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Interannual variability in krill off Baja California in the period 1997–2005

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In memory of my adviser Prof. Edward Brinton, expert in euphausiids and creator of one of the most complete and inspiring works in biogeography 'The distribution of Pacific euphausiids'.

ABSTRACT

We document interannual changes in the species composition of euphausiids inhabiting the waters off Baja California during the period of 1997–2005. Thirty-two euphausiid species were identified from seventeen cruises, with the dominant species being *Euphausia eximia*, *Euphausia gibboides*, *Nyctiphanes simplex*, *Thysanoessa gregaria*, *Nematoscelis difficilis*, and *Stylocheiron affine* (present in 74–92% of the samples). Species composition had the strongest difference between coastal (Vizcaino Bay and the Ulloa Gulf) and oceanic waters. The coastal shelf was dominated almost exclusively by *N. simplex* while the oceanic regions showed a high diversity. In oceanic waters the most abundant species was *N. difficilis* off both the northern (32–30°N) and the central (30–24°N) Baja California peninsula. The highest krill biomass, however, was recorded in the central region in January 1998 during an El Niño and consisted principally of abundant larvae of *E. eximia*. La Niña was characterized by an increase of the 'transition zone' species (*E. gibboides*, *N. difficilis*, *T. gregaria*) and the subarctic *Euphausia pacifica*. This last even entered in Vizcaino Bay but was not apparent in the central region compared to the north. High abundance of *E. pacifica* was also observed in July 2002 and was linked to subarctic water intrusion and July 2005. Some swarms of *Thysanoessa spinifera* were observed during April and July of 2005. The presence of subarctic species *E. pacifica* and *T. spinifera* in Baja California waters contrasted with their strong decrease in northern sectors of the California Current System during 2005. This biological information, joined with high upwelling activity (compared to delayed upwelling off Oregon and northern California), reinforces the importance of regional studies in eastern boundary currents.

1. Introduction

The systematic study of the California Current System (CCS) grew considerably during the second half of the 20th century as a result of broad surveys of the CALCOFI program, which comprised the California and Baja California sectors (42–23°N). Studies derived from the first CALCOFI period (1951–1978) reported on variability in the distribution of euphausiids (Brinton, 1962, 1967a, 1973) and zooplankton biomass (Bernal, 1981; Roesler and Chelton, 1987). Reduction of the spatial coverage of the CALCOFI program took the Baja California sector out of the sampling routine, with few sporadic incursions between 1981 and 1984. These last CALCOFI cruises entering the northern Baja California waters provided information about the distributional changes in euphausiids during the 1982–1983 El Niño. They showed the typical northward invasion of subtropical species such as *Nyctiphanes simplex* and *Euphausia eximia* (Brinton and Reid, 1986). Furthermore, the few isolated surveys off southern Baja California performed during the 1980s by Mexican researchers allowed documentation of the 1982–1983 El Niño effects on copepods (Hernández-Trujillo, 1999) and of the 1986–1987 El Niño on euphausiids (Gómez-Gutiérrez et al., 1995).

In the 1990s, Roemmich and McGowan (1995) warned of declining zooplankton biomass off southern California (35–32°N) that was related to the Pacific Decadal Oscillation (PDO). The decreases in pelagic tunicates (Lavaniegos and Ohman, 2003) were the main zooplankton taxa explaining the decline in zooplankton volume, although the carbon biomass of zooplankton did not decrease significantly (Lavaniegos and Ohman, 2007). Brinton and Townsend (2003) analyzed long-term changes in euphausiid species showing a positive correlation between the PDO and abundance anomalies of the subtropical coastal *N. simplex* and three oceanic species of the genus *Euphausia* (*E. eximia*, *Euphausia gibboides*, and *Euphausia recurva*) from southern California. Though these authors included data for California and Baja California, the correlation with the PDO was not attempted for the latter because of gaps in the time-series. It was evident, however, that *Thysanoessa spinifera*, a cold-water coastal species, experienced a reduction in California waters and a virtual disappearance off Baja California during the 1980s (Brinton and Townsend, 2003). At the same time, the abundance of subarctic euphausiids (*Euphausia pacifica* and *T. spinifera*) in the northern sectors of the CCS increased during the late 1980s and early 1990s off British Columbia while boreal and

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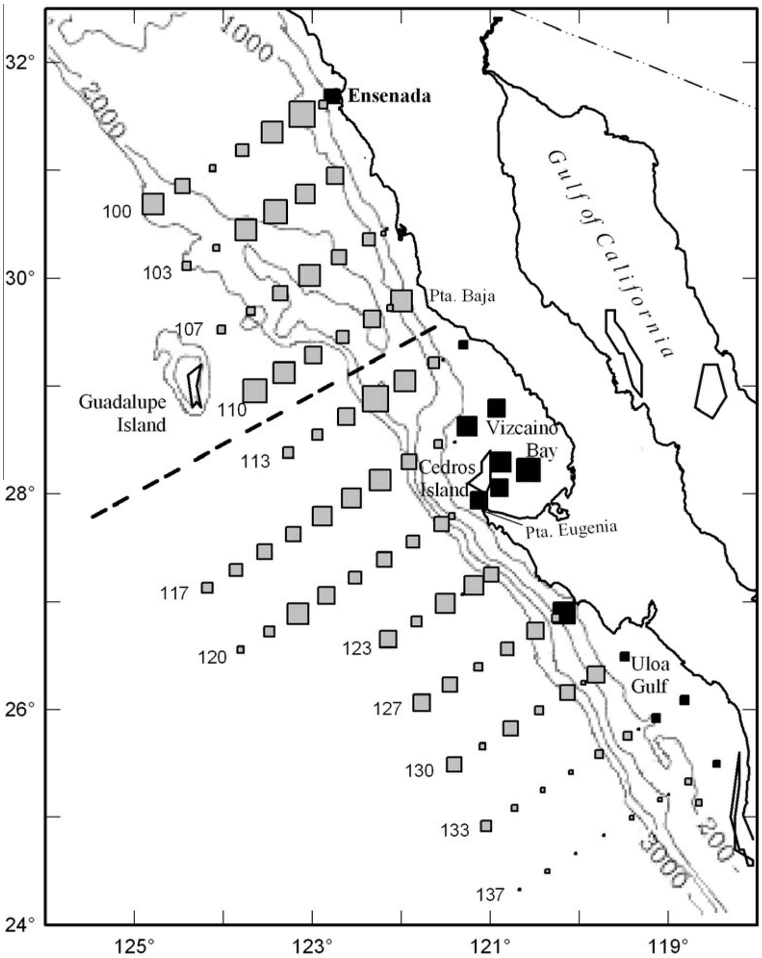

Fig. 1. Mexican sector of the California Current showing the IMECOCAL station grid. Symbol sizes are proportional to the number of times a station was sampled at night (ranging from 1 to 12) to collect zooplankton during the seventeen cruises analyzed in the present study. Black squares are coastal stations. The dashed line indicates the separation in north and central regions. The indentification number of transect lines is indicated. Gray lines are isobaths (m).

subarctic copepods decreased (Mackas et al., 2001). A diminution of boreal copepods was also observed off Oregon in samples collected between 1983 and 1998, compared to the period 1969–1973 (Peterson and Schwing, 2003).

