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CCE IV: El Niño-related zooplankton variability in the southern California Current System

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ABSTRACT

We analyzed seven El Niño events (springs 1958–59, 1983, 1992–93, 1998, 2003, 2010, and 2016) and the 2014–15 Pacific Warm Anomaly (spring 2015) for their impacts on zooplankton biomass and community composition in the southern sector of the California Current System (CCS). Although total mesozooplankton carbon biomass was only modestly affected during El Niño springs, community composition changed substantially. Carbon biomass of five major zooplankton taxa correlated negatively with San Diego sea level anomaly (SDSLA), a regional metric of El Niño physical impacts in the CCS. Additional taxa were negatively related to SDSLAs via a time-lagged response reflected in an autoregressive-1 (AR-1) model. All five SDSLAs-correlated taxa decreased in carbon biomass during most El Niño years compared to the surrounding years; the exception was the mild event of 2003. Principal Component Analysis revealed coherent species-level responses to El Niño within the euphausiids, copepods, and hyperiid amphipods. Percent similarity index (PSI) comparisons showed pronounced changes in the compositions of euphausiid and, to a lesser extent, calanoid copepod communities during El Niño. By grouping El Niños into Eastern Pacific (EP) versus Central Pacific (CP) events based on their expressions along the equator, we found that CCS zooplankton assemblages showed a tendency toward greater changes in species composition during EP than CP El Niños, although we had low statistical power for these comparisons. Several species showed consistent biomass changes across La Niña events as well, generally opposite in sign to El Niño responses, but overall community composition showed minimal change during La Niña. Carbon biomass and community composition returned to pre-Niño levels within 1–2 years following almost every event, suggesting high resilience of southern CCS zooplankton to El Niño perturbations to date.

1. Introduction

El Niño is a coupled atmosphere-ocean phenomenon that develops in the equatorial Pacific, with global impacts (Liu and Alexander, 2007). El Niño occurs when the equatorial Pacific trade winds weaken or reverse, and westerly wind bursts induce eastward propagation of Western Pacific Warm Pool waters via subsurface Kelvin Waves (Wyrtki, 1975; Cane, 1983; McPhaden, 1999). El Niño can significantly alter the highly productive ecosystems in the equatorial Pacific, particularly off South America. Studies have observed decreased magnitude and spatial extent of primary production (Cowles and Barber, 1977; Barber et al., 1996; Foley et al., 1997; Chavez et al., 1998) and reduced biomass of commercial fish stocks and guano-producing seabird populations (Barber and Chavez, 1983, 1986; Schreiber and Schreiber, 1984; Arcos et al., 2001; Chavez et al., 2003) associated with El Niño.

El Niño events vary widely in their physical expressions and biological impacts. ENSO variability has gained significant attention in recent years due in part to NOAA's 2003 official designation of the phenomenon as a sustained three-month period of SST anomalies in the central equatorial Pacific (Larkin and Harrison, 2005). This definition identified several central Pacific warm events that had not been previously detected off South America. Subsequent studies have investigated whether El Niño events dichotomize into Eastern Pacific (EP or 'canonical') versus Central Pacific (CP, also 'Dateline' or 'Modoki') events or span a continuum of expressions and forcing mechanisms. One view posits that EP events are caused by strong Kelvin Wave propagation from the Warm Pool to the eastern equatorial Pacific, while CP events are caused by local atmospheric forcing at the International Dateline (Ashok et al., 2007; Yu and Kao, 2007; Kao and Yu, 2009). A contrasting view suggests that all El Niño events are mixtures of these

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two types of forcing, and that variations in expression are due to the strength and timing of westerly wind bursts (Chavez et al., 1999; Karnauskas, 2013; Capotondi et al., 2015). El Niño can affect higher latitudes via three mechanisms: 1) coastally-trapped waves (CTWs, known as remote forcing) (Alexander et al., 2002; Schwing et al., 2002); 2) atmospheric teleconnections from the equator (Simpson, 1984; Strub and James, 2002; Frischknecht et al., 2015); or 3) anomalous advection of warm, saline water of southern or western origin into the CCS (Simpson, 1984; Bograd and Lynn, 2001; Lynn and Bograd, 2002; Jacox et al., 2016). Strong Kelvin Wave propagation associated with EP El Niños is thought to induce poleward-migrating CTWs, while CP-focused El Niños tend to show stronger evidence for atmospheric teleconnections to mid-latitudes (Chavez, 1996; Ashok et al., 2007; Frischknecht et al., 2015). The question of El Niño variability in the equatorial Pacific, and connective mechanisms to higher latitudes, is essential for our understanding of how El Niño affects mid-latitude ecosystems.

The California Current System (CCS) is a mid-latitude eastern boundary upwelling system home to a range of large pelagic species and commercially-valuable fisheries (Hickey, 1979; Chelton et al., 1982). A typical CCS El Niño response includes elevated ocean temperatures and sea surface height (SSH), depressed thermocline and nutricline, and increased poleward flow of the Inshore Countercurrent (Hayward, 1993; Chavez, 1996; Lynn and Bograd, 2002). El Niño-related physical perturbations can significantly alter biological production in the CCS. Primary production generally decreases and contracts nearshore (Fiedler, 1984; Hayward, 1993; Chavez, 1996; Kahru and Mitchell, 2000; Chavez et al., 2002), and the phytoplankton community can switch from diatom to picoplankton dominance due to reduced nutrient inputs (Chavez, 1996). Mesozooplankton have shown decreased biomass and reduced dominance by resident cool species during El Niño (Smith, 1985; Mullin, 1998), as well as low community similarity to other years (Rebstock, 2001). Non-resident offshore and southerly euphausiid species generally associate with El Niño-related warm water intrusions into the southern CCS (Brinton, 1960, 1981; Brinton and Townsend, 2003). However, individual El Niño event responses can vary widely. Some recent El Niños lacked evidence for CTWs and increased poleward flow (Simpson, 1984; Todd et al., 2011), suggesting variability in forcing mechanisms underlying individual events. Although some El Niño years show increases in subtropical euphausiid species off Southern and Baja California, and corresponding decreases in resident cool-water species (Brinton, 1981; Lavaniegos et al., 2002; Marinovic et al., 2002), other events do not have major associated influxes of subtropical species (Todd et al., 2011). Fisher et al. (2015) found that the magnitude of copepod community anomalies in the northern CCS correlated positively with both the magnitude and duration of El Niño events, and that years tended to group into EP versus CP responses. Similarly, Pares-Escobar et al. (2018) found significant variability in summer euphausiid communities off Baja California between 1998 and 2008, a period encompassing two EP and two CP El Niños, suggesting that zooplankton may respond differently depending on the type of equatorial El Niño.

CCS El Niños generally correlate with equatorial events, but several El Niños have also persisted in the CCS for 1–2 years beyond the initial equatorial perturbation, and some years show anomalous CCS conditions without associated equatorial changes (Fiedler and Mantua, 2017). Recently, the 2014–15 Pacific Warm Anomaly occurred in the Eastern North Pacific with no corresponding significant equatorial El Niño signal (Di Lorenzo and Mantua, 2016; Chao et al., 2017). The combination of perturbations from the 2014–15 Warm Anomaly and 2015–16 El Niño produced a 2–3 year period of positive temperature and negative nutrient anomalies in the CCS (Bond et al., 2015; Di Lorenzo and Mantua, 2016; Frischknecht et al., 2017), only partially interrupted by spring upwelling in 2015 (Jacox et al., 2016; Kahru et al., 2018). The 2014–15 Warm Anomaly was notable because 1) it produced much greater temperature anomalies than any previous CCS

warm event (Zaba and Rudnick, 2016), and 2) it preceded, rather than followed, an equatorial El Niño (Fiedler and Mantua, 2017). The Warm Anomaly may provide a glimpse into potential future ocean conditions of a warmer background state against which El Niño events occur.

The mechanisms by which El Niño influences CCS mesozooplankton are still not well understood. Quantifying variability in mesozooplankton community structure in response to individual events will help identify dominant forcing mechanisms of change, which can then be used to predict future El Niño-related mesozooplankton shifts and associated impacts on higher trophic levels. Toward this goal, the present paper addresses the following questions:

1. At what taxonomic level are CCS mesozooplankton responses to El Niño most pronounced?
2. Do CCS mesozooplankton respond consistently across all El Niños of the past 66 years?
3. Do responses vary between Eastern Pacific and Central Pacific El Niños?
4. How do the 2014–15 Warm Anomaly and 2015–16 El Niño compare to each other and to past El Niño events with respect to mesozooplankton shifts?
5. How resilient are CCS mesozooplankton to El Niño?

This study provides an initial analysis and categorization of El Niño-related mesozooplankton shifts in the southern CCS. We recognize the importance of spatial variations within the larger region, and of decadal-scale changes in background Eastern North Pacific conditions, but we focus here explicitly on the variability between individual El Niño events.

2. Methods

2.1. Study region

Our study focused on the southern region of the California Current System (CCS), defined as California Cooperative Oceanic Fisheries Investigations (CalCOFI) lines 80–93.3, stations 26.7–70 (SC region, cf., Lavaniegos and Ohman, 2007; see that publication for a map of the region). The region extends from just north of Pt. Conception, CA, south to the U.S.-Mexico border, and encompasses the southward-flowing core California Current and the northward-flowing Inshore Countercurrent and California Undercurrent.

2.2. El Niño indices

We used a combination of two equatorial Pacific El Niño indices and two local California Current System (CCS) indices to define El Niño occurrences that had an expression in the CCS. The Niño 3.4 (5°S–5°N, 170–120°W) and Niño 1 + 2 (0–10°S, 90–80°W) indices measure sea surface temperature (SST) at two different regions in the equatorial Pacific Ocean (Climate Prediction Center, 2017). The two local CCS indices are: San Diego detrended sea level anomaly (SDSLA) and the depth of the 26.0 kg/m³ density isopycnal in the nearshore 50 km along CalCOFI Line 90 ($Z_{26.0}$). The SDSLAs timeseries is maintained by the University of Hawaii Sea Level Center (University of Hawaii Sea Level Center, 2017). The SDSLAs data used here are monthly average anomalies, from which the seasonal cycle and long-term trend (1906–2016) were removed (data processed specifically using this method are available at: <http://oceaninformatics.ucsd.edu/datazoo/catalogs/ccelter/datasets/153>). Our $Z_{26.0}$ index was constructed using data from the CalCOFI program, which samples four times per year. CalCOFI density measurements are obtained from hydrocast bottle samples at discrete depths; for our index, the data were then interpolated between bottle depths to resolve the depth of the 26.0 kg/m³ isopycnal. Data for the index are only from CalCOFI Line 90, Stations 26.7–37, encompassing the nearshore 50 km, based on a similar $Z_{26.0}$

timeseries from Jacox et al. (2016) computed from merged Regional Ocean Modeling System (ROMS) and *Spray* glider *in situ* measurements, encompassing the time period 1981–2016. Our CalCOFI $Z_{26.0}$ index had a highly significant correlation with the ROMS-*Spray* index ($r = 0.89$, $p < 0.01$), confirming the suitability of using either index. We chose to utilize only the CalCOFI-based index here because it extends back to 1951, corresponding to the beginning of our zooplankton timeseries. The purpose of using both the SDSLA and $Z_{26.0}$ indices in our analyses is to capture different aspects of El Niño expression in the CCS: sea level anomaly can change due to changes in horizontal advection or local heating of water masses, while $Z_{26.0}$ is closely related to nutricline depths and primary production and can also be affected by local upwelling and wind changes (Jacox et al., 2016).

For each of the four El Niño indices, we calculated one average value per year based on wintertime monthly values (equatorial indices – November, December, and January (NDJ) average; CCS indices c December, January, and February (DJF) average). Each El Niño year refers to January of the average (e.g., ‘1958’ means Nov 1957–Jan 1958 for equatorial indices and Dec 1957–Feb 1958 for CCS indices). We chose to average these months because: 1) previous studies have shown that El Niño peak anomalies occur along the equator in November–December and in the CCS in January–February (Jacox et al., 2015); and 2) CCS zooplankton taxonomic analyses are only available in spring (sampled in March, April, or May) of each year, and we expect a two-three month time lag between CCS physical disturbances and zooplankton responses.

2.3. CCS El Niño classification

For this study, we defined El Niño perturbations in the CCS (hereafter: CCS El Niños) as three-month winter averages (see above) in which at least one Equatorial Index (Niño 3.4 or Niño 1 + 2) and at least one CCS index (SDSLA or $Z_{26.0}$) were both ≥ 1 S.D. above their respective long-term means. The following years fulfill these criteria: 1958, 1973, 1983, 1992, 1998, 2003, 2010, and 2016. CalCOFI did not sample zooplankton during spring 1973, so we removed that year from our analyses. We included 1959 and 1993 as El Niño Years 2 although they did not classify at the equator, because they were continuations of prior-year CCS El Niño events and were ≥ 1 S.D. in at least one CCS index. The equatorial signal during the 2014–15 Warm Anomaly was negligible (only > 0.5 S.D. in the Niño 3.4 Index) and the event was not considered an equatorial El Niño by NOAA standards, but we include 2015 in our analyses because of its extreme and unusual signals in the CCS. Therefore, our list of CCS El Niño Springs (indicating the spring period at the end of the fall-to-spring CCS El Niño cycle) is: 1958, 1959, 1983, 1992, 1993, 1998, 2003, 2010, and 2016, and the 2015 Warm Anomaly.

The Niño 1 + 2 index only reached ≥ 1 S.D. for years already classified by Niño 3.4, but we retained Niño 1 + 2 for use as a secondary means to categorize El Niño variability. Eastern equatorial Pacific-focused El Niño events (EP) are defined here as years when both the Niño 3.4 and Niño 1 + 2 indices exceed ≥ 1 S.D. (with corresponding ≥ 1 S.D. in at least one CCS index). Using this secondary classification, the CCS El Niño events classify as follows: EP – 1983, 1998, 2016; CP – 1958–59, 1992–93, 2003, and 2010. We did not classify the 2015 Warm Anomaly as either type of event.

We also defined a set of La Niña years for the CCS using the above metrics, where La Niña events are ≤ 1 S.D. below the mean. Under these criteria, the following are CCS La Niña Years: 1951, 1956, 1965, 1971, 1989, 1999, 2000, and 2008. CalCOFI zooplankton were not collected in 1971, so we excluded that year from our analyses. The same inter-year comparative analyses were performed on La Niña as on El Niño years. We considered 1999 and 2000 to be separate La Niña events because both years expressed significantly at the equator and the CCS.

