

Climate shifts the interaction web of a marine plankton community

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Abstract

Climatic effects in the ocean at the community level are poorly described, yet accurate predictions about ecosystem responses to changing environmental conditions rely on understanding biotic responses in a food-web context to support knowledge about direct biotic responses to the physical environment. Here we conduct time-series analyses with multivariate autoregressive (MAR) models of marine zooplankton abundance in the Northern California Current from 1996 to 2009 to determine the influence of climate variables on zooplankton community interactions. Autoregressive models showed different community interactions during warm vs. cool ocean climate conditions. Negative ecological interactions among zooplankton groups characterized the major warm phase during the time series, whereas during the major cool phase, ocean transport largely structured zooplankton communities. Local environmental conditions (sea temperature) and large-scale climate indices (El Niño/Southern Oscillation) were associated with changes in zooplankton abundance across the full time series. Secondary environmental correlates of zooplankton abundance varied with ocean climate phase, with most support during the warm phase for upwelling as a covariate, and most support during the cool phase for salinity. Through simultaneous quantitation of community interactions and environmental covariates, we show that marine zooplankton community structure varies with climate, suggesting that predictions about ecosystem responses to future climate scenarios in the Northern California Current should include potential changes to the base of the pelagic food.

Keywords: California Current, climate change, community interactions, MAR models, marine zooplankton, time series analysis

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Introduction

Overwhelming evidence exists that marine species are affected by changing climate conditions (Richardson, 2008; Hoegh-Guldberg & Bruno, 2010; Doney *et al.*, 2012), threatening the delivery of ecosystem goods and services necessary to human well-being. Reducing these threats requires diverse management actions aimed at increasing ecosystem resilience, and based upon a comprehensive understanding of how ecosystem structure and function will respond to changing climate (Lubchenco & Sutley, 2010). However, knowledge of community-level responses to climate change is limited (but see Cloern *et al.*, 2007; Kirby & Beaugrand,

2009), in part because indirect interactions can thwart expectations about biotic responses to environmental conditions (Wootton, 1994; Lytle & Poff, 2004). While the dynamics of individual populations are tightly linked to abiotic conditions (Walther *et al.*, 2002), ecological communities are more complex than simple collections of populations and, therefore, the effects of changing climate on communities cannot be predicted from studies of single, or even pairs of, species (Walther, 2010). Instead, community-wide analyses of long-term data sets (e.g., Atkinson *et al.*, 2004) are necessary to reveal responses to anthropogenic climate change, including the potential for thresholds and regime shifts (Hoegh-Guldberg & Bruno, 2010). Interactions among species structure communities, control energy flow through food webs (Paine, 1980) and influence emergent community properties including stability and resilience (Paine, 1969). Indeed, changes in community interactions can foretell important compositional

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reorganization (Lindegren *et al.*, 2009). Thus, quantifying community interactions, and the influence of climate on such interactions, is key to predicting community structure under future climate change.

The Northern California Current Ecosystem (NCCE) experiences well-documented seasonal, interannual and multi-decadal climate shifts associated with variability in ocean-atmospheric coupling in both the northern and equatorial Pacific Ocean, as characterized by the Pacific Decadal Oscillation (PDO) and El Niño/Southern Oscillation (ENSO), respectively (Francis & Hare, 1994; Mantua *et al.*, 1997). Alternating 'warm' and 'cool' phases in these indices are observable locally as positive and negative anomalies, respectively, in multiple oceanographic characteristics, including upwelling strength, salinity, and sea temperatures. Prolonged periods and extreme values of these anomalies can affect marine biota by expanding pelagic species ranges (Lluch-Belda *et al.*, 2005) or causing population-wide breeding failures of top predators (Sydeman *et al.*, 2006). Fluctuations in these large-scale climate signals have also been associated with changes in zooplankton biomass (McGowan *et al.*, 2003) and community composition (Peterson & Schwing, 2003; Hooff & Peterson, 2006; Mackas *et al.*, 2007). Specifically, copepod community composition cycles seasonally and interannually in association with ocean transport driven by large-scale climate patterns (Keister *et al.*, 2011), such that anomalies in the abundance of several copepod groups on the Oregon coast, which numerically dominate the zooplankton community, fluctuate with ocean currents (Peterson & Miller, 1977; Peterson & Keister, 2003). Furthermore, this shifting composition has been correlated with Pacific salmon survival (Peterson & Schwing, 2003). Sea temperatures and the frequency of large-scale climate cycles in the NCCE, as well as in other large-scale ecosystems, are likely to be different in the future (Auer *et al.*, 2006; IPCC, 2007). Therefore, understanding the effects of climate variability on NCCE plankton communities will be critical to developing adaptive strategies to minimize losses of ecosystem services, such as production of commercially important fishes, which rely heavily on zooplankton for food as juveniles and/or as adults.