Regional differences or similarities along the CCS have been difficult to address due to the isolated sampling efforts and methodological differences (Mackas et al., 2006). Nonetheless, there is evidence of notable spatial coherence in zooplankton biomass during strong El Niño events, as in 1958–1959 and 1982–1983 (Roesler and Chelton, 1987). Coherent responses were also observed in several zooplankton taxa between central and southern California (Lavaniegos and Ohman, 2007). In contrast, the strong El Niño of 1997–1998 showed a slight increase in biomass off Baja California compared to the collapse observed in southern California (Lavaniegos et al., 2002) and the northern California Current (Peterson et al., 2002). Though transition-zone copepod species suffered some decrease, other tropical and cosmopolitan species increased in abundance considerably during the 1997–1998 El Niño (Jiménez-Pérez and Lavaniegos, 2004) off Baja California, along with of salps (Hereu et al., 2006). There is also evidence of changes in euphausiid species composition (Linacre, 2004) based in the comparison of two autumns (1997 and 1999): higher abundances of species with tropical and equatorial affinity were associated with the warm event in 1997 relative to 1999, although analysis of the complete ENSO cycle is necessary to confirm the association.

Table 1
Sampling date and number of zooplankton nighttime samples by regions used in the present study (see Fig. 1).

IMECOCAL Cruises	Sampling date	Oceanic		Coastal shelf	
		North	Central	Vizcaino	Ulloa
9710	29 September–6 October 1997		13	4	
9801	25 January–11 February 1998	13	14	6	1
9807	15–30 July 1998	11	13	2	
9810	28 September–1 November 1998	12	19	5	1
9901	14–30 January 1999	14	10	3	
9904	30 March–16 April 1999	6	14	2	
9908	8–22 August 1999	12	17	3	3
9910	3–22 October 1999	11	22	5	3
0001	14 January–1 February 2000	14	24	5	3
0004	4–21 April 2000	12	14	5	
0007	10–30 July 2000	11	21	1	3
0010	10–29 October 2000	12	18	3	2
0207	12 July–1 August 2002	12	22	3	3
0501	21 January–10 February 2005	19	28	1	3
0504	14 April–5 May 2005	12	24	1	1
0507	14 July–4 August 2005	14	22	3	2
0510	13–27 October 2005	16	19	5	1

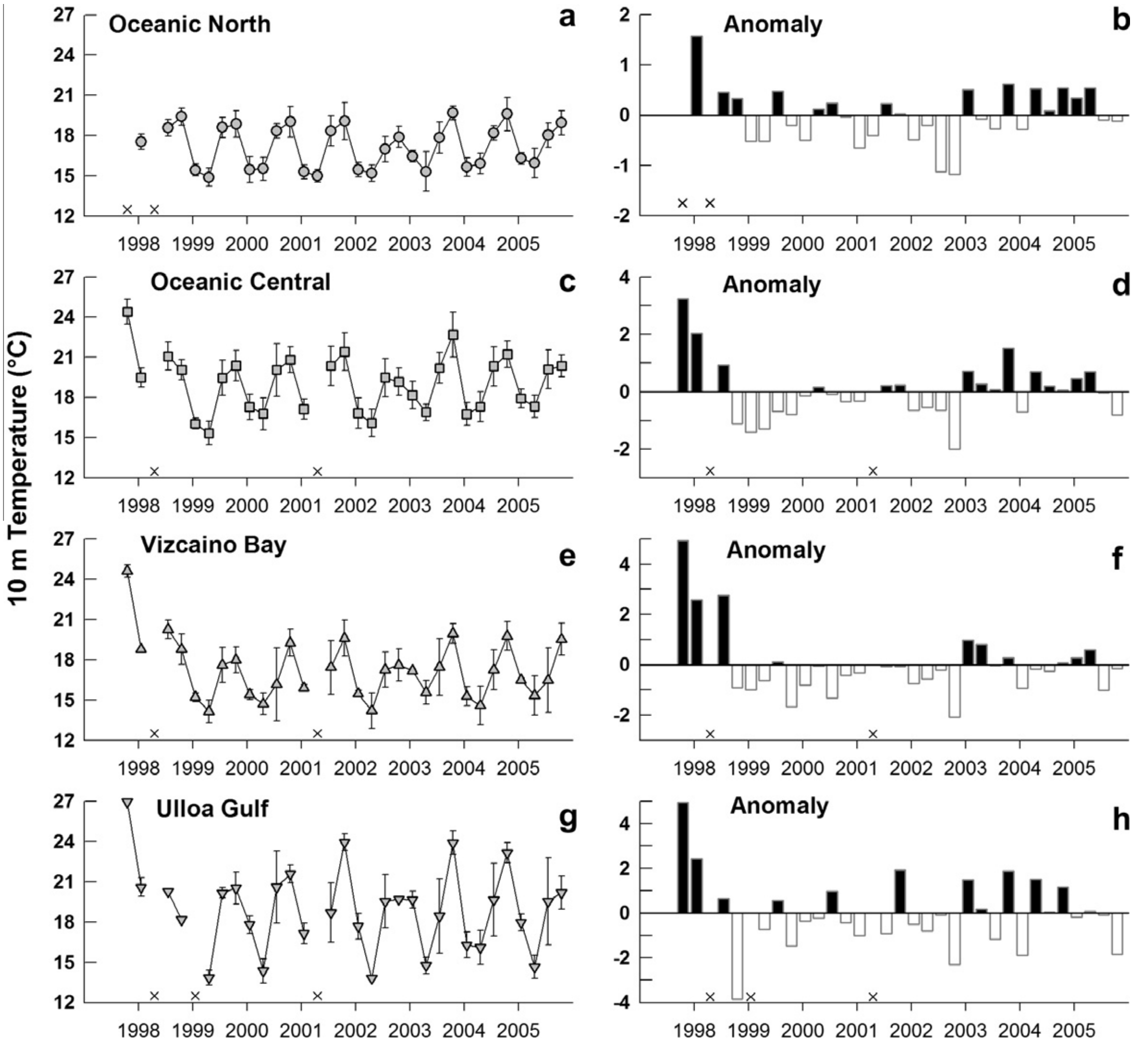

Fig. 2. Temperature and temperature anomalies at 10 m depth in oceanic regions (a–d) and coastal shelves (e–h) off Baja California. The mean and standard deviation per cruise are shown (a, c, e, g). Anomalies were estimated by removing seasonal means for the period 1997–2005 (b, d, f, h). Note the different scales of the anomalies in different regions. Missing data are indicated with *x* in this and subsequent figures.