2.4. Zooplankton data

2.4.1. Data collection and processing

Zooplankton samples were taken on quarterly CalCOFI cruises from 1951 to 2016 (reduced sampling years during the 1970s). Sampling net specifications changed during that period: from 1951 to 1968, a 1-m ring net with 550 μm mesh was towed obliquely from 0 to 140 m depth; from 1969 to 1977, 1-m ring net with 505 μm mesh was towed obliquely from 0 to 210 m; and since 1978 a twin-opening 0.71-m diameter bongo net with 505 μm mesh net has been towed obliquely from 0 to 210 m (Ohman and Smith, 1995). The effects of these changes on mesozooplankton have been discussed by Brinton and Townsend (1981), Ohman and Smith (1995), Ohman and Lavaniegos (2002), and Rebstock (2002), and do not influence the results presented here. Volumes filtered were based on calibrated flowmeter readings. Samples were preserved in sodium borate-buffered formaldehyde and archived in the Pelagic Invertebrate Collection at Scripps Institution of Oceanography.

CalCOFI spring zooplankton samples were enumerated by microscopy to species level where possible, otherwise to higher taxa. The carbon content of each organism was obtained from taxon-specific length-carbon regressions (Lavaniegos and Ohman, 2007), and summed to calculate total carbon biomass. Samples were pooled for all nighttime stations within the sampling domain described above, except for 14 years when samples were enumerated by individual station (unpooled samples) to assess long-term changes in spatial variability (see Lavaniegos and Ohman, 2007). Unpooled samples were then averaged across all stations in the sampling domain to create a consistent time-series across pooled and unpooled samples. Our purpose was to analyze the temporal variability within a standardized region, not to analyze within-region sampling variability. This approach has been successfully adopted for our sampling region by previous studies (Rebstock, 2001; Rau et al., 2003; Mackas et al., 2006; Lavaniegos and Ohman, 2007; Ohman et al., 2009).

Biomass was standardized to mg C m^{-2} to correct for changes in sampling depth, which could influence volumetric measurements. Salp abundances (used to calculate biomass) were multiplied by a net-correction factor of 2.68 for samples prior to 1978, to account for more accurate collection by the bongo net. See Lavaniegos and Ohman (2007) for full sampling details.

2.4.2. Copepod and euphausiid species

Our analyses involved two categories of copepod enumerations. The total copepods category includes length measurements for every copepod in a subsample, regardless of taxonomic order or life history stage. These copepods were not identified to species. A separate category, calanoid copepods, was enumerated to calanoid species. The calanoid community is a subset of the total copepods, but because animals are enumerated from separate subsamples, we cannot subtract the calanoid component from the total copepods. Therefore, for our analyses, we analyzed both categories (total copepods, calanoid copepods) for taxon-level biomass shifts, but only one category (calanoid copepods) for species-level assemblage shifts. Only adult female calanoid copepods were identified, except for *Neocalanus cristatus* and *N. plumchrus*, which only occur as copepodid stage 5 (C5) in the SC region. For three species (*Calanus pacificus*, *Eucalanus californicus*, *Rhincalanus nasutus*), adult males and C5s were also enumerated, but for consistency we used only the adult females in our analyses.

Euphausiids were enumerated to species and life history phase and/or length class (cf., Brinton and Townsend, 2003), from all individual nighttime samples within the region described above, then converted to carbon content from length-carbon relationships from Ross (1982).

2.4.3. Community-level analyses

Three taxa (euphausiids, calanoid copepods, hyperiid amphipods) showed significant correlation with at least one CCS El Niño index

(SDSLA or $Z_{26.0}$) and had sufficient species-level enumerations for more detailed taxonomic analyses. These three taxa were analyzed for species-level community (assemblage) shifts, where the community contained the consistently-enumerated species throughout the whole period (1951–2016). For this purpose, the euphausiid community includes 24 species, the calanoid copepods 40 species (a few enumerations could only be made to genus level, but were made consistently and are therefore included), and the hyperiid amphipods 13 species. Many additional rarer species are known from the region.

The hyperiid amphipod total biomass category includes all hyperiid amphipods and is therefore greater than the sum of the 13 individually enumerated species. Numerous hyperiids could only be identified to genus or family level, so we used only the 13 consistently identified species in order to understand species-level assemblage changes. For analyses involving taxon-level biomass, however, we used total hyperiid amphipod biomass.

Within the above three taxa, we also analyzed individual species that showed significant El Niño-related loadings in our Principal Component Analysis (PCA). We used the SDSLAs-correlated principal component to determine El Niño-responsive species within that taxon. Each taxon-specific threshold was determined visually based on a loading value surpassed by 6–9 species (generally several each of positive and negative correlations). For euphausiids, the loading threshold of PC1 was $|0.25|$; for calanoids, the PC2 threshold was $|0.20|$; for hyperiids, the PC1 threshold was $|0.30|$. Based on the sign of each species' loading on the PC, species were categorized as warm versus cool, where warm species are those with a positive correlation of PC loading with SDSLAs, suggesting elevation during El Niño events.

2.5. Data analysis and statistical treatments

All statistical computations and plots were run in R version 1.0.136 (R-core-team, 2015).

2.5.1. Log-transformations

Nearly half of the higher taxa and species analyzed here had non-normal distributions for untransformed biomass data, so we analyzed all data in \log_{10} -transformed form unless otherwise noted. Data are plotted with 95% confidence intervals (C.I.) calculated from the t-distribution. Euphausiid biomass has C.I.s for every year because data were always enumerated by individual station and then combined into a southern California (SC) regional average. We make no attempt to correct for temporal autocorrelation in timeseries because our sampling points are annual, a longer time-interval than the lifespan of most zooplankton.

2.5.2. El Niño vs. surrounding average biomass

For comparisons of biomass between El Niño and surrounding years, we calculated 'surrounding' as the average of the two years immediately preceding El Niño Year 1, and the second and third year following El Niño Year 1 or Year 2 (where applicable). For example, for the 1958–59 El Niño, surrounding biomass = mean(1956,1957,1961,1962), whereas for the 1983 El Niño, surrounding biomass = mean(1981,1982,1985,1986). We implemented the one-year lag to account for lagged biological responses due to reproduction. We used a Wilcoxon signed-rank matched pairs test to detect directional changes in biomass across El Niño years compared to surrounding average biomass.

2.5.3. Magnitude of zooplankton responses vs. magnitude of physical changes

The magnitude of the difference for each index (SDSLA, $Z_{26.0}$, zooplankton biomass, hereafter: $\text{mag}(\Delta\text{index})$) was calculated for each El Niño year minus its respective four-year surrounding average using the same method described in Section 2.5.2. The 2015 and 2016 events had only a two-year surrounding average (2013–14), because data were not

yet available after 2016.

2.5.4. Principal Component Analysis (PCA)

Prior to performing PCA, we standardized log-transformed biomass data for each taxon or species within a group using species mean and standard deviation. Standardized biomass = (individual yearly biomass-mean biomass)/SD(all biomass).

2.5.5. Percent Similarity Indices

Percent Similarity Indices (PSI) were calculated from Whittaker (1952):

$$PSI = 100 - 0.5 \sum |A_i - B_i| = \sum \min(A_i, B_i)$$

where A_i and B_i represent the percentages of species i in samples A and B , respectively. Untransformed biomass data were used for these calculations in order to assess proportions of each taxon within the community. PSIs were calculated for the total mesozooplankton (at the level of 15 taxa, hereafter referred to as "higher taxa"), and for species-level analyses of the euphausiid, calanoid copepod, and hyperiid amphipod communities. PSI calculations for each El Niño year were performed for two comparisons: 1) El Niño versus every other El Niño year, and 2) El Niño versus every non-El Niño year, using a Mann-Whitney U test.

3. Results

3.1. Physical indicators of El Niño in the CCS

California Current System El Niño events (CCS El Niños), as defined by our classifications, are indicated by vertical grey bands in Fig. 1. Each event is labeled by the year-spring of the latter portion of the event. Equatorial and CCS El Niño indices correlated significantly with

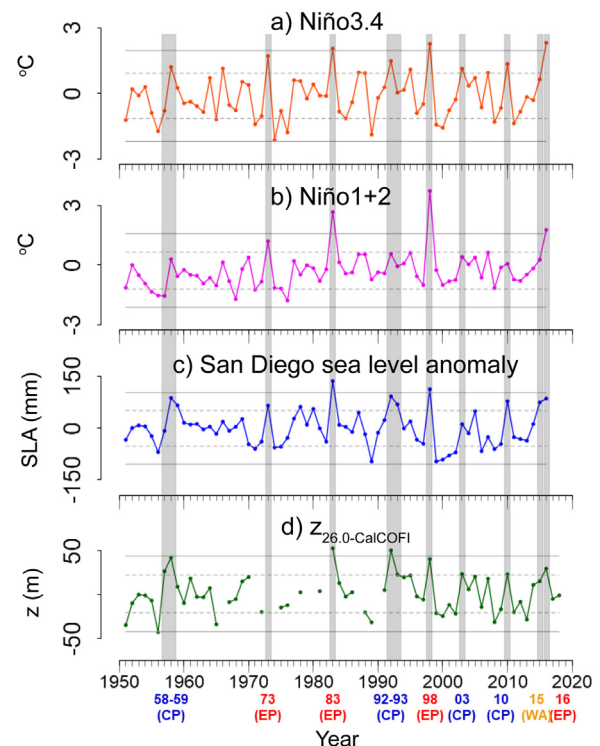


Fig. 1. El Niño indices. Equatorial: a) Niño 3.4, b) Niño 1 + 2; and California Current System-specific: c) San Diego sea level anomaly (SDSLA), d) $Z_{26.0} - \text{CalCOFI}$. Anomalies are from long-term mean; single three-month average per year. Horizontal grey lines indicate ± 1 S.D. (dashed) and ± 2 S.D. (solid). Vertical grey bars denote CCS El Niño years identified for this study. Labels are Eastern Pacific (EP) and Central Pacific (CP) El Niños and the 2014–15 Warm Anomaly (WA).

Table 1

Correlation coefficients between El Niño environmental indices. ** = $p < 0.01$.

	Niño 1 + 2	SDSLA	Z _{26.0}
Niño 3.4	$r = 0.81$ ($p < 0.01$)**	$r = 0.76$ ($p < 0.01$)**	$r = 0.77$ ($p < 0.01$)**
Niño 1 + 2	-	$r = 0.62$ ($p < 0.01$)**	$r = 0.65$ ($p < 0.01$)**
SDSLA	-	-	$r = 0.79$ ($p < 0.01$)**

each other, although Niño 3.4 had higher correlation values with CCS metrics than did Niño 1 + 2 (Table 1). Only three of the El Niño years (1983, 1998, 2016) for which we also had zooplankton data were classified as Eastern Pacific (EP) El Niños, although 1992 was just below the Niño 1 + 2 threshold. All other El Niños, including 1992–93, were classified as Central Pacific (CP) events (Fig. 1).

3.2. Total mesozooplankton- and taxon-level shifts

3.2.1. Biomass changes during El Niño

3.2.1.1. Responses to physical changes. Total mesozooplankton carbon biomass showed a weak but non-significant ($p > 0.25$) relationship with both CCS El Niño indices (Fig. 2a). However, five taxa correlated significantly ($p < 0.05$) with at least one CCS index, in all cases declining during El Niño: euphausiids, polychaetes, calanoid copepods, hyperiid amphipods, and appendicularians. Although thaliaceans (salps, doliolids, pyrosomes) and pelagic molluscs (pteropods and heteropods) showed small positive associations with the CCS El Niño indices, they were not significant ($p > 0.20$). We further analyzed the carbon biomass timeseries with first-order autoregressive-modeled biomass timeseries (AR-1-models, damping time scale $\tau = 3$ months, cf., Di Lorenzo and Ohman, 2013) forced by SDSL A and Z_{26.0} (Fig. 2b). Unlike measured carbon biomass, total mesozooplankton AR-1-modeled biomass correlated negatively with SDSL A ($p < 0.01$). All of the above El Niño-correlated taxa except hyperiid amphipods also correlated negatively with AR-1-modeled biomass, as did several additional taxa: chaetognaths, ostracods, and total copepods ($p < 0.05$).

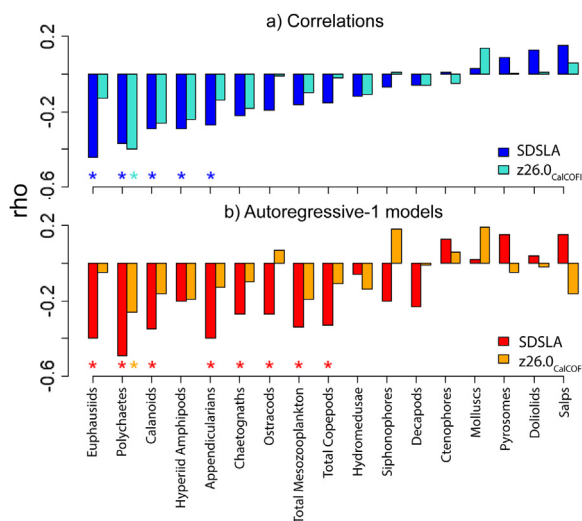


Fig. 2. Correlation coefficients for a) measured log C biomass versus SDSL A and Z_{26.0}, and b) AR-1-modeled C biomass (forced by SDSL A or Z_{26.0}) versus measured log C biomass for each major taxon. AR-1 models used damping scale of $\tau = 3$ months. Asterisk (*) = $p < 0.05$, color-coded by physical index. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

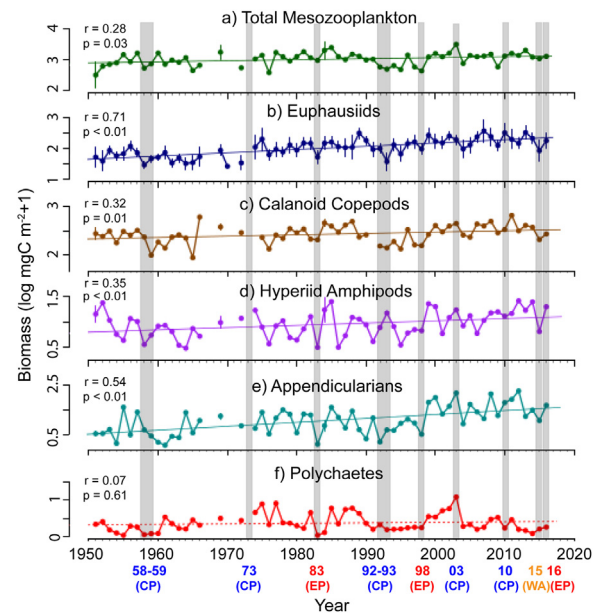


Fig. 3. Timeseries of log C biomass for a) total zooplankton, and the five taxa that correlated significantly with SDSL A: b) euphausiids, c) calanoid copepods, d) hyperiid amphipods, e) appendicularians, f) polychaetes. Linear trends and associated correlation coefficients are shown. The purpose of the linear trend-line is to indicate the overall non-stationarity of the timeseries, not to apply a descriptive model to the timeseries changes. Vertical grey bars indicate El Niño years (labels as in Fig. 1). Error bars indicate $\pm 95\%$ confidence interval.