Previous analyses of California Current zooplankton time series have shown long-term trends, as well as shifts associated with large-scale climate patterns in zooplankton abundance and species composition. Long-term declines in California Current zooplankton, as measured by displacement volume, have been observed in the latter half of the 20th century (Roemmich & McGowan, 1995). This trend, however, is not observable when zooplankton abundance is expressed as biomass (Lavaniegos & Ohman, 2007), and the bio-

volume decline may be owing to long-term declines in pelagic tunicates high in biovolume:biomass ratios (Lavaniegos & Ohman, 2003). Long-term increases in the abundances of individual plankton groups and species have been observed during the latter half of the 20th century, including in foraminifera (Field *et al.*, 2006), and siphonophores, appendicularians and polychaetes (Lavaniegos & Ohman, 2007). These long-term trends may be associated with warming (Roemmich & McGowan, 1995; Field *et al.*, 2006) and/or changes in density stratification of the water column (Lavaniegos & Ohman, 2007). Zooplankton communities also vary with large-scale climate drivers during the same time period. For example, the abundance of 'cool phase' pelagic tunicates declined (Lavaniegos & Ohman, 2003), and step changes in the abundance of calanoid copepods occurred (Rebstock, 2002) with the PDO shift of 1976–1977. At the same time, no ecosystem shift in zooplankton biomass or biovolume was observed in the latter half of the 20th century (Lavaniegos & Ohman, 2007), and community composition has been stable in copepods (Rebstock, 2001) but variable in pelagic tunicates (Lavaniegos & Ohman, 2003) across decadal regime shifts. While there have been many assessments of the varied responses of zooplankton abundance to climate and environmental variables through time, to date there has been little effort to describe California Current zooplankton interactions, and how those interactions respond to climate drivers.

Zooplankton populations are apt organisms for assessing the effects of climate conditions over long periods of time, as their relatively short generation times, and little legacy of population trends and effects from year to year, allow direct assessment of the effects of environmental conditions. Previous studies have demonstrated that zooplankton are responding to changing ocean conditions throughout the world's large marine ecosystems (Richardson, 2008; Kirby & Beaugrand, 2009; Loeb *et al.*, 2009). Here, we assess the effects of ocean climate change on zooplankton interactions in the NCCE through time series analysis of zooplankton abundances collected biweekly between 1996 and 2009 on the coast of Oregon, USA. With this long data set, we compare interaction networks during the major cool (8/1998–3/2002) and warm (8/2002–8/2005) climate phases during the time period (Fig. 1a). Simultaneously, we determine the key environmental correlates of zooplankton abundance to gain additional insight into how changing climate conditions might affect the base of the pelagic food web in the NCCE. Of particular interest here is the quantitation of interactions among community constituents, as interaction strength is a key component of food web models that predict community dynamics (Paine, 1980).

