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The impact of El Niño events on the pelagic food chain in the northern California Current

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Abstract

The zooplankton of the northern California Current are typically characterized by an abundance of lipid-rich copepods that support rapid growth and survival of ecologically, commercially, and recreationally valued fish, birds, and mammals. Disruption of this food chain and reduced ecosystem productivity are often associated with climatic variability such as El Niño events. We examined the variability in timing, magnitude, and duration of positive temperature anomalies and changes in copepod species composition in the northern California Current in relation to 10 tropical El Niño events. Measurable impacts on mesozooplankton of the northern California Current were observed during seven of 10 of these events. The occurrence of anomalously warm water and the response of the copepod community was rapid (lag of zero to 2 months) following the initiation of canonical Eastern Pacific (EP) events, but delayed (lag of 2–8 months) following 'Modoki' Central Pacific (CP) events. The variable lags in the timing of a physical and biological response led to impacts in the northern California Current peaking in winter during EP events and in the spring during CP events. The magnitude and duration of the temperature and copepod anomalies were strongly and positively related to the magnitude and duration of El Niño events, but were also sensitive to the phase of the lower frequency Pacific Decadal Oscillation. When fisheries managers and biological oceanographers are faced with the prospect of a future El Niño event, prudent management and observation will require consideration of the background oceanographic conditions, the type of event, and both the magnitude and duration of the event when assessing the potential physical and biological impacts on the northern California Current.

Keywords: climate change, copepod, Eastern Pacific and Central Pacific El Niño, ENSO, food chain, northern California Current, Pacific Decadal Oscillation, trophic transfer, zooplankton

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Introduction

The California Current is an eastern boundary current that supports a rich and diverse ecosystem valued for the immense productivity of its living marine resources. This high productivity is due, in part, to wind-driven coastal upwelling in the late spring and summer seasons. Upwelling during this period forces nutrient-rich waters on to the shelf in the northern portion of the California Current (NCC) which supports a nutritious, lipid-rich forage community of copepods, krill, and small pelagic fishes. This prey community is fed upon by higher trophic-level predators which migrate into the area in spring from the southern portion of the California Current (hake, sardine, and mackerel), from rivers of the Pacific Northwest (salmon), and from Hawaii and the south Pacific (Laysan and black-footed albatross, sooty shearwaters, humpback whales, and leatherback sea turtles, among others). These spe-

cies migrate to the NCC to feed on the lipid-rich food chain and accumulate fat and the nutriment needed both for reproduction and for their lengthy migration to overwintering and breeding (or spawning) habitats.

Seasonal and decadal variability in the productivity of this nutritious forage community in the NCC is related to local-scale physical processes associated with coastal upwelling (Peterson & Miller, 1975, 1977; Peterson *et al.*, 1979) and to low-frequency, basin-scale physical processes associated with the Pacific Decadal Oscillation (PDO) (Peterson & Schwing, 2003; Hooff & Peterson, 2006; Bi *et al.*, 2011; Keister *et al.*, 2011; Francis *et al.*, 2012). Intra-annual oscillations in the direction and magnitude of local winds (with typical poleward, downwelling-favorable winds in winter and equatorward, upwelling-favorable winds in summer) influence alongshore currents that modify the mesozooplankton community structure of the NCC by advection and local production. Decadal changes in the sign of the PDO are associated with similar community responses at a lower frequency. The PDO is defined as the first principal component of monthly sea-surface

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temperature (SST) anomalies in the North Pacific (poleward of 20°N) and is driven largely by changes in the Aleutian Low pressure atmospheric system in winter (Mantua *et al.*, 1997). When the PDO is negative [the eastern Pacific cold phase], the intensity of the Aleutian Low decreases and the North Pacific High increases, leading to increased southward wind stress. This results in increased equatorward transport of northern copepod species from the Gulf of Alaska which leads to positive anomalies in their contribution to the copepod community in the coastal NCC. Conversely, when the PDO is positive (the eastern Pacific warm phase), the strength of the Aleutian Low increases, resulting in increased onshore and poleward flow. During these periods, warm-water copepod species, typical of oceanic and subtropical waters from the south, contribute an anomalously larger fraction of the copepod biomass in the NCC (Bi *et al.*, 2011; Keister *et al.*, 2011). Changes in zooplankton composition across these different climate scenarios can greatly alter the bioenergetics of the food chain because the northern copepod taxa have large stores of wax esters that serve as long-term energy depots, whereas the warm-water, southern (subtropical) taxa have minimal lipid reserves (Lee *et al.*, 2006). Therefore, basin-scale climate variability can lead to a reduction in the abundance of the lipid-rich zooplankton, and thus, the productivity of forage fish communities in the NCC that in turn leads to reduced productivity of the higher trophic-level organisms (Peterson & Schwing, 2003; Field *et al.*, 2006; Peterson *et al.*, 2014).

While the relationship between the low-frequency variability in zooplankton community characteristics and the PDO is well understood, the influence of El Niño on higher frequency changes in zooplankton communities of the NCC is less clear. Some strong El Niño events have had widespread consequences for the pelagic ecosystem throughout the California Current. During the strong El Niño events of 1982–1983 and 1997–1998, regions of the southern California Current were characterized by a deep nutricline and a photic zone deplete of chlorophyll; and during the 1997–1998 event dramatic declines in zooplankton biomass were observed (Fiedler, 1984; McGowan, 1985; Bograd & Lynn, 2001). Anomalously warm surface water and low nutrients and primary productivity were also observed during 1997–1998 in the central California Current (Chavez *et al.*, 2002), and changes in zooplankton composition were observed during and following these strong events off British Columbia (Mackas & Galbraith, 2002). In the NCC, the impacts of the most recent strong events of 1982–1983 and 1997–1998 included declines in upwelling-favorable winds (Schwing *et al.*, 2002; Jacox *et al.*,

2015); altered physical water properties such as alongshore flow, temperature, salinity, and mixed-layer depth (Huyer & Smith, 1985; Huyer *et al.*, 2002; Jacox *et al.*, 2015); decreases in nutrients and chlorophyll (Pearcy & Schoener, 1987; Corwith & Wheeler, 2002); changes in the species compositions of zooplankton (Miller *et al.*, 1985; Peterson *et al.*, 2002; Keister *et al.*, 2005), fish (Pearcy, 2002), and whales (Benson *et al.*, 2002); and decreased reproductive success and increased mortality of seabirds (Pearcy & Schoener, 1987). On the contrary, other extreme El Niño events (such as the 1972–1973 event which was devastating to pelagic fish stocks off Peru) had no apparent physical or biological impact in the NCC (Cannon *et al.*, 1985; Wells *et al.*, 2013). Weaker El Niño events are less studied, and there are no studies to our knowledge that have attempted to assess differences in the biological responses across multiple events. Given the potential for El Niño to alter the pelagic ecosystem, and the potential for extreme events to increase in response to greenhouse warming (Cai *et al.*, 2014), we aim to investigate the impact of 10 El Niño events on the local hydrography, biogeochemistry, and species composition of the copepod community, and thus the bioenergetics of the food chain, in the NCC.