Another interannual event observed along the CCS was the subarctic water intrusion in 2002–2003 (Huyer, 2003; Durazo et al., 2005). The subarctic intrusion was associated with large-scale changes in the North Pacific Current and its bifurcation in the two branches; the north-flowing Alaska Current and the south-flowing California Current (Freeland and Cummins, 2005). This perturbation remained until mid-2003 and was coherent along the CCS but particularly disruptive in waters off Baja California because the zooplankton community rich in tropical species was carried to the north by the 2002–2003 El Niño (Lavaniegos, 2009).

Further in 2005, out of phase conditions occurred along the CCS, with the warming of surface water and delayed coastal upwelling from southern British Columbia to northern California, which was not observed off Baja California (Schwing et al., 2006). Negative abundance anomalies in total copepods and euphausiids in northern sectors of the CCS contrasted with positive anomalies off Baja California (Mackas et al., 2006). However, there was no information of copepod and euphausiid species from Baja California to compare with northern regions of the CCS.

In the present study we analyze the response of euphausiid species to the interannual perturbations off Baja California during the period 1997–2005. We selected samples from this time period to compare and contrast species composition between the warm event of El Niño 1997–1998 and three cool events: La Niña 1998–1999, the subarctic intrusion in July 2002, and the increased upwelling in April and July 2005.

2. Methods

2.1. Study area

The CCS as one of the eastern boundary upwelling ecosystems presents two main characteristics: (1) a latitudinal thermohaline gradient (Lynn and Simpson, 1987) which is enriched by tropical biota as it progress southward (Reid et al., 1978); and (2) an upwelling front from coast to offshore, resulting from the influence of the dominant winds (Huyer, 1983), which induces high biological productivity. During spring, the wind stress contributes to the enhancement of the equatorward flow and the intensification of coastal upwelling (Lynn et al., 2003). Off Baja California, the fertilization of surface waters activates the proliferation of plankton species associated with cool water (temperate) joined with subtropical species. The rest of the year the main equatorward flow continues, but the intensity gradually decreases, allowing the incursion of equatorial water from the southwest (Roden, 1971;

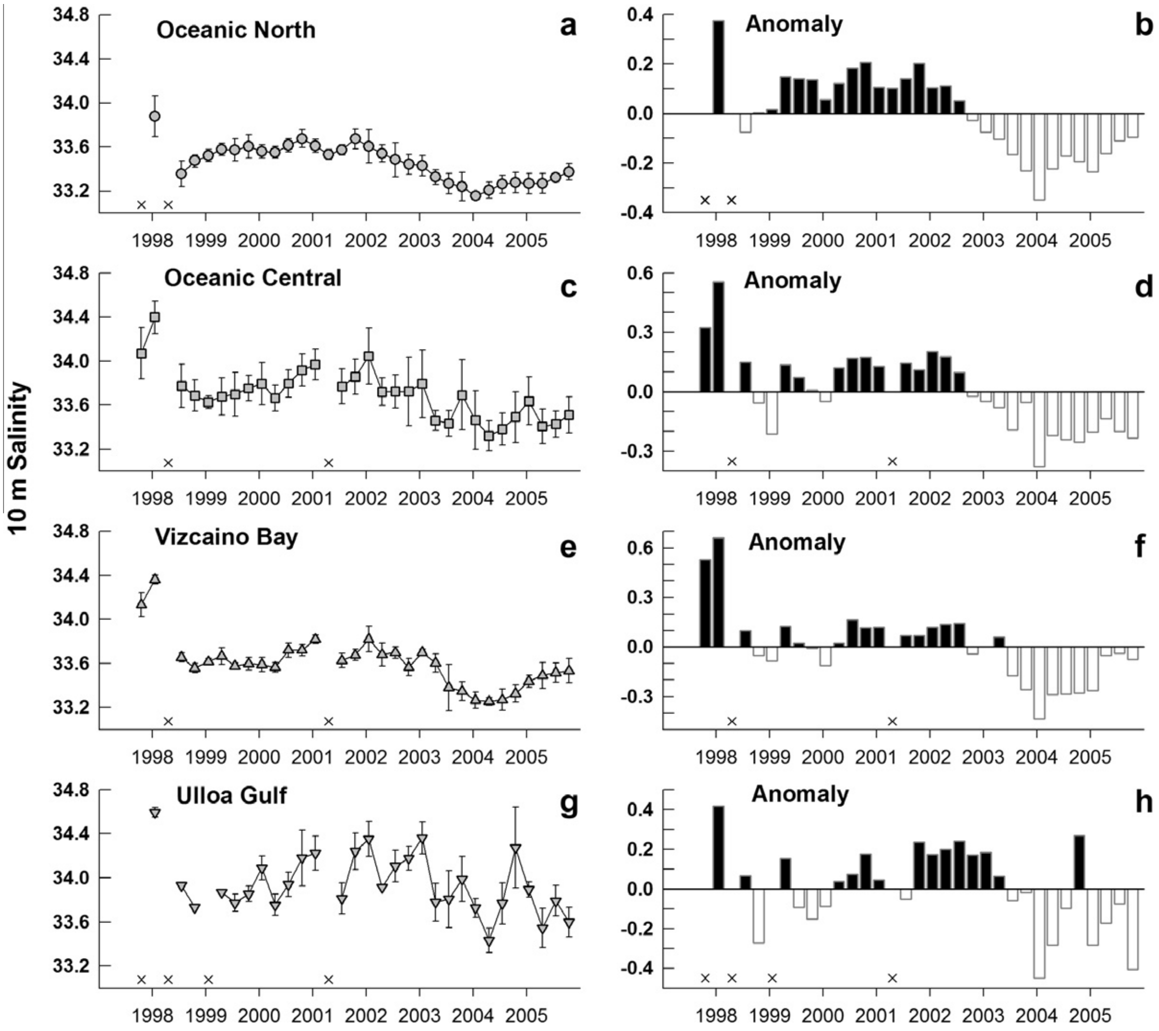

Fig. 3. Salinity and salinity anomalies at 10 m depth in oceanic regions (a–d) and coastal shelves (e–h) off Baja California. The mean and standard deviation per are is shown (a, c, e, g). Anomalies were estimated removing seasonal means for the period 1997–2005 (b, d, f, h). Note the different scales of the anomalies in different regions.