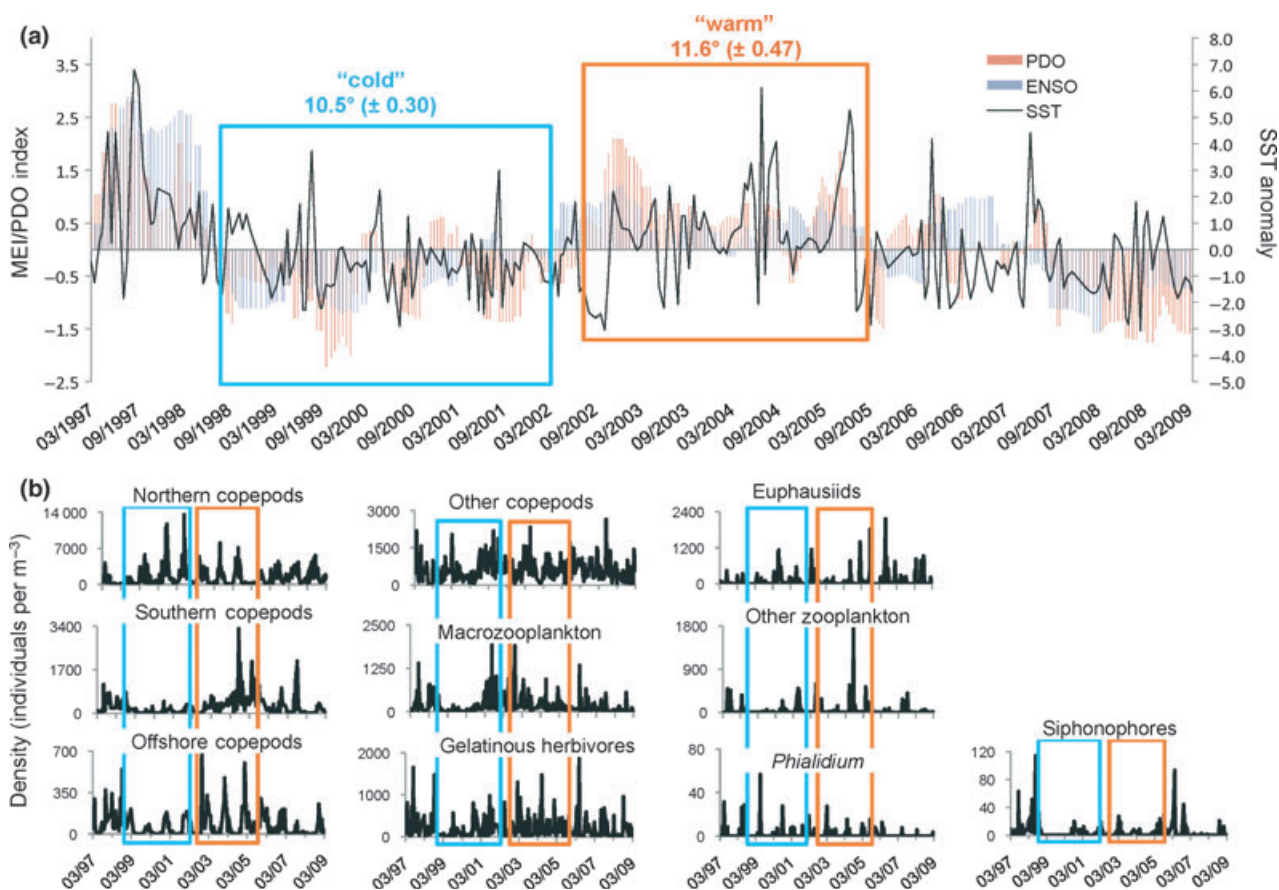


Fig. 1 Time series from 3/1997 to 4/2009 of (A) the Multivariate ENSO Index (MEI), Pacific Decadal Oscillation (PDO) and seasonal anomalies of sea surface temperature (SST); and (B) zooplankton sampled at station 5 on the Newport Hydrographic Line. Boxes are drawn around the major cool phase (blue), when the MEI and PDO were predominantly negative, and the major warm phase (orange), when the MEI and PDO were predominantly positive. Mean (SEM) temperature shown for each phase. SST is taken at 1 m depth during zooplankton sampling at Newport Hydrographic Line Station 5 (NH05).

Materials and methods

Data analysis

To investigate the effects of climate phase shifts on NCCE zooplankton, we used a time series of zooplankton collected off the coast of Oregon, USA, from 1996 to 2009. Zooplankton were collected at roughly biweekly intervals from the near-shore station of the Newport Hydrographic Line (station NH05), located 9 km from shore (44.65N, 124.18W) and at 60 m water depth. Sampling and laboratory methods have been detailed elsewhere (Peterson *et al.*, 2002; Peterson & Keister, 2003) and will be described briefly here. Zooplankton were collected using a 202 μm mesh net fitted to a 50 cm diameter bongo hauled vertically from 55 m depth to the surface. Over 95% of zooplankton samples were collected during daytime hours. In the laboratory, 1.1 mL subsamples were extracted from each sample, all zooplankton were identified by species and developmental stage (where possible), and the density of each taxonomic group (number of individuals per m^{-3}) was calculated. Our target was to count 200–400 individual

zooplankters per sub-sample, and to this end we enumerated zooplankton in between 2 and 5 subsamples.

For all analyses, we aggregated > 125 zooplankton species and life stages into 10 groups (see Table S2), including three previously identified copepod groups associated with specific regions in the eastern Pacific Ocean: 'Northern,' 'Southern,' and 'Offshore' copepods (Peterson & Keister, 2003; Hooff & Peterson, 2006). Anomalies in the abundance of these copepod groups, which numerically dominate the zooplankton at the study site (Fig. S1), are associated with ocean conditions and large-scale climate indices (Peterson & Miller, 1977; Peterson & Keister, 2003). The remaining zooplankton taxa were aggregated into seven additional groups based on trophic overlap and previous work (Ruzicka *et al.*, 2007). Subsequent to aggregation, but prior to analysis, zooplankton densities were log-transformed to improve the model fit (Ives, 1995), and standardized to a zero mean and unit variance to increase ease of comparison among zooplankton groups with very different abundances. We generated two time series representing two different sampling intervals: monthly means from 4/1998 to 9/2008, used for environmental covariate model selection; and

a biweekly time series incorporating the full set of dates, used for estimation of community interactions and secondary environmental drivers. We used linear interpolation to fill missing dates, and zeros in the data were replaced with a random number between zero and the minimum raw density observed for each taxon/life stage (Hampton & Schindler, 2006). Simulation exercises showed that the irregularity of the time series did not bias the results based on the biweekly intervals (see Supporting Information).

We included several environmental and climate variables as covariates in our model of zooplankton abundance through time. Local environmental variables that often are associated with zooplankton dynamics, and which were measured concurrently with zooplankton collection, included temperature (surface and at 50 m depth), salinity (at 50 m depth), chlorophyll *a* (surface), and density stratification (as density differences between the surface and 30 m, and the surface and 50 m), a measure of water column stability associated with salinity. In addition, because abundances of several zooplankton groups vary in concert with large-scale climate signals in the NCCE (Fig. 1b), we included as environmental covariates in the model the PDO index (<http://jisao.washington.edu/pdo/PDO.latest> for a description and data) and the Multivariate ENSO Index (MEI; calculated by Klaus Wolter at NOAA's Earth System Research Laboratory, <http://www.esrl.noaa.gov/psd/people/klaus.wolter/MEI/table.html>). Because the effects of both ENSO and the PDO on ecosystem processes along the Oregon Coast are delayed by 1–4 months, we included MEI and the PDO at lags from 0 to 4 months. We also included the monthly mean coastal upwelling index derived for 45N, 125W (Environmental Research Division of NOAA's Pacific Fisheries Environmental Laboratory, <http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html>). We also assessed the effect of planktivory on zooplankton abundance, calculated as an aggregate planktivore biomass based on quarterly model estimates from 1998 to 2008 of the major planktivores in the system (Ruzicka *et al.*, 2007). Finally, because most zooplankton species exhibit strong seasonal cycles in abundance, we included two terms in the model to account for seasonality (Ives *et al.*, 1999; Hampton & Schindler, 2006; Hampton *et al.*, 2006): month (i.e., month number of the year) and (month)².

