Interannual summer variability in oceanic euphausiid communities off the Baja California western coast during 1998–2008

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ABSTRACT

Euphausiids are a major component of the zooplankton biomass due to their large size, contributing with high carbon content to other trophic levels in the pelagic ecosystem. We analyzed the summer interannual variability in euphausiid species composition based on carbon mass of the Baja California oceanic domain during 1998–2008. Selection of one exclusive season allowed the emphasis of interannual changes in order to research possible biological impacts. During the period 1998–2008 prevailed intense interannual activity, with four El Niño events, two of them (1997–1998 and 2006–2007) with SST anomalies propagating toward the eastern Pacific (EP-El Niño), while the other two (2002–2003 and 2004–2005) had SST anomalies limited to the central Pacific (CP-El Niño). There were also La Niña events in 1998–2000 and 2007–2008. The species with higher biomass contribution off Baja California were *Nematoscelis difficilis*, *Euphausia gibboides*, *Thysanoessa gregaria*, *Euphausia eximia*, *Nyctiphanes simplex*, and *Euphausia pacifica*, with a global geometric mean of 156, 66, 38, 30, 21, and 13 µg C m^{-3} respectively. *N. difficilis* and *E. pacifica* were dominant in the northern area (29.5-32°N), *N. difficilis* and *E. gibboides* in the central area (27–29.5°N), and *E. eximia* dominated in the southern area (24.5–27°N). 1998–2008 biomass anomalies showed a variety of patterns by species with the clearest footprint, in most of the species, during the strong EP-El Niño 1997–1998. CP-El Niño events also left a footprint in the biomass of some species but this was not always by anomalies of the same nature as EP-El Niño. The best examples were *N. difficilis* and *N. simplex*, which presented lightly positive anomalies during July 1998 but were strongly negative in the summer of 2003 and 2004. The opposite was observed in *E. recurva*, with a negative anomaly in July 1998 but positive in 2004 and 2005. The biophysical coupling between the species assemblage and environmental variables, using canonical correspondence analysis (CCA), explained 22% of the biomass variability. The first axis was responsible for thermal conditions in the upper layer (temperature at 10 m, 50 m, and the gradient between 10 and 100 m depth), while the second axis concentrated the oxygen gradient, oxygen and salinity at 50 m depth, and 200 m temperature. A large group of tropical-subtropical species showed covariance with axis-1, while *E. pacifica* and *T. spinifera* had an inverse covariance. The equatorial species *E. distinguenda* and *E. lamelligera* were close to axis-2, though the stations were limited to slope water where intense upwelling bring oxygen depleted deep water. Transition zone species (*E. gibboides*, *N. difficilis*, *T. gregaria*, and *N. simplex*) were relatively inert to both axes. Their response to climatic variability was less predictable and new variables should be explored, including bottom-up and top-down mechanisms.

1. Introduction

During the last decades the knowledge of how zooplankton communities change through long-term scales has considerably increased (Beaugrand, 2003; Bograd et al., 2003; Mackas et al., 2012). Long-time series are necessary to evaluate interannual anomalies, decadal regime shifts and climate change. With that purpose the Baja California region of the California Current System (CCS) has been the subject of intense sampling since the end of the past century (Baumgartner et al., 2008;

Lavaniegos, 2009; Lavaniegos et al., 2015). Baumgartner et al. (2008) created a summary of the thermohaline conditions, chlorophyll concentration and zooplankton biomass during 1997–2007, while Lavaniegos (2009) analyzed the abundance of functional zooplankton groups from the same period. Furthermore, Lavaniegos et al. (2015) updated the time-series of zooplankton functional groups for an extended period (1997–2013). However, in those studies euphausiids and other zooplankton were analyzed per major taxonomic group, but without any distinction between species.

Long-term changes in euphausiid species abundance off Baja California and California were formerly investigated by Brinton and Townsend (2003), who analyzed the winter and spring variability through decadal periods during 1951–2002. Among the dominant species in the CCS, *Euphausia pacifica* and *Thysanoessa spinifera* were associated to low temperature, decreasing their abundances during warm El Niño events, while *Euphausia recurva*, *Euphausia eximia*, and *Euphausia gibboides* increased (Brinton and Townsend, 2003). In the southern California region, where the longest time-series was available, *Nyctiphanes simplex* and *E. eximia* presented decadal variability with a positive response during 1976–1998. However, the time-series for the Baja California sectors were shorter and with temporal gaps (surveys during 1951–1985 in the north and 1951–1981 in the central region), making the verification for a decadal response impossible (Brinton and Townsend, 2003).

Subsequently, Lavaniegos et al. (2010) and Lavaniegos and Ambriz-Arreola (2012) described interannual variability of the euphausiid community in Baja California waters based on 17 cruises carried out during 1997–2005. They found that *E. pacifica* and *T. spinifera* were absent during El Niño 1997–1998, reappearing in 1999, while *E. eximia* presented its highest abundance in 1997–1998. Even though this study presented gaps in 2001–2004, it was evident that typical species of the CCS as *E. pacifica*, *E. gibboides*, *Nematoscelis difficilis*, and *Thysanoessa gregaria* were abundant during the subarctic water intrusion occurring during July 2002 (Wheeler et al., 2003; Gómez-Gutiérrez et al., 2007; Lavaniegos, 2009). In addition, the high abundance of *E. pacifica* and *T. spinifera* drew attention during April and July of 2005, contrasting with observations in the northern sectors of the CCS. However, Lavaniegos and Ambriz-Arreola (2012) did not analyze CP-El Niño events of 2002–2003 and 2004–2005, due to missing data. In the present study, we display a more continuous and extended time-series based on biomass of summer euphausiid species collected during 1998–2008, to do a more complete analysis of interannual variability and possible long-term tendencies. This longer time-series will enable a more robust statistical analysis due to the possibility of estimating biomass anomalies.

The knowledge of euphausiid ecology in the CCS is reported mostly based on the abundance (Brinton, 1962; Gómez-Gutiérrez, 1995; Brinton and Townsend, 2003). However, the adult component of the euphausiid populations represents substantial biomass due to their large body sizes. Large species from the CCS are *E. eximia* and *E. gibboides* with adults up to 30 mm, *E. pacifica* has an intermediate size (11–25 mm), and *N. simplex* is a small sized species (8–17 mm; Brinton et al., 2000). Diversity in species and sizes represent a broad spectrum of preys for nektonic predators. Therefore, euphausiid biomass stands out as a key link in trophic webs and carbon cycling dynamics. Consequently, our research is based on biomass estimations rather than on abundance. The study will be restricted to the oceanic region because the coastal shelf stations are too few and the previous study showed categorical differences between oceanic and neritic euphausiid communities (Lavaniegos and Ambriz-Arreola, 2012). In the neritic region, *N. simplex* is dominant, with eventual occurrence of *T. spinifera* in the upwelling region off Punta Colonet (31°N), Punta Canoas (29.4°N), and Punta Eugenia (28°N). Thus, the focus of the present study is on the oceanic latitudinal differences of the summer euphausiid communities' biomass with a more extensive sampling coverage than those previously reported.

During the study period, the CCS underwent the influence of four El Niño events; two of them (1997–1998 and 2006–2007) with high SST anomalies propagating from the central Pacific toward the Eastern Pacific (EP-El Niño). According to the Oceanic El Niño Index (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml), the EP-El Niño 1997–1998 was strong, starting in May 1997 and ending in May 1998, while the EP-El Niño 2006–2007 was weak and short (September 2006–January 2007). Other two El Niño events showed positive SST anomalies limited to the central

Pacific (CP-El Niño, also named Modoki). The CP-El Niño 2002–2003 lasted from June 2002 to February 2003 and the CP-El Niño 2004–2005, from July 2004 to April 2005 (Lee and McPhaden, 2010). Regarding the cold phase of the ENSO cycle, only two events occurred, one in 1998–2000 and another in 2007–2008. La Niña 1998–2000 started in July 1998 and ended in February 2001, with two peaks of high intensity in the winters of 1998–1999 and 1999–2000. La Niña 2007–2008 presented two cold pulses, one between August 2007 and June 2008, and another from November 2008 to February 2009 (Hu et al., 2014). Moreover, an extra-tropical cooling event occurred from 2002 to 2003, which consisted in a subarctic water intrusion (Wheeler et al., 2003, Lavaniegos, 2009). The goal of the present study is to analyze the intense interannual activity that occurred in the region during 1998–2008. We expect to find changes in euphausiid biomass as a response to climatic variability taking as a reference the biogeographic knowledge of the species (Brinton, 1962; Brinton et al., 2000).

2. Methods

The study area off Baja California pertains to the subtropical sector of the CCS. Because of the strong latitudinal gradient in temperature and increasing southward influence of tropical species, the area was divided in three sections: north, central, and south. Each sector included four transect-lines, extending 240 km from coast to offshore, with the exception of two transects in the central region (117 and 120) that were 390 km long (Fig. 1).

2.1. Sampling

Zooplankton samples were collected with a bongo net towed obliquely between the surface and 200 m depth, with a velocity of 3.7 km h^{-1}. The net had 500 µm mesh width and 71 cm of mouth diameter (61 cm before 2000). The water filtered was measured with a flowmeter located in front of the net. The plankton was preserved using 4% formaldehyde with sodium borate. Only zooplankton samples from nighttime stations were selected to avoid strong variability due to vertical migration (Brinton, 1967). To discard seasonal variability, only summer cruises were selected. This gives 338 zooplankton samples from 11 cruises performed during the summers of 1998–2008 (see Appendix 1 for the list of stations and cruise used in the present study).

In all stations CTD/rosette casts were performed to 1000 m depth. Water samples from 0, 10, 20, 50, 100, and 150 m depth were taken with 5L Niskin bottles to determine chlorophyll *a*. The water was filtered with Whatman GF/F filters and these frozen for further fluorescence analysis in the laboratory.

2.2. Taxonomic analysis

Euphausiid species were identified and counted per life phases: calyptopis, furcilia, juvenil and adult. Subsamples (1/8 or 1/16) were used to count the most abundant species or a particular life phase, but the complete sample was analyzed for the less abundant species. Taxonomic identification was done with the interactive key of Brinton et al. (2000). The larvae of *Euphausia diomedeae*, *E. mutica*, *E. recurva*, and *E. eximia* were difficult to identify, and are reported as Group 1A (Brinton, 1962).

2.3. Data analysis

Euphausiid abundances were converted to carbon mass using the carbon mass-length function for *E. pacifica* estimated by Ross (1982): $Y = 0.337 (X)^{3.17}$, where *Y* is carbon mass (µg) and *X* the body length (mm) assuming all species have the same body weight-length relationship. The mean body length of each life phase was taken from Brinton et al. (2000). The biomass of all life phases was added to get the carbon mass of the total population of each species. Before the
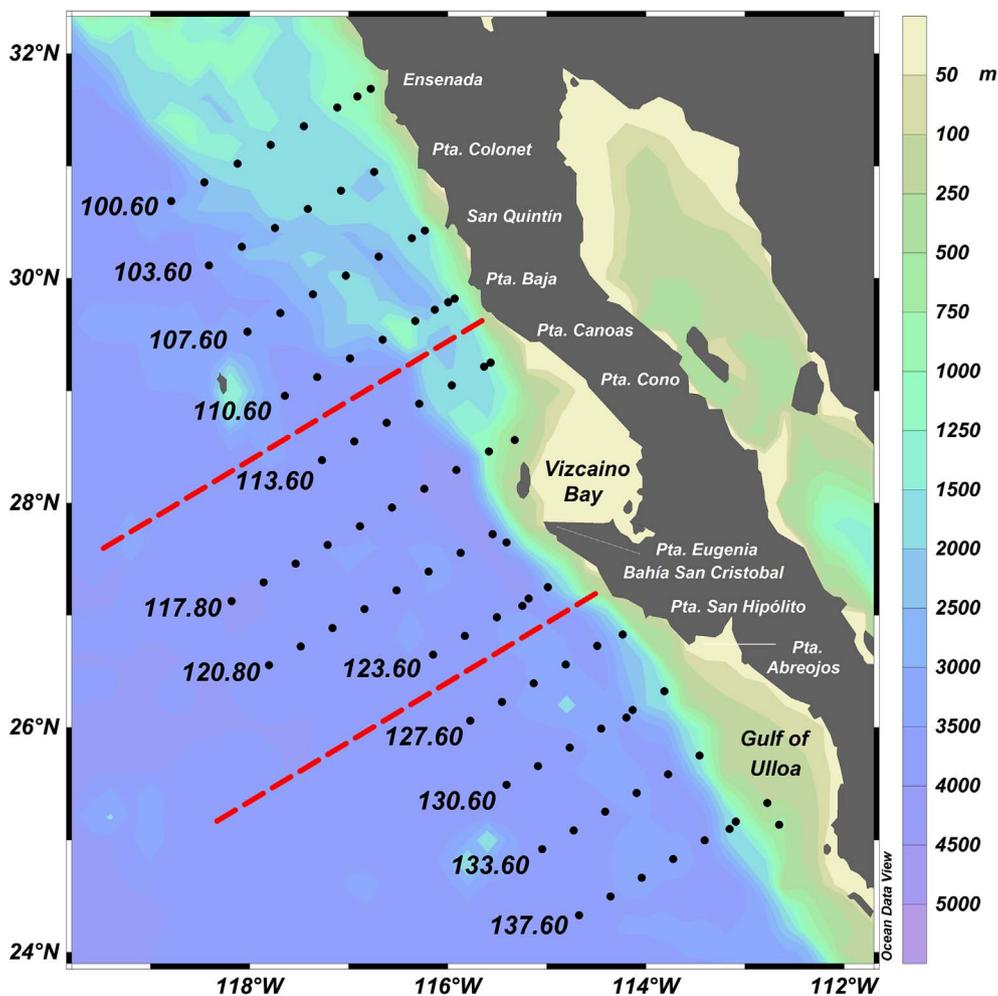
Fig. 1. Bathymetry and oceanic stations (> 200 m bottom depth) of the IMECOCAL grid, showing study regions. Number at the edge of the transect-lines indicates the station line (integers) and position from the coast (decimals). See Appendix 1 for the complete list of stations analyzed in each cruise.

calculation of the mean and confidence intervals, biomass data was log-transformed for the purpose of normalization. Biomass anomalies were calculated by subtracting the long-term mean of 1998–2008 to each annual mean. A similar procedure was done to calculate anomalies for 10 m temperature, 10 m salinity, 200 m dissolved oxygen and integrated chlorophyll *a* concentration. Only the data of chlorophyll were transformed to logarithms. Oxygen data for the summer of 2000 is missing.