Recent research has distinguished two different types (or 'flavors') of El Niño events. These events can be categorized as either Eastern Pacific (the canonical El Niño) or Central Pacific (CP; also referred to as Modoki meaning 'similar but different') (Ashok *et al.*, 2007; Weng *et al.*, 2007; Kao & Yu, 2009; Kug *et al.*, 2009; McPhaden *et al.*, 2011). EP El Niño events are characterized by positive temperature anomalies in the eastern tropical Pacific, whereas CP El Niño events are associated with anomalously warm waters in the central tropical Pacific, but SST-neutral or negative anomalies in the eastern and western tropical Pacific. Recent work by Kidwell *et al.* (2014) suggests that the size and distribution of the western Pacific warm pool are different during EP and CP events. EP events are characterized by a larger warm pool, are typically stronger in amplitude than CP events, and are generally followed by strong La Niña conditions. On the other hand, CP events tend to occur more often and are associated with a smaller spatial extent of the warm pool, yet CP events persist for much longer compared to EP events. CP events have also doubled in intensity over the past three decades (Lee & McPhaden, 2010), and future climate models suggest that the frequency of CP events may increase with increased anthropogenic greenhouse gasses (Yeh *et al.*, 2009).

Positive SST anomalies in the tropics associated with El Niño influence extratropical latitudes through two

distinct mechanisms: the poleward propagation of coastally trapped waves and through large-scale atmospheric teleconnections. Thermocline depth anomalies in the tropics are propagated poleward resulting in a deeper thermocline, increased sea level, and reduced upwelling of deep, nutrient-rich water (Ramp *et al.*, 1997; Chavez *et al.*, 2002; Hermann *et al.*, 2009). El Niño conditions also alter deep convection in the tropics that influences the upper atmosphere and impacts the strength of the North Pacific High and the Aleutian Low in the extratropics (McPhaden *et al.*, 1998; Alexander *et al.*, 2002). This results in locally forced changes in upwelling-generating alongshore winds (Schwing *et al.*, 2002; Checkley & Barth, 2009; Jacox *et al.*, 2015) and large-scale ocean circulation (Alexander *et al.*, 2002; Di Lorenzo *et al.*, 2013).

It has been suggested that the atmospheric pathways between the tropics and the northern Pacific differ depending on the 'flavor' of the El Niño event. Di Lorenzo *et al.* (2013) suggest that interannual El Niño fluctuations drive the decadal ocean–atmosphere variability of the PDO and the North Pacific Gyre Oscillation (NPGO). The NPGO is defined as the second dominant mode of sea-surface height anomalies in the northeast Pacific and is associated with decadal variations in the circulation of the North Pacific Gyre (Di Lorenzo *et al.*, 2008). Positive SST anomalies in the central Pacific during CP El Niño events may trigger atmospheric teleconnections to the extratropics through the North Pacific Oscillation that in turn are evidenced by changes in the NPGO (Alexander *et al.*, 2002; Newman *et al.*, 2003; Di Lorenzo *et al.*, 2010, 2013; Furtado *et al.*, 2012). Conversely, warm anomalies in the equatorial eastern Pacific during EP El Niño events are linked to extratropical locales through atmospheric teleconnections that affect the Aleutian Low and are manifested by changes in the PDO. These two different pathways affect alongshore transport in the extratropics differently, with the PDO being associated with variability in alongshore transport and changes in zooplankton communities in the NCC and the NPGO being indicative of transport and changes in zooplankton communities in the western Pacific Kuroshio-Oyashio Transition Region (Keister *et al.*, 2011; Chiba *et al.*, 2013; Di Lorenzo *et al.*, 2013).

Motivated by the potential for El Niño to alter the pelagic ecosystem, and the possibility that extreme events might become more frequent in future climate scenarios, we examined the effect of 10 El Niño events on the timing, magnitude, and duration of temperature and copepod community composition anomalies (and thus pelagic food-chain structure) in the NCC using a 20+ year time series of hydrographic and zooplankton samples collected fortnightly. Given the recent evidence

that there are two distinct 'flavors' of El Niño that differ in frequency and intensity and that influence the extratropics via different atmospheric teleconnections, we considered the potential for 'flavor-dependent' responses by the pelagic ecosystem. Further, we investigated whether these biological responses are dependent upon the intensity of the warm event.

Materials and methods

Characterization of El Niño events

The Niño-3.4 index was used to characterize equatorial SST anomalies over the study period from 1968 to 2014. The Niño-3.4 index is the monthly ERSST.v3b SST anomalies (1981–2010 base period) in the Niño-3.4 region (5°N-5°S, 120°-170°W; http://www.cpc.ncep.noaa.gov/data/indices/). Warm events are defined as occurring when the Niño-3.4 index exceeds 0.5 °C for two or more consecutive months. Extreme events are characterized by positive temperature anomalies >1.5 °C, whereas moderate events have SST anomalies between 0.5 and 1.5 °C. Each event was classified as either EP or CP based on whether the anomalous warming occurred in the eastern or central Pacific (after McPhaden *et al.*, 2011; Yu *et al.*, 2012) and was characterized by the timing (the month that the Niño-3.4 index exceeded 0.5 °C), duration (number of months the Niño-3.4 index exceeded 0.5 °C), magnitude (mean Niño-3.4 index), and intensity (average monthly Niño-3.4 index multiplied by the duration, i.e. degree months). Each event was further characterized by the sign, average, and intensity (as described above) of the monthly PDO (http://research.jisao.washington.edu/pdo/PDO.latest) values during the months of each El Niño event. The relationship between the intensity of El Niño and PDO was explored using pairwise correlation.

Local hydrographic, biogeochemical, and zooplankton data

Zooplankton, hydrography, nutrient, and chlorophyll data were collected at fortnightly to monthly intervals along the Newport Hydrographic Line (44.6°N, 124.2°W) at a station (NH 5) five miles (9 km) offshore of Newport, Oregon in 62 m of water. Zooplankton were collected from 1969 to 1973, 1983, and 1996 to 2014, and hydrography, nutrient, and chlorophyll data were collected from 1997 to 2014. Temperature was measured with a Seabird SBE 19 or SBE 25 CTD; measurements from the lower water column (50 m) were used to avoid the high-frequency variability of SST and the mixed layer. Surface (1 m) water samples were collected for nutrients and chlorophyll. Nutrients were analyzed by standard wet chemical methods using a Technicon Autoanalyzer (Gordon *et al.*, 1995). Chlorophyll samples were immediately filtered through precombusted 25-mm glass-fiber filters and stored at −20 °C. Chlorophyll-*a* was extracted for 12 h in the dark at −20 °C using 90% acetone as the solvent, and fluorescence was measured with a Turner Designs™ 10-au fluorometer

(Turner Designs, Sunnyvale, CA, USA). Temperature, nutrient, and chlorophyll values were averaged monthly, and monthly anomalies were calculated using 1997–2014 as the base period to remove the seasonal cycle.

Zooplankton sampled from 1996 to 2014 were collected with a 0.5-m diameter, 202-μm plankton net hauled vertically from a few meters above the sea floor to the sea surface. Zooplankton sampled prior to 1996 were collected using similar methods (see Peterson & Miller, 1975). The volume of water filtered during each net tow was estimated using a TSK flowmeter. In the laboratory, copepods were enumerated following methods outlined in Hooff & Peterson (2006), and all counts were converted to biomass using length-to-mass regressions and standardized to units of mg C m^{-3}. The biweekly copepod biomass data (mg C m^{-3}) were then averaged monthly and transformed $\log_{10}$ ($x + 0.01$), and monthly biomass anomalies were calculated for each species by removing the seasonal cycle using 1996–2014 as the base period (Mackas *et al.*, 2001). Zooplankton anomalies are on a $\log_{10}$ scale and represent a multiplicative (not additive) scaling relative to the average seasonal cycle: for example, an anomaly of +1 means that observations average 10× (1996–2014 climatology).