MAR modeling

A complete description of multivariate autoregressive (MAR) models is given by Ives *et al.* (2003) and they will be described briefly here. MAR models are stochastic models describing change in population abundance through time. Fitting a MAR model to population abundance time series allows for simultaneous quantitation of the effects of community interactions and environmental covariates on abundance, while accounting for temporal autocorrelation in abundance data and population density dependence. In matrix form, MAR models are written as:

$$\mathbf{X}_t = \mathbf{A} + \mathbf{B}\mathbf{X}_{t-1} + \mathbf{C}\mathbf{U}_{t-n} + \mathbf{E}_t, \quad (1)$$

where \mathbf{X}_t is the (log-transformed) community abundance vector at time t , \mathbf{A} is a vector of constants representing intrinsic growth rates; \mathbf{B} is the community interaction matrix,

in which the diagonal elements represent self effects (i.e., density dependence) and the off-diagonal elements represent effects between groups, such as predation or competition; \mathbf{C} is the matrix of environmental effects on abundance; \mathbf{U} is the matrix of environmental covariates at a chosen time lag n ; and \mathbf{E} is a vector of process errors.

Here we use both biweekly and monthly time steps, depending on the model. We assessed which environmental variables were the best correlates of zooplankton abundance by including environmental covariates in the MAR model (using monthly time steps) one at a time, and comparing each model fit using Akaike's Information Criterion (AIC; Hampton *et al.*, 2006; see Supporting Information for details). Next, because this exercise showed that large-scale climate variables (ENSO and PDO) were strong correlates of zooplankton abundance across the full time series, we compared zooplankton community interactions during the major cool (8/1998–3/2002) and warm (8/2002–8/2005) ENSO and PDO phases in the time series (Fig. 1a) using biweekly time steps. Abundances of several of the copepod groups vary in synchrony with these large-scale climate shifts (Fig. 1b). Lack of statistical power precluded our ability to estimate community interactions during strong but shorter climate shifts in the time series (e.g., the strong El Niño event of 1997–1998).

To compare community interactions during the two climate phases, we fixed the effects on zooplankton abundance of the environmental covariates chosen by the above model selection exercise, and used the resulting set of observations to estimate community interactions and local environmental effects at a biweekly sampling interval. We compared community interaction networks between (1) the full time series, (2) the warm period and (3) the cool period. We also compared the interactions estimated for the warm and cool climate periods with interactions estimated for 216 random consecutive time periods, each equal in length to the shorter warm climate period and starting with every possible date in the time series, to ensure that the observed differences between warm and cool periods were not due to random chance. MAR modeling was performed in MATLAB (2007, The MathWorks), using the open-source program LAMBDA (freely available from <http://conserver.iugo-cafe.org/user/e2holmes/LAMBDA>) and additional programming by the authors.

Results

Autoregressive models revealed different zooplankton interaction networks in warm and cool climate periods (Fig. 2; Table 1), which were in turn distinct from interactions across the full time series and in random time series (Table S1). The interaction network during the warm phase included many significant negative interactions, many of which were absent from the matrix estimated for the cold phase. There were significant negative effects of Northern Copepods on Offshore Copepods and Euphausiid Eggs/Larvae. Southern Copepods also had a negative effect on Offshore Copepods during the warm phase. There was a negative effect of Offshore Copepods on Other Zooplankton. Negative