Durazo and Baumgartner, 2002). As a result, from the end of summer but mainly in autumn and winter, oceanic species associated to the subtropical gyre advance toward the northeast, as well as species from the eastern tropical Pacific progress northward (Brinton, 1962).

The terminal part of the CCS passes off Baja California (Fig. 1), a sector less inhabited by temperate biota and the most enriched by tropical species (Lavaniegos and Jiménez-Pérez, 2006). It spans an extended area with the greatest latitudinal gradient, and may be differentiated in two regions: (1) northern Baja California (32–30°N), which is part of the southern California Bight recirculation and is characterized by marked stratification, minimal wind forcing and weak upwelling (US GLOBEC, 1994), and (2) the region between Punta Baja (Fig. 1) to the tip of the peninsula which has moderate upwelling throughout the year (Huyer, 1983), a greater influence of the Pacific equatorial water (Roden, 1971), and prominent mesoscale activity (Soto-Mardones et al., 2004).

2.2. Zooplankton sampling

The sampling routine of the IMECOCAL (Spanish acronym for 'Mexican Research of the California Current') program includes CTD casts and zooplankton tows during quarterly cruises conducted on the R/V *Francisco de Ulloa*. The present study includes physical data from 32 cruises performed between September 1997 and October 2005 through a grid of 92 stations (Fig. 1). The initial IMECOCAL grid did not include the last transect lines (133 and 137). In July 1999 line 133 was added and line 137 has been sampled since 2000. Usually the months sampled were January, April, July and October, with the exception of April 1998, and two short cruises (September 1997 limited to lines 110–127 and April 2001 to lines 100–113).

Zooplankton was collected with a bongo net of 505 μm meshwidth towed in double oblique hauls in the upper 210 m or from 10 m above the bottom to the surface at shallow stations. The diameter of the net was 61 cm before October 2001, after which it was replaced by one of 71 cm. The volume of water strained was measured with a flow-meter in the mouth of the net. Samples were preserved with 4% formalin and sodium borate.

2.3. Laboratory analysis

Euphausiid species were identified in zooplankton samples from 17 cruises: 12 from 1997 to 2000, cruise 0207 in July 2002 and four cruises in 2005. Only nighttime samples were selected for taxonomic analysis (Fig. 1); the juveniles and adults were counted from the whole sample while larval enumeration was limited to a fraction (1/2, 1/4, or 1/8). The total number of samples analyzed was 598, of which 84% were oceanic and 14% were from shallow stations in the Vizcaino Bay and the Ulloa Gulf (Table 1).

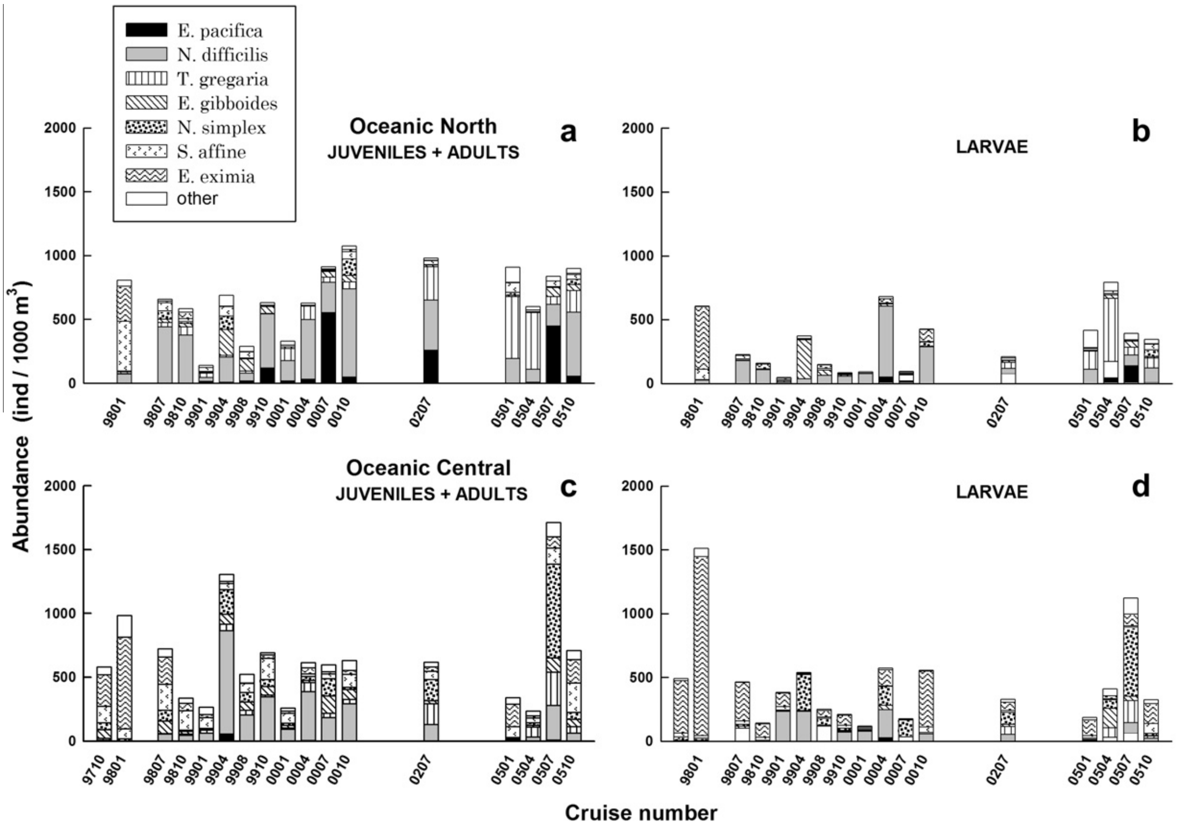

Fig. 4. Euphausiid species composition in two oceanic regions off Baja California: stacked bars are back-transformed geometric mean abundance. Larval abundance (b, d) is presented separately from the juveniles and adults (a, c). In both, data from each species were log-transformed prior to the calculation of log-means and then reported as back-transformed values. The species selected are a combination of the four species with the highest abundance in both regions. The cruise number indicates year (first two digits) and month (last two digits).

2.4. Data analysis

Euphasiid abundance was converted to carbon biomass using the equation from Ross (1982) for *E. pacifica*: $y = 0.337\ (x)^{3.17}$ where y = µg carbon and x = body length in mm. We applied this equation to all species using the mean body length of juveniles and adults combined. For euphausiid larvae an equation was estimated based on a combination of values estimated from equations given in Lindley et al. (1999) for furcilias of two species (*Nyctiphanes couchi* and *Thysanoessa longicaudata*). The resultant equation was: $y = 1.501\ (x)^{2.61}$ ($r^2 = 0.953$).

