associations of these planktivores with the environment were mediated through environmental influences on the abundance of their planktonic prey, based on a principal component analysis of the abundance of total calanoid copepods (Lavaniegos and Ohman, 2007), zooplankton displacement volume, and the abundance of three key euphausiid species, *E. pacifica*, *T. spinifera*, and *N. difficilis* (Brinton and Townsend, 2003, updated). The first PC explained 53% of the variance and was the only PC with an eigenvalue greater than one. All zooplankton variables loaded significantly on PC 1 (Table 6), indicating that PC 1 synthesized a coherent temporal pattern among these zooplankton groups. Zooplankton PC 1 displayed no significant temporal trend (correlation with Year: $r = 0.07$, ns).

Zooplankton PC 1 was negatively correlated with an aggregate variable based on the larval abundance of both epipelagic planktivores (sardine, anchovy, jack mackerel, and Pacific mackerel) and mesopelagic diel migratory planktivores ($r = -0.31$), but the correlation was not significant after correcting the degrees of freedom for autocorrelation (20 df, corrected). Disaggregating the planktivore variable, there was no correlation between zooplankton PC 1 and either the epipelagic planktivores ($r = 0.03$ ns) or the mesopelagic migratory planktivores with northerly affinities ($r = 0.09$ ns). However, there was a highly significant negative correlation between the zooplankton PC 1 and the abundance of mesopelagic migrators with warm-water affinities ($r = 0.60$, $p < 0.01$, 21 df, corrected). These results were consistent when the analysis was carried out in relation to the individual zooplankton variables: the small epipelagic planktivores and cool-water affinity migratory mesopelagics were not significantly correlated with any of the zooplankton taxa. However, the warm water affinity mesopelagic migrators were significantly negatively correlated with all zooplankton groups except *N. difficilis* (Table 7).

The negative correlation between the abundance of certain planktivores and their prey might indicate a top-down predator–prey interaction but might also be the result of a common correlation with a third factor. To examine their relationship with environmental forcing, we reduced the dimensionality of the oceanographic time series, since many of these variables are inter-related, *i.e.* SST, upwelling, advection of the California Current (*i.e.* sea level), deepwater oxygen concentrations, the MEI, PDO, and NPGO. The first PC of these time series explained 51% of the variance of the data set and was the only PC with an eigenvalues greater than 1. All variables loaded significantly on the