Copepod species were classified into two general groups based on their water-mass affinity: cold-water (northern) and warm-water (southern) species. Northern species (*Calanus marshallae*, *Pseudocalanus mimus*, and *Acartia longiremis*) dominate the coastal species assemblages of the Gulf of Alaska and Bering Sea, whereas the southern species (*Acartia tonsa*, *Calanus pacificus*, *Calocalanus* spp., *Clausocalanus* spp., *Corycaeus anglicus*, *Ctenocalanus vanus*, *Mesocalanus tenuicornis*, and *Paracalanus parvus*) dominate the coastal and oceanic species assemblages off central and southern California (Fleminger, 1967; Barnett & Jahn, 1987; Mackas *et al.*, 2001; Hooff & Peterson, 2006). The presence of one group vs. another in shelf waters off central Oregon depends on advective transport, with the presence of northern cold-water species indicating southward transport of subarctic waters and warm-water, southern species indicating northward or onshore transport of subtropical water. Species within these two groups are often referred to as 'indicator' or 'sentinel' species, as changes in their abundances are typically indicative of a substantial shift in ecosystem structure. Biomass anomalies were calculated for the southern and northern copepod groups by averaging the monthly biomass anomalies across species within each group (Mackas *et al.*, 2001).

Data analysis

We characterized the timing, duration, and magnitude of the 50-m temperature and copepod community anomalies in the NCC in response to each El Niño event. The lag in the timing of the local physical and biological change measured at station NH 5 in response to El Niño activity at the equator was defined as the number of months between the initiation of the Niño-3.4 index ≥0.5 °C and the observation of positive temperature anomalies >0.25 °C or positive (negative) biomass anomalies of southern (northern) copepods exceeding

0.1 mg C m^{-3} for two consecutive months. The duration of each physical and biological response was measured as the number of consecutive months with temperature anomalies >0.25 °C and biomass anomalies of southern and northern copepods exceeding the 0.1 mg C m^{-3} threshold until termination of each event. The termination of each event was defined to occur when temperature anomalies were <0.25 °C and biomass anomalies of southern (northern) neritic copepods were less (greater) than 0.1 mg C m^{-3} for two consecutive months. The overall magnitude and intensity of the physical and biological response to El Niño events were measured as the average (magnitude) and the average multiplied by the duration in months (intensity) of the temperature and biomass anomalies for each event. 'Flavor-dependent' patterns in the timing (lag) and intensity of the local hydrographic and biological response across EP and CP events were determined using one-way analysis of variance (ANOVA) with the lag and intensity of 50-m temperature and southern and northern copepod biomass anomalies as the dependent variables. The coherence among the monthly changes in the local physical and biological response to each El Niño event was explored using nonmetric multidimensional scaling (NMS). Monthly fluctuations in 50-m temperature and copepod biomass anomalies were smoothed with a 3-month running mean, and the dissimilarity in the temporal evolution of the temperature and biomass anomalies across events was quantified using Euclidean distance beginning with the earliest month of El Niño initiation across events (May) and extending 19 months (December of the following year). NMS explored the separation in the patterns of similarity in these monthly fluctuations. Nearby El Niño events on the NMS ordination plot had a similar temporal evolution in the physical and/or biological response compared to events that are farther apart. Finally, the relationship between the intensity of the physical and biological response to El Niño intensity was examined using linear regression.

Results

Zooplankton were sampled during 1969–1973, 1983, and 1996–2013. During this time period, 10 El Niño events (1968–1969, 1969, 1972–1973, 1982–1983, 1997–1998, 2002–2003, 2004–2005, 2006–2007, 2009–2010, and 2012) occurred (Table 1). Four events have been classified as CP events, and five events have been classified as EP events by McPhaden *et al.* (2011) and Yu *et al.* (2012). A warm event in 2012 was not classified as EP or CP by previous authors because it did not meet the conventional definition of an El Niño event as classified by NOAA of having SST anomalies in the Niño-3.4 region ≥0.5 °C for a period of at least five consecutive and overlapping 3-month periods. However, SST anomalies in the EP (Niño-3 region) were stronger than those in the western Pacific (Niño-4 region), and thus, we classified this event as an EP event.

Table 1 Characterization of 10 El Niño events that occurred during 20+ years of zooplankton sampling from 1969 to 1973, 1983, and 1996 to 2014. The lag of the local physical and biological change measured at station NH 5 in response to El Niño activity at the equator was defined as the number of months between the initiation of the Niño-3.4 index ≥ 0.5 °C and the observation of positive temperature anomalies >0.25 °C and positive (negative) biomass anomalies of southern (northern) copepods (exceeding a 0.1 mg C m^{-3} threshold) for two consecutive months. The duration (Dur.) of each physical and biological response was measured as the number of consecutive months with positive temperature anomalies >0.25 °C and biomass anomalies of southern (northern) copepods greater (less) than the 0.1 threshold. The intensity of a parameter is the mean times the duration of each signal

El Niño events					Niño-3.4 index		PDO			Hydrography 50-m T				Southern copepods				Northern copepods			
Type	Year	Start Date	End Date	Dur. (month)	Mean	Intensity	Phase	Mean	Intensity	Lag (month)	Dur. (month)	Mean	Intensity	Lag (month)	Dur. (month)	Mean	Intensity	Lag (month)	Dur. (month)	Mean	Intensity
CP	68–69	Nov-68	May-69	7	0.75	5.26	–	−0.72	−5.06	–	–	–	–	–	–	–	–	–	–	–	–
EP	72–73	Jun-72	Feb-73	9	1.40	12.58	–	−0.33	−3.00	–	–	–	–	–	–	–	–	–	–	–	–
EP	82–83	May-82	Jun-83	14	1.27	17.76	+	0.76	10.67	–	–	–	–	–	–	–	–	–	–	–	–
EP	1969	Sep-69	Dec-69	4	0.61	2.45	+	0.50	1.99	–	–	–	–	0	0	0.00	0.00	1	4	−0.31	−1.24
EP	97–98	May-97	May-98	13	1.64	21.32	+	1.67	21.69	0	17	1.30	22.18	2	17	0.35	5.95	1	17	−0.79	−13.49
EP	06–07	Sep-06	Jan-07	5	0.83	4.15	–	−0.21	−1.06	2	2	0.88	1.77	0	5	0.14	0.72	2	2	−0.25	−0.50
EP	2012	Sep-12	Oct-12	2	0.68	1.36	–	−1.50	−3.00	1	3	0.91	2.72	2	3	0.25	0.75	1	3	−0.23	−0.69
CP	02–03	May-02	Mar-03	11	0.91	10.00	+	0.83	9.12	8	5	1.09	5.44	6	9	0.22	2.01	8	2	−0.41	−0.82
CP	04–05	Jul-04	Jan-05	7	0.70	4.88	+	0.22	1.57	7	6	0.61	3.69	6	12	0.44	5.27	2	13	−0.66	−8.52
CP	09–10	Jul-09	Apr-10	10	1.07	10.70	+	0.29	2.90	6	6	0.81	4.87	6	10	0.24	2.37	2	9	−0.26	−2.35

CP, Central Pacific; EP, Eastern Pacific; –, no data; PDO, Pacific Decadal Oscillation.