We compared euphausiid biomass among areas (North, Central, and South) with the Kruskal-Wallis test. If the comparison of the medians was significantly different, areas were compared pair-by-pair using the Mann-Whitney test (Siegel and Castellan, 1988). The same tests were used to explore interannual differences in total euphausiid biomass within the areas.

2.4. Canonical correspondence analysis

All data were explored to detect outliers and the biomass euphausiid species was transformed (Log10 [x + 1]) to decrease data variance prior to multivariate analysis (McCune et al., 2002). A combination of 26 euphausiid species with the highest biomass (26 × 306 matrix) and thirteen environmental variables were used to address the relation between the species assemblage and climate variability using canonical correspondence analysis (CCA; PC-ORD 6.0, MjM software design, McCune et al., 2002). Species with an occurrence frequency of less than 2% were excluded from the analysis (Table 1). The environmental variables selected were temperature, salinity, and dissolved oxygen. All of them at three depths (10, 50 and 200 m), which are reference points for surface conditions, around the thermocline and the subsurface layer

influenced by the California Undercurrent. Temperature, salinity, and oxygen gradients (DT, DS, and DO respectively) were also used, considering the absolute difference between the value at 10 and 200 m depth. Integrated chlorophyll (Chl) was used as a proxy of the food available for euphausiids. Stations from the summer 2000 had to be excluded from the CCA due to missing oxygen data.

An exploratory analysis using principal components was carried out previous to the CCA, in order to detect potential multi-collinearity problems among the exploratory variables (Zuur et al., 2010). This resulted in high positive correlation (> 0.80) between 200 m temperature (T200) and 200 m salinity (S200), and inverse correlation between T200 and 200 m oxygen (O200). Therefore, T200 was kept while S200 and O200 were dropped, remaining eleven environmental variables (11 × 306 matrix) used in the CCA. The Monte Carlo permutation test was used to detect which exploratory variables best explain euphausiid biomass spatially and temporally (p < .05).

3. Results

3.1. Environmental conditions during 1998–2008

Temperature anomalies at 10 m depth showed high variability during summer of the period 1998–2008 (Fig. 2a–c). Though the peak of positive anomalies due to EP-El Niño 1997–1998 occurred before July 1998 (published elsewhere), positive temperature anomalies still remained in the central and southern regions (1.3° and 0.8 °C respectively) but near zero in the northern region. La Niña conditions were evident in the summer of 1999 with negative anomalies, low in the north (Fig. 2a) but stronger at central and south zones (Fig. 2b and c).

Table 1

Summer euphausiid species found during 1998–2008 showing the body length range of adults (BL), frequency of occurrence (FO) in samples, and the carbon mass estimated with the geometric mean (GM) and mean (M) combining all samples (N = 338). Species ordered in biogeographic groups based in Brinton (1962). Species codes will be used in canonical correlation analysis.

Code	Species and biogeographic groups	BL (mm)	FO (%)	GM (μg C m^{-3})	M (μg C m^{-3})
Subarctic					
Epa	*Euphausia pacifica*[a]	11–25	63.6	13.3	948.2
Toc	*Tessarabrachion occulatum*	20–26	1.2	< 0.1	< 0.1
Tsp	*Thysanoessa spinifera*[a]	16–25	38.8	2.1	72.4
Tac	*Thysanopoda acutifrons*	35–50	0.6	< 0.1	< 0.1
Transition zone					
Egi	*Euphausia gibboides*	16–29	90.8	66.3	302.8
Ndi	*Nematoscelis difficilis*	15–25	96.2	155.5	857.3
Nsi	*Nyctiphanes simplex*	8–17	82.0	21.4	467.5
Tgr	*Thysanoessa gregaria*	8–17	90.8	37.8	131.1
Subtropical central gyre					
Ehe	*Euphausia hemigibba*	8.5–14	51.8	1.5	5.3
Emu	*Euphausia mutica*[b]	7–15	52.4	1.9	10.1
Ere	*Euphausia recurva*[b]	7–16	74.9	9.6	49.8
Nat	*Nematoscelis atlantica*	10.5–15	18.9	0.2	1.1
Ssu	*Stylocheiron suhmii*	6–7	52.7	0.6	1.3
Tas	*Thysanopoda astylata*	12–18	43.5	0.8	3.2
Equatorial					
Edm	*Euphausia diomedeae*[b]	10–16	30.5	1.0	5.6
Eds	*Euphausia distinguenda*	10–14.5	4.4	0.1	0.5
Eex	*Euphausia eximia*[b]	15–30	68.0	30.2	494.2
Ela	*Euphausia lamelligera*	7–11	3.3	0.1	3.0
Ete	*Euphausia tenera*	7–9	17.5	0.1	0.2
Ngr	*Nematoscelis gracilis*	11–15.5	18.9	0.4	1.5
Warm-temperate cosmopolite					
Nbo	*Nematobrachion boopis*	20–25	0.3	< 0.1	0.2
Nfl	*Nematobrachion flexipes*	17–27	79.3	11.6	70.5
Nte	*Nematoscelis tenella*	13–20	39.3	0.9	2.9
Sab	*Stylocheiron abbreviatum*	12–17	6.5	0.1	0.1
Saf	*Stylocheiron affine*	5.4–8.5	94.7	7.3	13.7
Sca	*Stylocheiron carinatum*	6–12	4.1	< 0.1	0.1
Sel	*Stylocheiron elongatum*	11.5–18	1.8	< 0.1	0.1
Slo	*Stylocheiron longicorne*	6.5–10	68.0	0.8	2.2
Sma	*Stylocheiron maximum*	17–30	45.6	0.4	2.1
Tcr	*Thysanopoda cristata*	35–65	0.3	< 0.1	< 0.1
Teg	*Thysanopoda egregia*	51–62	0.3	< 0.1	< 0.1
Tmo	*Thysanopoda monacantha*	25–32	3.6	< 0.1	0.5
Tob	*Thysanopoda obtusifrons*	18–23	0.3	< 0.1	< 0.1
Tor	*Thysanopoda orientalis*	23–38	0.3	< 0.1	< 0.1

[a] *E. pacifica* and *T. spinifera* are also transition zone species, distributed throughout the California Current.

[b] Species pertaining to the group 1A which larvae were not identified to species. Therefore the carbon biomass shown included only the amount produced by juveniles and adults.

Strong negative anomalies also occurred in July 2002, reaching −1 °C in the north-central areas (Fig. 2a and b). This was associated to the subarctic water intrusion from the North Pacific. Summers of 2003 and 2004 showed lightly negative anomalies despite the occurrence of CP-El Niño events (2002–2003 and 2004–2005), probably due to their short-time influence during autumn-winter seasons. Other negative anomalies were recorded in July 2005 (from −0.5 to −1 °C) in the north and south regions (Fig. 2a and c). The anomalies changed again to positive in 2006 due to a weak EP-El Niño in 2006–2007. At the end of the study period, La Niña 2007–2008 affected Baja California but was only evident in the south region by a low negative anomaly (Fig. 2c). In contrast, the north region presented a high positive anomaly and close to zero at the central region (Fig. 2a and b).

Salinity anomalies at 10 m depth followed a multiyear pattern with high temporal coherence among regions (Fig. 2d–f). Formerly, there was a period of positive anomalies from 1998 to the 2002 (beginning in 1999 in the north). After this "saline" period, there was a period of negative salinity anomalies in 2003–2006, limited to 2003–2005 in the north. The decrease in salinity was associated to the subarctic water intrusion since July 2002. The saline stratification persisted the following three years, apparently related with CP-El Niño events. Finally, the stratification was broken by intense upwelling during La Niña 2007–2008.

Oxygen at 200 m depth showed a decreasing tendency since 2005, which was coherent among regions and consistent with a northward expansion of the oxygen minimum layer (Fig. 2 g–i). In contrast, previous summers showed inconsistencies in oxygen anomalies from one region to another.

Integrated chlorophyll (Fig. 2j–l) followed a similar pattern as the salinity (Fig. 2d–f). The exception was in 1998, when negative or null chlorophyll anomalies occurred linked to subtropical water, particularly influential in the central and south regions. During 1999–2002 there were positive chlorophyll anomalies, with the highest value in 2002. Later, a strong shift to a negative anomaly occurred in July 2003, starting a four year period of low chlorophyll, coincident with the low salinity. Also during the summer of 2008 there was a positive anomaly associated to high salinity and enhanced upwelling.

3.2. Oceanic euphausiid community

There were 34 euphausiid species identified over the entire research period (Table 1). *N. difficilis*, *Stylocheiron affine*, *E. gibboides*, and *T. gregaria* were the most common species with an occurrence frequency greater than 90%. These species have different sizes, reflecting unequal species biomass contributions to the ecosystem. *N. difficilis* was the most common species (96.2%), and contributed with the highest carbon
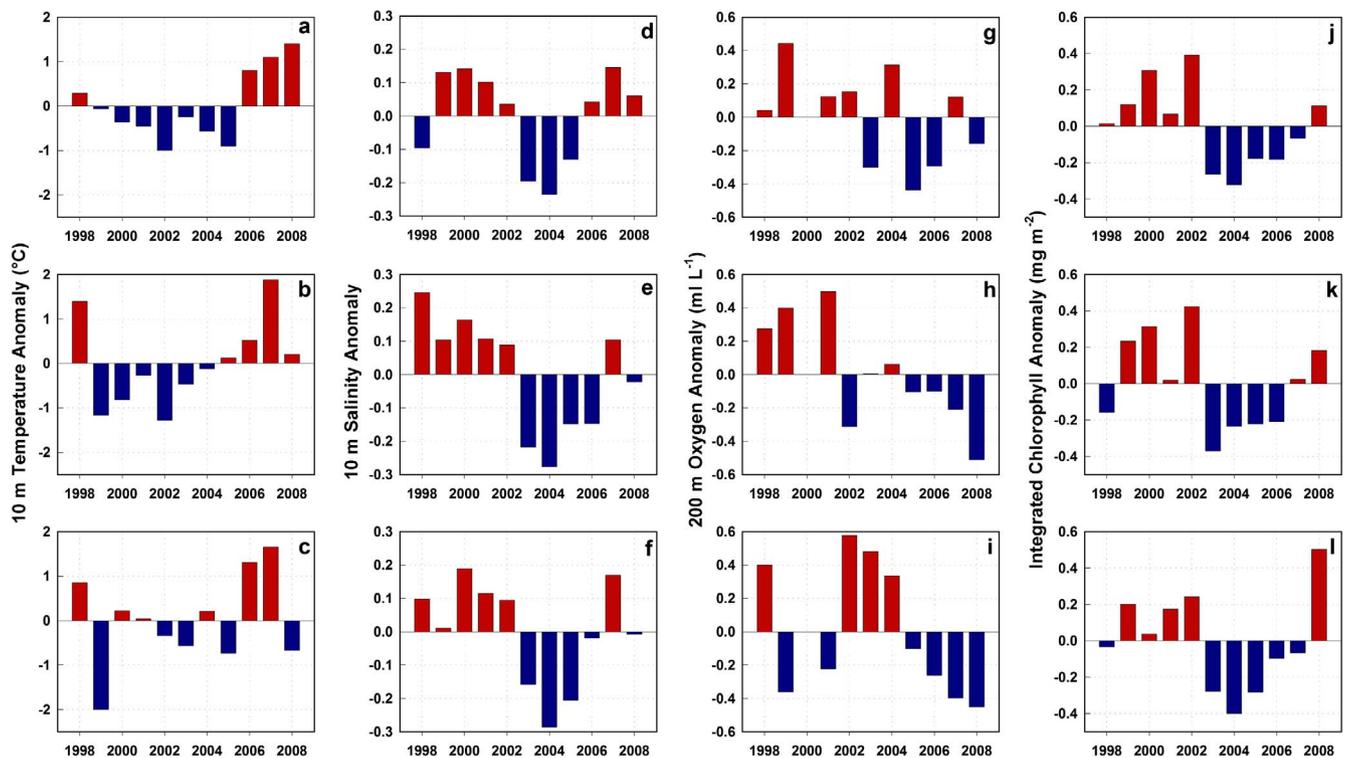
Fig. 2. Summertime anomalies of environmental variables in the three regions off Baja California: North (a, d, g, j), Central (b, e, h, k), and South (c, f, i, l).