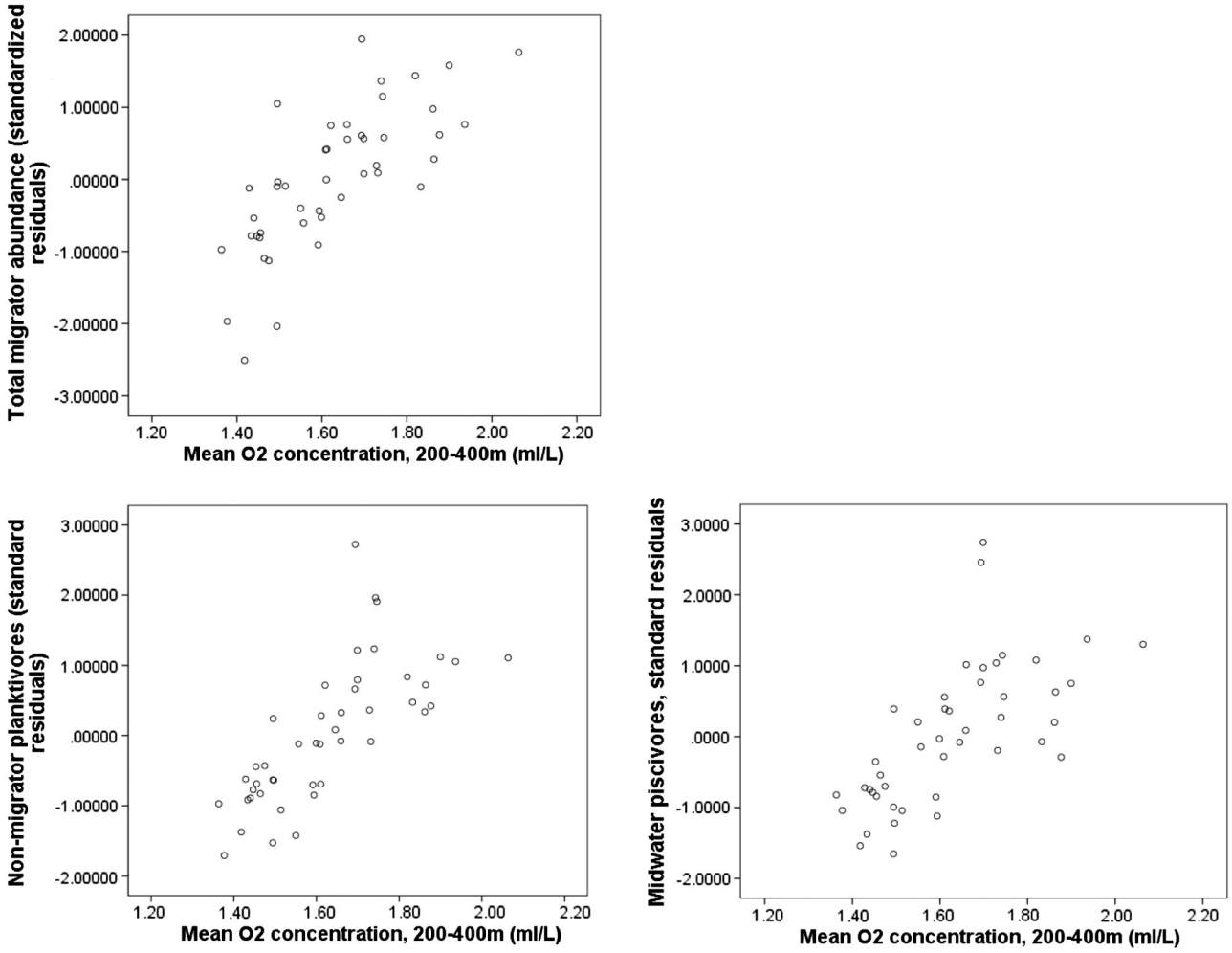

Fig. 3. The standardized residuals for the annual mean abundance of total midwater migratory fishes, non-migratory planktivores and non-migratory piscivores plotted against mean annual oxygen concentration at 200–400 m depth (ml/l). The linear correlations are all highly significant, and the plots indicate nonlinearity with steeper rates of decline at very low oxygen concentrations and asymptotic relationships at relatively high oxygen concentrations.

oceanographic PC 1 (Table 8). There was no significant trend in the time series (correlation with Year: $r = 0.15$, ns).

The oceanographic PC 1 was significantly negatively correlated with the zooplankton PC 1 ($r = -0.42$, corrected $df = 33$, $p < 0.05$) and the combined time series for all epipelagic and mesopelagic migrator planktivores ($r = 0.54$, corrected $df = 31$, $p < 0.01$). When the influence of the physical environment (oceanographic PC 1) and predation (total epipelagic and migratory mesopelagic planktivores) on zooplankton PC 1 was examined jointly in a multiple regression, only the oceanographic PC 1 entered significantly. Its standardized regression coefficient (β) was approximately three-fold larger than that of the planktivores (Table 9). The time series for oceanographic PC 1 and mesopelagic migrators with warm-water affinities were highly correlated ($r = 0.69$, corrected $df = 31$, $p < 0.001$).

Table 3
Correlations of the abundance of diel migratory planktivores, non-migratory planktivores, and mesopelagic piscivores with the abundance of key epipelagic planktivores, northern anchovy, Pacific mackerel, jack mackerel, Pacific hake, and Pacific sardine, based on larval abundances in the CalCOFI area, 1951–2008. Degrees of freedom corrected for autocorrelation shown in parentheses with significance level: ns: $p > 0.10$; †: $p < 0.10$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

	Anchovy	Pacific mackerel	Jack mackerel	Pacific hake	Pacific sardine
Vertical migrators	0.43† (17)	0.46* (23)	0.32* (43)	0.51** (24)	−0.29 ns (19)
Non-migratory planktivores	0.57* (14)	0.62** (19)	0.39** (44)	0.51* (20)	−0.20 ns (17)
Mesopelagic piscivores	0.53* (14)	0.38† (20)	0.21 ns (43)	0.43* (21)	−0.13 ns (17)