There was no 'flavor-dependent' pattern in the magnitude of events. The five strongest El Niño events were initiated in 1972 (EP), 1982 (EP), 1997 (EP), 2002 (CP), and 2009 (CP) (Fig. 1). The mean SST anomalies in the equatorial Pacific during these events exceeded 0.9 °C, and persisted for 9–14 months (Table 1). The other five events (two CP and three EP events) were relatively weak with mean SST anomalies ranging from 0.61 °C (1969) to 0.83 °C (2006–2007; Table 1). These weaker events ranged in duration from the most prolonged (7 months) in 1968–1969 and 2004–2005 to the shortest duration event of 2 months in 2012 (Table 1). The 10 warm events also occurred over a range of negative and positive PDO values. Of these 10 events, four occurred when the PDO was in negative phase (1968–1969, 1972–1973, 2006–2007, and 2012) and six occurred when the PDO was in positive phase (Fig. 1). While weak and strong El Niño events occurred during both positive and negative phases of the PDO, there was a significantly positive trend in the relationship of El Niño intensity and PDO intensity (Fig. 1; $r = 0.80$; P-value = 0.006) that was not dependent on the 'flavor' of events.

A local hydrographic and biogeochemical signal of El Niño was observed at 44.6°N by the occurrence of nutrient- and chlorophyll-deplete warm water and a change in the copepod community composition. Anomalously warm water with low-nitrate concentrations was observed during and/or following the six events for which data are available (1997–2014; Fig. 2d, e). Coincident with the warm, low-nitrate surface waters, chlorophyll concentrations were also generally low
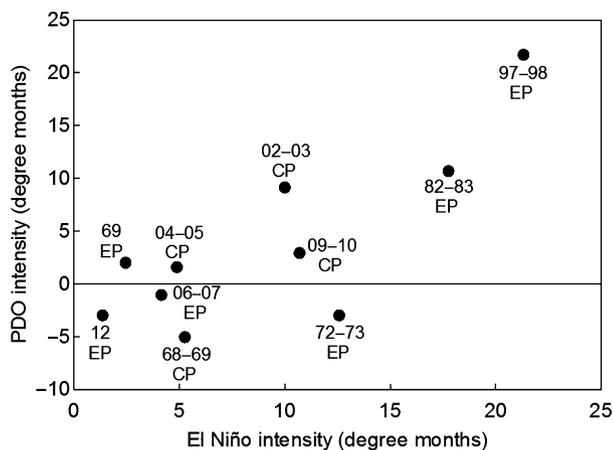
during and/or following all events except 2002–2003 when chlorophyll concentrations were moderately higher than average (Fig. 2f). During the 20+ year time series of zooplankton collections, anomalously high biomass anomalies of southern, warm-water copepods and anomalously low biomass of northern, cold-water copepods were observed during and/or following seven of the 10 warm events: 1982–1983, 1997–1998, 2002–2003, 2004–2005, 2006–2007, 2009–2010, and 2012 (Fig. 2b, c). There was no detectable effect on the southern or northern copepod communities associated with the strong 1972–1973 event and only a slight effect on the southern copepod community associated with the 1968–1969 events (although sampling was less comprehensive than during events after 1996).

The temporal pattern of the hydrographic and biological response at the station NH 5 to warming events at the equator closely resembled the evolution and temporal pattern of the Niño-3.4 index from initiation to the demise of each event. These patterns generally differed between EP and CP events. With the exception of the strong and prolonged event of 1997–1998, the EP events of 1969, 2006–2007, and 2012 began in September and were relatively short with durations of 2–4 months (Table 1, Fig. 3a). Warm temperatures and increased biomass of southern copepods and decreases in northern copepods were also relatively short with durations of zero to 2 months (Table 1, Fig. 3b–d). Peaks in temperature and the copepod response occurred in November–December during these events. In contrast, the CP events of 2002–2003, 2004–2005, and 2009–2010 began in May or July and persisted for 6–8 months (Table 1, Fig. 3a). The hydrographic and biological responses were also prolonged, persisting for 5–13 months with the exception of the northern copepod community that persisted for only 2 months in 2002–2003. Following the initiation of an event, the pattern of warm-water anomalies at NH 5 peaked in February–March (Fig. 3b), while the increase in the biomass of the southern copepods and the decrease in biomass of the northern copepods peaked during March–June (Fig. 3c, d).

The time lag between initiation of an El Niño event at the equator and the occurrence of positive temperature anomalies and a change in the copepod community off Oregon differed between the two types of El Niño events (Table 1, Fig. 3). Anomalously warm deep water was observed at NH 5 significantly quicker during EP events (0- to 2-month lag) compared to CP events (6- to 8-month lag; Table 1; $F = 54.0$, P-value = 0.002). Similarly, positive biomass anomalies of southern copepods were observed more rapidly following EP events (0–2 months) compared to CP events (6 months; Table 1; $F = 53.6$, P-value < 0.001). However, the tim-

Fig. 1 El Niño intensity in relation to the PDO intensity during each El Niño event. Intensity is measured as the average SST anomalies (°C) multiplied by the duration (months) of each event. Numbers represent El Niño years and (CP) Central Pacific and (EP) Eastern Pacific; PDO, Pacific Decadal Oscillation; SST, sea-surface temperature.
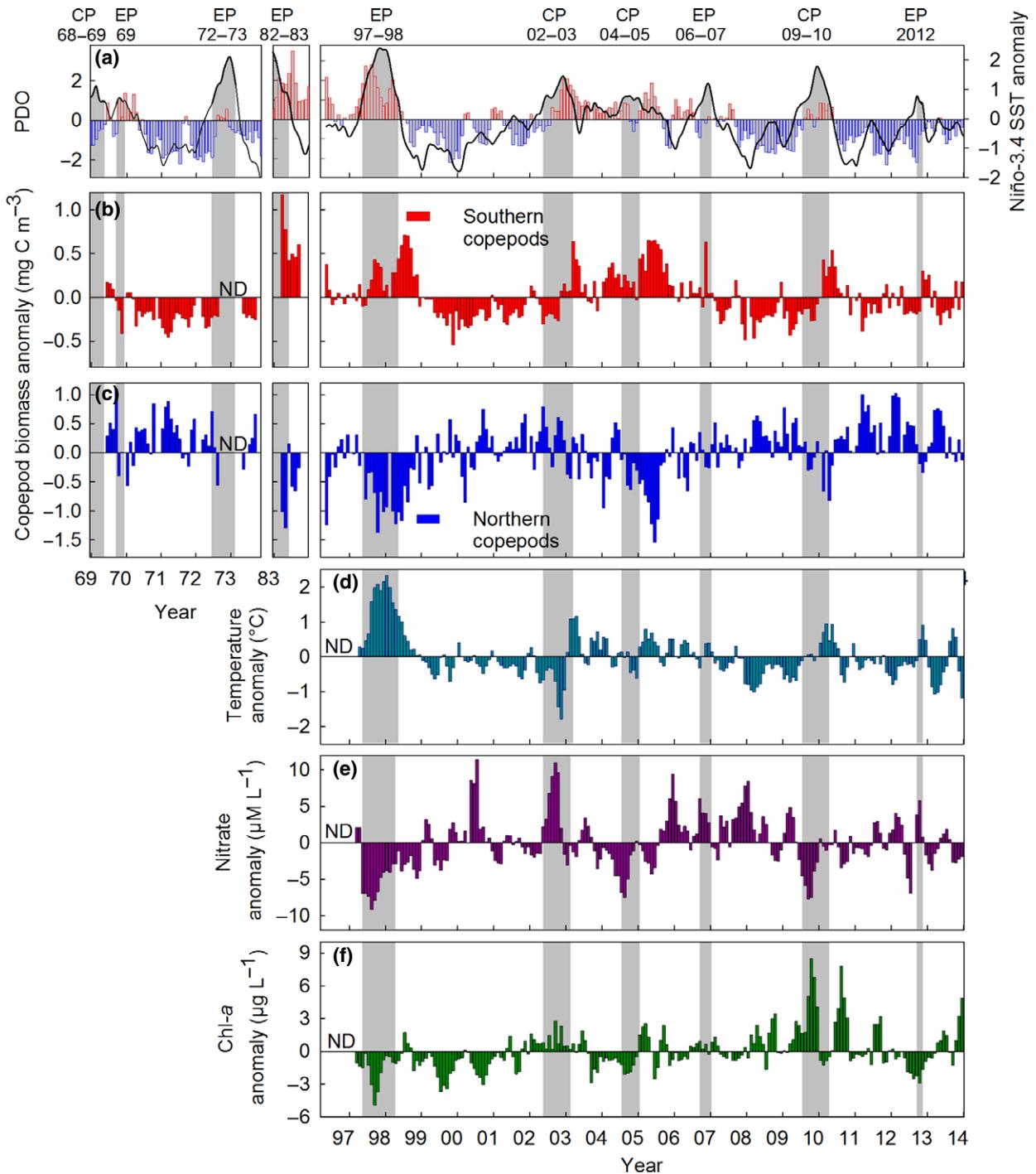
Fig. 2 Time series of El Niño events and the PDO compared to monthly averaged biomass anomalies of copepod groups, hydrography, and biogeochemistry at NH 5 (44.6°N). (a) Niño-3.4 index (°C; line) and the PDO (red and blue bars), and time interval spanned by each El Niño event (gray vertical bars). Monthly anomalies of (b) southern, (c) northern copepods (mg C m^{-3}), (d) deep-water (50-m) temperature (°C), (e) nitrate (μM L^{-1}), and (f) chlorophyll-a (μg L^{-1}). Temperature, nitrate, and chlorophyll-a data are smoothed with a 3-month running mean to remove high-frequency variability. ND, no data; PDO, Pacific Decadal Oscillation.