Total mesozooplankton carbon biomass, as well as four of the five taxa that covaried with SDSL A, showed significant long-term upward trends (Fig. 3, $p < 0.05$). In order to avoid comparisons confounded by such long-term secular trends and other changes in background ocean state (e.g., due to the Pacific Decadal Oscillation, Mantua et al. 1997), we have chosen to compare individual El Niño events only to their four immediately surrounding years. We also

found that SDSL A yielded stronger correlations than Z_{26.0} for all analyses, so we do not further report Z_{26.0} results.

3.2.1.2. Consistency of biomass changes across El Niño events. Fig. 4 compares biomass of each El Niño year with its four-year surrounding average, for total mesozooplankton and the five El Niño-responsive taxa. Only total calanoid copepod biomass showed a significant directional change across all El Niño events (Fig. 4c; Wilcoxon signed rank = 32, $p = 0.05$). Total mesozooplankton and all five taxa increased in biomass during the weak El

Niño of 2003, and euphausiid biomass also increased in 2010 (Fig. 4b). All four taxa besides polychaetes had larger biomass decreases during the 2015 Warm Anomaly than during the 2016 El Niño, when all biomasses returned to average or slightly elevated levels. We further consider responses to individual events, including possible differential responses to EP versus CP events, below.

3.2.1.3. Magnitude of biomass change in relation to physical forcing. Only polychaetes and chaetognaths had weak negative correlations ($p < 0.10$) of the magnitude of change in biomass between El Niño and the surrounding four years with the corresponding

magnitude of change in SDSL A. This suggests that the magnitude of change in biomass of higher taxa during an El Niño event is not determined by event magnitude.

3.2.1.4. Biomass resilience to El Niño. Total mesozooplankton and the four El Niño-related taxa besides appendicularians returned to pre-El Niño biomass levels within one year following each event except 1992–93 and 2003 (Fig. 3; see Suppl. Fig. 1 for changes in additional

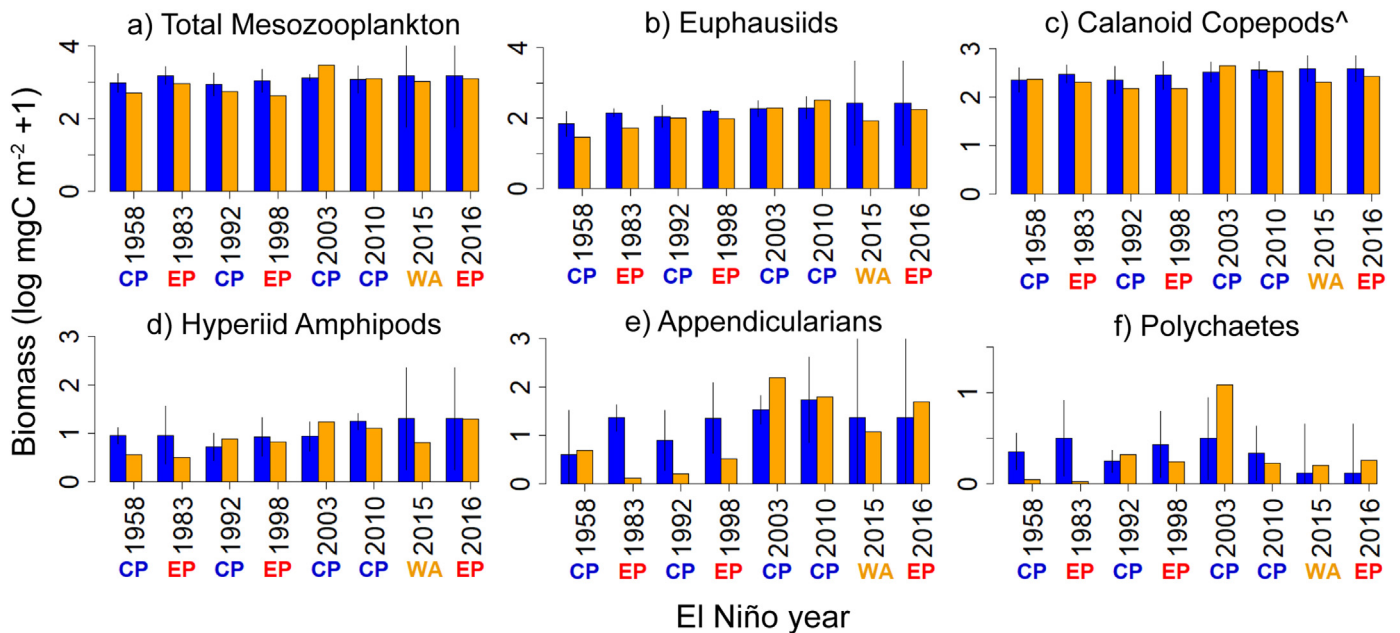


Fig. 4. Comparisons of log C biomass during El Niño years (light orange bars) and average log C biomass of the 4 surrounding years (dark blue bars). Error bars are 95% confidence interval for surrounding averages. Year labels indicate El Niño year. Only El Niño Years 1 are shown (1959 and 1993 of two-year events excluded). \wedge = $p = 0.05$ (Wilcoxon matched pairs signed-rank test). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

taxa). Biomass of the above taxa remained at low levels after 1992–93, while biomass for all taxa declined substantially in the 1–3 years after 2003 from elevated levels during the event.

3.2.2. Community compositional changes during El Niño

3.2.2.1. Consistency of community composition across El Niño events. We used the percent similarity index (PSI) as a measure of how similar zooplankton communities (assemblages) were between individual El Niño events (Fig. 5). The total mesozooplankton community, differentiated into 15 higher taxa, did not show a consistently higher similarity of El Niño years to other El Niño years than similarity between El Niño years and non-El Niño years (Fig. 5a; orange dots indicate PSI values comparing a given El Niño year to each other individual El Niño; blue dots indicate PSI between that El Niño year and each individual non-El Niño year. Bars are the color-coded median values for the two types of comparisons. See figure caption for details). Both types of comparisons had similar ranges of values, and no El Niño year yielded a significant difference between medians for the two types of comparisons (Fig. 5a; $p > 0.30$ for all, using Mann-Whitney U test). Median PSIs were overall high (~ 0.80), except for 1983 (PSI < 0.40), which had a substantially lower PSI because of extremely high proportions of salps compared to all other years. When salps were removed, all PSI values and both median comparison values for 1983 were ~ 0.80 .

Species-level compositional changes within individual higher taxa were often much greater than changes in the total community analyzed at the level of higher taxa. The euphausiid community had significantly higher median PSIs for community comparisons between El Niño years (Fig. 5b, orange symbols) than for El Niño versus non-El Niño comparisons (blue symbols; $* = p < 0.01$). The only non-significant comparisons were 1959, 2003 (identical median PSIs), and 2015. These results imply that the community of euphausiid species generally shifts to a relatively consistent “El Niño” composition that differs significantly from non-El Niño years. Additionally, the 1983 and 1998 El Niños showed largest differences in median euphausiid community composition from all other years, suggesting that these events may have produced greater community impacts or had different forcing mechanisms than other El Niño events.

In contrast, the calanoid copepod community did not show consistently higher inter-El Niño similarities than El Niño versus non-El Niño, suggesting that the species composition of the calanoid community does not shift to one consistent composition during El Niño, but that individual events can produce quite different community compositions. Only two years had significant differences between inter-El Niño and El Niño versus non-El Niño median values: 2003 (higher El Niño/non-El Niño comparison) and 2015 (higher inter-El Niño comparison; Fig. 5c). Three El Niño years (1983, 1992, 1998) showed somewhat higher inter-El Niño median comparison values but no significant difference between the two types of medians ($p > 0.05$).

In contrast to both of the above taxa, the hyperiid amphipod assemblage showed no significant difference between median values for the two types of comparisons during any El Niño event (Fig. 5d). Additionally, median similarity values were the lowest (~ 0.40 – 0.60) of the four taxa analyzed, and the 2015 medians were notably low (PSI < 0.30). This finding of overall low similarity suggests that the hyperiid amphipod assemblage varies more between any given individual years than specifically in response to El Niño perturbations.

3.2.2.2. Magnitude of community change in relation to physical forcing. Only the calanoid copepod species-level community showed a significant correlation between the magnitude of change of community composition during El Niño and the corresponding magnitude of change of SDSLA across El Niño years relative to their four-year surrounding averages (Fig. 6, $r = 0.67$, $p < 0.05$). The euphausiid community showed a significant correlation when the 2010 El Niño was excluded ($r = 0.82$, $p = 0.01$).

3.2.2.3. Community composition resilience to El Niño. To test for mesozooplankton community resilience to El Niño, we analyzed the total mesozooplankton community and the three species-enumerated taxa for PSI of each El Niño compared to its preceding five and following five years (Fig. 7). In nearly all cases, communities returned to pre-El Niño similarity by the following year. One exception was the euphausiid

community in 1958–59, which gradually returned to pre-El Niño levels over the following three years. The calanoid copepod community

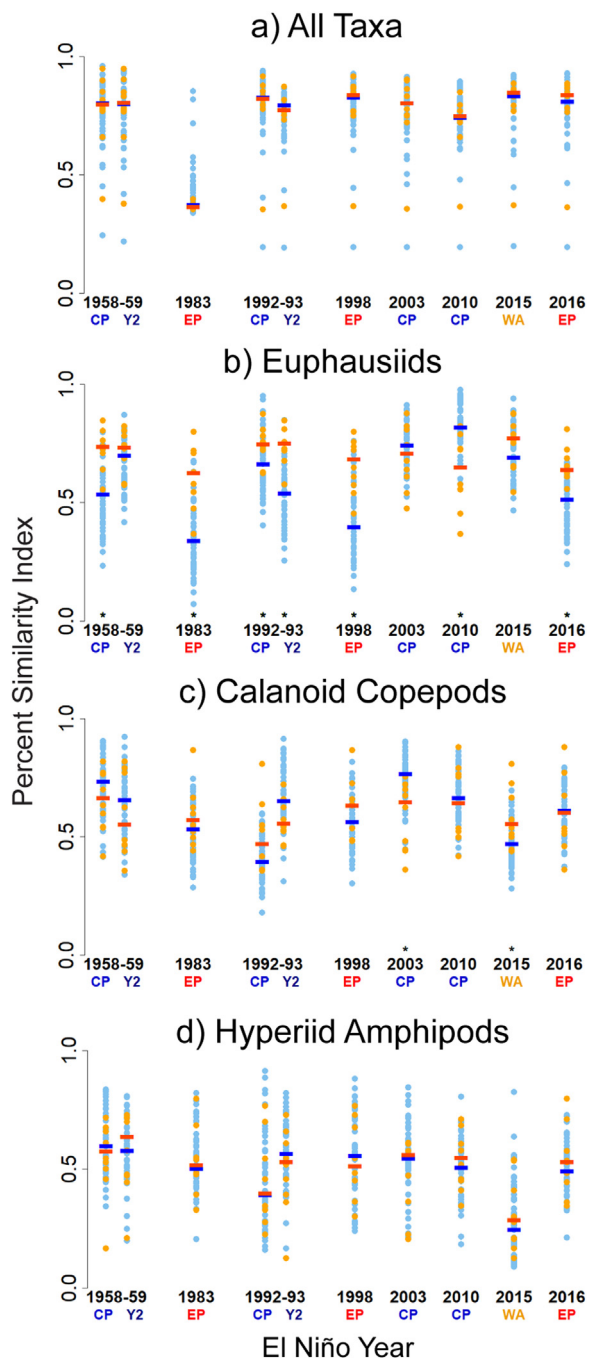


Fig. 5. Percent Similarity Index (PSI) comparing each El Niño with every other year in the timeseries. Dots represent the individual similarities between that El Niño year and each other El Niño year (orange dots; red bars = median) or each non-El Niño year (blue dots; blue bars = median). a) all taxa, b) euphausiids, c) calanoid copepods, d) hyperiid amphipods. Year-labels indicate El Niño type: Eastern Pacific (EP), Central Pacific (CP), or Year 2 (Y2) El Niño, or the Warm Anomaly (WA). Asterisks above El Niño year labels indicate significant difference between median inter-El Niño comparison and median El Niño/non-El Niño comparison, using a Mann-Whitney *U* test.

showed decreased similarity in the two years before the 2010 El Niño, but the event itself was similar to other surrounding years ($PSI \geq 0.80$).