4. Discussion

We observe a striking pattern of positive correlations between a large suite of potentially competing mesopelagic planktivores, between mesopelagic planktivores and their midwater predators, and between potentially competing mesopelagic diel migrators and several key epipelagic planktivores, such as northern anchovy, Pacific mackerel, jack mackerel, and Pacific hake (Tables 2, 3). These taxa also display a fairly consistent pattern of marginal-to-significant correlations with a suite of basin-scale ocean environment indices, such as the MEI, PDO, and NPGO (Table 4); some groups were also correlated with coastal sea level, a proxy for the advection of the California Current. Mesopelagic planktivores with southerly biogeographic affinities were also negatively correlated with several key zooplankton taxa with predominantly Transition Zone and sub-Arctic distributions (Table 7). What does this web of correlations tell us about the dynamics of the pelagic ecosystem off southern California?

Correlation analysis is often denigrated ("correlation does not imply causation"). However, correlations may be used to *pose* or to *disprove* hypotheses, consistent with Popperian methodology, as well as to

Table 4
Correlations of the abundance of epi- and mesopelagic planktivores based on larval abundances in the CalCOFI area, 1951–2008 with local oceanographic variables and large-scale ocean environmental indices. All variables except Pacific mackerel, hake, MEI, and NPGO showed significant trend and were detrended. Degrees of freedom corrected for autocorrelation shown in parentheses with significance level: ns: $p > 0.10$; †: $p < 0.10$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. Degrees of freedom not corrected for non-significant correlations.

	O_2 (200–400 m)	SST (10 m)	Upwelling	Sea level (SF)	MEI	PDO	NPGO
Migrators	0.74** (14)	0.06 ns (44)	−0.32 * (44)	0.40 ** (44)	0.44 ** (35)	0.29 † (39)	−0.37† (23)
Non-migrators	0.74** (11)	0.13 ns (44)	−0.14 ns (44)	0.39 ** (44)	0.42 ** (33)	0.43** (34)	−0.41 * (22)
Mesopelagic Piscivores	0.67* (11)	0.02 ns (44)	−0.10 ns (44)	0.34 * (44)	0.34 * (34)	0.21 ns (44)	−0.27 ns (20)
Northern anchovy		0.00 ns (44)	0.25 ns (44)	0.14 ns (44)	0.22 ns (44)	0.32 * (40)	−0.17 ns (44)
Jack mackerel		0.29 † (36)	0.25 ns (37)	0.36 * (35)	0.26 † (43)	0.28 † (35)	−0.37 * (28)
Pacific mackerel		0.25 ns (34)	−0.12 ns (44)	0.17 ns (44)	0.30 † (35)	0.59 *** (27)	−0.11 ns (44)
Pacific hake		−0.06 ns (44)	0.06 ns (44)	0.20 ns (44)	0.18 ns (44)	0.32 * (44)	−0.36 * (36)
Pacific sardine		0.14 ns (44)	0.04 ns (44)	−0.03 ns (44)	−0.14 ns (44)	−0.13 ns (44)	0.09 ns (44)

attempt weakly to infer causal relationships. That is the approach we propose to follow here.

Simple food web models, such as Ecopath, and other ecosystem models pose a particular set of hypotheses about the structure and functioning of marine ecosystems. Based on steady state, near-equilibrium conditions, competitive and predator–prey interactions dominate in such models. If resources are limiting, then the abundance of dominant competitors should be negatively correlated with each other, such that increases in one lead to declines in its competitor. Trophic cascades may be observed, with negative correlations between successive trophic levels, as inferred for the northwest Atlantic (Frank et al., 2005). The "wasp-waist" paradigm for eastern boundary currents assumes similar tight coupling between the dominant planktivores in these systems and the zooplankton they prey upon and the piscivores consuming them.

The pattern of correlations observed in our study fails to meet key predictions of these models. First, none of the potentially competing planktivores were negatively correlated, indicating the ecosystem is not near equilibrium and resource-limited. Furthermore, the preponderance of correlations was positive, indicative of bottom-up or other physical forcing.