ing of the change from positive to negative biomass anomalies of northern copepods did not differ between event types (Table 1; $F = 2.6$, P-value = 0.17).

Regardless of event type, negative biomass anomalies of northern copepods occurred rapidly (1–2 months) following the initiation of events in the tropics, with
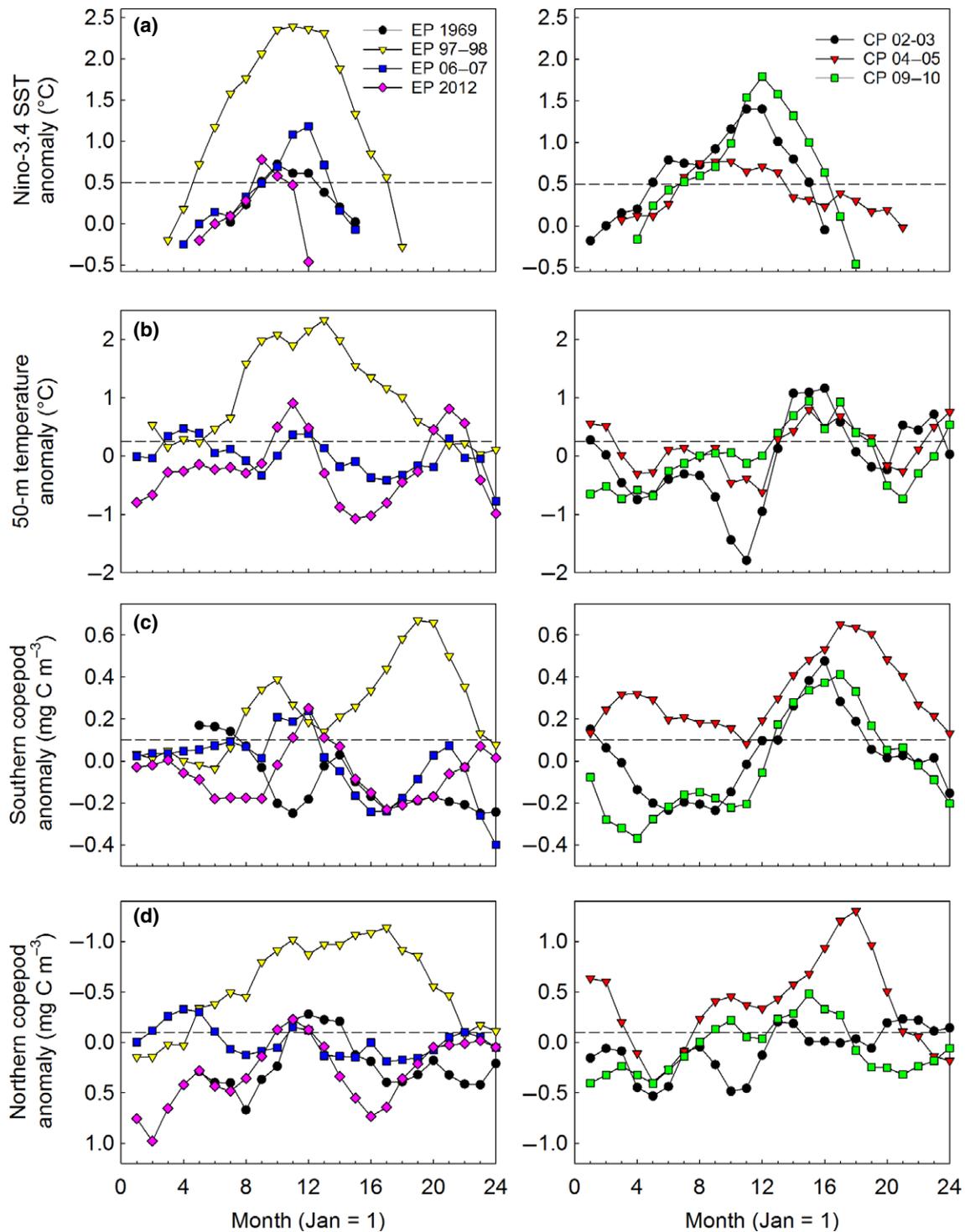
Fig. 3 Monthly changes in equatorial SST anomalies and local temperature and zooplankton across EP (left panels) and CP (right panels) El Niño events. (a) Niño-3.4 index (°C), (b) 50-m temperature anomaly, (c) southern, and (d) northern copepod biomass anomaly mg C m^{-3} from NH 5 (44.6°N). Local hydrography and biological data are 3-month running means. Dashed lines depict thresholds for the start/end of El Niño events (for Niño-3.4 index ≥0.5 °C; 50-m temperature anomaly >0.25 °C; southern copepods >0.1 mg C m^{-3}; northern copepods less than −0.1 mg C m^{-3}). CP, Central Pacific; EP, Eastern Pacific; SST, sea-surface temperature.

one exception during the CP event of 2002–2003 when negative biomass anomalies were not observed until 8 months after the initiation of the event at the equator. This event followed a 4-year period of predominantly positive PDO values (Fig. 2a).