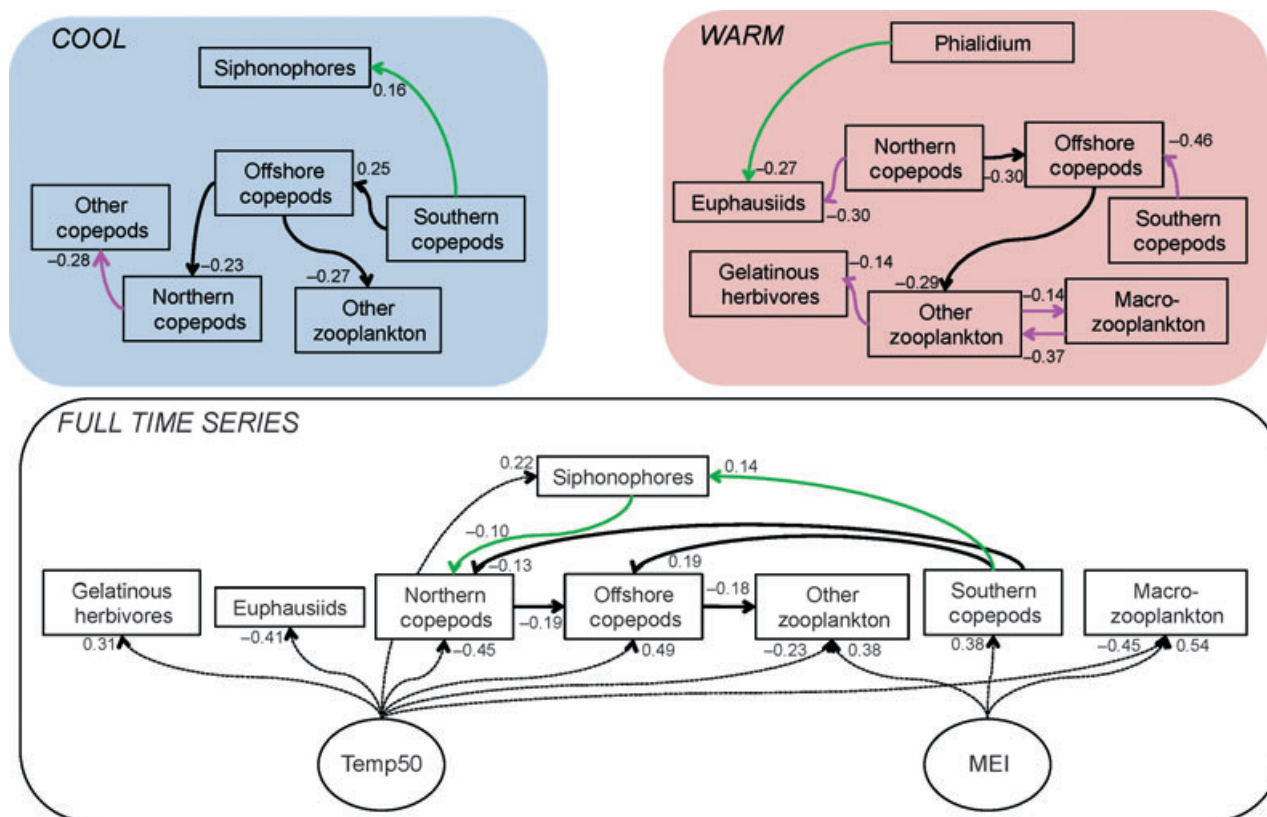


Fig. 2 Zooplankton community interactions in the Northern California Current during cool and warm phases, and across the full time series. Only groups with significant interspecific interactions are shown. Green arrows indicate predator-prey interactions, fuchsia arrows indicate competition; solid black arrows indicate community composition shifts resulting from transport of zooplankton; dashed black arrows indicate environmental effects. Interspecific coefficients are given next to arrows. Model fit statistics (conditional and regular R^2 values) are given in Table S6. Zooplankton aggregations are given in Table S1.

coefficients were estimated between Other Zooplankton, a group primarily comprised of the branchiopod *Podon*, and Macrozooplankton, an aggregation of mostly bivalve and barnacle larvae. Other Zooplankton also had a negative effect on Gelatinous Herbivores, dominated by the larvacean *Oikopleura*. Finally, predatory *Phialidium* had a negative effect on Euphausiid Larvae/Eggs.

The autoregressive model of the cool climate phase identified fewer significant negative interactions: Northern Copepods had a negative effect on Other Copepods; and Offshore Copepods had negative effects on Northern Copepods and Other Zooplankton. Positive interaction coefficients were also estimated by the MAR model of the cool phase, of Southern Copepods on Offshore Copepods, and of Other Copepods on predatory Siphonophores (Fig. 2).

Bivariate abundance plots of zooplankton pairs reveal two patterns associated with negative interactions identified by the MAR model (Fig. 3). First, asynchronous cycles exist between transient zooplankton groups, groups whose abundance on the

Oregon coast has been previously associated with seasonal ocean currents that drive compositional shifts in the coastal zooplankton community (Fig. 3a). Bivariate plots between non-transient zooplankton groups, i.e., those zooplankton groups whose abundance is not driven by advection, show no such seasonal asynchrony (Fig. 3b). These interactions may potentially represent biological interactions, e.g., competition or predation.

Across the entire time series, we found greatest support for a model that included sea temperature at 50 m depth (Temp50) and the MEI lagged 6 weeks, meaning that MEI values were strongly related to zooplankton densities 6 weeks later (Fig. 2; Table S4). We found little support for models that included chlorophyll, planktivory, or density stratification as covariates of change in zooplankton abundance.

The MEI had a positive effect on abundances of Southern Copepods, Macrozooplankton and Other Zooplankton (Fig. 2; Table S5). Among the models contributing to 98% of the total AIC weight was one that

Table 1 Inter- and intraspecific interaction coefficients estimated by MAR models, with fixed effects of El Niño and temperature (see text). Shown are mean (\pm 95% confidence intervals) coefficient estimates for the cool phase and warm phase. Inter-group interactions (off-diagonal elements) strengthen as they approach 1, and intra-group (i.e., density dependence; diagonal elements) interactions weaken as they approach 1. *Phialidium* were not retained in the model of the cool phase