3.3. Species-level changes during El Niño

3.3.1. Biomass responses to physical changes

We used PCA to test for coherent species-level El Niño responses

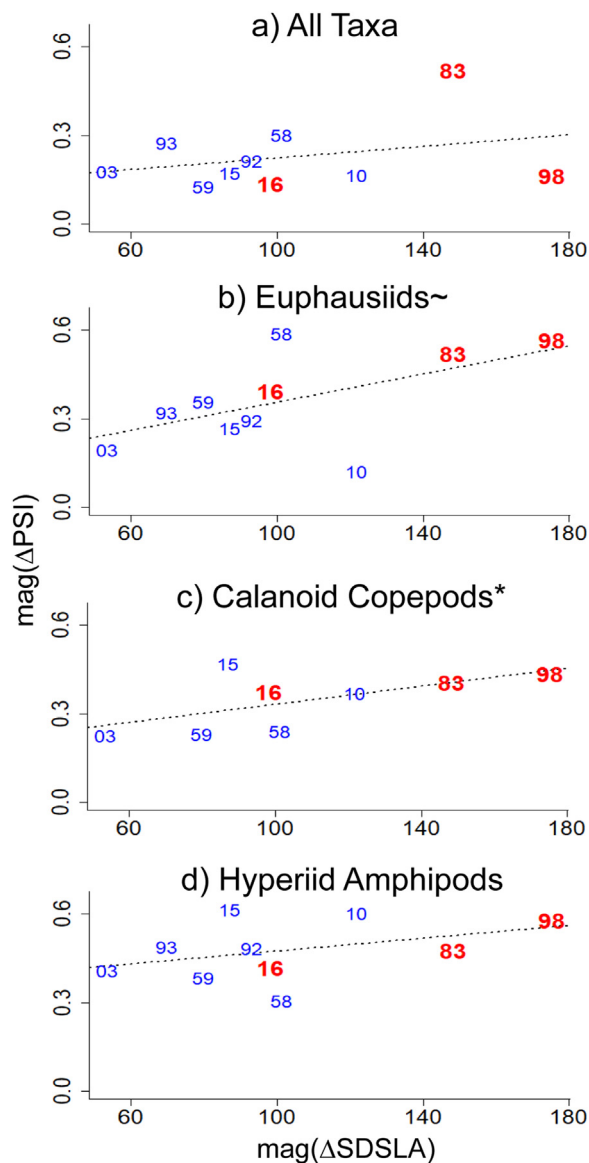


Fig. 6. Magnitude of change in PSI compared to corresponding magnitude of change in SDSLA. Magnitude of change is calculated as: (El Niño)-(average of 4 surrounding years). EP El Niño years are shown in bold red, CP years in thin blue. Dotted line indicates linear regression. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

within euphausiids, calanoid copepods, and hyperiid amphipods. The first two principal components of the euphausiid species-level community recovered 19.8% and 14.5% of variance, respectively (Fig. 8a,b). The euphausiid PC1 timeseries (Fig. 8c) correlated positively with SDSLA ($p < 0.01$), while PC2 did not ($p > 0.60$). We further used the PC1 loadings to identify individual species that showed consistent responses to El Niño events (Fig. 8a). We chose loading thresholds to determine El Niño-responsiveness based on values that identified approximately 6–9 species as ‘El Niño responsive’ (see Section 2 for full details). We used a loading threshold of $|0.25|$ for euphausiid PC1: the dominant CCS euphausiid, *Euphausia pacifica* showed a ‘cool-water species’ response, while six warm-water species showed ‘warm-water’ responses.

The first two principal components of the calanoid copepod community recovered 14.5% and 13.2% of variance, respectively (Fig. 9a,b). In contrast to the other assemblages, calanoid PC1 did not correlate with SDSLA, but did show a long-term upward trend (Fig. 9c;

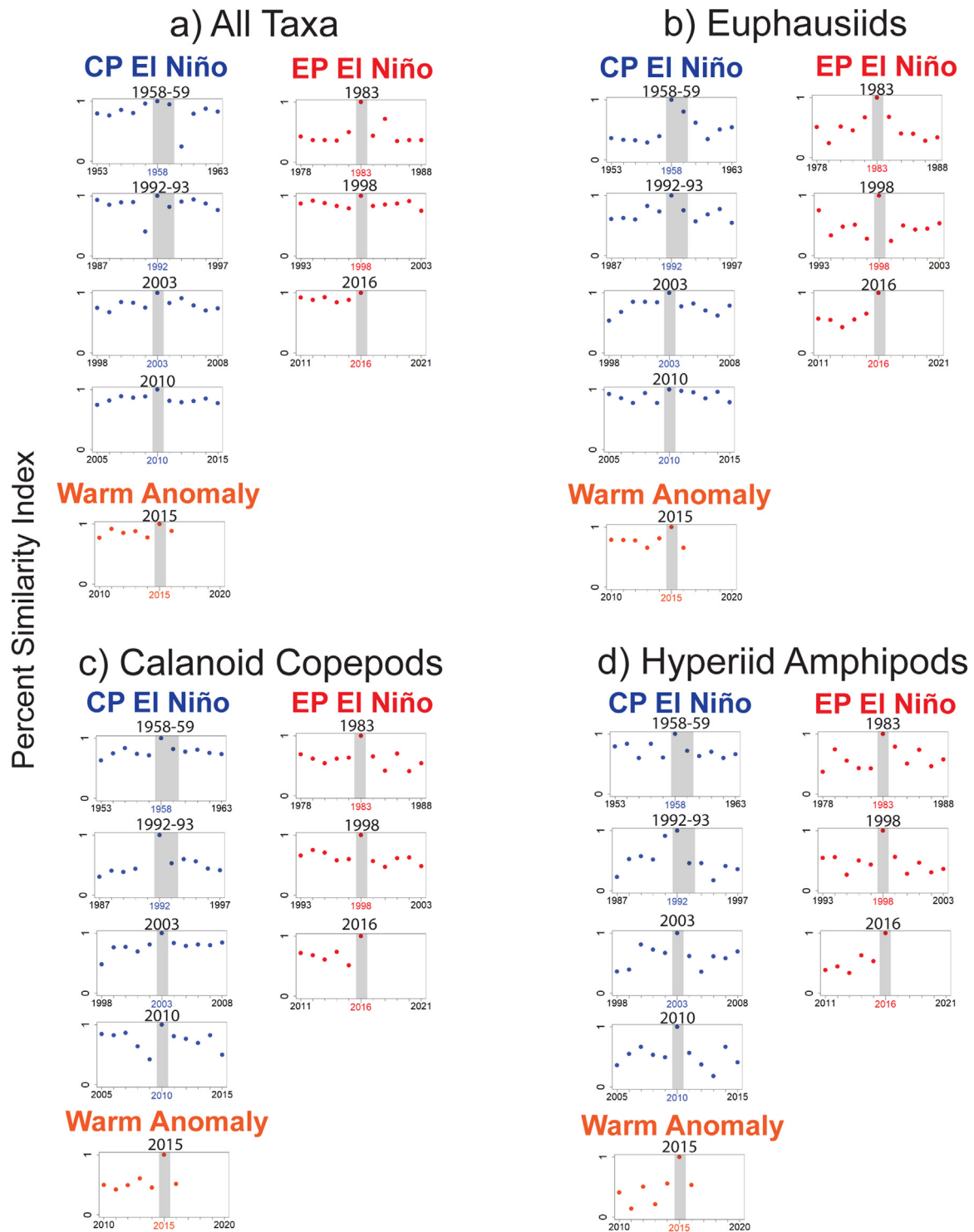


Fig. 7. Percent Similarity Index (PSI) comparing each El Niño with the preceding five and following five years, for a) all taxa, b) euphausiids, c) calanoid copepods, and d) hyperiid amphipods. El Niño years are divided into (left) EP and (right) CP events, and (bottom) the Warm Anomaly. For two-year El Niños, only the first year was used in PSI calculations. Vertical dashed lines denote El Niño years. Lack of dots indicate years of no data.

$r = 0.73$, $p < 0.01$). PC2 correlated significantly negatively with SDSLA, so we used that to identify El Niño-responsive species (Fig. 9b). We used a loading threshold of $|0.20|$ for calanoid PC2: three calanoid species showed a ‘warm-water’ and six species a ‘cool-water’ response (see Fig. 9 legend).

The first two principal components of the hyperiid amphipod species assemblage recovered 19.7% and 14.3% of variance, respectively (Fig. 10a,b). In contrast to the total mesozooplankton

and euphausiid assemblages, hyperiid amphipod PC1 correlated negatively with SDSLA (Fig. 10c, $r = -0.28$, $p = 0.03$). All species except *Paraphronima crassipes* loaded positively on PC1. We used a threshold of > 0.30 for El Niño responses; six species loaded above that mark (Fig. 10a).

The euphausiid PC1 and calanoid PC2 timeseries correlated with each other (Fig. 11, $r = 0.74$, $p < 0.01$) and showed corresponding dips during nearly all CCS El Niño events. Two different years were the

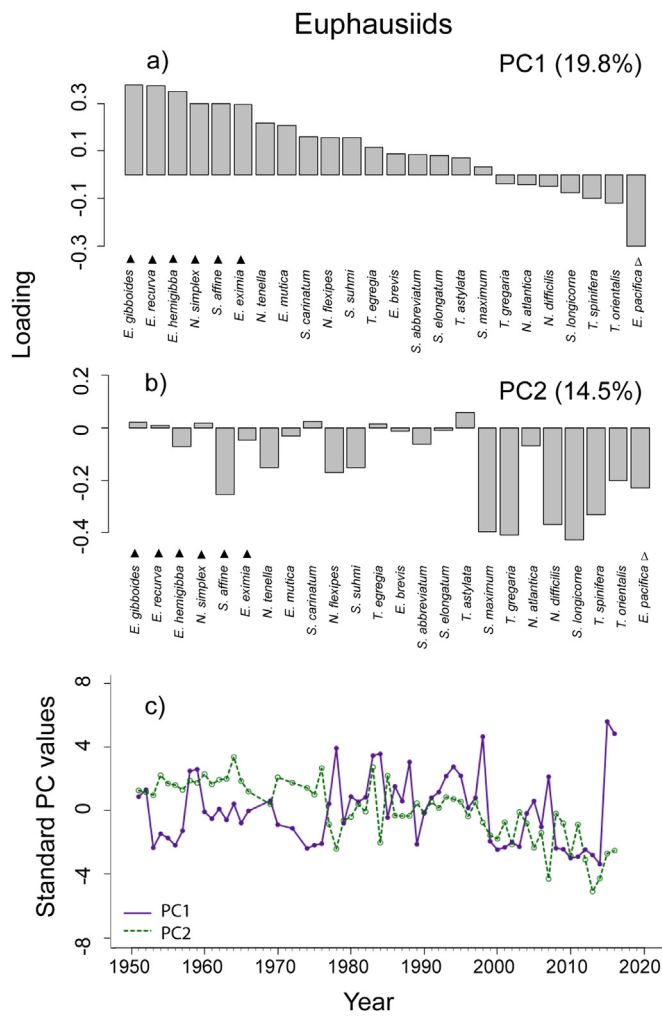


Fig. 8. Principal component analysis of the euphausiid species-level community. Shown are loadings by species on a) PC1 and b) PC2, with corresponding % variance. c) Timeseries of PC1 (solid purple) and PC2 (dashed green). Triangles in a) and b) denote the cool-water (open) and warm-water (filled) species. PC1 is correlated with SDSLA ($r = 0.58$, $p < 0.01$), but PC2 is not ($r = -0.01$, $p = 0.92$). Species names are as follows: *Euphausia gibboides*, *Euphausia recurva*, *Euphausia hemigibba*, *Nyctiphanes simplex*, *Stylocheiron affine*, *Euphausia eximia*, *Nematoscelis tenella*, *Euphausia mutica*, *Stylocheiron carinatum*, *Nematobrachion flexipes*, *Stylocheiron summi*, *Thysanopoda egregia*, *Euphausia brevis*, *Stylocheiron abbreviatum*, *Stylocheiron elongatum*, *Thysanopoda astylata*, *Euphausia maximum*, *Thysanoessa gregaria*, *Nematoscelis atlantica*, *Nematoscelis difficilis*, *Stylocheiron longicorne*, *Thysanoessa spinifera*, *Thysanopoda orientalis*, *Euphausia pacifica*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1977–78 CCS warm period (not classified as an El Niño in our analyses but identified in previous studies as a PDO sign change) and the 2015 Warm Anomaly. In 1977–78, calanoid PC2 decreased twice as much as euphausiid PC1, whereas in 2015 euphausiid PC1 decreased more than twice as much as calanoid PC2. These differences suggest that, while the two assemblages experience overall similarity in El Niño responses, they have differing additional sensitivities that cause year-specific variability.

Based on the PC loading thresholds described above, we further analyzed the El Niño-responsive species for inter-event variability in biomass. The six warm-water El Niño-responsive euphausiid species correlated positively with SDSLA, while the dominant cool species correlated negatively ($p < 0.05$). The nine calanoid copepod species showed similar directional correlations, although only two cool species (negative) and four warm species (positive) correlated significantly

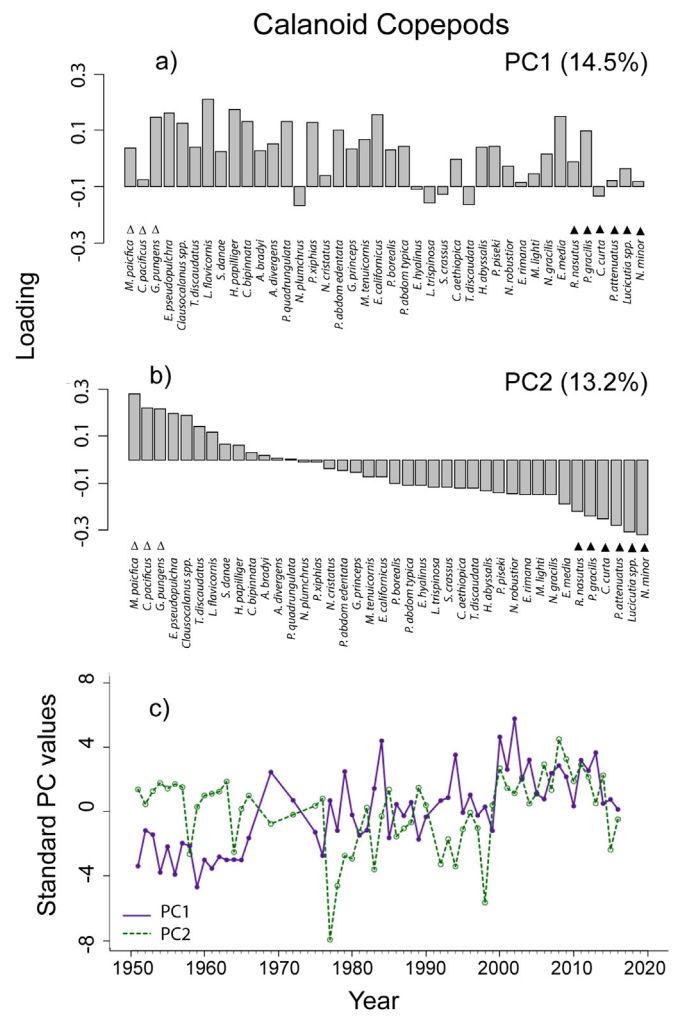


Fig. 9. As in Fig. 8, but for calanoid copepod species. Triangles in a) and b) indicate cool-water (open) and warm-water (filled) species. Both PC loading plots are ordered by PC2 loadings. PC1 is not correlated with SDSLA ($r = -0.13$, $p = 0.33$), but PC2 is ($r = -0.53$, $p < 0.01$). Species names are as follows: *Metridia pacifica*, *Calanus pacificus*, *Gaidius pungens*, *Euchirella pseudopulchra*, *Clausocalanus spp.*, *Tortanus discaudatus*, *Lucicutia flavicornis*, *Scolecithrix danae*, *Heterorhabdus papilliger*, *Candacia bipinnata*, *Aetideus bradyi*, *Aetideus divergens*, *Pleuromamma quadrangulata*, *Neocalanus plumchus*, *Pleuromamma xiphias*, *Neocalanus cristatus*, *Pleuromamma abdominalis edentata*, *Gaussia princeps*, *Mesocalanus tenuicornis*, *Eucalanus californicus*, *Pleuromamma borealis*, *Pleuromamma abdominalis typica*, *Eucalanus hyalinus*, *Labidocera trispinosa*, *Subeucalanus crassus*, *Candacia aethiopia*, *Temora discaudata*, *Heterorhabdus abyssalis*, *Pleuromamma piseki*, *Neocalanus robustior*, *Euchaeta rimana*, *Mesocalanus lighti*, *Neocalanus gracilis*, *Euchaeta media*, *Rhincalanus nasutus*, *Pleuromamma gracilis*, *Candacia curta*, *Pareucalanus attenuatus*, *Lucicutia spp.*, *Nannocalanus minor*.

with

SDSLA ($p < 0.05$). The six hyperiid amphipod species all classified as cool, and only two correlated significantly with SDSLA ($p < 0.01$). Species-level AR-1 model correlations generally matched correlation patterns of measured biomass with physical indices, although with fewer significant results for euphausiid and calanoid species. Only three calanoid and two hyperiid amphipod species showed significant long-term trends ($p < 0.01$), all upward except *Candacia curta*.