The local pattern of the temperature response based on the NMS showed separation of the EP and CP events with the strong event of 1997–1998 separated from the other five events (Fig. 4a). The pattern of response of the southern and northern copepod assemblage also partially separated out by EP and CP events. The two exceptions were the patterns of response for both the southern and northern copepod groups during the strong EP event of 1997–1998 and the CP event of 2004–2005, when the PDO was persistently positive for 2 years preceding this event (Fig. 4b, c). The pattern of biomass change for the southern copepods during the other two CP events (2002–2003 and 2009–2010) grouped closely together, as did the three EP events (1969, 2006–2007, and 2012), and these two groups were distinctly separated from one another and from the coherent pattern of response during the 1997–1998 and 2004–2005 event (Fig. 4b). The pattern of biomass change for the northern copepods was not as strongly separated across CP and EP events; however, the 1997–1998 and 2004–2005 events were strongly separated from the other events and from each other (Fig. 4c).

The intensity of each El Niño event was strongly related to the intensity of the hydrographic and the biological signal observed during events. There was a positive relationship between the intensity (degree months) of the six El Niño events (for which we have hydrographic data) and the intensity of positive temperature anomalies (degree months) observed at NH 5 (Fig. 5a; $R^2 = 0.86$, $P = 0.008$). There was also a strong positive relationship between the intensity of El Niño events and the intensity of biomass anomalies of southern copepods (Fig. 5b; $R^2 = 0.96$, $P < 0.001$) and the decrease of northern copepods (Fig. 5c; $R^2 = 0.78$, $P = 0.02$). The 2004–2005 event was excluded from this analysis because there were prolonged increases (decreases) of southern (northern) copepod biomass anomalies likely due to the prolonged and persistently positive phase of the PDO for the 2 years preceding this event. This indicates that both the magnitude and the duration of each event were highly correlated with the magnitude and duration of the change in local hydrography and copepod community composition and that these changes are modulated by the background state of the Pacific Ocean prior to the onset of the event. However, the robustness of these conclusions is low due to a relatively few number of observations, and
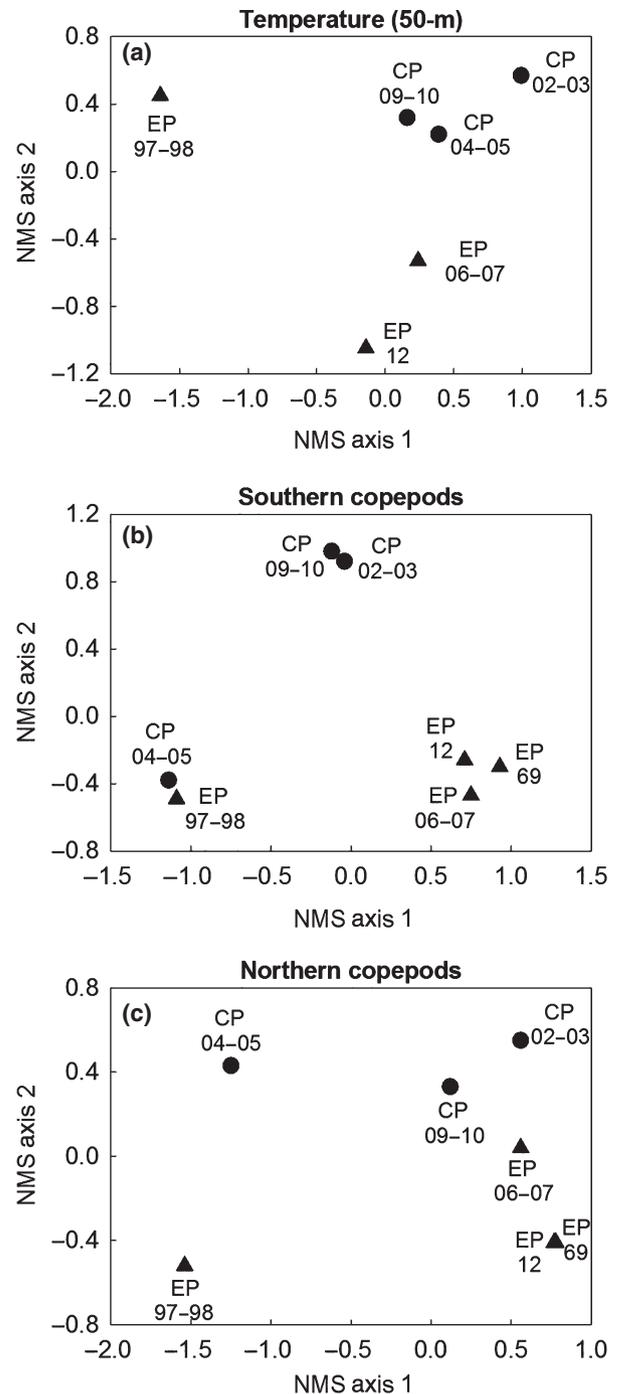
Fig. 4 Nonmetric multidimensional scaling (NMS) plot showing separation of the interannual differences in the monthly changes in (a) 50-m temperature anomalies, biomass anomalies of (b) southern and (c) northern copepods collected at NH 5 (44.6°N). Numbers represent El Niño years, and symbols represent the type of event (i.e. EP or CP). CP, Central Pacific; EP, Eastern Pacific.

the significance of the relationships for the temperature and northern copepods is largely dependent on observations during the extreme 1997–1998 event.

Temperature (50-m)

(a)

Southern copepods

(b)

Northern copepods

(c)
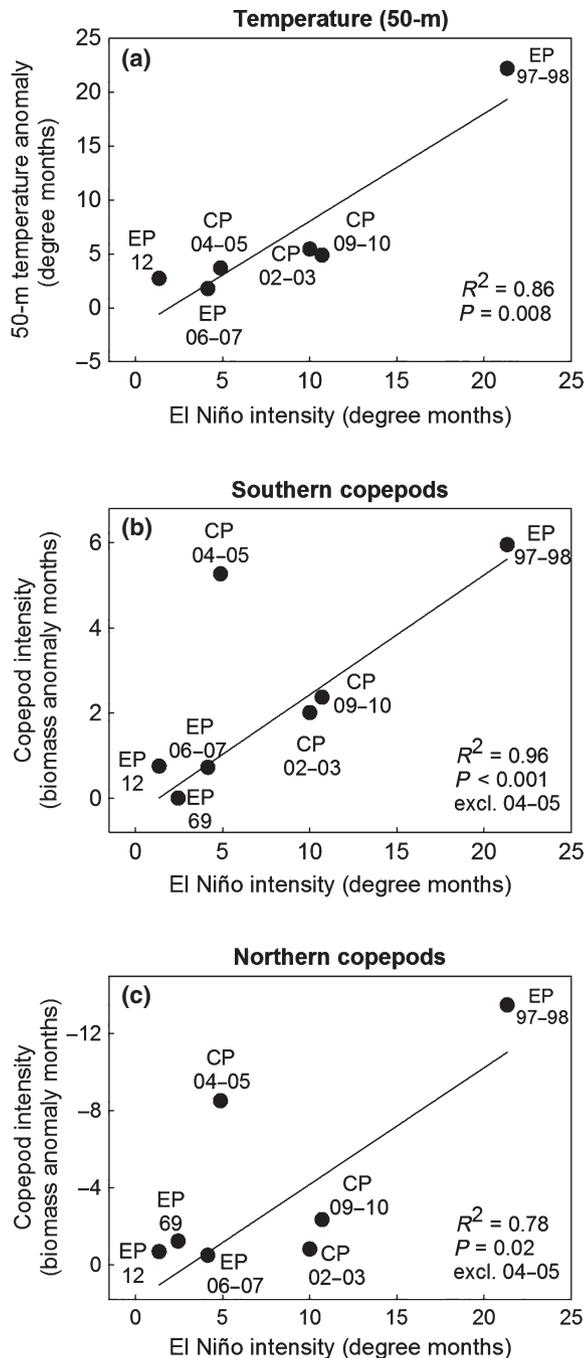
Fig. 5 Relationship of El Niño intensity measured by the average of the SST anomalies in the Niño-3.4 region multiplied by the number of months that those anomalies were >0.5 °C (degree months) vs. the (a) 50-m temperature anomaly (b) southern and (c) northern copepod intensity measured as the average temperature or biomass anomalies multiplied by the number of months when positive temperature anomalies (>0.25 °C) or positive (negative) biomass anomalies of warm (cold) greater than (less than) 0.1 mg C m^{-3} were observed for two consecutive months at NH 5 (44.6°N). SST, sea-surface temperature.