Warm Phase	NoCo	SoCo	OffCo	OtherCo	Eu	GelHe	Mac	OtZo	Phia	Siph
NoCo	0.66 [0.47, 0.8]									
SoCo		0.38 [0.15, 0.57]								
OffCo	-0.3 [-0.48, -0.15]	-0.46 [-0.83, -0.08]	0.54 [0.27, 0.69]							
OtherCo				0.54 [0.33, 0.72]						
Eu	-0.3 [-0.58, 0]				0.47 [0.25, 0.64]				-0.27 [-0.46, -0.09]	
GelHe						0.44 [0.19, 0.64]		-0.14 [-0.26, -0.02]		
Mac							0.27 [0.04, 0.47]	-0.14 [-0.26, -0.02]		
OtZo			-0.29 [-0.57, -0.03]				-0.37 [-0.7, -0.03]	0.41 [0.19, 0.6]		
Phia									0.4 [0.19, 0.59]	
Siph										0.31 [0.1, 0.51]
Cool phase	NoCo	SoCo	OffCo	OtherCo	Eu	GelHe	Mac	OtZo	Siph	
NoCo	0.34 [0.14, 0.51]		-0.23 [-0.39, -0.09]							
SoCo		0.39 [0.16, 0.61]								
OffCo		0.25 [0.09, 0.41]	0.47 [0.26, 0.64]							
OtherCo	-0.28 [-0.56, -0.02]			0.57 [0.37, 0.74]						
Eu					0.38 [0.2, 0.56]					
GelHe						0.24 [0.05, 0.7]				
Mac								0.55 [0.35, 0.70]		
OtZo			-0.27 [-0.48, -0.05]						0.35 [0.15, 0.52]	
Siph		0.16 [0.01, 0.32]								

NoCo, Northern Copepods; SoCo, Southern Copepods; OffCo, Offshore Copepods; OtherCo, Other Copepods; Eu, Euphausiids; GelHe, Gelatinous Herbivores; Mac, Macrozooplankton; OtZo, Other Zooplankton; Phia, *Phialidium*; Siph, Siphonophores.

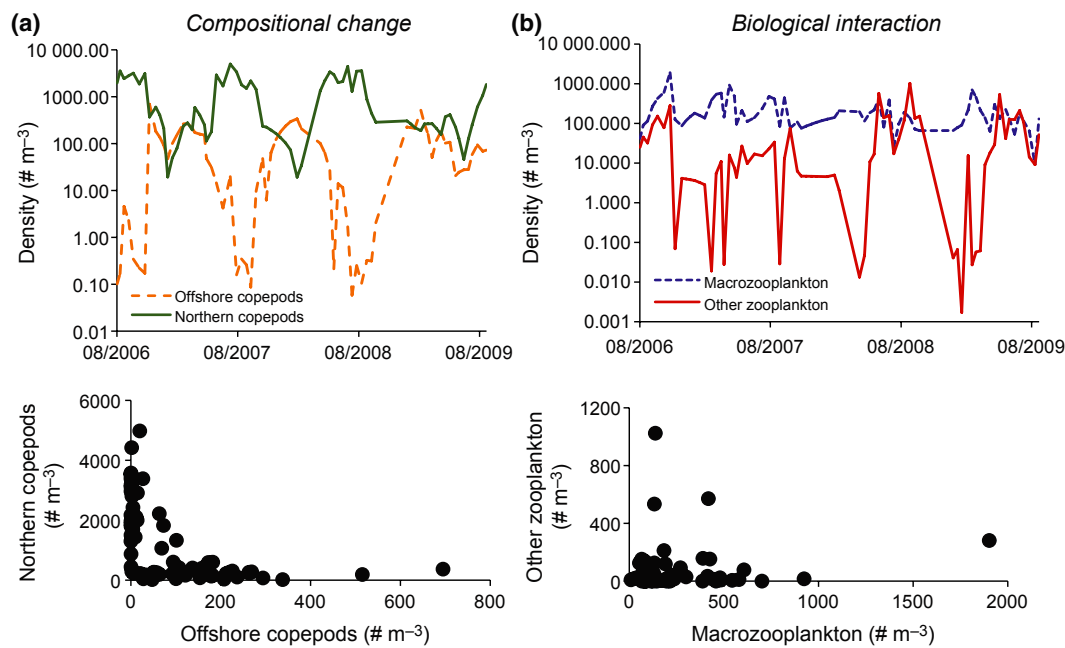


Fig. 3 Zooplankton time series showing two types of negative interactions during the ‘warm’ climate phase: biological interaction (competition), and compositional change. Competition appears as a negative correlation (bottom left panel) without clear evidence of seasonal discordance (top left panel). In contrast, compositional shifts appear as a negative correlation (bottom right panel) with seasonal asynchrony (top right pane). Dates for all data are 8/2002–8/2005.

Table 2 Best fit model interaction coefficients for the local environmental covariates during the warm and cool climate phases. Shown are bootstrapped mean values with 95% confidence intervals in brackets

Climate phase	Covariate	Zooplankton group	Coefficient
Warm	Upwelling	Northern Copepods	0.77 [0.45, 1.11]
		Other Copepods	1.12 [0.69, 1.67]
		Euphausiids	0.82 [0.25, 1.45]
		Gelatinous Herbivores	0.38 [0.08, 0.68]
Cold	Salinity	Southern Copepods	−0.34 [−0.54, −0.15]
		Offshore Copepods	−0.34 [−0.49, −0.20]
		Macrozooplankton	0.21 [0.03, 0.41]
		<i>Phialidium</i>	0.29 [0.06, 0.52]

included the PDO lagged 12 weeks (Table S4), a result that confirms previous conclusions about time lags between the PDO signal and zooplankton abundance on the Oregon coast (Hooff & Peterson, 2006). There was most support for upwelling as an environmental covariate during the warm phase, after fixing the effects of temperature and MEI, affecting most groups positively (Tables 2 and S4). During the cool phase, in contrast, salinity received the most model support. Increased salinity was associated with lower densities of copepods from equatorial (Southern Copepods) and offshore waters (Offshore Copepods).