biomass with a total geometric mean (GM) of 155 μg C m^{-3}. Although *S. affine* was present in almost the same number of stations as *N. difficilis*, it had a biomass GM = 7.3 μg C m^{-3} (4.7% of the value found in *N. difficilis*) due to its small body size. The use of the geometric mean is indispensable, because the mean overestimates the biomass between two and six times its actual value, more so with *E. pacifica*, *N. simplex*, and *T. spinifera* (Table 1). Compared with the transition zone species, other biogeographic groups presented a low contribution to biomass, with the exception of the equatorial *E. eximia* (GM = 30.2 μg C m^{-3}). Other species of modest carbon biomass were *Nematobrachion flexipes* and *E. recurva* (GM = 11.6 and 9.6 μg C m^{-3} respectively). The rest of species had a low biomass contribution during summer.

Total euphausiid biomass showed a latitudinal north-south increase, with GMs of 1369, 1815, and 1940 μg C m^{-3} for the three areas respectively. The statistical comparison of the GM was significant (H = 8.7, p = .013), due to a lower euphausiid biomass in the north compared to central and south areas (Mann-Whitney tests, p < .02). Considering the regions separately, the interannual variability in the north and south was relatively weak (Fig. 3a–c), while the central area presented significant interannual differences (H = 26.9, p = .003). The summers of 2003, 2004, and 2006 showed low euphausiid biomass (GM < 500 μg C m^{-3}); significantly lower than the summers of 2000, 2002, 2005, 2007, 2008 (GM > 2300 μg C m^{-3}). The summers of low biomass were under the influence of El Niño, while the group of high biomass was influenced by cooling events. There were no long-term tendencies in biomass anomalies (Fig. 3d–f), nor a coherent pattern of anomalies among regions.

3.3. Regional biomass contribution of the euphausiid species

The carbon biomass of each region presented a dominance of certain euphausiid species and substantial changes in composition among regions. In the north, *N. difficilis* accounted for 51% of the total biomass, followed by 23% for *E. pacifica* (Fig. 4a). If the biomass of *E. gibboides* and *T. gregaria* is added, the cumulative biomass increases to 93%. Thus, the north region was mainly a transition zone and subarctic fauna

(Table 1). In the central region, two transition zone species (*N. difficilis* and *E. gibboides*) represented 64% of the euphausiid biomass (Fig. 4b). In this region, the coastal species *N. simplex* had a modest contribution, similar to that of the oceanic *E. eximia*. Although both showed a slight increase compared to the north zone. In contrast, *E. pacifica* had a strong decrease. In the south region, *E. eximia* prevailed with 45% of the euphausiid biomass while *N. difficilis* and *E. gibboides* decreased (13 and 8% respectively), and *E. pacifica* was virtually absent (Fig. 4c). Other species increasing biomass in the south region were *N. simplex* and *N. flexipes*. Larval stages of non-identified species pertaining to the Group 1A (*E. diomedeae*, *E. eximia*, *E. mutica*, and *E. recurva*) showed a low biomass contribution in the three regions.

In order to compare the biomass among regions, some species had to be excluded due to low occurrence in samples (< 5%). The excluded species are shown in Table 1. Biomass of the remaining 22 species compared among regions showed significant differences (α = 0.01) in 18 of them (Table 2, Fig. 4) with the following characteristic patterns:

(1) Species that decrease from north to south. *E. pacifica* and *S. maximum* were characteristic of this pattern but the bulk of biomass in the north region originated from *E. pacifica* while *S. maximum* was negligible (GM = 109 and 1 μg C m^{-3} respectively). *N. difficilis* and *T. gregaria* could be included in this pattern even though they did not present differences between north and central regions.

(2) Species with higher biomass in the central zone. This pattern was recorded in four species of different biogeographic groups, the transitional *E. gibboides*, the subtropical gyre inhabitants *Euphausia hemigibba* and *E. recurva*, and the subarctic neritic *T. spinifera*. However, only *E. gibboides* presented a substantial contribution in biomass reaching a GM = 154 μg C m^{-3} in the central region.

(3) Species that increase from north to south. The equatorial *E. eximia* and *Nematoscelis gracilis*, the central gyre inhabitant *Stylocheiron suhmii*, and the warm cosmopolite *N. flexipes* shared this pattern. However, the last three had modest contribution to southern biomass (GM < 50 μg C m^{-3}) in relation to *E. eximia* (GM = 233 μg C m^{-3}).
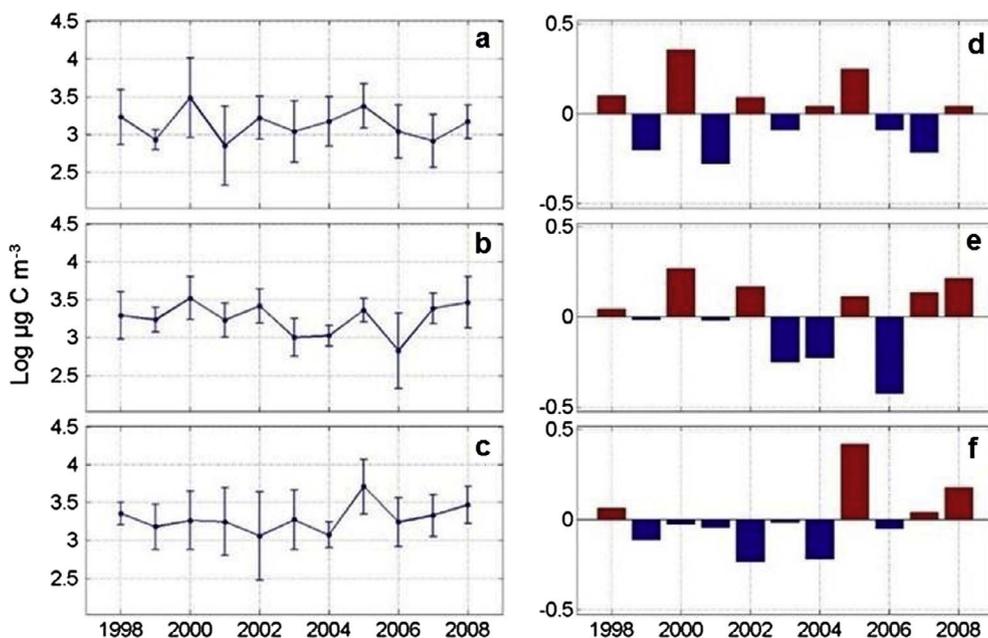
Fig. 3. Total euphausiid carbon biomass during summer in the three regions off Baja California: North (a, d), Central (b, e), and South (c, f). Mean and 95% confidence interval are shown on the left while anomalies are on the right.

(4) Species with high biomass in central and south regions. This pattern was presented in six species of different biogeographic groups. They were *N. simplex*, *E. mutica*, *Nematoscelis atlantica*, *E. tenera*, *Nematoscelis tenella*, and *S. affine*. *N. simplex* had the main contribution to biomass with a GM of 36 and 73 µg C m^{-3} in central and south regions respectively.

3.4. Interannual variability of euphausiid species

Given the remarkable latitudinal variability in euphausiid biomass of the different species, it is appropriate to follow-up interannual variability per regions. As could be expected, there were multiple responses depending on the species, though some patterns may be traced. The temporal variability in selected species, those with the highest contribution in carbon biomass, are described as follows:

The subarctic *E. pacifica* had high biomass in the north region and had interannual variability mainly associated with the strong EP-El Niño and La Niña events from 1998 to 2000 (Fig. 5). This response was expected, resulting in large negative anomalies in the north and central regions (Fig. 5d and e). In 1999, the anomaly was still negative in the north despite the biomass increase of 450% in relation to the previous year (Fig. 5d). *E. pacifica* had a complete recovery by the year 2000 in

the north region (GM = 572 µg C m^{-3}). During CP-El Niño events there were no relevant anomalies. Subsequently, the highest positive anomaly occurred during the summer of 2005, which could be associated to local upwelling enhancement. Another pronounced positive anomaly occurred in 2008 but only in the central area (Fig. 5e). The biomass in the southern area was too low during the entire study period with negligible anomalies with the exception of 2005 (Fig. 5f). *T. spinifera*, another subarctic species, had a modest contribution to the biomass, but showed an increasing trend particularly in the south region (Appendix 2).

N. difficilis, the most characteristic transition zone species off Baja California, presented an even biomass in the north zone (Fig. 6a) with a long-term mean of 282 µg C m^{-3}, contrasting with the central and south areas where strong negative anomalies occurred in 2003 and 2004 (Fig. 6e and f). Contrary to *E. pacifica*, the biomass of *N. difficilis* changed little during EP-El Niño 1997–1998. The positive anomalies in 2007–2008 were coincident with records of *E. pacifica* and *T. spinifera* from the central zone. *T. gregaria*, also showed low biomass variability in the north (Fig. 7a). The main negative anomalies occurred in 1998 and 2003 in the central and south regions probably associated to EP-El Niño 1997–1998 and CP-El Niño 2002–2003 (Fig. 7d–f).

N. simplex had negative anomalies as did *N. difficilis* during
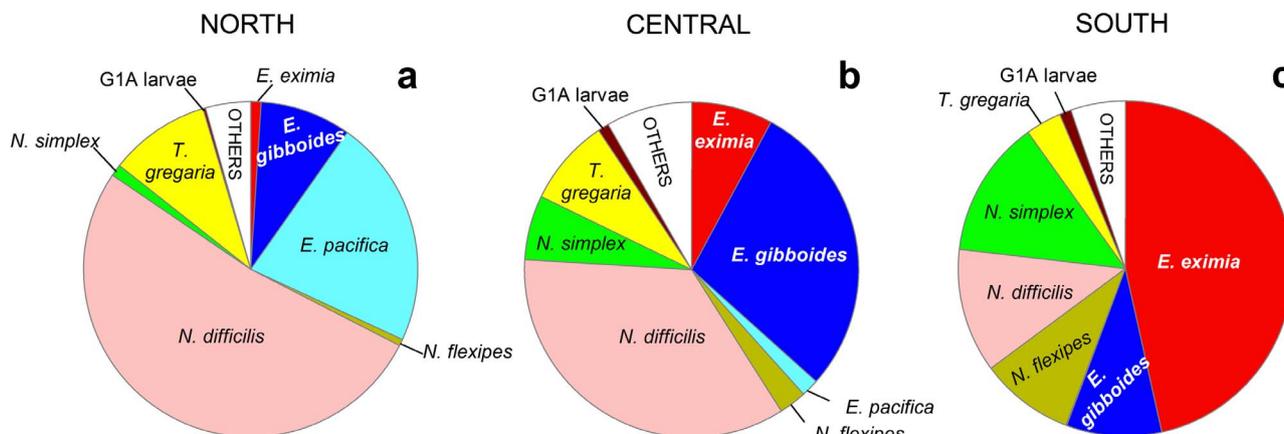

Fig. 4. Euphausiid species composition in the three oceanic regions off Baja California: North (a), Central (b), and South (c). Species with a carbon biomass that presented a geometric mean < 10 µg m^{-3} in any area were grouped in the category 'Others'. 'G1A' is the larval biomass of the Group 1A *Euphausia*.

Table 2
Euphausiid carbon biomass (µg C m^{-3}): geometric mean by species and area, and results of the Kruskal-Wallis test comparing areas (North, Central, and South). Species ordered depending on spatial patterns found with the Mann Whitney test. Species with occurrence frequency < 5% were excluded. Results significant at 0.001 highlighted.