3.3.2. Consistency of biomass changes across El Niño events

Biomass fluctuations of individual species during El Niño revealed more consistent directional trends than for higher taxa. Two warm euphausiid species (*Euphausia eximia*, *E. gibboides*) increased and the

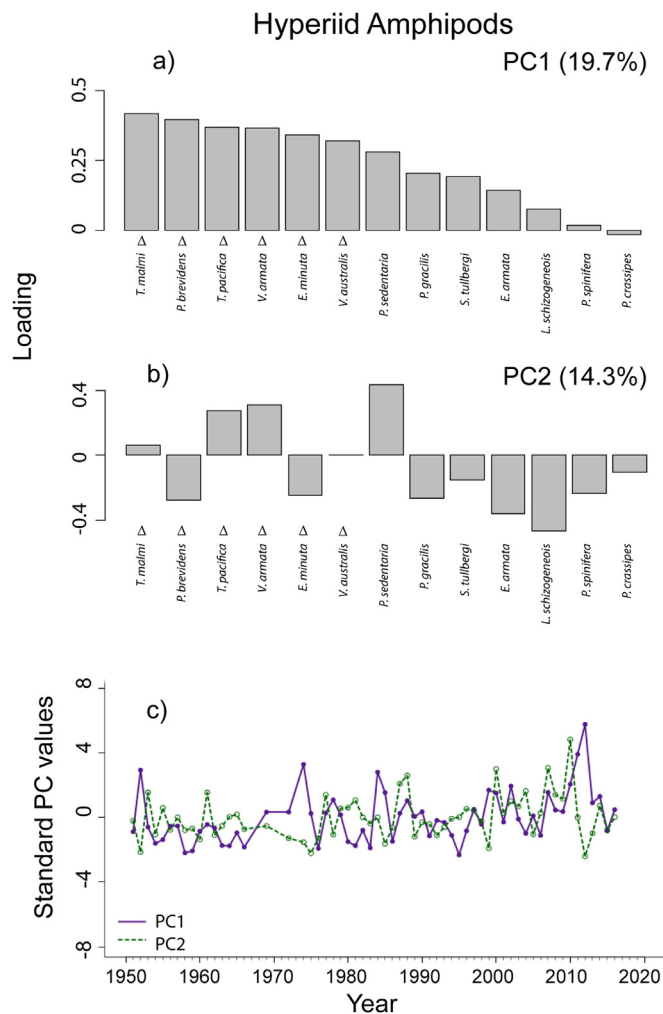


Fig. 10. As in Fig. 8, but for hyperiid amphipod species. Triangles in a) and b) indicate cool-water (open) species (no warm species identified). PC1 is correlated with SDSL (A) ($r = -0.28$, $p = 0.03$), but PC2 is not ($r = 0.02$, $p = 0.89$). Species names are as follows: *Tryphana malmi*, *Primno brevidens*, *Themisto pacifica*, *Vibilia armata*, *Eupronoe minuta*, *Vibilia australis*, *Phronima sedentaria*, *Paraphronima gracilis*, *Scina tullbergi*, *Eupronoe armata*, *Lestrigonus schizogeneois*, *Phronimopsis spinifera*, *Paraphronima crassipes*.

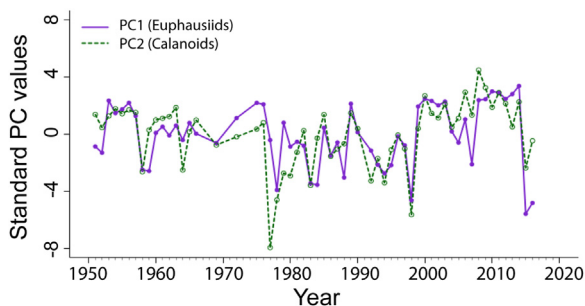


Fig. 11. Timeseries of euphausiid PC1 (solid purple) and calanoid copepod PC2 (dashed green). The two timeseries are highly correlated ($r = 0.74$, $p < 0.01$). Note that the euphausiid PC1 timeseries is flipped to align with calanoid copepod PC2. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

cool euphausiid species (*E. pacifica*) decreased (Fig. 12a); one warm calanoid species (*Pleuromamma gracilis*) increased and two cool species (*Metridia pacifica*, *Gaidius pungens*) decreased (Fig. 12b); and two cool hyperiid amphipod species (*Primno brevidens*, *Themisto pacifica*)

decreased (Fig. 12c) during almost all El Niños (Wilcoxon signed rank, $p \leq 0.05$ for all species mentioned). The six warm euphausiid species differed in their responses in 2015 and 2016: three species reached higher biomass levels in 2015 and then decreased in 2016, while the other three had higher biomass in 2016. In contrast, only two warm calanoid species increased in 2015 and 2016 compared to surrounding years, while three species were completely absent. Only one hyperiid amphipod species (*Eupronoe minuta*) increased substantially, while another (*Vibilia australis*) was completely absent in both 2015 and 2016. One hyperiid amphipod species also had a significant negative correlation ($p < 0.05$) between the magnitude of change in biomass during El Niño and the corresponding magnitude of change in SDSL. These results corroborate our findings that El Niño responses are more strongly expressed at the species, rather than higher taxon, level.

3.3.3. Warm-water species indices

As a metric of the extent to which warm species dominate over cool species during El Niño, we calculated composite warm-water species indices for euphausiids, calanoid copepods, and hyperiid amphipods by subtracting the sum of dominant warm minus cool species. The euphausiid ($r = 0.63$) and calanoid ($r = 0.50$) indices correlated with SDSL (A) (Fig. 13a-b, $p < 0.01$). Both indices showed peaks in 1983 and 1998 corresponding to highest peaks in SDSL, but the overall highest peaks for the warm-water indices were 2015–16 (euphausiids) and 1977–78 (calanoids). The indices showed fourth highest peaks in 1958–59 (euphausiids) and 1992 (calanoids). These indices corroborate the euphausiid PC1 and calanoid PC2 timeseries comparison, which showed similar overall correlation of the two taxa but differences between individual events. The hyperiid amphipod index, which was comprised only of cool species (hence the reversed index sign in Fig. 13c), did not correlate with SDSL, which corroborates our findings that hyperiid amphipods did not vary principally on El Niño timescales.

3.4. EP versus CP El Niños

We compared Eastern Pacific (EP) versus Central Pacific (CP) El Niño responses in terms of i) taxonomic similarity (PSI) and ii) carbon biomass. The taxonomic comparisons (for 15 higher taxa and the euphausiid, calanoid copepod, and hyperiid amphipod species) all showed larger changes in percent similarity index during EP relative to CP events, but no comparison was significant at $p < 0.05$ (Fig. 14a-d; red filled dots are individual EP events and blue open dots are individual CP events for all plots). The calanoid and euphausiid declines in PSI were greater for EP El Niños than for nearly every CP El Niño (Wilcoxon rank sum test; calanoids: $W = 0$, $p = 0.06$; euphausiids: $W = 0.01$, $p = 0.011$). Considering the small number of El Niños in each category (3 EP, 6 CP), our statistical power is low. In contrast, mean percentage changes in biomass were nearly identical between EP and CP events for three of four groups, and the fourth (hyperiid amphipods) had large ranges in values for both EP and CP events (Fig. 14e-h). Separating warm and cool species within the euphausiids, calanoid copepods, and hyperiid amphipods (Fig. 14i-m; EP – red filled triangles (warm spp.) or squares (cool spp.); CP – blue open triangles (warm spp.) or squares (cool spp.)), the dominant cool euphausiid species had a greater biomass depression in EP than CP events, though the difference was not significant (Fig. 14j; $W = 2$, $p = 0.10$). The warm euphausiid species showed the greatest percentage increase during El Niño events, but also had large ranges across individual events, and therefore no significant difference in magnitude of increase between EP and CP events (Fig. 14i).

3.5. La Niña events

3.5.1. Biomass fluctuations

Only the total hyperiid amphipod community (increase), three

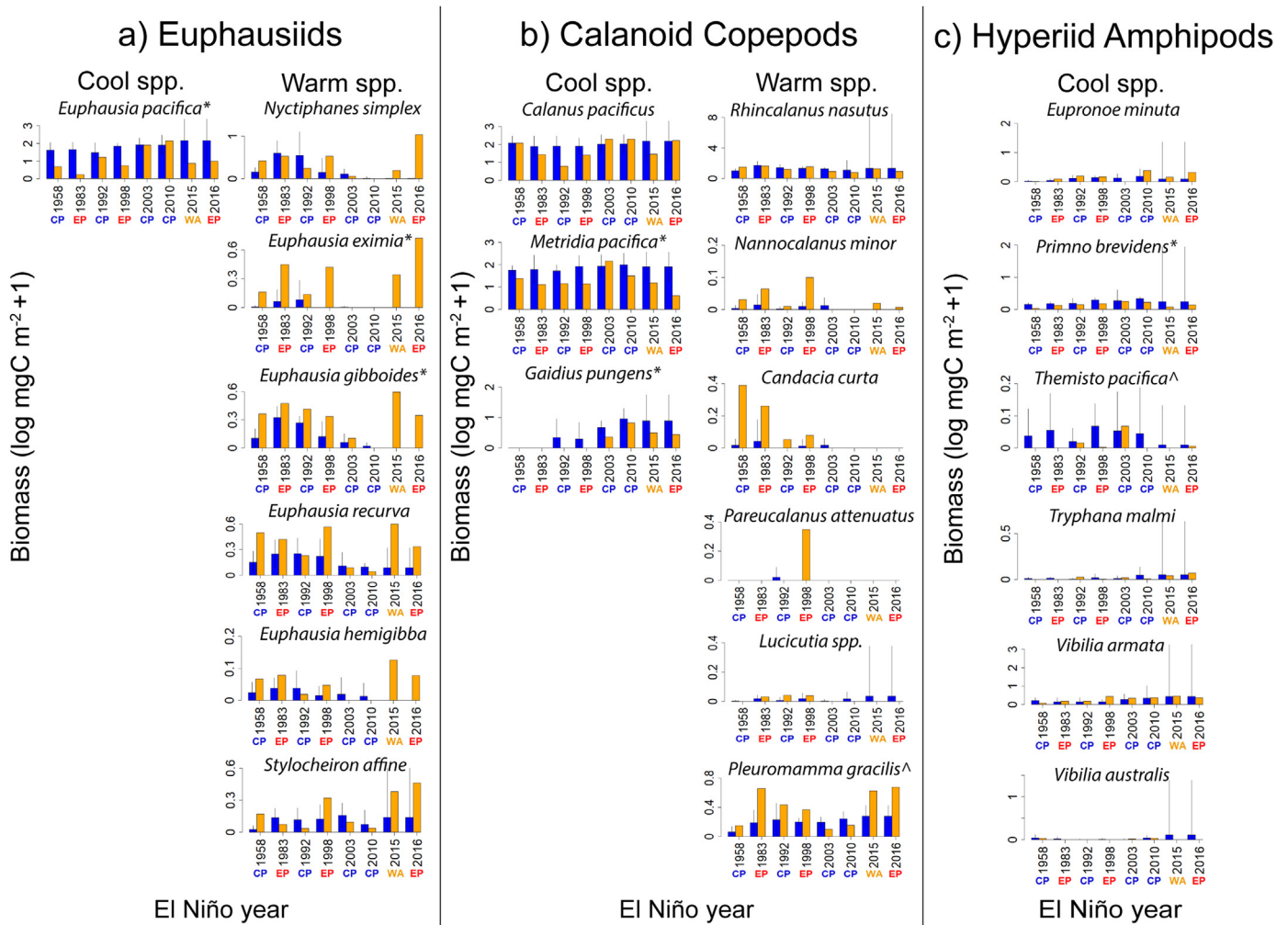


Fig. 12. As in Fig. 4, but for El Niño-responsive cool-water (left) and warm-water (right) species for a) euphausiids, b) calanoid copepods, and c) hyperiid amphipods. \wedge = $p = 0.05$, * = $p < 0.05$ (Wilcoxon matched pairs signed-rank test).

warm euphausiid species (decrease), and two warm calanoid species (decrease) showed significant directional changes in biomass during La Niña compared to surrounding years (Suppl. Figs. 2–3). The euphausiid *Euphausia eximia* was completely absent during all La Niña years, and *E. gibboides* was nearly zero during the 1989–2008 events. Testing for proportional changes in biomass relative to change in SDSLA yielded a significant relationship for only one hyperiid amphipod species, although euphausiids, chaetognaths, and pyrosomes suggested weak relationships in the direction of greater biomass increase during stronger La Niña events ($p < 0.10$).

3.5.2. Community composition

Comparisons of community similarity across La Niña years (using PSI, described above) showed significantly different mean inter-La Niña similarity (purple symbols) compared to La Niña/non-La Niña similarity in five years (blue symbols; Suppl. Fig. 4) for both the euphausiids and calanoid copepods, though the significant years differed. The total mesozooplankton community had significant differences between medians in 1951 and 1999. Unlike El Niño years, the magnitude of change in community similarity across La Niña did not correlate with change in SDSLA for any assemblage (Suppl. Fig. 5), although in all cases there was a tendency toward a negative relationship. In terms of resilience to La Niña, similarity generally returned to pre-Niña levels within 1–2 years after each event, although surrounding years sometimes showed higher variability in percent similarity to La Niña events compared to El Niño surrounding years (Suppl. Fig. 6).