Discussion

Based on a priori knowledge of potential ecological interactions among community constituents, interaction matrix coefficients estimated by MAR models can be interpreted to represent biological interactions (Ives *et al.*, 2003). For example, negative interactions can represent competition (between potentially competitive groups) or predation (between predators and prey). Positive coefficients can represent bottom-up effects of a prey on its predator, or facilitation. Likewise, interaction coefficients may be associated with other patterns driving changes in abundance. In the NCCE, where zooplankton community composition shifts result from passive ocean transport (Keister *et al.*, 2011), negative coefficients among groups affected by transport can be additionally interpreted as cohort replacements associated with advection by ocean currents (Fig. 3). Similarly, positive coefficients may represent coherent increases in abundance driven by ocean currents.

During the cool phase, we found that most negative interactions estimated by the MAR model represented seasonal asynchrony either between transient groups (Offshore vs. Northern copepods), or between transient and non-transient groups (Offshore Copepods vs. Other Zooplankton, and Northern Copepods vs. Other Copepods). Similarly, several negative interactions during the warm phase were between transient groups

(Northern vs. Offshore Copepods, and Southern vs. Offshore copepods) and between transient and non-transient groups Northern Copepods vs. Euphausiids, Offshore Copepods vs. Other Zooplankton). The mechanism behind alternating cycles of Northern, Southern, and Offshore copepods has been related to changes in advection of surface waters in the NCCE that occur both seasonally or during El Niño events (Hooff & Peterson, 2006), and interannually as driven by the PDO (Keister *et al.*, 2011). Southward flows of cool, sub-Arctic Pacific water masses bring a higher abundance of boreal copepod species to the Oregon coast. During warmer conditions, increasing influence of the northward-flowing Davidson current brings increased abundance of both subtropical coastal (Southern) and oceanic (Offshore) copepod species (Hooff & Peterson, 2006). Thus, during the cool phases, a positive effect of Southern Copepods on Offshore Copepods represents coherent seasonal increases in abundance when densities of Southern and Offshore copepods are low on the Oregon coast, and advection of offshore waters brings Southern Copepods and Offshore Copepods to coastal waters (Hooff & Peterson, 2006). In contrast, during warm conditions when Southern Copepods abundances are anomalously high, seasonal downwelling transports Offshore Copepods to coastal waters while production of Southern Copepods, already located onshore, declines owing to weakened upwelling and low primary productivity, resulting in a negative interaction between Southern and Offshore copepods. Ordination analyses of the time series data supported this interpretation of interaction coefficients, identifying unique community compositions during cool and warm phases (Fig. S2; Table S3), a result that has been found in previous studies (Mackas *et al.*, 2001, 2007; Morgan *et al.*, 2003; Peterson & Keister, 2003; Hooff & Peterson, 2006).

Overall, the warm phase interaction matrix included more interactions not associated with zooplankton whose abundance is controlled by ocean transport than the cool phase. There were several additional negative interactions estimated by the MAR model of the warm phase that did not involve transient copepod species, including between Other Zooplankton, primarily comprised of the cladocerans *Podon* and *Evadne* (Table S2), and two other zooplankton groups: Macrozooplankton, an aggregation of mostly bivalve and barnacle larvae; and Gelatinous Herbivores, dominated by the larval *Oikopleura* (Fig. 2; Table S2). *Oikopleura* and most of the taxa comprising Macrozooplankton are particle-feeders that ingest prey ranging in size from 1 to 250 μm but favor particles $< 25 \mu\text{m}$, primarily ciliates and dinoflagellates (Urban *et al.*, 1992; Acuna *et al.*, 1996; Katechakis & Stibor, 2004; Sanchez *et al.*, 2011).

The cladocerans found on the Oregon coast also ingest small particles including ciliates, nanoflagellates, picoplankton and diatoms (Katechakis & Stibor, 2004; Katechakis, 2005). Thus, there is overlap in the preferred prey of these groups, indicating the potential that the negative interaction coefficient represents competition among these groups. Alternatively, the two-way negative interaction could reflect seasonal variation in food availability, i.e., small particles (favoring Macrozooplankton and Gelatinous Herbivores) vs. diatoms (favoring Other Zooplankton). In coastal California, small-celled phytoplankton and small zooplankton are favored by nutrient-limiting conditions, while high-nutrient conditions found in onshore upwelling zones favor larger phytoplankton and larger zooplankton (Ryckaczewski & Checkley, 2008). While we found no significant difference in the abundance of these small-particle selecting zooplankton taxa between the low-productivity warm phase and high-productivity cool phase, the potential competition among taxa over smaller-sized prey may signify that this prey type is limited during warmer conditions.

The MAR model also estimated effects of interactions between gelatinous zooplankton predators and other zooplankton taxa. During the cool phase, increased abundance of siphonophores, carnivorous colonial hydrozoa that prey predominantly on copepods, was positively associated with increases in Southern Copepods (Fig. 2), suggesting siphonophore populations are supported by increases in these copepods. Additionally, across the full time series, siphonophores had predatory effects on Southern Copepods and Northern Copepods and their density was positively associated with temperature (Fig. 2; Table 1). *Phialidium*, small, predatory hydroids, had a negative effect on Euphausiid eggs/larvae during the warm period. *Phialidium* show strong preference for egg prey in the Pacific Northwest (Costello & Colin, 2002), as do larger jellyfish species in the NCCE not sampled here (Brodeur *et al.*, 2008b), and here they appear to be selecting Euphausiid eggs as prey during the warm climate phase. These results suggest that the effects of predacious jellyfish populations, which include trophic overlap with planktivorous fishes (Brodeur *et al.*, 2008b), may be enhanced by warmer temperatures, as has been suggested for larger scyphomedusae jellyfish in the Bering Sea (Brodeur *et al.*, 2008a).