Areal pattern	Species code	North	Central	South	H	p
North biomass > Central > South	Epa	109.3	9.3	0.4	151.5	< .001
	Sma	0.9	0.3	0.1	43.6	< .001
North and Central biomass > South	Ndi	240.9	191.6	66.9	19.6	< .001
	Tgr	44.3	44.8	24.8	6.7	.035
Central biomass > North and South	Egi	44.2	153.9	40.3	25.1	< .001
	Ehe	1.0	2.5	1.3	13.2	**.001**
	Ere	6.8	18.8	6.3	20.2	< .001
	Tsp	1.3	4.1	1.5	8.8	.012
Central and South biomass > North	Emu	1.0	2.9	2.5	16.9	< .001
	Ete	< 0.1	0.2	0.2	9.7	.008
	Nat	0.1	0.3	0.3	8.5	.014
	Nte	0.5	1.2	1.2	11.9	.003
	Nsi	4.9	35.6	72.7	65.8	< .001
	Saf	5.2	8.8	8.9	13.3	**.001**
South biomass > Central > North	Eex	4.4	40.5	232.9	98.8	< .001
	Nfl	3.0	13.4	49.2	88.0	< .001
	Ngr	< 0.1	0.2	1.3	68.5	< .001
	Ssu	0.3	0.6	1.0	28.5	< .001
No differences among areas	Edm	0.8	1.3	0.8	0.9	.637
	Sab	0.1	0.1	< 0.1	1.4	.510
	Slo	0.9	0.7	0.7	4.2	.122
	Tas	0.6	1.1	0.7	2.1	.359

2003–2004 (Fig. 8d–f), contrasting with positive anomalies during July 1998 in the north-central area. Decreased biomass in that area in 1999 indicated a tropical-type response. The opposite occurred in the south zone. *N. simplex*, as other transition species (*E. pacifica*, *T. spinifera*, and *T. gregaria*), showed a strong positive anomaly during 2005, though restricted to the central-south area. A long-term decrease was apparent in the north region.

E. gibboides showed mixed responses to interannual events. In the north, it presented positive anomalies associated to La Niña events (1999 and 2008), and negative anomalies during 2001–2003 (Fig. 9d). In the south, the pattern was the opposite (Fig. 9f). However, in the central region where the main biomass concentration was present it had relatively lower variability (Fig. 9b and e).

The Subtropical central gyre species *E. recurva* showed an increasing trend in the north and central regions (Fig. 10a and b). Negative anomalies from 1998 to 2000 were associated to EP-El Niño and La Niña events (Fig. 10d and e), while in the south area the negative anomaly was only in July 1998 (Fig. 10f). *Nematoscelis atlantica* and *S. suhmii* had similar tendencies but their biomass was considerably low, while other central species (*E. hemigibba*, *E. mutica*) did not present a clear tendency in the north and central regions as *E. recurva*, however, they decreased in the south area. *Thysanopoda astylata* decreased in all areas with a strong positive anomaly during 1999 in the north and central regions (see Appendix 2).

E. eximia was the only one of the equatorial species assemblage with a remarkable contribution to carbon biomass due to its large body size and relatively high abundance. It showed a clear response to the ENSO 1997–2000 reaching record values in the north and central regions
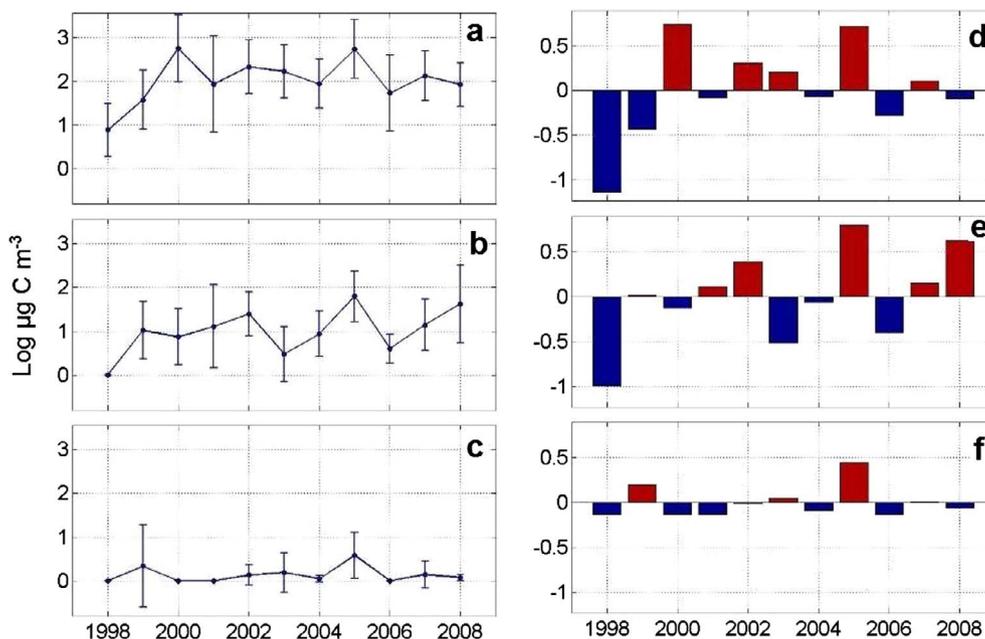

Fig. 5. *Euphausia pacifica* carbon biomass during summer in the three regions off Baja California: North (a, d), Central (b, e), and South (c, f). Mean and 95% confidence interval are shown on the left while anomalies are on the right.
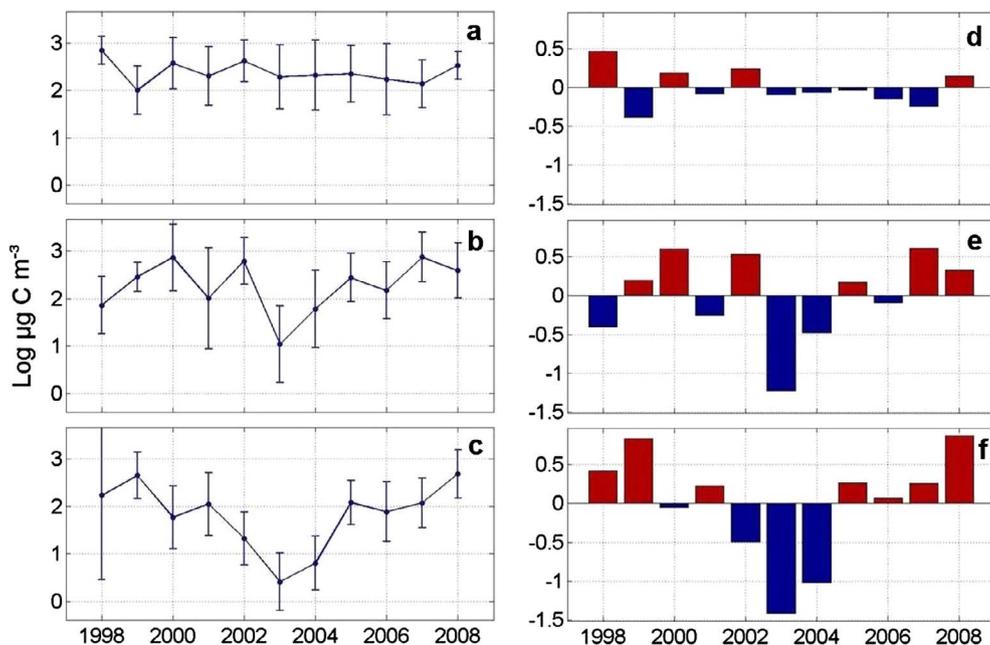
Fig. 6. *Nematoscelis difficilis* carbon biomass during summer in the three regions off Baja California: North (a, d), Central (b, e), and South (c, f). Mean and 95% confidence interval are shown on the left while anomalies are on the right.

during 1998 (Fig. 11a and b). In the south area, it had a more consistent biomass during the study period with positive anomalies in 1998 and 2003 (Fig. 11c and f). Other equatorial species as *E. diomedeae* showed positive anomalies during 1998–2000 and the remainder of the period was mainly negative in all areas. *N. gracilis* was virtually absent in the north and central regions, but showed an increasing tendency in the south (Appendix 2).

S. affine, the most common warm-water cosmopolite species, presented a regular biomass, with its highest values during both El Niño types, with positive anomalies in 1998 and 2003–2004 in the central region (Fig. 12). Negative anomalies were associated to La Niña in 2000 and 2007–2008. A strong negative anomaly was observed in 2003 at the south region. *N. flexipes* also had a regular biomass in central and south regions but presented a different response during La Niña 2007–2008. The low biomasses from other cosmopolite species make the tendencies observed in anomalies unreliable (see Appendix 2).

3.5. Biophysical coupling between euphausiids and climate

The CCA model revealed nine variables that significantly explained 22% of the carbon biomass variability ($p < .05$, Monte Carlo permutation test) taking the first three axis. The first CCA axis accounted for 10.8% of the total variance and was responsible for thermal conditions in the upper 100 m, considering high loads found in T10m, T50m and the thermal gradient (Fig. 13, Appendix 3). The second CCA axis, with 9% of variance, was driven by the oxygen gradient, related with the covariates T200m and S50m and inversely with O50m. The third axis explained less than 3% of the variance and only the salinity gradient had a high score.

The load scores for species plotted for the first two axes, showed a group of seven subtropical-equatorial species (*E. distinguenda*, *E. tenera*, *N. atlantica*, *N. gracilis*, *N. tenella*, *S. carinatum*, and *T. astylata*) driven by axis-1, is to say, by thermal conditions in the upper layer (Fig. 13a,
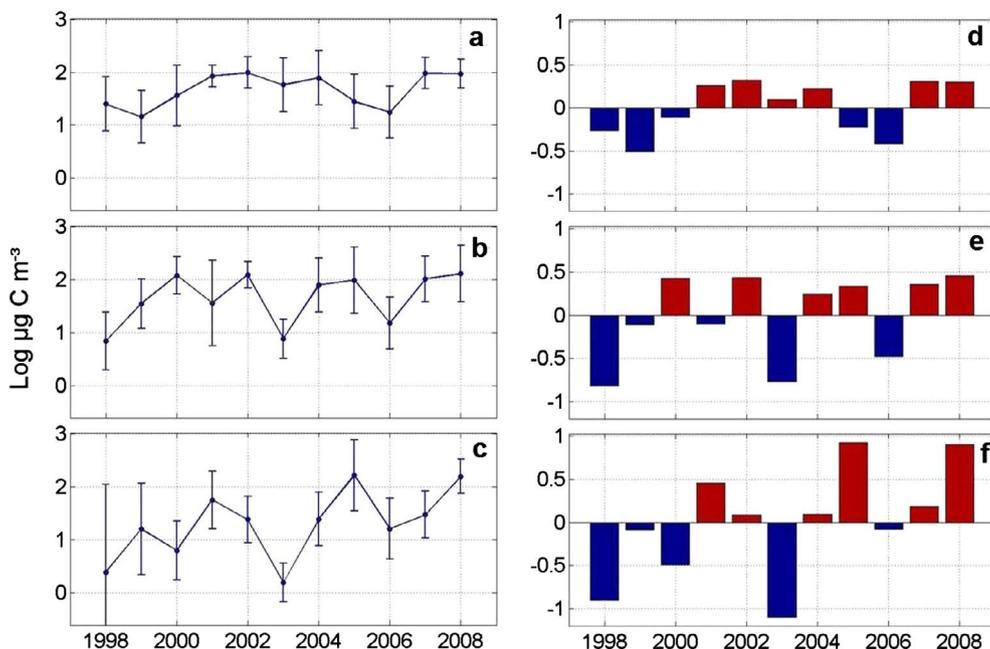

Fig. 7. *Thysanoessa gregaria* carbon biomass during summer in the three regions off Baja California: North (a, d), Central (b, e), and South (c, f). Mean and 95% confidence interval are shown on the left while anomalies are on the right.