Are these different taxa indeed competing for resources? Competition is difficult to quantify, and the diet and fine-scale vertical resolution of most midwater taxa in our region are poorly known. However, available studies of our meso- and epipelagic faunas indicate there is substantial diffuse competition (*sensu* MacArthur, 1972) among these taxa in the California Current ecosystem: most taxa feed initially on copepods and prey increasingly on krill and to varying extents other pelagic crustaceans and fish through ontogeny (Arthur, 1976; Emmett et al., 2005; Koslow, 1981; Suntsov and Brodeur, 2008). The lack of significant continental shelf habitat also leads to less onshore–offshore segregation of mesopelagic and epipelagic planktivores in the California Current than in other eastern boundary currents, such as off Peru (Cornejo and Koppelmann, 2006). However, diel differences in feeding and spatial segregation among taxa vertically and horizontally (Checkley et al., 2000; MacCall, 1990) as well as a degree of feeding specialization (Rykaczewski and Checkley, 2008; Suntsov and Brodeur, 2008) no doubt lead to finer-scale resource partitioning, as shown elsewhere (Hopkins and Gartner, 1992).

Although it is difficult to ascertain the precise degree of competitive overlap among meso- and epipelagic planktivores in the California Current ecosystem, the observed pattern of positive correlations among them is difficult to conceive except in a non-equilibrium, non-steady state ecosystem driven predominantly by bottom-up or physical forcing. The large number of species involved in this pattern also brings into question the "wasp-waist" paradigm, which posits that just one or two plankton feeders, such as anchovy and sardine, are critical for food web dynamics in eastern boundary currents. Eleven out of the 20 most abundant taxa in the CalCOFI ichthyoplankton data set are mesopelagic planktivores. Mesopelagic planktivores from three families of fishes, the bathylagid *Leuroglossus stilbius*, the phosichthyid *Vinciguerria lucetia*, and the myctophid *Stenobrachius leucopsarus*, are among the 6 most abundant taxa in the data set (Moser and Watson, 2006).

The general pattern of correlations is not only opposite to that predicted by simple food web models, the correlations between planktivores and oceanographic conditions are also generally opposite to those expected if bottom-up forcing through ecosystem productivity were driving ecosystem dynamics (Table 4). Thus, mesopelagic fishes (both planktivores and piscivores), northern anchovy, Pacific hake, jack mackerel and Pacific mackerel are generally correlated with El Niño (rather than La Niña) conditions, the warm phase of the PDO, high sea level (low southward flow of the California Current), and negatively correlated with the NPGO (low nutrient, low chlorophyll conditions). These are all conditions indicative of low rather than high primary production.

Further, we do not believe that the negative correlation between certain planktivores and potential zooplankton prey supports the hypothesis of top-down forcing. The dominant euphausiid taxa in our

Table 5
Correlations of the summed mean annual abundance of mesopelagic fishes with warm- or cool-water affinities (see Table 1) based on larval abundances in the CalCOFI area, 1951–2008 with local oceanographic variables and large-scale ocean environmental indices. All variables except upwelling, deepwater O_2, MEI and NPGO showed significant trend and were detrended. Degrees of freedom corrected for autocorrelation shown in parentheses with significance level: ns: $p > 0.10$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. Degrees of freedom not corrected for non-significant correlations.

	Warm affinity	Deep O_2	SST	Upwelling	SF Sea level	MEI	PDO	NPGO
Cool affinity	0.25 ns (20)	0.56 ** (18)	−0.24 ns (44)	−0.15 ns (44)	0.04 ns (44)	0.19 ns (44)	0.03 ns (44)	−0.09 ns (44)
Warm affinity		0.63 ** (17)	0.41 * (38)	−0.35 * (37)	0.63 *** (39)	0.50 ** (36)	0.49 ** (38)	−0.47 * (20)

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Table 6
The factor loadings between zooplankton PC 1 and the variables entered into the PC analysis. All zooplankton variables were log-transformed prior to analysis. The factor loadings are equivalent to the correlations of the variable and PC 1 time series. Significance levels are based on the nominal (uncorrected) df (44): *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

	Calanoid copepods	*Euphausia pacifica*	*Thysanoessa spinifera*	*Nematoscelis difficilis*	Displacement volume
Factor loadings	0.85***	0.88***	0.78***	0.43**	0.61***