Across the full time series, there was most support for a model that included ocean temperature and ENSO. Temperature and ENSO have been previously correlated with copepod biodiversity at this site (Hooff & Peterson, 2006), and here temperature had a positive effect on Offshore Copepods and Siphonophores, no effect on Southern Copepods or *Phialidium*, and a nega-

tive effect on all other groups (Fig. 2; Table S5). While predictions about the effects of climate change on the NCCE vary, future conditions may include changes in sea temperature and the frequency and intensity of regional climate signals (Lee & McPhaden, 2010), and therefore these results suggest that climate change is likely to affect zooplankton community dynamics.

The secondary correlates of zooplankton abundance varied between cool and warm periods. During the warm phase, there was most support for a model that included upwelling. Coastal upwelling is a key structuring feature of the NCCE at multiple trophic levels (Morgan *et al.*, 2003; Peterson & Keister, 2003; Brodeur *et al.*, 2005; Scheuerell & Williams, 2005). During the annual summer upwelling season, southward flow transports boreal copepod species to the Oregon coast; this increased abundance is reflected in a positive effect of upwelling, forced by alongshore winds, on the Northern Copepod group. In addition, nutrient delivery from deep waters to surface waters during upwelling periods fuels primary production and boosts zooplankton populations, reflected in the positive effects of upwelling on non-transient zooplankton groups, including Other Copepods and Gelatinous Herbivores. During the warm climate phase, the baseline abundances of Northern Copepods and other non-equatorial taxa are typically lower, thus the effect of upwelling on these groups may be stronger during the warm phase than the cold. During the cool period, in contrast, the best model of zooplankton abundance included salinity as a secondary environmental correlate, which was negatively associated with copepods whose abundances are relatively depressed during cool conditions. This reflects the seasonal upwelling of deeper, more saline water masses to coastal habitats and associated transport of Southern and Offshore copepods offshore during summer.

Though there was little support in the data for chlorophyll *a* as a driver of zooplankton abundance, both ENSO and the PDO are strongly correlated with chlorophyll in the Pacific at different time lags (Fig. S3), and we assume the effect of chlorophyll is incorporated into the regional climate coefficients. Nevertheless, it is worth noting that there was more support in the MAR model for environmental variables associated with water transport (upwelling, salinity) than for bottom-up forcing. Both the community interactions and key environmental covariates show that there is a fundamental shift between warm and cool phases in the importance of climate/oceanographic processes in structuring the NCCE zooplankton community.

While the appropriateness of using observational data in food web models to describe interaction strength has been demonstrated (Wootton, 1997), cau-

tion should be exercised in interpreting interaction coefficients. Here, we use a conservative approach, limiting possible interactions in the model to only ecologically reasonable ones, such as competition among competing grazer zooplankton groups or predation between known predator and prey groups. Furthermore, rather than interpreting interaction coefficients precisely, we take a qualitative view of our results, concluding that community interactions among zooplankton groups are different between the two ocean climate phases. Estimating mean effects during the warm and cool phases, as well as across the full time series, achieves two ends: First, it reveals interactions that are specific to a unique climate phase that might otherwise be lost by estimating mean interactions across the full time series. Second, it dampens the effects of single-season events (e.g., the delayed spring transition of 2005) by averaging effects across a wide range of dates. Also, by deliberately using a MAR(1) model (i.e., estimating interaction effects with a lag of a single time step), we deliberately ignore potential biotic interactions occurring at lags > 2 weeks that could be important in structuring zooplankton communities in the North Pacific.

Our results demonstrate that climate-induced changes in fundamental ecosystem properties propagate up through pelagic food webs and alter zooplankton community dynamics and abundance. Although there is uncertainty about exactly how climate change will alter oceanographic conditions in the NCCE, there is little doubt that conditions will be different, and our results may foretell a fundamental shift in zooplankton communities in the future. In particular, these results suggest that the configuration of community interactions will vary, as will changes in the relative importance of biological interactions vs. abiotic structuring forces. Because zooplankton are key prey resources in the NCCE pelagic food web, we can expect climate change would also have consequences for upper trophic levels of immense economic and cultural value. While it is difficult to extrapolate from intra-annual variation to future trends, these results point to the likelihood that the Northern California Current Ecosystem of the future may depart dramatically from its current state.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Interaction coefficients estimated by MAR models for full time series and 216 random models.

Table S2. Zooplankton aggregation key.

Table S3. Constrained Analysis of Principal Components (CAP) scores.

Table S4. Covariate model selection AIC scores.

Table S5. Interaction coefficients for full time series including temperature and MEI.

Table S6. Conditional and R^2 values for best fit models of the full time series.

Figure S1. Zooplankton community composition.

Figure S2. Ordination analysis results.

Figure S3. Cross-correlations between chlorophyll, MEI and PDO.

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