Fig. 8. *Nyctiphanes simplex* carbon biomass during summer in the three regions off Baja California: North (a, d), Central (b, e), and South (c, f). Mean and 95% confidence interval are shown on the left while anomalies are on the right.
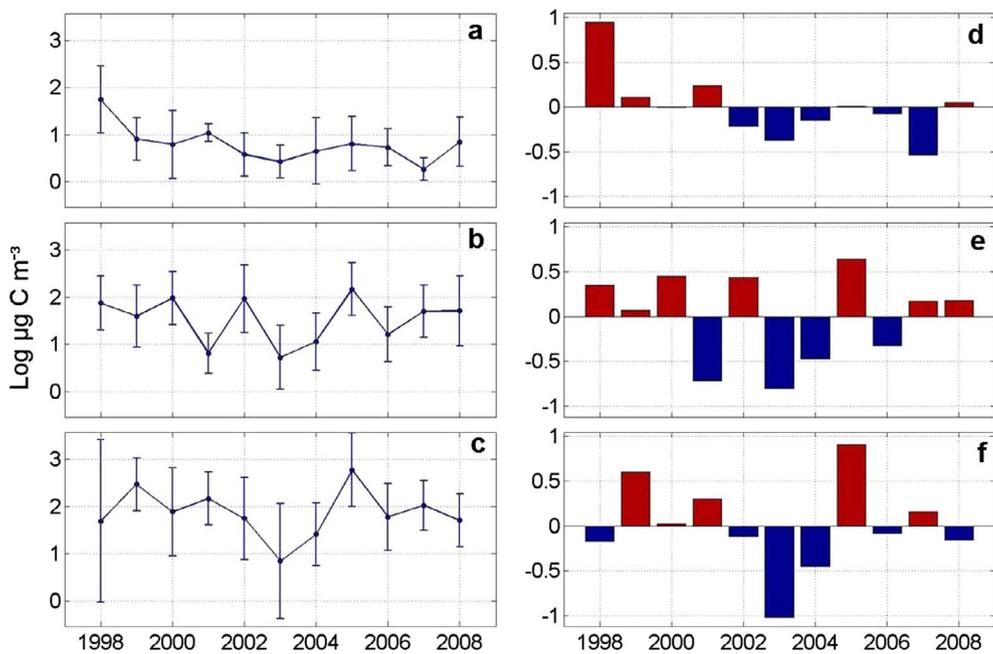
Appendix 3). Other subtropical-equatorial species (*E. diomedeae*, *E. eximia*, *E. hemigibba*, *E. lamelligera*, *E. mutica*, *N. flexipes*, and *S. suhmii*) showed also negative but lower scores in axis-1. Most of the sampling points where these environmental variables had negative scores in the biplot belonged to central-south stations (Fig. 13b).

If the bulk of tropical-subtropical species responded in the same way, increasing biomass when temperature is warm in the mixed layer and DS strong, the opposite was true for the subarctic species *E. pacifica* and *T. spinifera*, and the mesopelagic *S. maximum* and *T. monacantha* (Fig. 13a, Appendix 3).

A different response was found for *E. lamelligera*, and *E. distinguenda*, which had high scores in axis-2 (Fig. 13a). High values of T200 m (and S200 m) are typical of the California Undercurrent, flowing along the continental slope. Undercurrent water is low in oxygen, and consequently DO is strong in the water column of the slope stations (Fig. 13b). In contrast, a low DO determined the biomass of some

mesopelagic species (*T. monacantha*, *S. abbreviatum*, and *S. maximum*), which is more typical in the north-central offshore stations.

The biomass variability of *N. difficilis*, *T. gregaria*, and *N. simplex*, had low loads in both axes (Fig. 13a, Appendix 3). Similarly, three environmental variables (Chl, DS, and S10m) had low influence on the CCA, but could be important for *N. difficilis*, *T. gregaria*, and *N. simplex*.

The north, central, and south regions had a reasonable separation in function of the axis-1 (Fig. 13b). Since there were points of the three regions along the axis-2, this is indicative of a strong thermal gradient in some stations from any area, presumably representing offshore stations (positive loads), while in slope stations the stratification is broken due to coastal upwelling (negative loads). Displaying the years, we observed that more negative values in axis-2 corresponded mainly to slope stations from 2005, 2007 and 2008 (Fig. 3c) denoting higher DO, probably due to intense upwelling bringing oxygen depleted deep water. However, this temporal tendency can be partially caused by
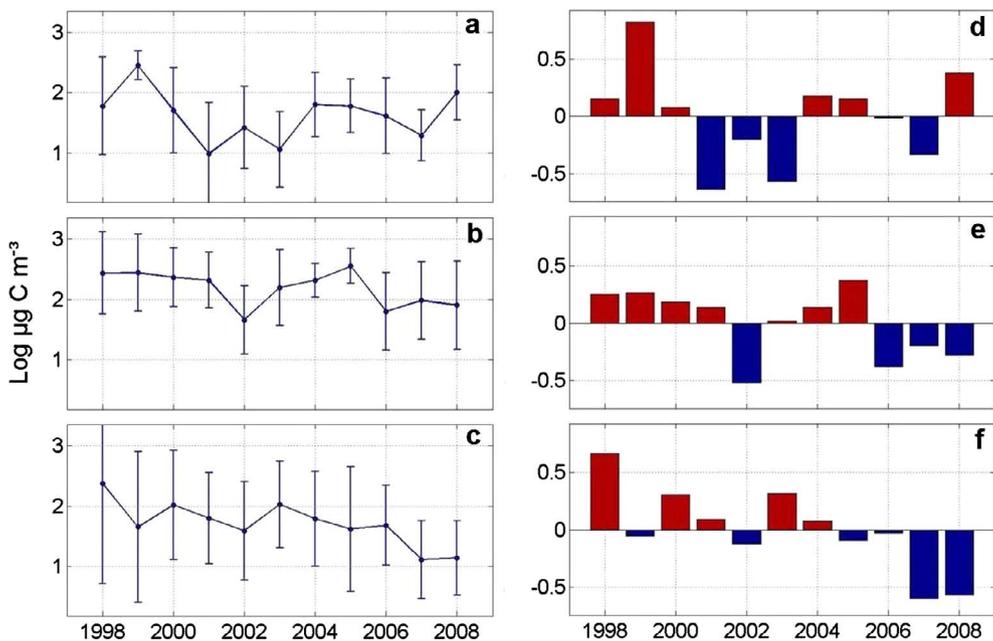

Fig. 9. *Euphausia gibboides* carbon biomass during summer in the three regions off Baja California: North (a, d), Central (b, e), and South (c, f). Mean and 95% confidence interval are shown on the left while anomalies are on the right.

Fig. 10. *Euphausia recurva* carbon biomass during summer in the three regions off Baja California: North (a, d), Central (b, e), and South (c, f). Mean and 95% confidence interval are shown on the left while anomalies are on the right.

Fig. 11. *Euphausia eximia* carbon biomass during summer in three regions off Baja California: North (a, d), Central (b, e), and South (c, f). Mean and 95% confidence interval are shown on the left while anomalies are on the right.
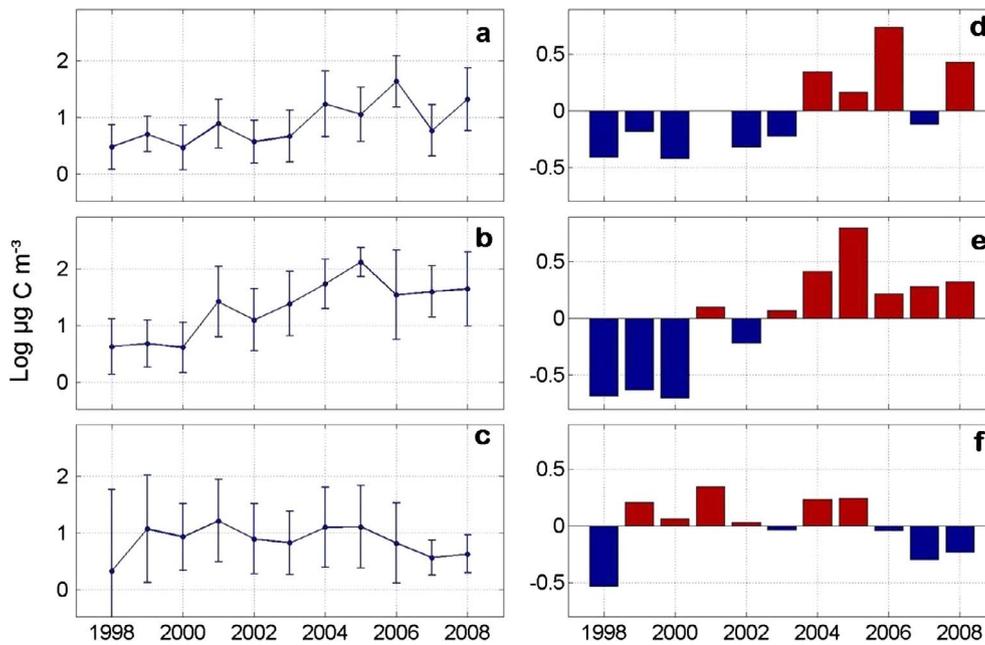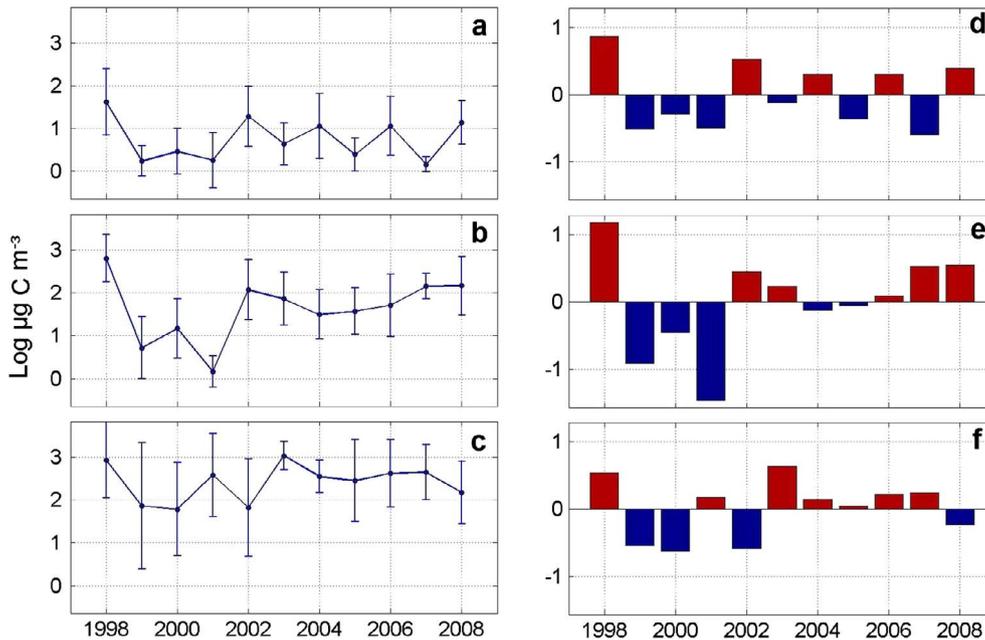
sampling bias, with more nighttime samples taken from slope waters in those years (Appendix 1).

A light tendency to more negative scores in axis-1 of the CCA was observed for the summers of 1998 and 2006, with 54–62% of the stations having scores between -0.5 and -1.5, while other years were in the range of 15–39%. This is indicative of higher temperature in the upper layer and higher DT during EP-El Niño events. In relation to the axis-2, the summers of 1999 presented scores > 0.5 in 66% of the stations in covariance with O50m, suggesting well oxygenated conditions in or around the thermocline during this La Niña event.

4. Discussion

4.1. How does euphausiid biomass off Baja California compare with other regions?

There are only a few studies of oceanic euphausiid biomass despite

their relevant function in offshore pelagic food webs and carbon flow (Kaplan et al., 2013). *E. pacifica* is one of the most studied species in the North Pacific (Table 3), although these studies are mainly related to secondary productivity in the Canadian coast (Heath, 1977; Tanasichuk, 1998a), southern California (Brinton, 1976), and Japan waters (Iguchi and Ikeda, 1999; Taki, 2006; Kim et al., 2009). The Strait of Georgia and adjacent fjords recorded the highest and most variable biomass during summer season, ranging between zero and 5935 mg C m^{-2} (Heath, 1977; Romaine et al., 2002; Mackas et al., 2013). Summer is only the beginning of the productive season for *E. pacifica* in Canadian waters, considering that Heath (1977) found a monthly increase from June to November averaging 13,640 mg C m^{-2} in the Jervis Inlet. The open Canadian coast appears to be less productive with a mean summer biomass ranging from 113 to 491 mg C m^{-2} estimated in Barkley Sound during 1991–1996 (Tanasichuk, 1998a). High summer biomass was also found in the western subarctic Pacific, with similar tendency to higher values in protected areas such as Toyama Bay
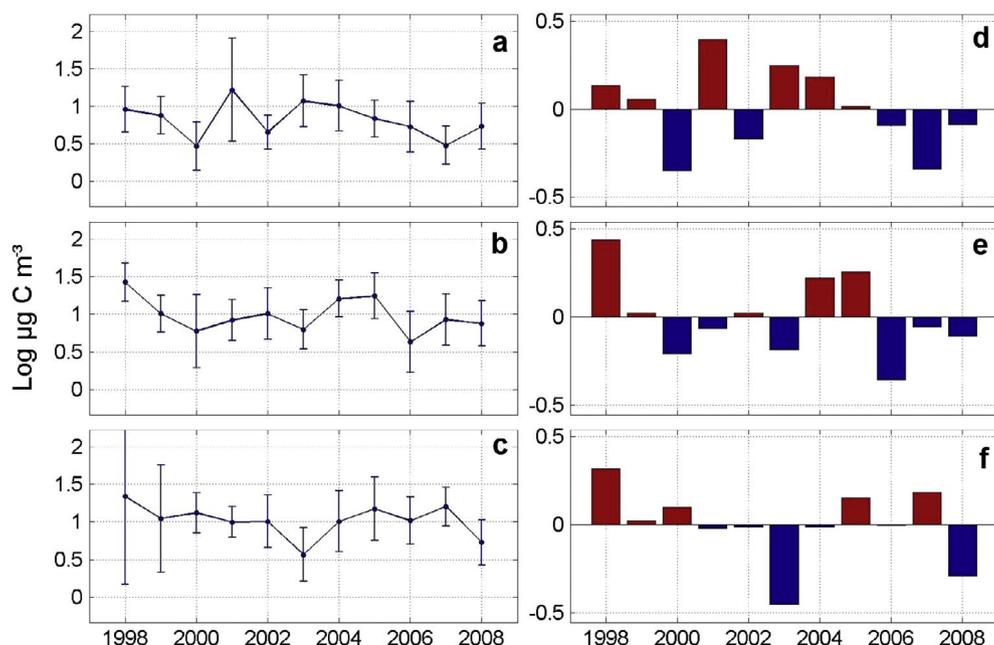
Fig. 12. *Stylocheiron affine* carbon biomass during summer in the three regions off Baja California: North (a, d), Central (b, e), and South (c, f). Mean and 95% confidence interval are shown on the left while anomalies are on the right.