4. Discussion

4.1. Taxonomic levels of resolution that respond to El Niño

Our findings suggest that El Niño signals in the southern California Current System (CCS) express most strongly at the levels of species and individual taxonomic groups, while total mesozooplankton biomass and composition of higher taxa are not consistently affected. Differential responses of taxonomic levels suggest that species in the southern CCS can undergo rearrangements in dominance without substantially impacting total mesozooplankton biomass. Species rearrangements during El Niño can have important implications for foraging success and survival of higher trophic levels, as well as for carbon export. Many species of seabirds, fishes, and marine mammals are known to selectively target specific zooplankton taxa for foraging (Lee et al., 2007; Nickels et al., 2018). Zooplankton also vary in nutritional value: cool-water calanoid copepods tend to have higher lipid reserves than subtropical species (Lee et al., 1971; Hooff and Peterson, 2006), which can affect the net energy gain by higher trophic levels. The 1992–93 and 1997–98 El Niños caused significant reductions in survival and breeding success of Cassin's auklets (Lee et al., 2007) and altered distributions of marine mammal off California (Keiper et al., 2005). Both changes were attributed in part to reduced prey zooplankton availability, particularly certain species of euphausiids, which our results corroborate.

Zooplankton taxonomic composition can also significantly alter carbon export. Lavaniegos and Ohman (2007) noted that communities

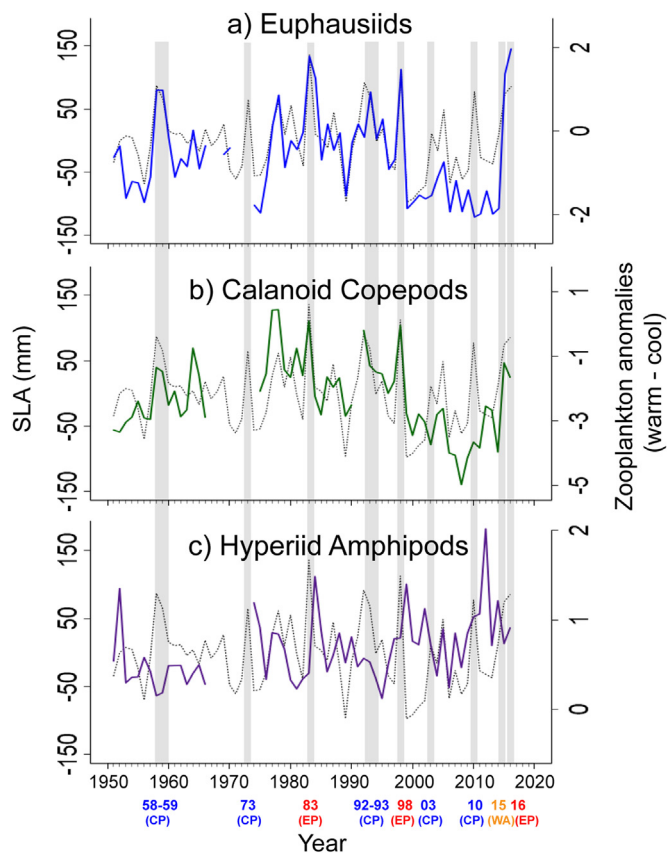


Fig. 13. Indices of the difference between dominant warm species biomass minus cool species biomass. a) euphausiids, b) calanoid copepods, c) hyperiid amphipods. Dotted grey line is SDSLA timeseries. The hyperiid amphipod index is shown in reverse (cool species as positive).

dominated by gelatinous tunicates such as salps tend to be less palatable and nutritious to higher trophic levels, although salps promote rapid carbon export (Michaels and Silver, 1988; Lavaniegos and Ohman, 2007; Smith et al., 2014). The 1983 El Niño was notable for exceptionally high proportions of salps relative to all other years in our timeseries. Such changes in zooplankton community composition, and the subsequent effects on higher ecosystem levels, make it essential for us to understand the underlying mechanisms causing zooplankton changes, and their variability between individual events.

4.2. Consistency of responses across individual El Niño events

Only the euphausiid species-level community composition showed a consistent change during most El Niños compared to non-El Niño years. This change appears to be due in part to increased proportions of subtropical species during almost every event. Brinton (1981) and Brinton (1960) found that non-resident southerly and offshore euphausiid species intruded into the southern and central CCS during the 1958–59 El Niño and 1977–78 CCS warm period, in some locations even displacing resident cool-water species. These past studies and our findings

suggest that most El Niño events are associated with some level of subtropical euphausiid intrusion into the SC region, although we note exceptions to this pattern below. The lack of a consistent El Niño-related change in the calanoid copepod community, and greatest species-level reordering during different years than for euphausiids, suggests that specific biological characteristics and life-histories cause calanoids to respond differently than euphausiids to a given perturbation. Brinton (1960) noted that euphausiids are long-lived (on the order of one year) compared to other zooplankton and are thus ‘conservative’ in terms of

reflecting inter-seasonal and interannual, rather than shorter-term, changes in ocean conditions. Such time-

lagged responses under the double-integration mechanism previously proposed by Di Lorenzo and Ohman (2013). Euphausiid species also strongly associate with specific physical ocean environments on a biogeographic scale (Brinton, 1960, 1981). In contrast, calanoid copepods have shorter life-spans, and several dominant CCS species undergo wintertime dormancy (Ohman et al., 1998). Our findings here of greatest euphausiid responses to 1958–59 and 2016 versus greater calanoid copepod responses to 1977–78 further suggest differential responses of the two taxa to the same forcing mechanisms. In contrast to both euphausiids and calanoid copepods, hyperiid amphipod community variability is likely determined more by variability in their gelatinous hosts than in direct response to El Niño, which likely explains why they show stronger year-to-year variability than consistent El Niño-related patterns (Lavaniegos and Ohman, 1999; Lavaniegos and Hereu, 2009; Lavaniegos, 2014).

The weak El Niños of 2003 and 2010 present unusual cases of anomalously elevated biomass and high compositional similarity to non-El Niño years. Both events occurred during the relatively cool 2000s, which experienced a sequence of back-to-back weak El Niño and La Niña events (Pares-Escobar et al., 2018). The 2003 event has been associated with southward-flowing subarctic water intrusions into the CCS, in contrast to increased poleward flow usually observed during El Niño (Murphree et al., 2003; Lavaniegos, 2009; Pares-Escobar et al., 2018). Subarctic-origin flows may have increased nutrient inputs to the southern CCS, enhancing growth of the existing community. Southward flows may have also delivered more subarctic-origin organisms to the southern CCS and reduced introduction of warm species from the south and offshore. Fisher et al. (2015) noted that chlorophyll concentrations were moderately higher than average off Oregon during the 2002–03 El Niño, supporting suggestions of increased high-nutrient flows and favorable conditions for resident species. Those authors also measured elevated biomass of southerly copepod species (e.g., *Calanus pacificus*, the dominant calanoid copepod in the southern CCS) off Oregon during the event. Our finding of increased biomass of *C. pacificus* in the southern CCS suggests that this species may have expanded its range in response to favorable habitat throughout the CCS, perhaps aided by submesoscale water movements in opposition to the larger southward flow. The 2010 El Niño, in contrast, showed evidence for atmospherically-forced El Niño perturbations in the CCS, but no anomalous oceanic poleward advection (Todd et al., 2011). The complete absence of subtropical euphausiids in the southern CCS during 2010 corroborates this lack of influx by subtropical- and offshore-origin flows.

The anomalous responses of zooplankton during the relatively weak 2003 and 2010 events suggest that our classification of CCS El Niños may benefit from further refinement incorporating additional physical metrics and zooplankton responses to various events. Although the 2003 and 2010 events both classified as CCS El Niños based on our physical index thresholds, their anomalous zooplankton responses suggest that these events likely had different forcing mechanisms or factors compared to other El Niños. We also note past findings of the importance of multi-decadal variations in the background ocean state of the CCS (e.g., PDO, North Pacific Gyre Oscillation (NPGO)) in perturbing mesozooplankton communities (Brinton and Townsend, 2003; Lavaniegos and Ohman, 2003, 2007; Keister et al., 2011; Di Lorenzo and Ohman, 2013), and acknowledge that background state may have confounding effects on zooplankton responses. However, we had too few El Niño events within any given multi-decadal state to systematically analyze the possible interactions of those sources of variation.

4.3. EP vs. CP El Niño events

Both the euphausiid and calanoid copepod communities show differentiation of El Niño responses into EP versus CP categories, highlighting the apparent sensitivity of these taxa to event magnitude or

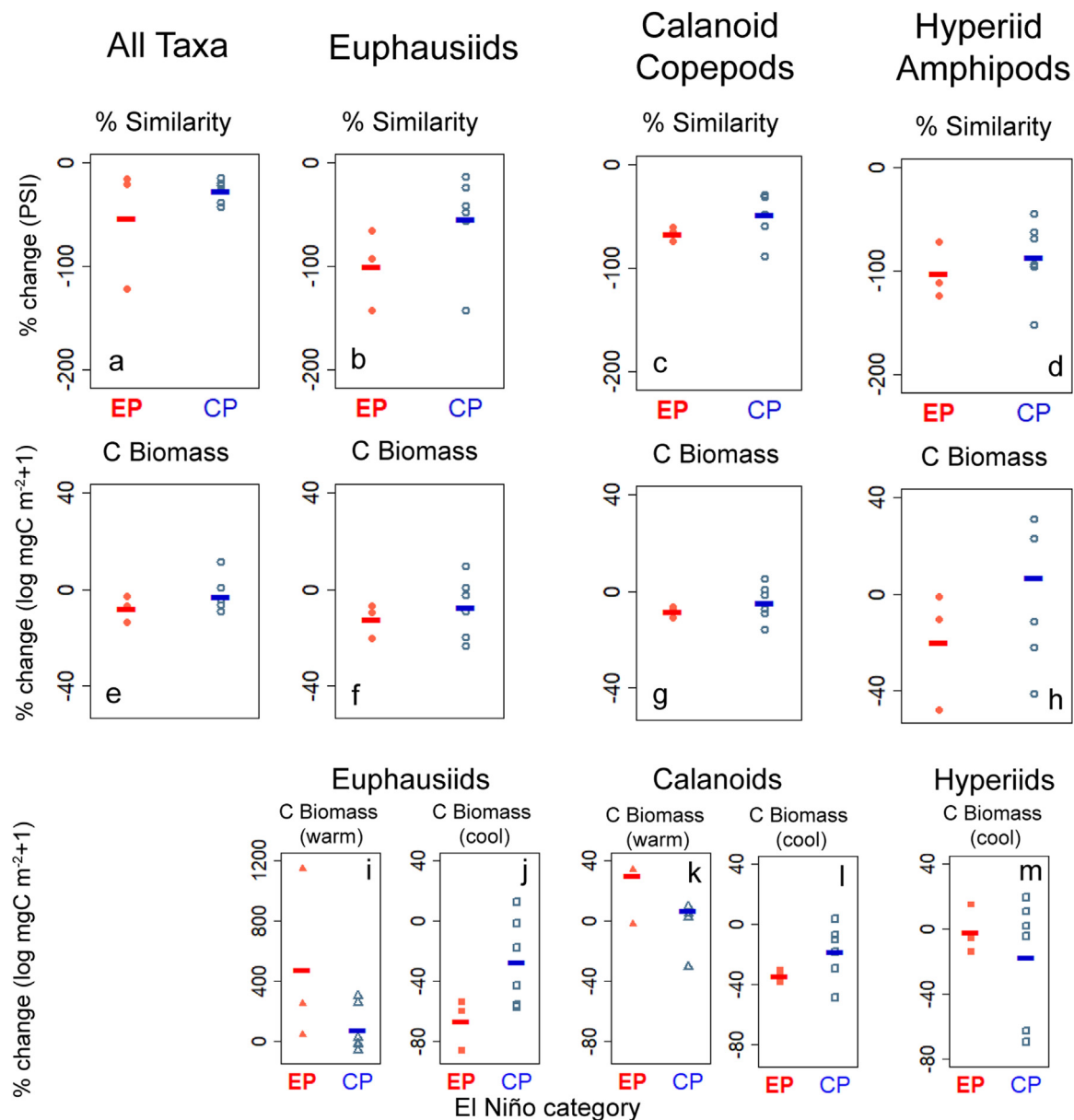


Fig. 14. El Niño-related changes in (upper row) Percent Similarity Index and (middle-lower rows) biomass for (a,e) all taxa, (b,f,i,j) euphausiids, (c,g,k,l) calanoid copepods, and (d,h,m) hyperiid amphipods. El Niño years are categorized as EP or CP. Dots indicate values for each individual El Niño year (EP – red filled, CP – blue open); bars indicate means for EP (red, left) or CP (blue, right) categories. C biomass was further subdivided into total biomass (e-h; EP – red filled circles, CP – blue open circles), and warm-water (i,k; EP – red filled triangles, CP – blue open triangles) and cool-water species (j,l,m; EP – red filled squares, CP – blue open squares). Biomass of warm-water euphausiids is shown on different a y-scale. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

event-specific forcing mechanisms. EP events, which tend to be oceanically-forced and stronger than CP events, appear to induce corresponding greater community changes in both taxa. Two of three EP El Niños (1998, 2016) show evidence for coastally-trapped wave (CTW) propagation and increased poleward flow in the CCS (Lynn and Bograd, 2002; Jacox et al., 2016; Frischknecht et al., 2017). Assuming a direct link between increased subtropical-origin waters and subtropical euphausiid species, we would expect such proportional changes in euphausiid community composition. The 1983 EP El Niño presents a different case: Simpson (1984) suggested that it showed evidence for onshore flow of gyre waters rather than CTWs. We found that the percent change in the euphausiid community during 1983 was substantially higher than during the other two EP years, perhaps due to higher proportions of offshore species in 1983. *Euphausia eximia* and *E. hemigibba* were the two subtropical euphausiid species with the largest

increases during 1983; these species tend to associate with Baja California and Central Pacific Gyre waters, so their presence corroborates onshore flow.

The southern CCS has been previously shown to experience rearrangement of dominant calanoid copepod species during El Niño (Rebstock, 2001). Our results, notably the significantly different percent change in community composition for EP versus CP years, and the significant correlation of magnitude of community change with SDSL, further suggest that calanoid responses to El Niño vary depending on event strength. These findings align with findings from the northern CCS during the 1997–98 El Niño, which displaced boreal copepods with the more southerly *Calanus pacificus* (Peterson et al., 2002) and even caused influxes of subtropical and offshore euphausiid species off Oregon (Keister et al., 2005), possibly due to horizontal advection of surface waters (Keister et al., 2011). Similarly, Fisher et al. (2015)

found that the magnitude of northern CCS copepod community change was strongly correlated with both the magnitude and duration of El Niño events, and that community composition was generally different during EP versus CP events. Our results suggest that such proportional shifts may occur across multiple parts of the CCS.