There was no clear distinction in the hydrographic or biological intensity between EP and CP events.

The importance of the background state of the pelagic ecosystem prior to an El Niño event is further illustrated by the coupling of the PDO, El Niño, and the biomass anomalies of the two copepod groups. The PDO explains 23% and 28% of the variability in biomass anomalies of the southern and northern copepods, respectively (Fig. 6a; $R^2 = 0.23$, $P < 0.001$ and Fig. 6b; $R^2 = 0.28$, $P < 0.001$). Twenty-seven percent and 24% of the residual variance in the southern and northern copepod biomass anomalies are explained by the Niño-3.4 index (Fig. 6c; $R^2 = 0.27$, $P < 0.001$ and Fig. 6d; $R^2 = 0.24$, $P < 0.001$). This illustrates that the PDO and El Niño are both associated with significant variability in the North Pacific, making it difficult to assess the relative effects of one on the copepod community independent of the other.

Discussion

Dramatic shifts in primary productivity and zooplankton biomass and species composition have been documented in the extratropics during and/or following some strong El Niño events, but this study provides the first evidence that even short duration or weak events can alter the pelagic food chain in the NCC. A clear hydrographic and biogeochemical signal of El Niño was observed at 44.6°N during and/or following seven of 10 El Niño events in this study regardless of the magnitude of the signal at the equator. However, the timing, magnitude, and duration of the response varied depending on the type and magnitude of the equatorial event and the background state of the Pacific Ocean prior to the event. The signal was manifested off Oregon by the occurrence of positive temperature anomalies, decreased surface nitrate, and chlorophyll concentrations and a zooplankton community that was dominated by southern copepods. From satellite data and modeling studies, similar patterns of increased temperature and decreased nutrient and chlorophyll concentrations were observed in the NCC across El Niño events of varying magnitude (Thomas *et al.*, 2012; Frischknecht *et al.*, 2015; Jacox *et al.*, 2015). During these studies, the net impact on zooplankton and higher trophic levels was inferred. However, our data now show how reduced productivity in the NCC in response to El Niño is also associated with a shift toward a subtropical zooplankton community known to have minimal lipid reserves (Lee *et al.*, 2006), thereby creating a forage community with a lower bioenergetic content and lower food quality, further exacerbating the potential consequences for upper trophic levels. An
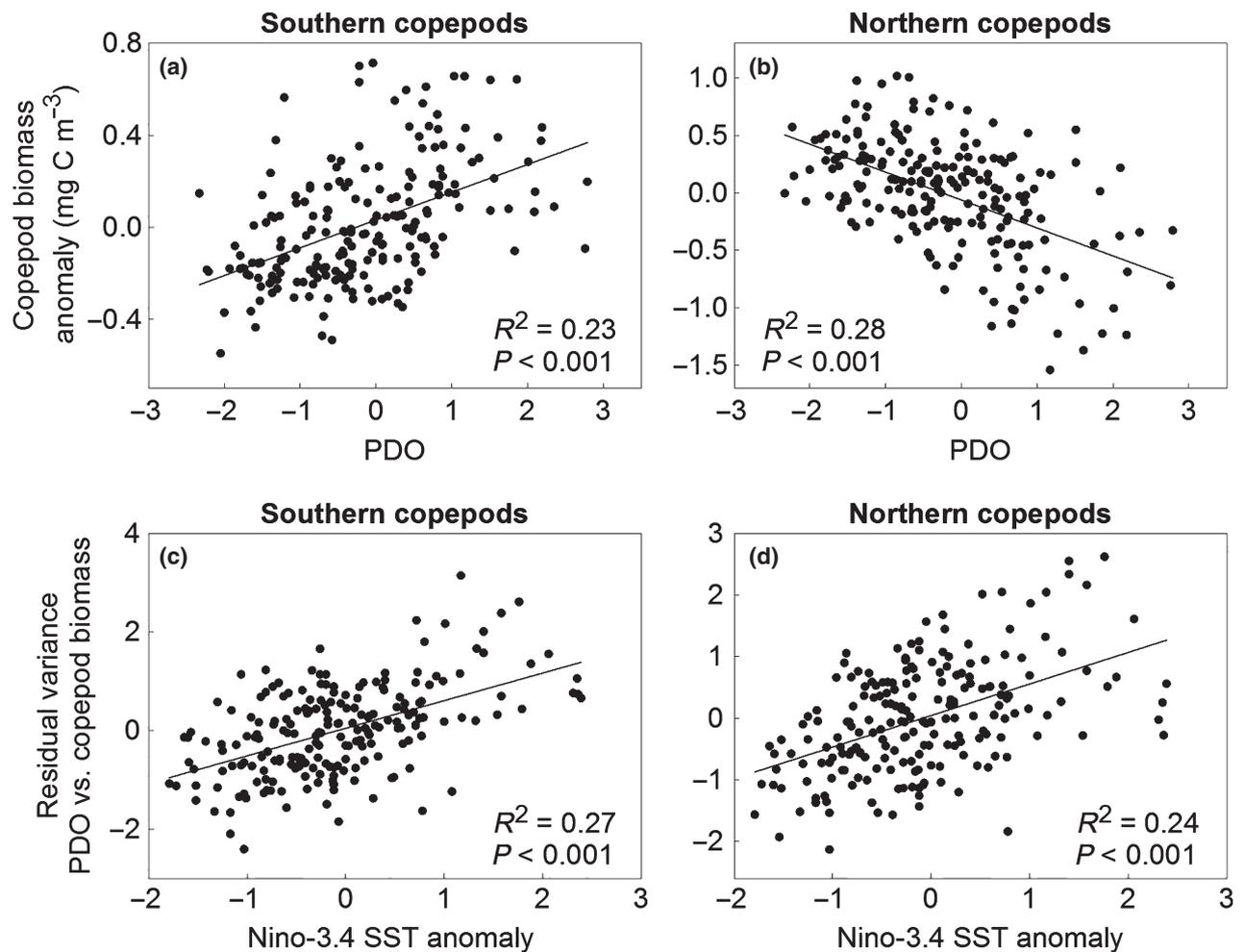
Fig. 6 Relationship of the PDO vs. (a) southern and (b) northern copepod biomass anomaly (mg C m^{-3}) and the relationship of the residual variance not explained by the PDO for the (c) southern, (d) northern copepod biomass anomaly (mg C m^{-3}) vs. the El Niño-3.4 index (°C). PDO, Pacific Decadal Oscillation.

important topic of future research would assess the sensitivity of upper trophic levels to variability in the persistence of these low productivity periods. If El Niño-like conditions become more frequent with human induced climate change (Timmermann *et al.*, 1999; Cai *et al.*, 2014), there could be prolonged periods of reduced productivity in the NCC that could lead to widespread negative biological impacts on upper trophic levels.