(3925 mg C m^{-2}) in the Japan Sea (Iguchi and Ikeda, 1999) when compared with 1100–1600 mg C m^{-2} in the oceanic region of Oyashio (Kim et al., 2009). Recent hydro-acoustic surveys revealed lower levels in Canadian coasts (Romaine et al., 2002; Mackas et al., 2013), hence indicating strong variability in the area. Since *E. pacifica* is harvested for commercial uses in the productive areas of the subarctic, a monitoring of euphausiid biomass is necessary to appropriately manage this resource, which is a forage food for numerous species of the marine ecosystem.

In the subtropical region, *E pacifica* represented 70% less biomass compared to the subarctic region (Table 3). Taki (2006) recorded a summer biomass of 120–440 mg C m^{-2} from three coastal locations off the eastern Japan coast. Meanwhile, in California and Baja California the summer mean ranged from zero to 3825 mg C m^{-2} (Brinton, 1976; Brinton and Reid, 1986, this study). Northern Baja California was the only region where *E. pacifica* presented a high biomass, but also a strong interannual variability with extreme values during the ENSO (7–3825 mg C m^{-2}). These values correspond to the warm phase (July 1998) and cool phase (July 2000), with a mean of 481 mg C m^{-2} for the

period 1998–2008. Strong fluctuations in *E. pacifica* population were also documented off California during El Niño by Brinton and Townsend (2003). Distribution of this species during El Niño 1958–1959 was constrained to the northern part of its range (Brinton and Reid, 1986) and the biomass sum for the California and northern Baja California areas was 66 mg C m^{-2} in April 1958, in contrast with a 110% higher value during April 1962 (Table 3).

In Barkley Sound, Canada, *T. spinifera*, presented a summer mean ranging 105–945 mg C m^{-2} during 1991–1996 (Tanasichuk, 1998b), while in the Strait of Georgia it ranged from zero to 1906 mg C m^{-2} during 1990–1995 with a mixture of *Thysanoessa* species (Mackas et al., 2013). Off Baja California, *T. spinifera* presented a low summer biomass mainly in slope waters, with the minimum in the north region (0–17 mg C m^{-2}) and the maximum in the central region (0–198 mg C m^{-2}). Only in the shelf break of Vizcaino Bay the species has a higher biomass tendency, but in later years it has also been seen in the shelf break of the Gulf of Ulloa (Table 3).

N. simplex showed a tendency to increase biomass from north to south in slope waters of the oceanic region. However, this is a coastal
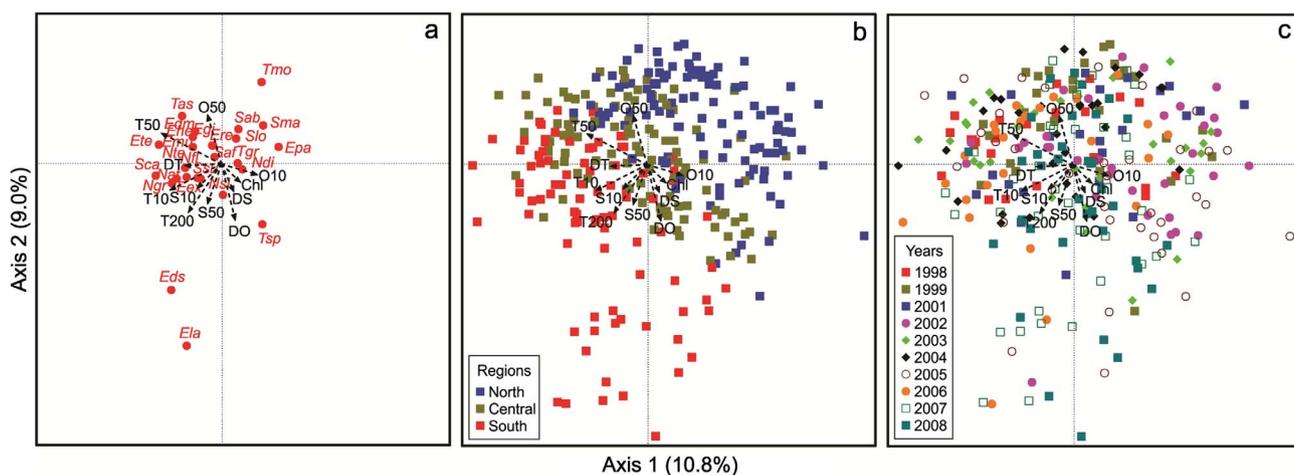
Fig. 13. Canonical correspondence analysis ordination biplots. The black arrows represent environmental variables in all biplots. Symbols in (a) are euphausiid species, (b) sampling sites colored by regions, and (c) sampling sites colored by year. Independent variables are integrated chlorophyll (Chl), thermal gradient (DT), salinity gradient (DS), dissolved oxygen gradient (DO), temperature at 10, 50, and 200 m depth (T10, T50, and T200), salinity at 10 and 50 m depth (S10 and S50), and dissolved oxygen at 10 and 50 m depth (O10 and O50). Species abbreviations are given in Table 1.

Table 3

Mean biomass of euphausiid species reported in the California Current and other locations in the North Pacific. In order to make them comparable, all values are expressed in mg per square meters, multiplying by sampling depth those originally in mg per cubic meters. (CS) coastal shelf, (O) oceanic, (D) day, (N) night, (1) Brinton (1976), (2) Brinton and Reid (1986), (3) Gómez-Gutiérrez et al. (1996), (4) Heath (1977), (5) Hirota et al. (1982), (6) Iguchi and Ikeda (1999), (7) Kim et al. (2009), (8) Lavaniegos and Ambriz-Arreola (2012), (9) Mackas et al. (2013), (10) Romaine et al. (2002), (11) Taki (2006), (12) Tanasichuk (1998a), (13) Tanasichuk (1998b), (14) This study.

Species	Geographic region		Date/Hour	Biomass (mg C m^{-2})	Source
Euphausia pacifica	Canada				
	Strait of Georgia	CS	Aug 1975/N	1200[a,e]	4
			Jul-Aug 1990–1995/D–N	0–5935[c,g]	9
	Jervis Inlet	CS	Jul 1975/N	1000[a,e]	4
			Jul 1994	92–109[b,c]	10
	Saanich Inlet	CS	Jul–Aug 1975/N	338–1200[a,e]	4
	Barkley Sound	CS	Jul–Aug 1991–1996/N	113–491[a,c,g]	12
	Southern California	CS–O	Jul–Aug 1953–1956/N	50–292[a,d]	1
	California-North Baja California	CS–O	Apr 1958/D–NApr 1962/D–N	66[d]	2
				139[d]	2
	Baja California				
	North	O	Jul–Aug 1998–2008/N	7–3825	14
	Central	O	Jul–Aug 1998–2008/N	0–86	14
	South	O	Jul–Aug 1998–2008/N	0–4	14
	Japan				
	Toyama Bay	O	Aug 1990/N	3925	6
	Oyashio	O	Aug 2002–2004/D–N	1100–1600 [a]	7
	Northeast (Hokkaido, Sanriku, Joban)	CS–O	Aug 1997/N	120–440[a,f]	11
Nematoscelis gracilis	Baja California				
	North	O	Jul–Aug 1998–2008/N	0–0.1	14
	Central	O	Jul–Aug 1998–2008/N	0–1	14
	South	O	Jul–Aug 1998–2008/N	0–4	14
	Japan				
	Sagami Bay	CS	1977–1980/D–N	11[d]	5
Nyctiphanes simplex	California-North Baja California	CS–O	Apr 1958/D–N	4[d]	2
			Apr 1984/D–N	287[d]	2
	Baja California				
	North	O	Jul–Aug 1998–2008/N	1–236	14
	Vizcaino Bay	CS	Jul 1998/N	2014	8
			Jul 2005/N	508	8
	Central	O	Jul–Aug 1998–2008/N	2–141	14
	South	O	Jul–Aug 1998–2008/N	15–1239	14
	Gulf of Ulloa	CS	Jul. 2005/N	8400	8
	W Magdalena Bay	CS mainly	Jun–Aug 1986	15–34[c]	3
Thysanoessa spinifera	Canada				
	Strait of Georgia	CS	Jul–Aug 1990–1995/D–N	0–1906[c,g,h]	9
	Barkley Sound	CS	Jul–Aug 1991–1996/N	105–945[a,c]	13
	Baja California				
	North	O	Jul–Aug 1998–2008/N	0–17	14
	Central	O	Jul–Aug 1998–2008/N	0–198	14
	South	O	Jul–Aug 1998–2008/N	0–67	14

[a] Data approximated from a graph of monthly mean biomass.

[b] Biomass estimated from hydro-acoustic methods.

[c] Conversion from dry weight (DW): Carbon = 42% DW (Lasker, 1966).

[d] Conversion from wet weight (WW): Carbon = 7.2% WW (Lasker, 1966).

[e] Conversion from WW: Carbon = 5% WW.

[f] Conversion from DW to Carbon using equivalences by size between 37 and 43% DW (Iguchi and Ikeda, 1998).

[g] Adult euphausiids.

[h] Mixture of *Thysanoessa* species.

species, and may reach a high biomass in the coastal shelf as was observed by Lavaniegos and Ambriz-Arreola (2012) in Vizcaino Bay and the Gulf of Ulloa during July 2005 (508 and 8400 mg C m^{-2}, respectively). Previous summer values recorded by Gómez-Gutiérrez et al. (1996) off Magdalena Bay were low (15–144 mg C m^{-2}), suggesting strong variability in the preferred coastal habitat of this species.

The equatorial species *N. gracilis,* had a low biomass off Baja California in the three oceanic regions, barely reaching a maximum of 4 mg C m^{-2} in the south region. In Sagami Bay, Japan, Hirota et al. (1982) reported a lightly higher annual mean (11 mg C m^{-2}). The presence of *N. gracilis* at 35°N is due to the influence of the warm Kuroshio Current in the west Pacific, while in the CCS this species is rare and limited to southern stations near the equatorial currents (Brinton, 1975, 1979).

4.2. How different was the response of the euphausiid community for the two types of El Niño?

The existence of two types of El Niño events makes the analysis of biological effects a complex problem. There are difficulties in identifying the physical effect during CP-El Niño due to the absence of warmth propagation to the eastern Pacific (Ashok et al., 2007; Lee and McPhaden, 2010). It is thus interesting to question whether the biological effect would be of similar nature, less intense, or completely different during both El Niño types. There is a consensus about the strength of the EP-El Niño 1997–1998, which was one of the most intense of the 20th century (McPhaden, 1999). The footprint of this event off Baja California was detected by the present study during the summer 1998 by a virtual absence of *E. pacifica* in the north region. This species together with *N. difficilis* would usually be the main euphausiids

contributing to carbon biomass off north Baja California (Fig. 3). The same situation of negative anomaly for *E. pacifica* was observed during the spring of 1998 coming from the adjacent region of southern California, although no information for the summer was available (Brinton and Townsend, 2003). In contrast, northern sectors of the CCS presented an increase in abundance of *E. pacifica* during the summer of 1998 contrary to 1997 in Monterey Bay (Marinovic et al., 2002) and near the Oregon coast (Feinberg and Peterson, 2003). In the Strait of Georgia, a positive biomass anomaly (annual mean) was observed during 1998 (Mackas et al., 2013) indicating a retreat of *E. pacifica* to the north.