Equatorial EP versus CP classifications do not always align with southern CCS zooplankton responses to El Niño, however. The 1958–59 El Niño was classified here as a CP event but produced changes in euphausiid biomass and community composition comparable to EP events, while the 1992–93 El Niño was just below our EP threshold but showed only moderate changes in taxon compositions. The 1958–59 event occurred during a cool PDO phase, in contrast to 1983 and 1998 (warm phase) but may have still experienced EP-like forcing mechanisms, resulting in higher-magnitude assemblage change from surrounding years. Brinton (1981) noted that subtropical euphausiid intrusions did not occur in the southern CCS at any point from 1949 to 1979 except during 1957–59, supporting our findings of substantial community change. Euphausiid community recovery after 1958–59 was also slower than after other events, suggesting lingering effects of the prolonged warm period. In contrast, the 1992–93 El Niño showed evidence for CTW forcing into the CCS (Chavez, 1996), so it is surprising that 1992 did not resemble EP zooplankton responses. Spring 1993 had prolonged warm anomalies in the CCS after the 1991–92 equatorial signal but showed greater differences in subtropical species biomass and composition from non-El Niño years than did 1992. These unusual changes might have been due to later arrival of perturbations into the CCS, or perhaps a year-lag response by zooplankton to the initial perturbation. Regardless, multi-year El Niño events present complications to EP versus CP classification and warrant further investigation to elucidate event-specific mechanisms. Some evidence suggests that CP El Niño events have doubled in intensity over the past three decades (McPhaden et al., 2011) and may be increasing in frequency (Yeh et al., 2011), although the evidence is not definitive (Newman et al., 2011). Understanding mesozooplankton responses to CP events, as well as differences between individual CP years, may be especially important for predicting future community changes.

4.4. The 2014–15 Warm Anomaly and 2015–16 El Niño

The 2014–15 Warm Anomaly was caused by atmospheric changes in the Eastern North Pacific, with no associated equatorial signal, but it induced El Niño-like conditions in the southern CCS. These included near-surface temperatures of +5 °C, thermocline depression > 20 m, and near-zero nitrate and chlorophyll levels for the entire period (Lilly, 2016; Zaba and Rudnick, 2016; Frischknecht et al., 2017). The Warm Anomaly differed from most El Niños, however, in its lack of enhanced poleward advection and dominance by near-surface temperature anomalies (Zaba and Rudnick, 2016). In contrast, the 2015–16 El Niño resembled 1997–98 in its early equatorial and CCS development and evidence for oceanic CTWs, although they were weaker than in previous El Niños (Frischknecht et al., 2017).

Our zooplankton findings roughly corroborate these differences. Euphausiid assemblage responses aligned with past EP and CP distinctions, in terms of a moderate 2015 response most similar to 1992 and a stronger change in 2016 but still less than past EP events. The presence of subtropical euphausiids in 2015 is somewhat surprising given the apparent lack of increased poleward flow during the Warm Anomaly. However, Zaba and Rudnick (2016) noted that, although alongshore velocities were not anomalous, nearshore salinity was anomalously fresh and corresponded to reduced coastal upwelling, indicating onshore flow of fresh offshore core California Current waters. Offshore subtropical euphausiids had higher-magnitude changes than coastal subtropical species and were perhaps transported onshore in conjunction with these flows or with small-scale changes in circulation. Alternately or in conjunction, the extreme temperature anomalies during 2014–15 may have produced a more favorable inshore

environment for offshore species or caused northward contraction of cool species out of the southern CCS. Peterson et al. (2017) found that the arrival of the Warm Anomaly brought previously unrecorded copepods to the very nearshore environment of the northern CCS, although these species are well known to occur farther offshore. This finding suggests onshore transport of a water mass with different origins than those typically brought by El Niño events.

The moderate changes in the 2016 zooplankton composition compared to past EP El Niños may have been due to upwelling winds in fall 2015 countering the effects of CTW arrival to the CCS (Frischknecht et al., 2017). Corresponding nitrate and chlorophyll anomalies during fall 2015 were slightly negative to neutral, but higher than in 1983 and 1998, suggesting more favorable ocean conditions for resident cool-water species. The significant change in the calanoid community in 2015 but neutral response in 2016 may also suggest responses to local temperature anomalies rather than to changes in ocean circulation.

4.5. Mesozooplankton resilience to El Niño

Mesozooplankton biomass and community composition in the southern CCS appear generally resilient to El Niño. We found that the total mesozooplankton community and the three species-enumerated assemblages (euphausiids, calanoid copepods, hyperiid amphipods) return to pre-El Niño composition within one year after almost every event. Even if subtropical species appear in the southern CCS in high proportions during El Niño, they do not appear to proliferate and maintain their presence following the perturbation. This pattern of rapid increase and subsequent decrease suggests either direct El Niño-related advective influxes or short-term favorable habitat changes without a sustained ability to reproduce and establish substantial populations post-El Niño. One exception is the subtropical euphausiid *Nyctiphanes simplex*, which remained elevated for 10 years during the 1980s–90s. This may have been due to confounding PDO influences (Brinton and Townsend, 2003; Di Lorenzo and Ohman, 2013). Although the dominant cool-water euphausiid (*Euphausia pacifica*) and calanoid copepod (*Calanus pacificus*, *Metridia pacifica*) species generally decrease during El Niño, their rapid recovery within 1–2 years suggests either they have developed the ability to rapidly repopulate after short-term perturbations or they receive renewed population seeding with the return of pre-El Niño flow patterns. *Metridia pacifica* does not undergo deep water column wintertime dormancy like other dominant CCS calanoids (Ohman et al., 1998), and may be more susceptible to the winter-focused physical effects and changes in horizontal advection associated with El Niño.

It is also notable that the species with strongest El Niño responses are not necessarily the dominant biomass contributors within their taxa. Several numerically dominant cool-water euphausiid species (*Nematoscelis difficilis*, *Thysanoessa gregaria*, *T. spinifera*) in the southern CCS did not show any correlation with our El Niño indices. Pares-Escobar et al. (2018) found that, off Baja California, *N. difficilis* and *T. gregaria* did not covary with temperature or other physical variables during a multi-El Niño/La Niña period from 1998 to 2008, suggesting that dominant CCS species may have adapted to withstand the effects of short-term perturbations such as El Niño. Additionally, these species are known to live below the thermocline (at average depths of 400 m) and may be less susceptible to El Niño-related changes in advection strength and circulation of the upper 200 m. Mackas et al. (2007) reasoned that zooplankton species in the northern CCS have evolved to withstand seasonal fluctuations in temperature and stratification,

and that these adaptations can be effective against environmental perturbations of similar magnitude. The southern CCS is a dynamic region influenced by water masses ranging from tropical to subarctic origin (Checkley and Barth, 2009). High variability in physical conditions has likely selected for resident zooplankton species with characteristics that allow them to withstand physical perturbations associated with El Niño without major reductions in fitness.

We observed almost no significant long-term trends in El Niño-correlated species. In contrast, many species that were not El Niño-correlated showed significant upward trends (data not shown). It appears that El Niño responses and long-term trends tend not to co-occur in individual species but can co-occur at the taxon level. This difference suggests functional complementarity and compensatory changes among related species within a taxon (Lindgren et al., 2016).

4.6. Conclusions

Our goal in quantifying mesozooplankton variability during El Niño was to identify patterns of change that could suggest possible mechanisms affecting biomass and community composition. El Niño may affect mesozooplankton in several ways: changes in advection can produce species influxes from different regions; oceanic and atmospheric forcing can alter in situ physical and biological conditions, including temperature, thermocline and nutricline depths, and food sources (phytoplankton and microzooplankton); and altered species interactions may occur via predation, parasitism or competition for food (Ohman et al., 2017). Evidence for increased poleward and onshore advection during past El Niño events suggests that this is frequently an important forcing mechanism of species transport. In our study of the southern CCS, presence of offshore and southern euphausiid species suggest some component of advective forcing: their high-magnitude but transient increases during El Niño events, with no time-lag to indicate local population growth or reproduction, suggests a direct physical forcing mechanism such as advection. The near-absence of subtropical species off Southern California during the 2003 and 2010 El Niños, in conjunction with a lack of enhanced poleward or onshore flow, further supports this interpretation.

The stronger associations of mesozooplankton higher taxa and species with SDSLA than with $Z_{26.0}$ may further highlight dominant forcing mechanisms underlying El Niño-related zooplankton variability. Increases in sea level can be caused by thermal expansion or by relaxation of upwelling and associated onshore flow, indicating water mass intrusion. Thermocline depth can be influenced by local wind-driven changes in upwelling and can convey signals related to reduced nutrient availability for primary production. Our evidence for species-level changes within communities suggests at least partial forcing by altered flow, but changes to in situ temperature and productivity likely interact to produce the responses to each individual event. Our CCS El Niño classifications may benefit from adding another physical metric such as the magnitude of alongshore flow in the core California Current.

The 2014–15 Pacific Warm Anomaly, although forced differently than El Niño, induced zooplankton community shifts similar to some past El Niños, particularly the moderate and prolonged 1992–93 event. The Warm Anomaly did not, however, clearly modify subsequent zooplankton responses to the 2015–16 El Niño, which most closely resembled 1997–98. Although individual El Niño events vary in their zooplankton responses, evidence for some consistency across El Niños, particularly in the euphausiid community, suggests that certain species and higher taxa may serve as useful tracers of physical and biological forcing mechanisms. Understanding the specific mechanisms that cause responses to each event will be the topic of future study.

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Contributions

L. Lilly and M. Ohman developed the questions and analyses. L. Lilly conducted all analyses. L. Lilly and M. Ohman wrote the manuscript.

Competing interests

The authors declare no competing interests.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2018.07.015.

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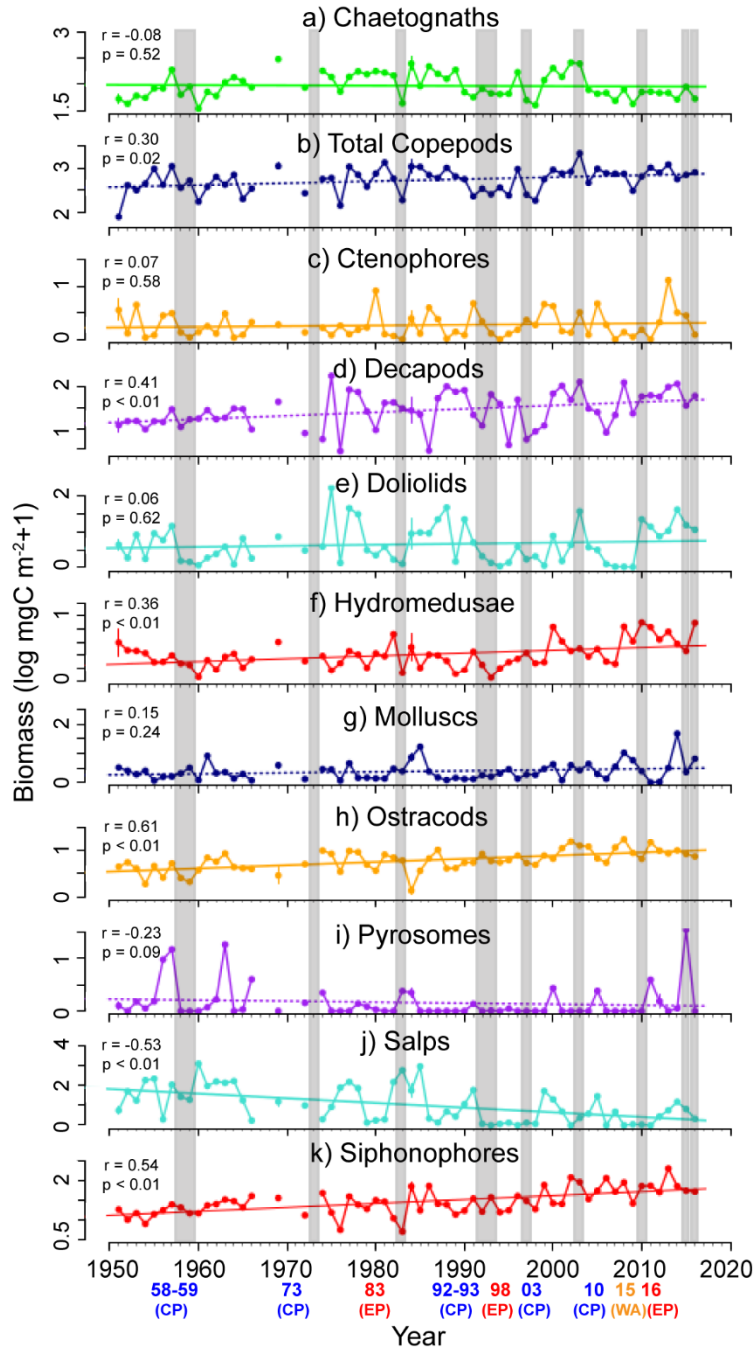
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CCE IV: El Niño-related zooplankton variability in the southern California Current System