Table 8
The factor loadings (equivalent to the correlations) between the oceanographic PC 1 and the variables entered into the PC analysis. San Francisco sea level and SST were detrended prior to the PCA. All correlations were significant with 43 df: *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

	SF sea level	SST	Deep O_2	Upwelling	MEI	PDO	NPGO
Factor loadings	0.86***	0.73***	0.59***	−0.44**	0.87***	0.75***	−0.66***

study have cool-water affinities: *E. pacifica*, *N. difficilis*, and *T. spinifera* (Brinton, 1962), as do the dominant calanoid copepods in the California Current, *Calanus pacificus* and *Metridia pacifica* (Rebstock, 2001). These zooplankton taxa were significantly negatively correlated only with mesopelagic plankton feeders with warm water affinities, which suggests that the correlation is based on a common association with ocean conditions fostering either a strong or weak California Current (Table 7). This result is supported by regression analysis, which statistically examined the relative importance of total planktivore abundance in the upper water column (both epipelagic and mesopelagic migrator planktivores) and environmental factors. Only the environmental factors entered the regression significantly; its standardized regression coefficient (β) was approximately three times as large.

What, then, underlies the web of inter-correlations among several key epipelagic planktivorous fishes, the mesopelagic fish fauna, and the zooplankton taxa that we examined? There appear to be several interrelated factors. First, the strong synchrony among diverse mesopelagic families, including migrators and non-migrators, plankton feeders and piscivores (correlations on the order of 0.7–0.9), indicates a single ultimate driver, which we suggest here to be changes in deepwater oxygen concentration. Mesopelagic fishes with cool water and warm water affinities were both highly correlated with midwater oxygen concentration and no other variable (Table 5). Habitat compression and increased vulnerability to predation is a potential proximate cause (Koslow et al., 2011).

Deutsch et al. (2011) showed that the PDO predominantly regulates the pool of sub-oxic intermediate water in the Pacific through its influence on the depth of the deep thermocline and microbial respiration. Midwater oxygen concentration in the California Current, the key driver of mesopelagic fish abundance there, is significantly correlated with the MEI, NPGO, and coastal sea level, a proxy for the advection of the Current, as well as the PDO (Table 10). And the PDO is itself closely correlated as well with coastal sea level ($r = 0.56$, corrected $df = 39$, $p < 0.001$) and SST in the CalCOFI area ($r = 0.61$, corrected $df = 39$, $p < 001$, all time series detrended).

This web of oceanographic interrelations appears to mediate the links between the mesopelagic fauna and key zooplankton taxa and epipelagic plankton feeders in the California Current. In their principal component analysis of the CalCOFI ichthyoplankton data set, Koslow et al. (2013) found that the dominant pattern (PC 1) was of the large number of mesopelagic taxa that were predominantly influenced by changing midwater oxygen conditions. However, their PC 2 and PC 3 time series were most highly influenced by advection of the California Current (coastal sea level) and SST. PC 2, which represented six out of the seven most abundant ichthyoplankton taxa in the CalCOFI time series included both epi- and mesopelagic taxa (*e.g.* anchovy, hake, rockfishes (*Sebastes* spp.), *S. leucopsarus*, and *L. stilbius*) that were either California Current endemics or had cool water affinities. This PC time series was significantly correlated with strong flow of the California Current and cool SST (Pacific sardine also loaded highly on PC 2, but with opposite sign from the aforementioned taxa). PC 3 was predominantly represented by coastal and reef fish species with warm water affinities, and PC 3 was oppositely correlated with coastal sea level and SST. Thus, the correlations between trophic levels (planktivores and zooplankton, mesopelagic piscivores and their planktivorous prey) and between potentially competing meso- and epipelagic planktivores appear to be artifacts, mediated through their correlations with a suite of inter-related local, regional, and basin-scale environmental forcing variables. Di Lorenzo and Ohman (2013) illustrate how the abundance of relatively long-lived pelagic organisms may respond in a time-lagged manner to ocean variability from low frequency forcing such as the PDO.