In contrast, the biomass of *E. eximia* experienced a strong increase in July 1998. During EP-El Niño 1997–1998, this species showed a remarkable expanded distribution in the north region (Lavaniegos and Ambriz-Arreola, 2012); although, its distribution is usually centered in the south Baja California region and the tropical east Pacific (Brinton, 1962; Gómez-Gutiérrez, 1995; Brinton et al., 2000). However, *E. eximia* may be found in low abundance further north in offshore stations during fall-winter, when the CC is weak or during warm events (Brinton and Townsend, 2003). *E. pacifica* and *E. eximia* were used as indicators of interannual variability by Brinton and Reid (1986), observing a shrinking of *E. pacifica* distribution and abundance to the north of Guadalupe Island in warm years 1958 and 1984 while it expanded its distribution to the Gulf of Ulloa in the cool year of 1962. Simultaneously, *N. simplex* and *E. eximia* presented the opposite effect, decreasing in onshore and oceanic domains respectively.

The EP-El Niño 2006–2007 had similar effects to the EP-El Niño 1997–1998 but in lesser magnitude for several species. Resulting in negative biomass anomalies in the summers of 1998 and 2006 for *E. pacifica* and *T. gregaria*, but positive for *E. eximia*. However, other species did not present consistent responses during the EP-El Niño events of the study period. The negative anomaly for *E. pacifica* biomass during 2006 coincided with observations in the Strait of Georgia, Canada, though in this region was part of a period of negative anomalies between 2003 and 2007 (Mackas et al., 2013) and a possible effect of previous CP-El Niño events cannot be excluded. Subtropical central gyre species (*E. hemigibba*, *E. mutica*, and *E. recurva*) increased biomass in the north Baja California region during EP-El Niño 2006–2007. This suggests that they could be transported by advection from the southwest during 2006–2007, as occurred during the EP-El Niño 1997–1998. A comparison with EP-El Niño 1997–1998 sheds conflicting evidences for subtropical gyre species being transported northward, because *E. recurva* presented strong negative anomalies in all areas during July 1998; while *E. hemigibba* only presented positive anomaly in the south region. Keister et al. (2005) recorded the presence of *E. recurva* and *E. mutica* during spring but not in summer of 1998 in coastal waters off Oregon.

CP-El Niño events 2002–2003 and 2004–2005 occurred in a brief period. We expected a reduced effect of these two CP-El Niños on the euphausiid populations given the modest increase of SST (Lavaniegos, 2009; McClatchie et al., 2009). However, the biomass of *N. flexipes*, *T. gregaria*, *N. difficilis*, and *N. simplex* recorded a strong decrease during July 2003 and in July 2004 for the last two. These species, excepting *N. simplex*, are not diel vertical migrants (Brinton, 1967; Youngbluth, 1976). Juvenile and adults of *N. difficilis* and *T. gregaria* live in the thermocline, while the mesopelagic *N. flexipes* lives deeper; therefore they should not be so vulnerable to surface warming but could be sensitive to changes in subsurface temperature. Negative biomass anomalies found in 2003 and 2004 are probably a response to interference of subarctic water intrusion and the CP-El Niño in 2002–2003, resulting in thermohaline stratification (Lavaniegos, 2009, and references therein), and causing thermal and osmotic shocks to the organisms. The saline stratification was more persistent than thermal stratification which remained until July 2006. However, *N. difficilis* and *T. gregaria* did not covariate with temperature or any other variable used in the CCA. Therefore, it is probable that top-down factors could be controlling the biomass of these species (Imsand, 1981; Hipfner, 2009).

In contrast, tropical species covariate with thermal gradient in the CCA, meaning that they are prone to attain large biomasses at regions with stratified waters. Some of them (*E. diomedeae*, *E. eximia*, *E. hemigibba*, *E. mutica*, *E. recurva* and *T. astylata*) are diel vertical migrants (Brinton, 1967; Youngbluth, 1976), adapted to vertically migrate across a wide range of temperature and salinity on a daily basis. This argument stands for the thermal gradient but not for the salinity gradient in the CCA (Fig. 13). The stratified condition was a combination of the subarctic water intrusion and CP-El Niño in 2002–2003. Even so a strongly negative temperature anomaly was observed only in July 2002 in the present study, while negative salinity anomalies persisted until July 2006. The subtropical central gyre species (*E. hemigibba*, *E. mutica*, *E. recurva*) are adapted to stratified and oligotrophic conditions but did not show a clear response to CP-El Niños 2002–2003 and 2004–2005, as they did in the EP-El Niño 2006–2007.

4.3. How similar were La Niña events during the study period?

Brinton and Townsend (2003) noted maximum levels of *E. pacifica* abundance associated to several strong La Niña events occurring between 1949 and 2002, with a rebound of the population at the beginning of La Niña 1995–1996, or delayed one year after for La Niña events of 1955–1956, 1967–1968, and 1998–2000, or even two years after (La Niña 1970–1971). The delay observed in the recovery of this species in Baja California waters during La Niña 1999–2000 could be attributable to the intense warming recorded during the previous El Niño 1997–1998, and because the transition to cool conditions appeared to be more gradual in the north compared with the central and south regions (Fig. 2a–c). Feinberg and Peterson (2003) found more intense spawning of *E. pacifica* during the second year of La Niña in Oregon waters, concluding that productivity delay was due to the life span of this species maturing after 9 months, and therefore increasing spawning until the second year of improved ocean conditions. In contrast, in the Strait of Georgia the biomass of this species had a negative anomaly during 1999 (Mackas et al., 2013).

The response to La Niña 1998–2000 for other transition zone species like *N. difficilis* and *T. gregaria* presented some differences between Baja California and other northern regions of the CCS. In southern California, Brinton and Townsend (2003) recorded positive abundance anomalies for both species during April of 1997–2000 regardless of the ENSO phases. In the present study, we obtained mixed responses of *N. difficilis* biomass off Baja California depending on the region, with increments in the central and south area during summer 1999 compared to 1998. The opposite was observed in Monterey Bay for *N. difficilis*, which increased in 1998 in relation to 1997; decreasing again in 1999, particularly during summer (Marinovic et al., 2002). *E. eximia* showed a similar decrease during La Niña between Baja California and southern California, and disappeared from this last region during 1999–2002 (Brinton and Townsend, 2003).

During the second half of 2005, there were negative SST anomalies in the central Pacific. But only few authors considered this period as La Niña event (Lee and McPhaden, 2010). This cooling followed a period of consecutive CP-El Niño producing strong positive biomass anomalies of subarctic species (*E. pacifica* and *T. spinifera*) during July 2005. Wind forced upwelling enhancement off Baja California since April 2005, after one year of negative upwelling anomalies (Lavaniegos, 2009). In northern sectors of the CCS, delayed upwelling documented in spring of 2005 (Schwing et al., 2006) induced displacements of numerous nektonic organisms along the North American western coast (Brodeur et al., 2006; Sydeman et al., 2006). For example, in British Columbia and central California, the planktivore Cassin's auklet (*Ptychoramphus aleuticus*) abandoned the breeding colonies during 2005 linked to poor biomass of *E. pacifica* and *T. spinifera* (Sydeman et al., 2006). In the Strait of Georgia, *E. pacifica* and *Thysanoessa* spp. presented a low biomass during 2005, the lowest recorded for the period 1990–2010

(Mackas et al., 2013). Massive bird migrations occurred in 2005, reached southern California and Baja California where euphausiids increased their abundance. Lavaniegos and Ambriz-Arreola (2012) suggested that Baja California served as refuge for temperate species looking for better temperature and food conditions. On the other hand, the arrival of abundant populations of micronektonic species (such as euphausiids and small pelagic fishes) and larger predators to refuge areas off Baja California created pressure on small size zooplankton, like young amphipods (Lavaniegos, 2017). Thus, the changing climate during 2005 showed a diversity of ecosystem responses in different taxa and locations of the CCS.

The influence of La Niña was observed again in 2007–2008. However, the summer seasons analyzed in the present study may not be the best period to show the cooling phase produced by La Niña event. Local SST anomalies showed positive numbers, particularly of high magnitude in 2007. These were a result of the sampling done in August instead of July (Fig. 2a–c). Other regions of the CCS also showed positive anomalies during the summers 2007 and 2008 (McClatchie et al., 2009) due to a relaxation during summer in both La Niña years. The highest intensity of La Niña 2007–2008 was in spring, when enhanced upwelling and increased chlorophyll occurred off Baja California (Gaxiola-Castro et al., 2008). High primary productivity recorded during La Niña 2007–2008 was also reported for the equatorial Pacific (Kim et al., 2011). This high primary productivity induced high reproductive activity and growth of euphausiids, perceived in summer as positive biomass anomalies of subarctic and transition species. Mackas et al. (2013) also observed a strong increase of subarctic species in the Strait of Georgia during 2008.

4.4. Is it possible to detect long-term trends during 1998–2008?

During 1998–2008 we found an apparent increase in biomass for *E. recurva*, *N. atlantica*, *N. gracilis*, *S. suhmii*, *T. spinifera*, and a decrease in *E. diomedeae*, *E. mutica*, and *T. astylata*, and in the southern region for *E. gibboides*. Most of these species were rarely collected or had low abundance, with only *E. recurva*, *E. gibboides*, and *T. spinifera* having a regular frequency occurrence and contributing relatively more to carbon biomass. The biogeography of these species is quite different, with *T. spinifera* akin to cool water and a neritic habit, while *E. recurva* inhabiting the subtropical north Pacific gyres (Brinton, 1962). However, an increase of *E. recurva* in the oceanic domain, and *T. spinifera* near the coast, fits well with the hypothesis of global warming promoting a progressive enhancement of coastal upwelling (García-Reyes and Largier, 2010; Bakun et al., 2015; Wang et al., 2015). Stronger winds induce enhanced upwelling by differential land-ocean temperatures (Bakun et al., 2015). Thus, the cooling of water is only in a narrow band along the coast, providing an adequate habitat for temperate species. However in the oceanic region, the warming is relentless promoting tropicalization of the ecosystem.

Our results for 1998–2008 are also consistent with findings by Brinton and Townsend (2003) for southern California during 1951–2002, with a correlation of the Pacific Decadal Oscillation (PDO) and shifting abundances of warm-water species (*N. simplex*, *E. eximia*, *E. gibboides*, *E. recurva*). However, these authors only found significant difference between a cool regime (1950–1976) and a warm regime (1977–1998) for *N. simplex*, increasing during the latter. After 1998, the abundance of *N simplex* decreased again in southern California apparently associated to a new regime shift (Brinton and Townsend, 2003). Consistently, the present study for the north Baja California area recorded an apparent decreasing trend in 1998–2008 in *N simplex* biomass (Fig. 8a). However, this result remains valid only for the slope stations analyzed here. Similar increasing biomass for *E. recurva* during 1998–2008 off north and central Baja California (Fig. 10a and b) are also consistent with the PDO tendency. However, the results for *E. eximia* are not so clear, but more positive anomalies have occurred in the last six years (Fig. 11e and f), and could be associated to PDO as

observed Brinton and Townsend (2003) in southern California for previous decades. In the case of *E. gibboides* our results showed a decreasing tendency in southern Baja California (Fig. 9b and c). These contrasting trends of *E. recurva* and *E. gibboides* in different regions are unexpected, given that Brinton and Townsend (2003) considered both as warm water species co-occurring in offshore regions in intermediate waters (mixing of Pacific Central and California Current waters).

Another issue is the relation between El Niño and climate change. Some authors argued a higher frequency of CP-El Niños due to climate change (Yeh et al., 2009; Lee and McPhaden, 2010). In the light of the results obtained in the present study, impacts of CP-El Niño on the biogeographic group of transition species (*N. difficilis*, *T. gregaria*, *N. simplex*) are probable in future scenarios of climate warming.

In summary, we were able to show the interannual variability of oceanic euphausiid biomass and the necessity for more objective estimations using the geometric mean rather than just the mean. *E. pacifica* may reach a high biomass in the north Baja California region but also presented strong fluctuations mainly associated to EP-El Niño 1997–1998. The response of tropical species results more predictable for EP-El Niño with SST than the thermal stratification of the water column for CP-El Niño. The response of transition-zone species is less predictable in both types of events, though there is a hint that CP-El Niño negatively affects non-vertical migrant species. This suggests a probable future tropicalization of the oceanic euphausiid community that can be attributed to climate change. However, the time series must be more extensive in order to clarify the influence of ENSO and other time-scale influences.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2017.11.009.