Data of euphausiid abundance and carbon biomass were log-transformed to normalize the data. Therefore the mean used in this paper is the geometric mean resulting from retransformation of the log-mean.

Temperature and salinity data were used to characterize the abiotic environment. Data for all stations (2276) performed during 1997–2005 were used. Anomalies were estimated by removing seasonal means of the period 1997–2005 for each oceanic region and the two coastal shelves considered in this study (Fig. 1).

3. Results

3.1. Physical environment

Temperature at 10 m depth during the period 1997–2005 showed high values associated with the 1997–1998 El Niño (Fig. 2). Positive anomalies up to 3 °C were recorded during the autumn of 1997 in the oceanic region (Fig. 2d) and up to 5 °C in the coastal shelf (Fig. 2f and h). The warming of the surface layer continued in winter with anomalies between 1.5 and 3 °C (Fig. 2b, d, f and h). After El Niño, negative anomalies persisted for 4 years, with those of 1999 and part of 2000 being associated with La Niña. The highest negative anomalies, however, were associated with the intrusion of subarctic water in July 2002 in the northern region (Fig. 2b) and October 2002 in all regions (Fig. 2b, d, f and h). Positive anomalies of low magnitude were associated with the 2002–2003 El Niño as well as subsequent years. The high variability and shifting direction of anomalies in the Ulloa Gulf (Fig. 2g and h) only partially reflect the dynamic nature of this coastal shelf as the mean values were based in five or fewer stations.

Salinity at 10 m depth presented high values in the beginning of time-series and a decreasing tendency at the end (Fig. 3). High salinity occurred during El Niño owing to the influence of equatorial water, but decreased during La Niña when more subarctic water was coming with the strengthening of the California Current. However, these would be moderate negative anomalies compared to those resulted from further freshening of the surface layer in 2002–2005. The decrease in salinity was gradual from the middle of 2002 to January 2004 (Fig. 3b, d and f) with a delay of 1 year in the Ulloa coastal shelf (Fig. 3h). The delay could be the result of the influence of El Niño 2002–2003, which produced positive anomalies during 2002 and part of 2003.

3.2. Euphausiid abundance

The seventeen IMECOCAL cruises analyzed for euphausiid species included the evolution of the ENSO cycle of 1997–1999, one cruise during the subarctic water intrusion (July 2002) and all of

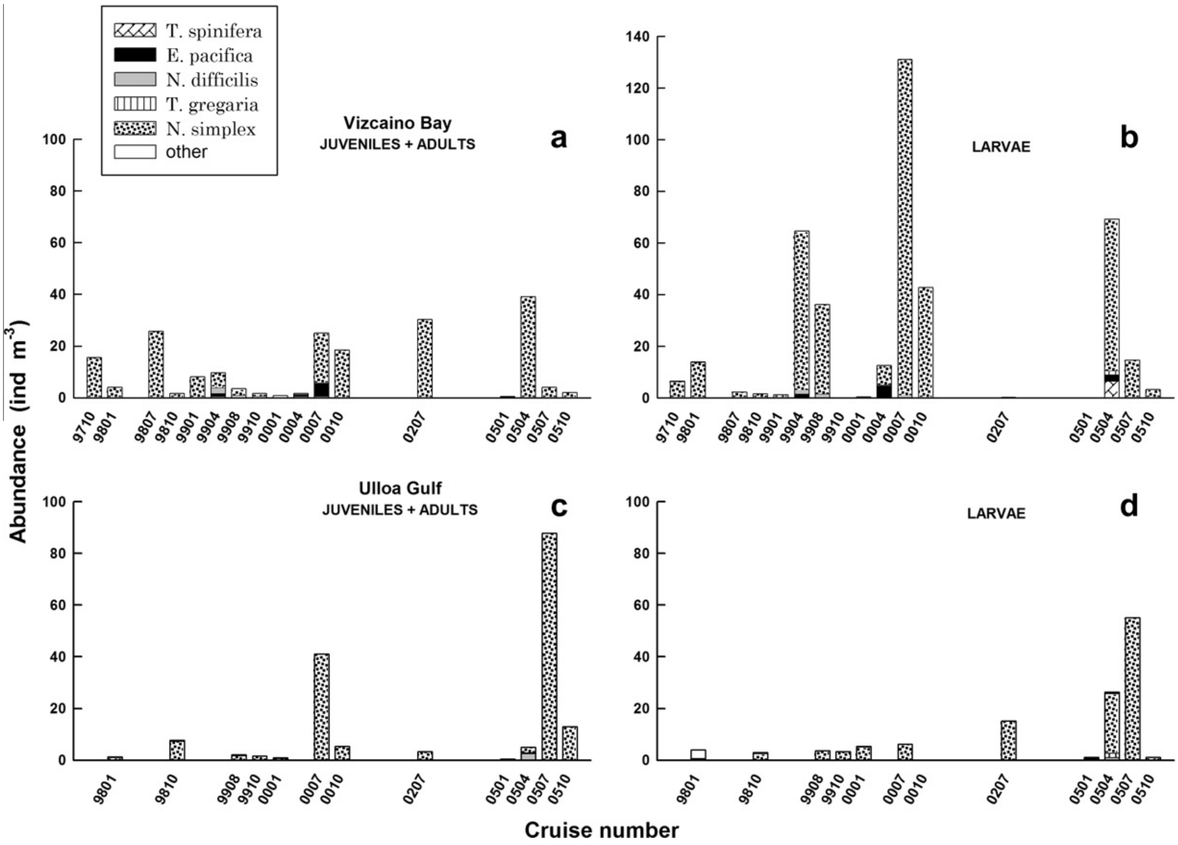

Fig. 5. Euphausiid species composition in two coastal shelves off Baja California: stacked bars are geometric mean abundance. Larval abundance (b, d) is presented separately from the juveniles and adults (a, c). In both, data from each species were log-transformed prior to the calculation of log-means and then reported as back-transformed values. The species selected were the five most abundant species in Vizcaino Bay.

2005. There were 32 euphausiid species identified, but eleven of them occurred in less than 5% of the samples (Supplemental Table 1). In the oceanic region, the abundance of larvae (calyptopes and furcilia) tended to be lower than that of juveniles and adults (Fig. 4), excepting during the 1997–1998 El Niño when larvae of *E. eximia* were abundant (Fig. 4b and d). Apart from the increased importance of *E. eximia* during El Niño, this species combined with *N. simplex* was more characteristic of the central region than north oceanic region. In contrast, *Euphausia pacifica* was scarce in the central region (Fig. 4a and b). Juveniles and adults of *E. pacifica* were particularly abundant in the summers of 2000, 2002 and 2005 (Fig. 4a). While July 2000 and 2002 were linked to cool events, such as La Niña and the subarctic water intrusion, the dominance of *E. pacifica* could be to the result of enhanced upwelling in July 2005.