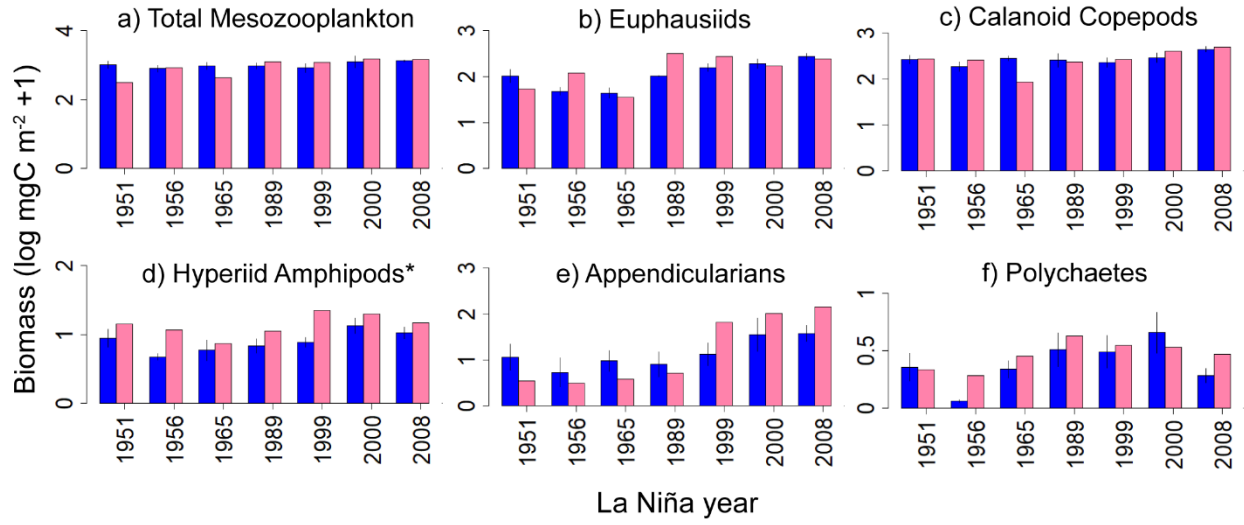
Laura E. Lilly^{a*} and Mark D. Ohman^a

DSRI 2941

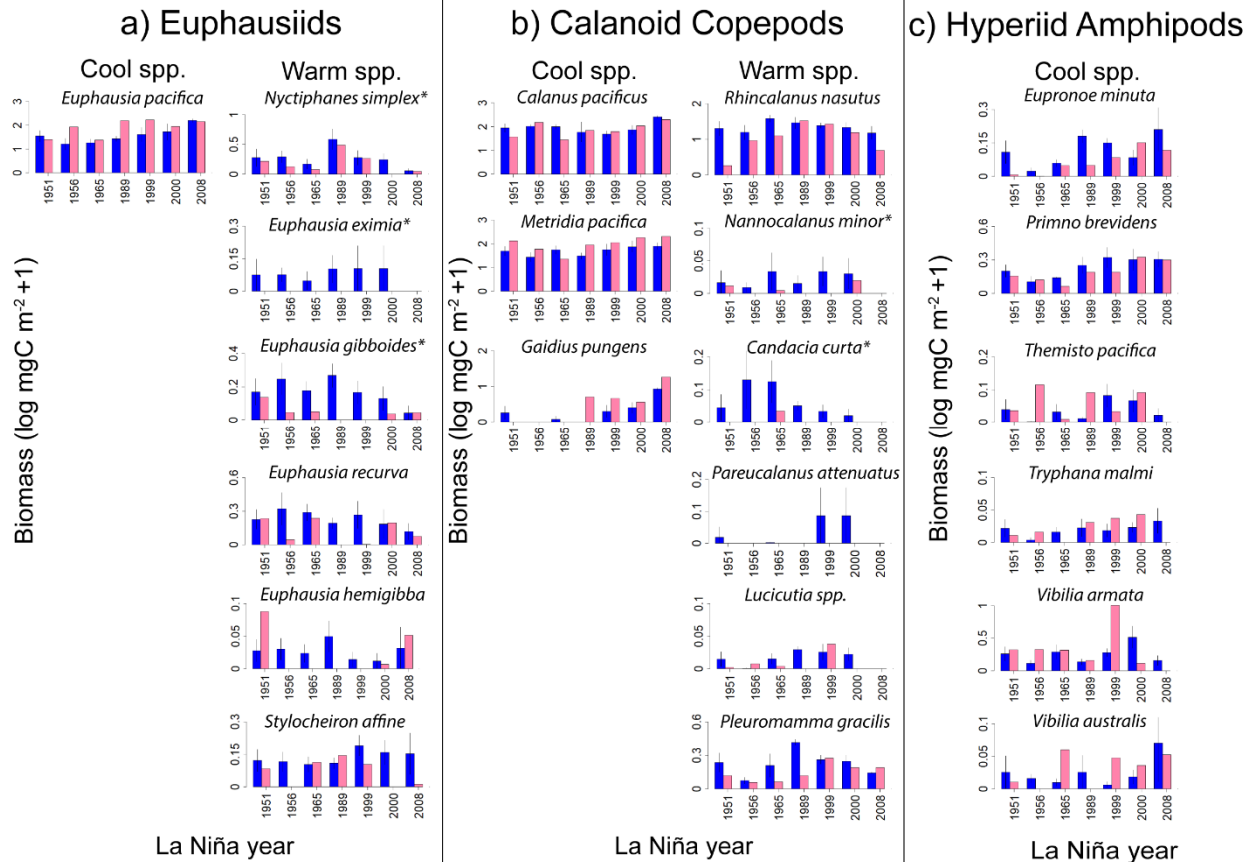
SUPPLEMENTAL FIGURE CAPTIONS



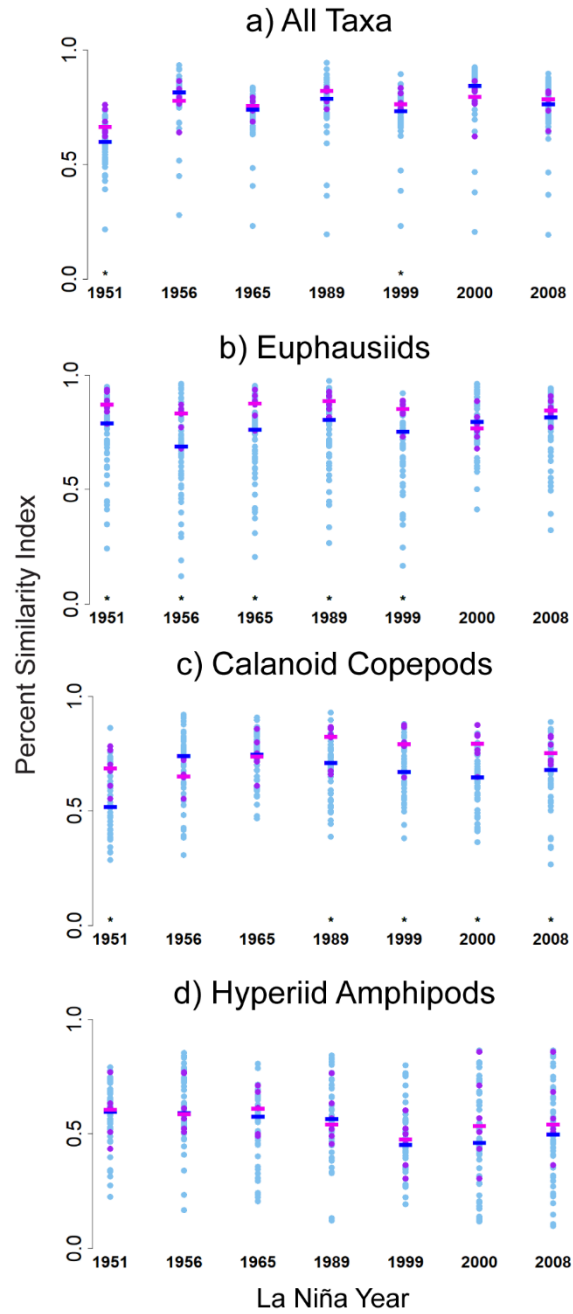
Supplemental Figure 1. Timeseries of log C biomass for enumerated taxa not already shown in Fig. 3. Linear trends and associated correlation coefficients are shown. Vertical grey bars indicate El Niño years (labels as in Fig. 1).



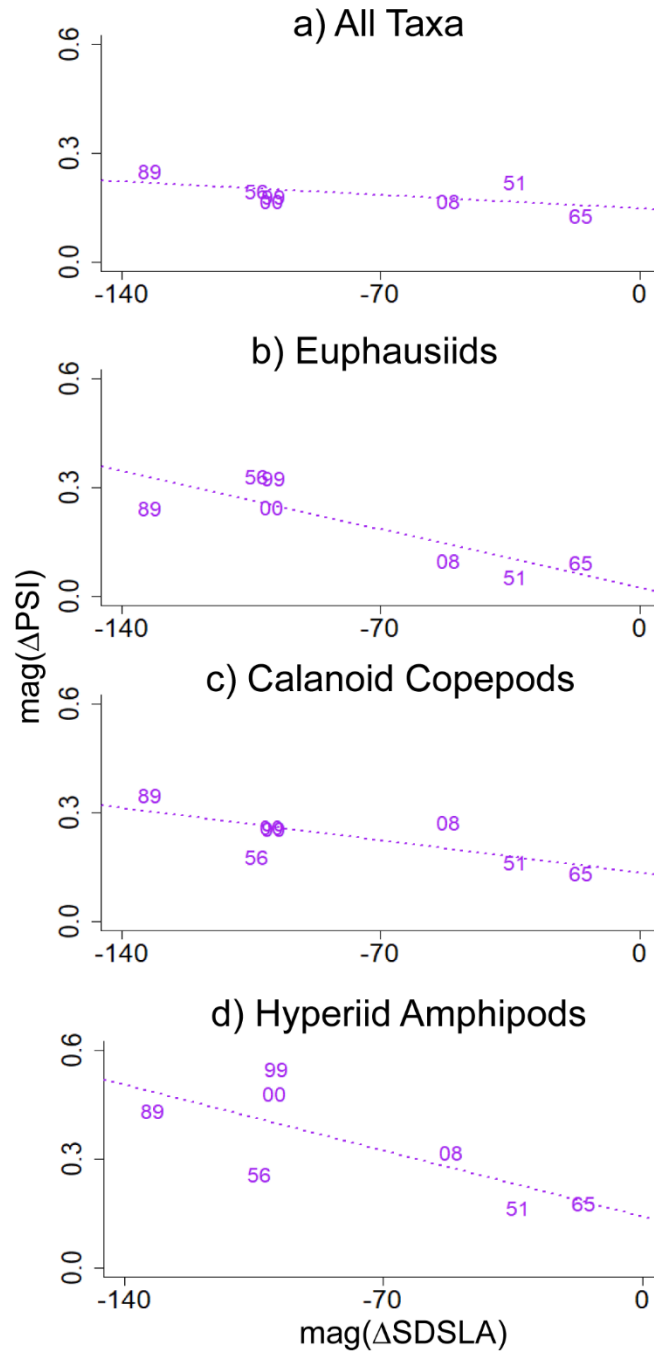
Supplemental Figure 2. As in Fig. 4, but for La Niña years (purple bars) versus average of the 4 surrounding years (blue bars). *significant Wilcoxon signed-rank value.



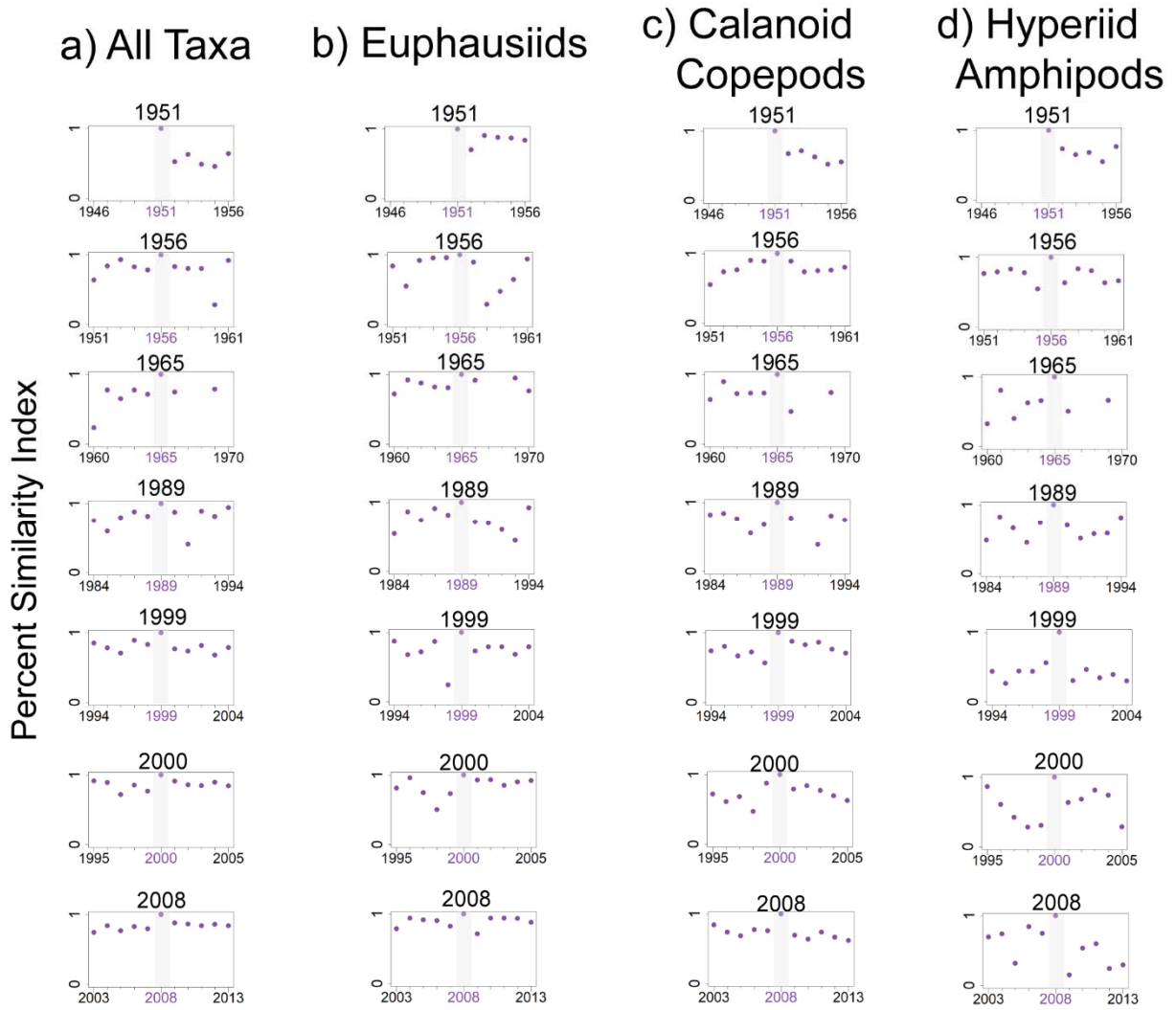
Supplemental Figure 3. As Suppl. Fig. 2, but for La Niña-responsive cool-water (*left*) and warm-water (*right*) species for a) euphausiids, b) calanoid copepods, and c) hyperiid amphipods. *significant Wilcoxon signed-rank value.



Supplemental Figure 4. As in Fig. 5 using the Percent Similarity Index, but for La Niña-La Niña comparisons (purple symbols) and La Niña-non-La Niña comparisons (blue symbols). a) All taxa, b) euphausiids, c) calanoid copepods, d) hyperiid amphipods.



Supplemental Figure 5. As in Fig. 6, but for La Niña correlations of $\text{mag}(\Delta\text{PSI})$ vs. $\text{mag}(\Delta\text{SDSLA})$. Dotted line indicates linear regression.



Supplemental Figure 6. As in Fig. 7, but Percent Similarity Index (PSI) comparisons of each La Niña with the preceding five and following five years. Lack of a dot indicates year of no data.