It may appear anomalous that in our present study we found mesopelagic fishes with tropical/sub-tropical distributions but not those with northerly affinities significantly correlated with indicators of the status of the California Current (Table 5). Smith and Moser (2003) also found that mesopelagic fishes with southerly affinities responded more strongly and consistently than those with northerly affinities to the 1976–1977 regime shift to the warm PDO phase. It appears that only a sub-set of endemics or species with northerly affinities respond to shifts in the California Current, the group extracted by the multivariate analysis as PC 2 in Koslow et al. (2013). In general, however, the tropical/sub-tropical component of the pelagic fauna off southern California appears to be more sensitive to advective processes. The region off southern California is often characterized as a mixing zone between northerly and southerly faunas (Fleminger, 1967). However, the cool water or Transition zone fauna appears to generally dominate (Brinton, 1962), such that the warm water fauna is more dependent on advection into the region during El Niños or warm PDO conditions. This is likely because a frontal zone, sometimes including the Ensenada Front, a recurrent feature separating waters and faunas of sub-Arctic/Transition Zone and warmer water origins, is found at the southern edge of the Southern California Bight and offshore (Haury et al., 1993; Landry et al., 2012; Lara-Lopez et al., 2012; Moser and Smith, 1993). Thus water and faunas of northerly origin generally predominate in the Southern California region, with more southerly water and faunas relying more on anomalous intrusions.

The present study thus affirms the conclusions of an earlier generation of oceanographers (Brinton, 1962; Fleminger, 1967; McGowan, 1971) that the core CalCOFI study area is an ecotone, whose

Table 7
The correlations between mesopelagic migrators with tropical/subtropical affinities and zooplankton taxa. All zooplankton variables were log-transformed prior to analysis. *Thysanoessa spinifera*, *Nematoscelis difficilis*, and zooplankton displacement volume displayed significant trend and were detrended. Degrees of freedom corrected for autocorrelation shown in parentheses with significance level: ns: $p > 0.10$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. Degrees of freedom not corrected for non-significant correlations.

	Calanoid copepods	*Euphausia pacifica*	*Thysanoessa spinifera*	*Nematoscelis difficilis*	Displacement volume
Warm water migrators	−0.61** (19)	−0.49** (28)	−0.34* (31)	−0.23 ns (43)	−0.44* (25)

Table 9
Results of multiple regression analysis showing the standardized regression coefficients (β) for the influence of total planktivores (epipelagic + migratory mesopelagics) and physical oceanographic variables (PC 1) on zooplankton abundance (zooplankton PC 1). The multiple regression overall explained 18.5% of the variance, $p < 0.05$.

	β	t	Significance
Oceanographic PC 1	−0.35	−2.15	0.04
Total planktivores	−0.12	−0.75	0.46

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Table 10
Correlations of midwater oxygen concentration in the southern California Current with regional and local oceanographic indices. Degrees of freedom corrected for autocorrelation shown in parentheses with significance level: ns: $p > 0.10$; †: $p < 0.10$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. Degrees of freedom not corrected for non-significant correlations.

	MEI	PDO	NPGO	SST	Upwelling (33°S × 119°W)	SF sea level
Deep O_2	0.47** (36)	0.39* (34)	−0.39† (23)	0.25 ns	−0.21 ns	0.46** (43)

zooplankton and micronekton fauna is largely linked to major water masses that extend well beyond it. Some of the patterns observed here, such as the coherent response of mesopelagic taxa with both warm and cold water affinities to changes in midwater oxygen concentration, reflect large-scale ecological processes. However, the extent of their spatial coherence across the North Pacific is still not known, although there is considerable coherence within the California Current (Chelton et al., 1982; Lavaniegos and Ohman, 2007). Thus shifts in the abundance of faunas with predominantly cool- or warm-water affinities across the CalCOFI sampling area may largely reflect changes in the transport of the California Current and of the assemblages associated with particular water masses. The predictions of equilibrium-based food web models that assume near-steady state ecological conditions are therefore unlikely to be validated in this dynamic region. Rather, ecological change appears to be dominated by basin-scale drivers, such as the PDO, which drive underlying biogeochemical processes (*e.g.* deoxygenation and denitrification Deutsch et al., 2011), as well as the relative predominance of the region's key water masses. Comparative analysis bringing together data sets from the full extent of the California Current System and from the Transition Zone and sub-Arctic to the north and Equatorial Tropical Pacific to the south will be required to understand the extent of spatial coherence in the Northeast Pacific and the mechanisms that underlie large-scale ecological change.

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