Nyctiphanes simplex was of little importance in the oceanic region (Fig. 4), contrasting with its high abundance on the coastal shelf (Fig. 5). Geometric means for juveniles and adults ranged from 3 to 736 ind/1000 m^3 in the central oceanic region (Fig. 4c) while at Vizcaino Bay they ranged from 35 to 39,000 ind/1000 m^3 (Fig. 5a) and the Ulloa Gulf had between 64 and 87,837 ind/1000 m^3 (Fig. 5c). The abundance of *N. simplex* larvae was higher in Vizcaino Bay (Fig. 5b) compared to the Ulloa Gulf (Fig. 5d) though there were many cruises without data from the latter. There were small numbers of *Nematoscelis difficilis* and *E. pacifica* onto the coastal shelf during La Niña. In contrast *E. eximia* rarely entered Vizcaino Bay, even during El Niño, in contrast with their high biomass in the oceanic region (Figs. 4 and 5). The only sample from the Ulloa Gulf in January 1998 showed the small presence of *E. eximia* during El Niño. A few *T. spinifera* was present in Vizcaino Bay during 2005 (Fig. 5).

3.3. Euphausiid biomass

One of the best ways to combine data on the abundance of euphausiid life phases is to express the abundance in units of carbon biomass. Remarkable changes in species dominance were evident in the oceanic regions (Fig. 6) through the ENSO cycle. A good indicator of warm water influence was the oceanic species *E. eximia*, which was dominant during January 1998 in both northern and central Baja California regions. After the warmest phase of El Niño, *N. difficilis* recovered rapidly in July 1998 in the northern region (Fig. 6a), while in the central region recovery was delayed until April 1999 (Fig. 6b). A longer delay was apparent for *E. pacifica* (Fig. 6a). *Euphausia gibboides* was another 'transition zone' species (Brinton, 1962), with increasing biomass in April 1999 though it was also present during El Niño (cruises 9710 and 9807). *Thysanoessa gregaria*, also considered by Brinton (1962) to be a transition zone species, showed a moderate increase during La Niña with a stronger increase apparent in July 2002, and during January and April 2005, particularly in the northern region (Fig. 6a). Regional differences in the species composition of the northern and central oceanic communities were intensified during July 2002, and for all of the 2005 cruises. During these periods, the number and biomass of both subarctic and temperate species increased in the northern region while they decreased in the central region. Warm-water species, however, increased only in biomass in the central region during these periods. These differences reflect a significant divergence in the character of the euphausiids communities in the northern and central oceanic regions.

In Vizcaino Bay, the changes in *N. simplex* are better shown in the form of carbon biomass (Fig. 7a), with a similar importance throughout the time-series. Interannual differences in euphausiid

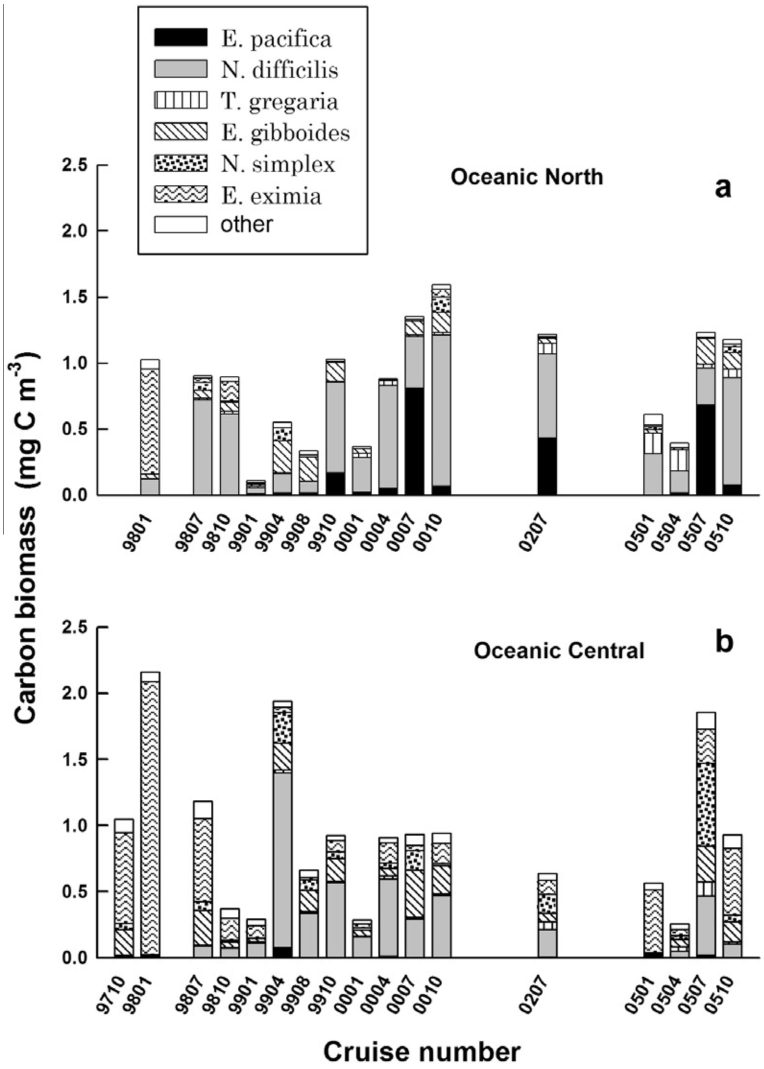

Fig. 6. Euphausiid species composition in two oceanic regions off Baja California: stacked bars are geometric means of carbon biomass. Nighttime data of all life phases from each species were log-transformed prior to the calculation of log-means and then reported as back-transformed values. The species selected are a combination of the four species with the highest carbon biomass in both regions.

community were due to the incursion of *N. difficilis* and *E. pacifica* during La Niña. *Thysanoessa spinifera* was present in small densities in Vizcaino Bay during April and July of 2005 (Fig. 7a). However the distribution of this species during those months indicated a more substantial biomass in locations adjacent to Vizcaino Bay (Fig. 8). The carbon biomass of *N. simplex* from the Gulf of Ulloa was impressive in July 2000 and even more so in July 2005, reaching 84 mg C m^{-3} (Fig. 7b).