Changes to the physical and biological ecosystem in the NCC related to climatic variability in the tropics are dependent on the background climatic state of the northeast Pacific prior to El Niño events. During our study, the PDO was in positive phase from 2002 to 2005, and the copepod community in the NCC remained in an 'El Niño state' during this 3-year period, regardless of SST values in the equatorial region. While the relative influence of the PDO and El Niño

on ocean conditions in the NCC is difficult to distinguish, it is clear that warm, oligotrophic water and a southern copepod community dominates during El Niño conditions in the NCC, regardless of the phase of the PDO. It is likely, however, that the zooplankton community can return to a lipid-rich northern community quicker during negative PDO years as was observed during 2006–2007 and 2012 when southern copepods persisted for only 5 and 3 months, respectively.

Changes to the species composition of the copepod community off Oregon appear to be more sensitive to El Niño activity at the equator compared to changes in the deep-water temperature. During some events, positive anomalies of southern copepods and negative anomalies of lipid-rich northern copepods preceded the occurrence of positive temperature anomalies and decreases in nutrients and phytoplankton off Oregon.

An equatorial signal of El Niño impacts the NCC both through remote forcing as the northward propagation of coastally trapped waves and via local atmospheric forcing that reduces upwelling-generating alongshore winds and alters circulation in the California Current (Hermann *et al.*, 2009; Di Lorenzo *et al.*, 2013; Frischknecht *et al.*, 2015). A southern copepod community in the NCC is thought to be the result of advective processes associated with atmospheric forcing that alters alongshore transport as opposed to local processes associated with upwelling (Bi *et al.*, 2011; Keister *et al.*, 2011). Variability in modeled SST in the NCC appears to be driven almost equally by both local and remote forcing during moderate and strong El Niño events (Frischknecht *et al.*, 2015). Therefore, variability in the timing of the physical vs. biological response related to El Niño could be the result of multiple pathways altering the ecosystem in the NCC differentially.

The time lag following the initiation of an El Niño event at the equator to the appearance of a signal off Oregon was strongly linked to the type of tropical event. Increased temperature anomalies and a change in copepod species composition to a southern, lipid-poor community was observed within 0–2 months following the four EP events (1969, 1997–1998, 2006–2007, and 2012), but responses to CP events lagged initial tropical anomalies by 6–8 months. The atmospheric bridge responds to tropical anomalies within 2 weeks (Alexander *et al.*, 2002), and poleward propagating coastally trapped waves travel at speeds of 210–250 km day^{-1} (Frischknecht *et al.*, 2015) potentially reaching our study region from an equatorial source within 1 month. Therefore, the difference in timing cannot be solely attributed to local vs. remote forcing, but does suggest that the physical processes through which tropical El Niño events influence physical and biological changes in the NCC differ between EP and CP events. The dominant mode of climate variability driving ocean dynamics in the NCC is the PDO, while the NPGO is thought to have greater influence on dynamics in the Gulf of Alaska and latitudes equatorward of 40°N (Chhak *et al.*, 2009). A large portion of the low-frequency variability associated with the PDO and the NPGO can be explained by the North Pacific sea-level pressure anomaly pattern of EP and CP events, respectively (Di Lorenzo *et al.*, 2013). Therefore, it appears that rapid changes in the physical and biological environment in the NCC during and/or following EP events could be the result of the complex coupling of EP events to the Aleutian Low that manifests a signal through changes in the PDO, thereby affecting alongshore transport and altering the physical and biogeochemical properties in the NCC more rapidly than during CP events.

While the timing of response in the NCC differed across EP and CP events, the magnitude and duration of temperature anomalies and of both northern and southern copepod biomass anomalies off Oregon were directly related to the magnitude and duration of tropical events. Following the pattern of the tropical signal, a southern lipid-poor copepod community persisted for much longer during CP events compared to EP events. This could have profound impacts on the bioenergetics of the pelagic food chain because CP events have increased in frequency and have doubled in intensity over the past three decades (Lee & McPhaden, 2010). Whether the increased frequency of CP events is due to natural climate variability (McPhaden *et al.*, 2011; Yeh *et al.*, 2011) or increased greenhouse gases (Yeh *et al.*, 2009) is a topic of ongoing research.

The delay between the initiation of a tropical SST anomaly and the appearance of the associated biological anomaly in the NCC copepods may be critical when considering the potential impacts of El Niño on higher trophic levels that are sensitive to environmental perturbations during different portions of the seasonal cycle. The tropical El Niño cycle is phase-locked to the annual cycle with CP and EP events, generally beginning in the spring and fall, respectively, both peaking in winter, and then ending the following spring or early summer. Because of the variable lags in the timing of a physical and biological response between events, impacts on the NCC generally peak in the winter during EP events and in the spring during CP events. Species-specific life histories and migration cycles are often phase-locked to seasonal cycles coinciding with physical and ecological conditions favorable for survival or successful reproduction. For instance, reproductive success of the common murre may be especially susceptible to prey conditions in late winter just prior to breeding, while growth rates of juvenile salmon are more sensitive to the seasonal peak in ocean productivity in spring when first entering the ocean (Black *et al.*, 2011; Peterson *et al.*, 2014). We hope that increased understanding of specific time periods (arrival timing, magnitude, and duration) during which an El Niño event may disrupt the transfer of lipids from phytoplankton and zooplankton to higher trophic levels may allow managers to better anticipate the impact on specific marine populations. Recognizing the differences in the timing, magnitude, and duration of impacts associated with different El Niño events is a first step in building this understanding and allows the ability to plan for future climate scenarios.

Given the direct relevance of the composition of the copepod community to the efficiency at which energy

and biomass are transferred to higher trophic levels in the NCC, an index based on the biomasses of local copepod species may serve as a more effective index of the regional biological impact of El Niño than standard basin-scale indices. Our research highlights some subtleties in using equatorial SST anomalies to estimate the influence of a particular El Niño event on the extratropics. We have shown that most El Niño events since 1968 have had measurable impacts on the pelagic food chain of the NCC. Anomalously warm-water deplete of nutrients and phytoplankton along with negative biomass anomalies of lipid-rich copepod species and positive biomass anomalies of southern, lipid-poor copepod species were observed during both strong and weak El Niño events. However, the magnitude and duration of these physical and biological anomalies were directly proportional to the magnitude and duration of the tropical signal. Tropical events that were stronger and persisted for longer exhibited prolonged biological impacts on the NCC pelagic ecosystem compared to shorter, low-intensity events. Further, the timing of appearance of a local signal following a tropical event was 'flavor-dependent'. When fisheries managers and biological oceanographers are faced with the prospect of a future El Niño, prudent management and observation will require consideration of the type of event, both the magnitude and duration of the event, and the phase of the PDO when assessing possible impacts on the bioenergetics of the pelagic food chain.

Acknowledgements

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