References

Ashok, K., Behera, S.K., Rao, S.A., Weng, H., Yamagata, T., 2007. El Niño Modoki and its possible teleconnection. J. Geophys. Res. Oceans 112 (C11). http://dx.doi.org/10.1029/2006JC003798.

Bakun, A., Black, B.A., Bograd, S.J., García-Reyes, M., Miller, A.J., Rykaczewski, R.R., Sydeman, W.J., 2015. Anticipated effects of climate change on coastal upwelling ecosystems. Curr. Clim. Change Rep. 1, 85–93.

Baumgartner, T., Durazo, R., Lavaniegos, B., Gaxiola, G., Gómez, J., García, J., 2008. Ten years of change from IMECOCAL observations in the southern region of the California Current Ecosystem. GLOBEC Int. Newslett. 14, 43–54.

Beaugrand, G., 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. Fish. Oceanogr. 12, 270–283.

Bograd, S.J., Checkley, D.A., Wooster, W.S., 2003. CalCOFI: a half century of physical, chemical, and biological research in the California Current System. Deep Sea Res. II 50, 2349–2353.

Brinton, E., 1962. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr. Univ. California, La Jolla 8 (2), 51–269.

Brinton, E., 1967. Vertical migration and avoidance capability of euphausiids in the California Current. Limnol. Oceanogr. 12, 451–483.

Brinton, E., 1975. Euphausiids of Southeast Asian waters. Naga Report vol. 4, part 5, Scripps Institution of Oceanography, University of California, 287 p.

Brinton, E., 1976. Population biology of *Euphausia pacifica* off southern California. Fish. Bull. 74, 733–762.

Brinton, E., 1979. Parameters relating to the distribution of planktonic organisms, especially euphausiids in the eastern tropical Pacific. Prog. Oceanogr. 8, 125–189.

Brinton, E., Ohman, M.D., Townsend, A.W., Knight, M.D., Bridgeman, A.L., 2000. Euphausiids of the World Ocean. World Biodiversity Database CD-ROM Series, Expert

Center for Taxonomic Identification, University of Amsterdam. [Available in the Marine Species Identification Portal http://species-identification.org/about.php].

Brinton, E., Reid, J.L., 1986. On the effects of interannual variations in the circulation and temperature upon the euphausiids in the California Current. UNESCO Tech. Papers Mar. Sci. 49, 35–41.

Brinton, E., Townsend, A., 2003. Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. Deep-Sea Res. II 50, 2449–2472.

Brodeur, R.D., Ralston, S., Emmett, R.L., Trudel, M., Auth, T.D., Phillips, A.J., 2006. Anomalous pelagic nekton abundance, distribution, and apparent recruitment in the northern California current in 2004 and 2005. Geophys. Res. Lett. 33, L22S08. http://dx.doi.org/10.1029/2006GL026614.

Feinberg, L.R., Peterson, W.T., 2003. Variability in duration and intensity of euphausiid spawning off central Oregon, 1996–2001. Prog. Oceanogr. 57, 363–379.

García-Reyes, M., Largier, J., 2010. Observations of increased wind-driven coastal upwelling off central California. J. Geophys. Res. 115, C04011. http://dx.doi.org/10.1029/2009JC005576.

Gaxiola-Castro, G., Durazo, R., Lavaniegos, B., DeLaCruz-Orozco, M., Millán-Núñez, E., Soto-Mardones, L., Cepeda-Morales, J., 2008. Pelagic ecosystem response to interannual variability off Baja California. Cienc. Mar. 34, 263–270.

Gómez-Gutiérrez, J., 1995. Distribution patterns, abundance and population dynamics of the euphausiids *Nyctiphanes simplex* and *Euphausia eximia* off the west coast of Baja California, Mexico. Mar. Ecol. Prog. Ser. 119, 63–76.

Gómez-Gutiérrez, J., De Silva-Dávila, R., Lavaniegos, B.E., 1996. Growth production of the euphausiid *Nyctiphanes simplex* on the coastal shelf off Bahia Magdalena, Baja California Sur, Mexico. Mar. Ecol. Prog. Ser. 138, 309–314.

Gómez-Gutiérrez, J., Feinberg, L.R., Shaw, T.C., Peterson, W.T., 2007. Interannual and geographical variability of the brood size of the euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* along the Oregon coast (1999–2004). Deep-Sea Res. I 54, 2145–2169.

Heath, W.A., 1977. The Ecology and Harvesting of Euphausiids in the Strait of Georgia. PhD Thesis, University of British Columbia, Vancouver, 1977, 187 p.

Hipfner, J.M., 2009. Euphausiids in the diet of a North Pacific seabird: annual and seasonal variation and the role of ocean climate. Mar. Ecol. Prog. Ser. 300, 277–289.

Hirota, Y., Nemoto, T., Harumo, R., 1982. Seasonal variation and horizontal distribution of euphausiids in Sagami Bay, Central Japan. Bull. Plankton Soc. Jpn. 29, 37–47.

Hu, Z.Z., Kumar, A., Xue, Y., Jha, B., 2014. Why were some La Niñas followed by another La Niña? Clim. Dyn. 42, 1029–1042.

Iguchi, N., Ikeda, T., 1998. Elemental composition (C, H, N) of a euphausiid *Euphausia pacifica* in Toyama Bay, southern Japan Sea. Plankton Biol. Ecol. 45, 27–32.

Iguchi, N., Ikeda, T., 1999. Production metabolism, P:B ratio of *Euphausia pacifica* (Crustacea: Euphausiacea) in Toyama Bay, southern Japan Sea. Plankton Biol. Ecol. 46, 68–74.

Imsand, S., 1981. Orientation of armored euphausiid prey in the stomachs of myctophid fishes. Crustaceana 41, 104–107.

Kaplan, I.C., Brown, C.J., Fulton, E.A., Gray, I.A., Field, J.C., Smith, A.D.M., 2013. Impacts of depleting forage species in the California Current. Environ. Conserv. 40, 380–393.

Keister, J.E., Johnson, T.B., Morgan, C.A., Peterson, W.T., 2005. Biological indicators of the timing and direction of warm-water advection during the 1997/1998 El Nino off the central Oregon coast, USA. Mar. Ecol. Prog. Ser. 295, 43–48.

Kim, H.J., Kim, D., Yoo, C.M., Chi, S.B., Khim, B.K., Shin, H.R., Hyeong, K., 2011. Influence of ENSO variability on sinking-particle fluxes in the northeastern equatorial Pacific. Deep Sea Res. Part I 58, 865–874.

Kim, H.S., Yamaguchi, A., Ikeda, T., 2009. Abundance, biomass and life cycle patterns of euphausiids (*Euphausia pacifica, Thysanoessa inspinata* and *T. longipes*) in the Oyashio region, western subarctic Pacific. Plankton Benthos Res. 4 (2), 43–52.

Lasker, R., 1966. Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. J. Fish. Res. Board Can. 23, 1291–1317.

Lavaniegos, B.E., 2009. Influence of a multiyear event of low salinity on the zooplankton from Mexican eco-regions of the California Current. Prog. Oceanogr. 83, 369–375.

Lavaniegos, B.E., 2017. Changes in composition of summer hyperiid amphipods from a subtropical region of the California current during 2002–2008. J. Mar. Syst. 165, 13–26.

Lavaniegos, B.E., Ambriz-Arreola, I., 2012. Interannual variability in krill off Baja California in the period 1997–2005. Prog. Oceanogr. 97–100, 164–173.

Lavaniegos, B.E., Ambriz-Arreola, I., Hereu, C.M., Jiménez-Pérez, L.C., Cadena-Ramírez,

J.L., García-García, P., 2010. Variabilidad estacional e interanual del zooplancton en la sección mexicana de la Corriente de California. In: Gaxiola-Castro, G., Durazo, R. (Eds.), Dinámica del ecosistema pelágico frente a Baja California, 1997–2007. CICESE/UABC/INE, México, D.F., pp. 87–126.

Lavaniegos, B.E., Molina-González, O., Murcia-Riaño, M., 2015. Zooplankton functional groups from the California Current and climate variability during 1997–2013. CICIMAR Océanides 30, 45–62.

Lee, T., McPhaden, M.J., 2010. Increasing intensity of El Niño in the central-equatorial Pacific. Geophys. Res. Lett. 37, L14603. http://dx.doi.org/10.1029/2010GL044007.

Mackas, D., Galbraith, M., Faust, D., Masson, D., Young, K., Shaw, W., Romaine, S., Trudel, M., Dower, J., Campbell, R., Sastri, A., Bornhold-Pechter, E.A., Pakhomov, E., El-Sabaawi, R., 2013. Zooplankton time series from the Strait of Georgia: results from year-round sampling at deep water locations, 1990–2010. Prog. Oceanogr. 115, 129–159.

Mackas, D.L., Pepin, P., Verheye, H., 2012. Interannual variability of marine zooplankton and their environments: within- and between-region comparisons. Prog. Oceanogr. 97–100, 1–14.

Marinovic, B.B., Croll, D.A., Gong, N., Benson, S.R., Chavez, F.P., 2002. Effects of the 1997–1999 El Niño and La Niña events on zooplankton abundance and euphausiid community composition within the Monterey Bay coastal upwelling system. Prog. Oceanogr. 54, 265–277.

McCune, B., Grace, J.B., Urban, D.L., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McClatchie, S., Goericke, R., Schwing, F.B., Bograd, S.J., Peterson, W.T., Emmett, R., Charter, R., Watson, W., Lo, N., Hill, K., Collins, C., Kahru, M., Mitchell, B.G., Koslow, J.A., Gomez-Valdes, J., Lavaniegos, B.E., Gaxiola-Castro, G., Gottschalck, J., L'Heureux, M., Xue, Y., Manzano-Sarabia, M., Bjorkstedt, E., Ralston, S., Field, J., Rogers-Bennet, L.L., Munger, L., Campbell, G., Merkens, K., Camacho, D., Havron, A., Douglas, A., Hilderbrand, J., 2009. The state of the California current, spring 2008–2009: cold conditions drive regional differences in coastal production. Calif. Coop. Ocean. Fish. Invest. Report 50, 43–68.

McPhaden, M.J., 1999. Genesis and evolution of the 1997–98 El Niño. Science 283, 950–954.

Romaine, S.J., Mackas, D.L., Macaulay, M.C., 2002. Comparison of euphausiid population size estimates obtained using replicated acoustic surveys of coastal inlets and block average vs. geostatistical spatial interpolation methods. Fish. Oceanogr. 11, 102–115.

Ross, R.M., 1982. Energetics of *Euphausia pacifica*. I. Effects of body carbon and nitrogen and temperature on measured and predicted production. Mar. Biol. 68, 1–13.

Schwing, F.B., Bond, N.A., Bograd, S.J., Mitchell, T., Alexander, M.A., Mantua, N., 2005. Delayed coastal upwelling along the U.S. West Coast in 2005: a historical perspective. Geophys. Res. Lett. 33, L22S01. http://dx.doi.org/10.1029/2006GL026911.

Siegel, S., Castellan, N.J., 1988. In: Nonparametric Statistics for the Behavioral Sciences, second ed. McGraw-Hill, New York, pp. 399.

Sydeman, W.J., Bradley, R.W., Warzybok, P., Abraham, C.L., Jahncke, J., Hyrenbach, K.D., Kousky, V., Hipfner, J.M., Ohman, M.D., 2006. Planktivorous auklet Ptychoramphus aleuticus responses to ocean climate, 2005: unusual atmospheric blocking? Geophys. Res. Lett. 33, L22S09. http://dx.doi.org/10.1029/2006GL026736.

Taki, K., 2006. Biomass and production of the euphausiid *Euphausia pacifica* along the coastal waters off north-eastern Japan. Fish. Sci. 72, 221–232.

Tanasichuk, R.W., 1998a. Interannual variations in the population biology and productivity of *Euphausia pacifica* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. Mar. Ecol. Prog. Ser. 173, 163–180.

Tanasichuk, R.W., 1998b. Interannual variations in the population biology and productivity of *Thysanoessa spinifera* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. Mar. Ecol. Prog. Ser. 173, 181–195.

Wang, D., Gouhier, T.C., Menge, B.A., Ganguly, A.R., 2015. Intensification and spatial homogenization of coastal upwelling under climate change. Nature 518, 390–394.

Wheeler, P.A., Huyer, A., Fleischbein, J., 2003. Cold halocline, increased nutrients and higher chlorophyll off Oregon in 2002. Geophys. Res. Lett. 30, 8021. http://dx.doi.org/10.1029/2003GL017395.

Yeh, S.W., Kug, J.S., Dewitte, B., Kwon, M.H., Kirtman, B.P., Jin, F.F., 2009. El Niño in a changing climate. Nature 46, 511–515.

Youngbluth, M.J., 1976. Vertical distribution and diel migration of euphausiids in central region of California Current. Fish. Bull. 74 (4), 925–936.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14.