4. Discussion

We found evidence of strong interannual changes in krill communities off Baja California during 1997–2005 based on the collections of the IMECOCAL program. The differences in euphausiid communities inhabiting the north and central oceanic regions justify the separation of two eco-regions (Lavaniegos, 2009), taking to Punta Baja (30°N) as the zoogeographic boundary for the temperate species *E. pacifica* and *T. spinifera*. Low abundances of these species in the northern region usually denote seasonal changes, but their total absence is indicative of anomalous warming events. Brinton and Townsend (2003) analyzed spring time-series in northern Baja California waters, identifying negative anomalies in 1977–1985 in the abundance of *E. pacifica* and during 1980–1985 in the case of *T. spinifera* that were associated with a warm decadal climate regime. Therefore, the invasion of the central region by *E. pacifica* and *T. spinifera* between 1999 and 2005 (particularly in and around Vizcaino Bay) is indicative of anomalous cooling events (Figs. 6–8).

The increase in the densities of ‘transition zone’ species in 1999–2000 in association with La Niña and during the subarctic water intrusion in 2002 was more evident in North Baja California, particularly during the summer. In central Baja California, the distribution of *E. pacifica* expanded although abundances were low. Those were episodes of re-colonization of Baja California waters. Invasion of the central region by *T. spinifera* better demonstrates re-colonization. The presence of this species in the central region was delayed until 2000, after La Niña, and was observed again in the summer of 2002 and in the spring–summer of 2005. These observations acquire relevance when contrasted with the virtual absence of *T. spinifera* off central Baja California between 1958 and 1978 (Brinton and Townsend, 2003).

High abundances of *E. pacifica* during spring and summer of 2005, particularly of larvae, suggest active swarming for

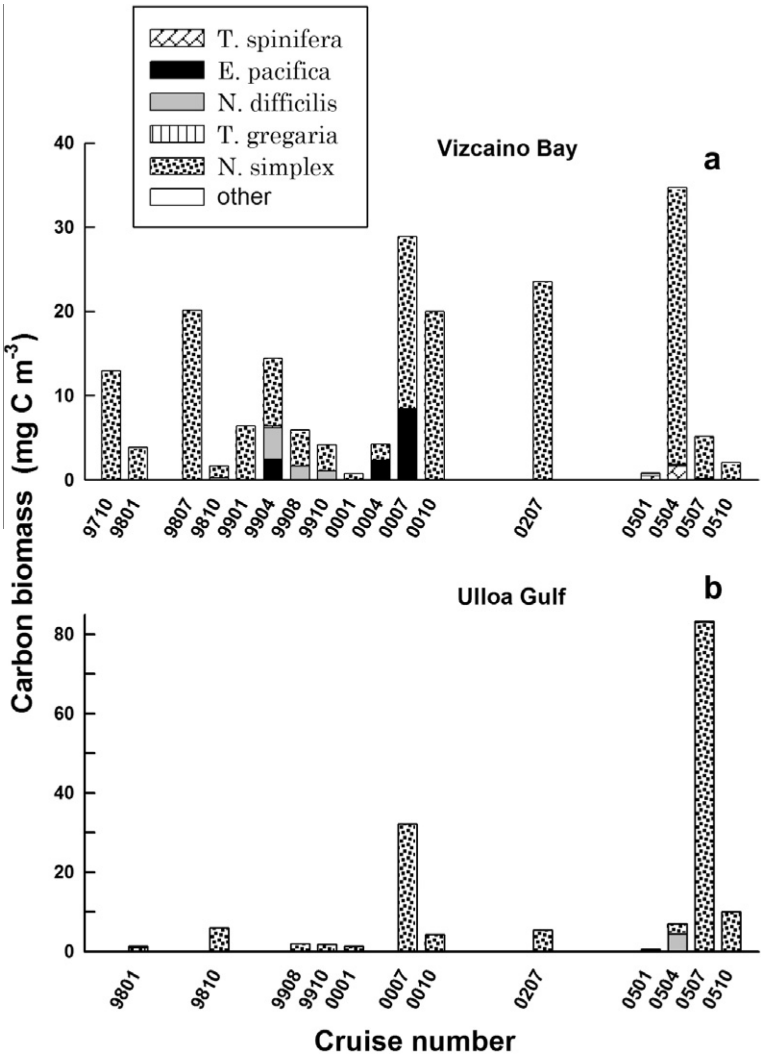

Fig. 7. Euphausiid species composition in two coastal shelves off Baja California: stacked bars are geometric means of carbon biomass. Nighttime data of all life phases from each species were log-transformed prior to the calculation of log-means and then reported as back-transformed values. The species selected were the five more abundant in Vizcaino Bay.

reproduction in northern Baja California. This is in strong contrast with the collapse observed in the northern sectors of the CCS (Sydeman et al., 2006), as a result of the warming conditions prevalent there (Schwing et al., 2006; Mackas et al., 2006; Thomas and Brickley, 2006). Warm SST affected euphausiid populations off both central California (37°N) and southern British Columbia (50°N) with consequences to higher trophic levels (Sydeman et al., 2006). In contrast, abundance of *E. pacifica* was typical off southern California, and was high for *T. spinifera* (Sydeman et al., 2006). The present study revealed abundances similarly high for these species off Baja California where slightly cool SSTs prevailed (Peterson et al., 2006). Regions south of Point Conception (34.5°N) served as refuges for temperate euphausiid species during 2005. The shifting distribution of the target euphausiids affected the reproductive success of Cassin's auklet (*Ptychoramphus aleuticus*) (Sydeman et al., 2006; Wolf et al., 2009). Despite the high densities of *E. pacifica*, *T. spinifera N. difficilis*, *T. gregaria*, and *E. gibboides* in adjacent waters to San Benito Islands, Baja California, this did not result apparently in a benefit to the auklets, for which the breeding success was as low as in the northern CCS locations (Wolf et al., 2009).

The coastal *N. simplex* presented different types of responses to interannual events. It did not show significant changes through the ENSO cycle (Ambriz-Arreola, 2007), but during the summers of 2002 and 2005 a considerable increase was recorded (at Vizcaino Bay in July 2002 and the Ulloa Gulf in July 2005). This suggests that the main breeding center of *N. simplex* may have moved southward, from Vizcaino Bay to the Gulf of Ulloa. The geographic movement of *N. simplex* may be explained by the enhancement of coastal upwelling since 2005 (Rykaczewski and Checkley, 2008; Lavaniegos, 2009). Though *N. simplex* lives in the zone of coastal upwelling activity, it has a narrow range of temperature in the subtropics and could be affected by extreme cooling. Long-term SST summer mean (and standard deviation) from Vizcaino Bay in the period 1998–2005 was 17.5 ± 1.2 °C. In July 2005 SST from Vizcaino Bay was 1° below the long term mean. The strong increase of temperate and subtropical species in 2005 as well as total zooplankton biomass in 2003–2007 (Baumgartner et al., 2008; Lavaniegos, 2009) could be a response to higher primary productivity driven by intensified coastal upwelling, which has provided a refuge for temperate species advected to Baja California with the subarctic water.

Perhaps the most disconcerting fact during the summer of 2005 was the simultaneous occurrence of high densities of two oceanic euphausiids: the tropical species *E. eximia* and the North Pacific gyre species *E. recurva*. *Euphausia eximia* is usually found in the

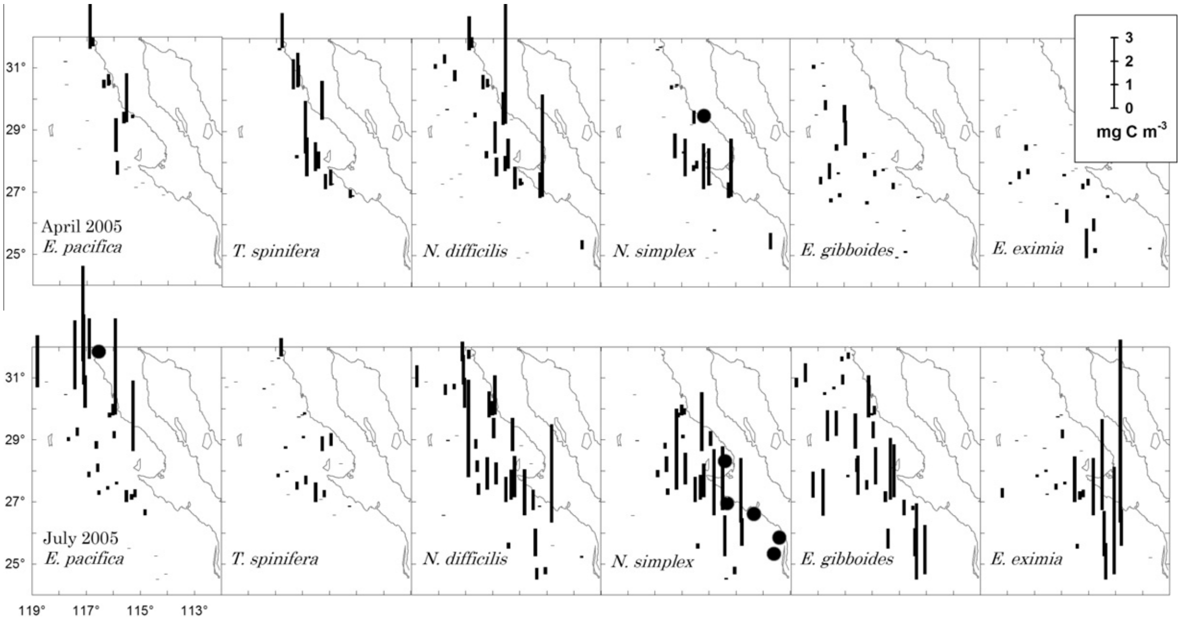

Fig. 8. Distribution of euphausiid species during April (upper panels) and July 2005 (lower panels). The first five species (*Euphausia pacifica*, *Thysanoessa spinifera*, *Nematoscelis difficilis*, *Nyctiphanes simplex*, *Euphausia gibboides*) are typical of the California Current System and *Euphausia eximia* is associated with warm water of the eastern tropical Pacific. Black circles indicate dense aggregations of krill with biomass out of scale (ranging 14–168 mg C m^{-3}).

central oceanic region of Baja California, particularly at offshore stations in autumn and winter. This species experienced remarkable changes in dominance during the ENSO cycle in the central region, being very abundant during El Niño, decreasing further with the transition to cool conditions. *Euphausia eximia* is the strongest indicator of warm water coming from the southwest during El Niño (Durazo and Baumgartner, 2002). The time-series of *E. eximia* abundance showed substantial increase during El Niño 1958–1959 (similar to El Niño 1997–1998) as well as positive anomalies after the warm regime shift in 1976–1977 (Brinton and Townsend, 2003).

Excluding the warm phase of El Niño 1997–1998, euphausiid carbon biomass was apparently higher in the oceanic north region (Fig. 6), due to favorable conditions during cool interannual events. The dominance of *N. difficilis* as the main oceanic species in most of the cruises also deserves mention. This species as well as *T. gregaria* are not vertical migrators, and the majority of the adults live below the thermocline (Brinton, 1967b). Avoiding the upper sea layer they have probably survived better than migrating species which enter the sea surface layers on a daily basis (Brinton, 1967b). *Nematoscelis difficilis* and *T. gregaria* could increase in the future with global warming, to the extent that they can avoid the surface layer. In contrast, the prevalence of cool water species (*T. spinifera* and *E. pacifica*) in the study area depends on transport and continuity in the intensification of upwelling activity (Lavaniegos, 2009). Thus, evidence presented here is indicative of the differences in regional processes along the CCS (Mackas et al., 2006; Baumgartner et al., 2008).

Phenological changes are also important. Bograd et al. (2009) analyzed upwelling occurrence and intensity through the CCS during 1967–2007 concluding that northern sectors presented a trend towards a later and shorter upwelling season. They excluded the Baja Californian sector in their analysis because of the prevalence of a different upwelling pattern, particularly the restricted presence or complete absence of downwelling in winter. Phenological changes off Baja California could be taking place also, but the upwelling season probably is occurring early in the year, as suggested by high biomass recorded in the winters of 2005–2007 (Lavaniegos, 2009) and significantly higher than in the period 1951–1966 (Lavaniegos et al., 2010).

5. Conclusions

- The strength of the 1997–1998 El Niño showed the expected influence on tropical species, with *E. eximia* being the best indicator off Baja California.
- *Nyctiphanes simplex* dominated the coastal shelf waters of Vizcaino Bay and the Gulf of Ulloa, with no particular changes in abundance being associated to the ENSO cycle, compared with their influence in northern CCS in the warm phase.
- Cool events (the 1998–2000 La Niña and the subarctic water intrusion in 2002) impacted the California Current. In both cases occurred an increase of ‘transition zone’ species (*E. gibboides*, *N. difficilis*, and *T. gregaria*) as well as the subarctic *E. pacifica*.
- Apart from the 1997 to 1998 El Niño, the only evidence of warming may be attributed to the 2002–2003 El Niño in the central Baja California region, although it did not result in a large increase in the abundance of tropical euphausiids but instead was associated with a decrease in the abundance of all krill species.
- Coastal shelves recorded small incursions of *N. difficilis* and *E. pacifica* from oceanic waters during La Niña, and of the northern *T. spinifera* during April and July of 2005 probably due to the local increase of coastal upwelling.
- The occurrence of high densities of species from different biogeographic origin (temperate, subtropical and tropical) in 2005 contrasted with northern sectors of the California Current that were impoverished of krill.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pocean.2011.11.008.

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