



# Changes in composition of summer hyperiid amphipods from a subtropical region of the California current during 2002–2008



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## ABSTRACT

Interannual changes in the assemblages of hyperiid amphipods during the period 2002 to 2008 are analyzed for the first time in the coastal Pacific area comprised between Ensenada (32°N) and Punta Baja (30°N), Baja California, Mexico. The study period witnessed diverse climatic events, such as a subarctic water intrusion in 2002, three El Niño events (in 2002–2003, 2004–2005, and 2006–2007) and one La Niña event in 2007–2008. Multivariate analysis of summer hyperiid amphipods based on the Bray–Curtis similarity index indicated that July 2005 contrasted with the rest of the summer seasons, showing a low abundance of amphipods, characterized particularly by the scarcity of *Lestrigonus schizogeneios*. The second most different summer was July 2002, characterized by the increased abundance of *Primno brevidens* and the presence of the subarctic species *Themisto pacifica*. Despite the marked decrease of *L. schizogeneios* in 2005, this species showed a pronounced recovery in 2006. Therefore, physical conditions under the influence of El Niño did not appear to be a direct factor in changing the abundances of *L. schizogeneios*, and the collapse of its populations during July 2005 could be the result of strong predation on small *Lestrigonus* juveniles by euphausiids, which were extremely abundant in spring and summer 2005. With the exception of 2005, the dominant species were relatively constant. Similarity analysis revealed a core contribution of the characteristic subtropical species in the California Current System (*L. schizogeneios*, *P. brevidens*, *Vibilia armata*, and *Eupronoe minuta*), indicating a resilience of these key species to climatic events.

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## 1. Introduction

There is increasing scientific interest in climatic variability and its repercussions for marine biota. Multi-year time-series of the mesozooplankton can provide useful information about climate-ecosystem interactions (Mackas and Beaugrand, 2010). In the California Current system (CCS) the copepods are the most studied component of the zooplankton, with time series available from British Columbia to California waters (Mackas et al., 2006). There are also long-time series of euphausiid abundances off California and Baja California, although collection in the latter region was limited to the period 1950 to 1985 (Brinton and Townsend, 2003). Other zooplankters analyzed for long-term variability in their abundance and species composition off southern California are hyperiid amphipods (Lavaniegos and Ohman, 1999), and salps (Lavaniegos and Ohman, 2003). Extended time-series both in time and space has allowed regional comparisons, revealing a considerable synchrony in decadal changes of copepod species assemblages (Mackas et al., 2006).

Additional studies on interannual and long-term variability of zooplankton populations are required for other taxa with different traits

to determine if they exhibit similar responses to climatic variability. Hyperiid amphipods are good candidates for the investigation of responses to climatic effects given that they are a diverse taxonomic group that reaches high abundance in the CCS, particularly in the subtropical region, south of Point Conception (34.5°N), as documented in previous studies (Brusca, 1967a, 1967b; Lavaniegos and Hereu, 2009; Lavaniegos, 2014). The focus of these studies, however, was mainly on seasonal variability. Lavaniegos and Hereu (2009) showed that hyperiids off Baja California, Mexico, exhibited strong seasonality, with low abundances in winter and species composition dominated by *Anchylomera blossevillei* and *Platyscelus ovoides*. During the rest of the year the California Current showed a well-defined flow with an assemblage characterized by the dominance of *Vibilia armata*, *Lestrigonus schizogeneios*, *Eupronoe minuta*, and *Primno brevidens*. Further, Lavaniegos (2014), looking for evidence of an event of subarctic water intrusion in the CCS during July 2002, documented the presence of *Themisto pacifica*, a species with cool water affinity.

Fish and other vertebrates are known to prey on amphipods (Miller et al., 2010; Young et al., 2015). In the northern regions of the CCS there are reports of fish that occasionally consume amphipods (Pinkas et al., 1971; Brodeur et al., 1987). However, abundant amphipods have been also reported in the stomachs of some fish species such as Chinook salmon *Oncorhynchus tshawytscha* (Schabetsberger et al., 2003) and

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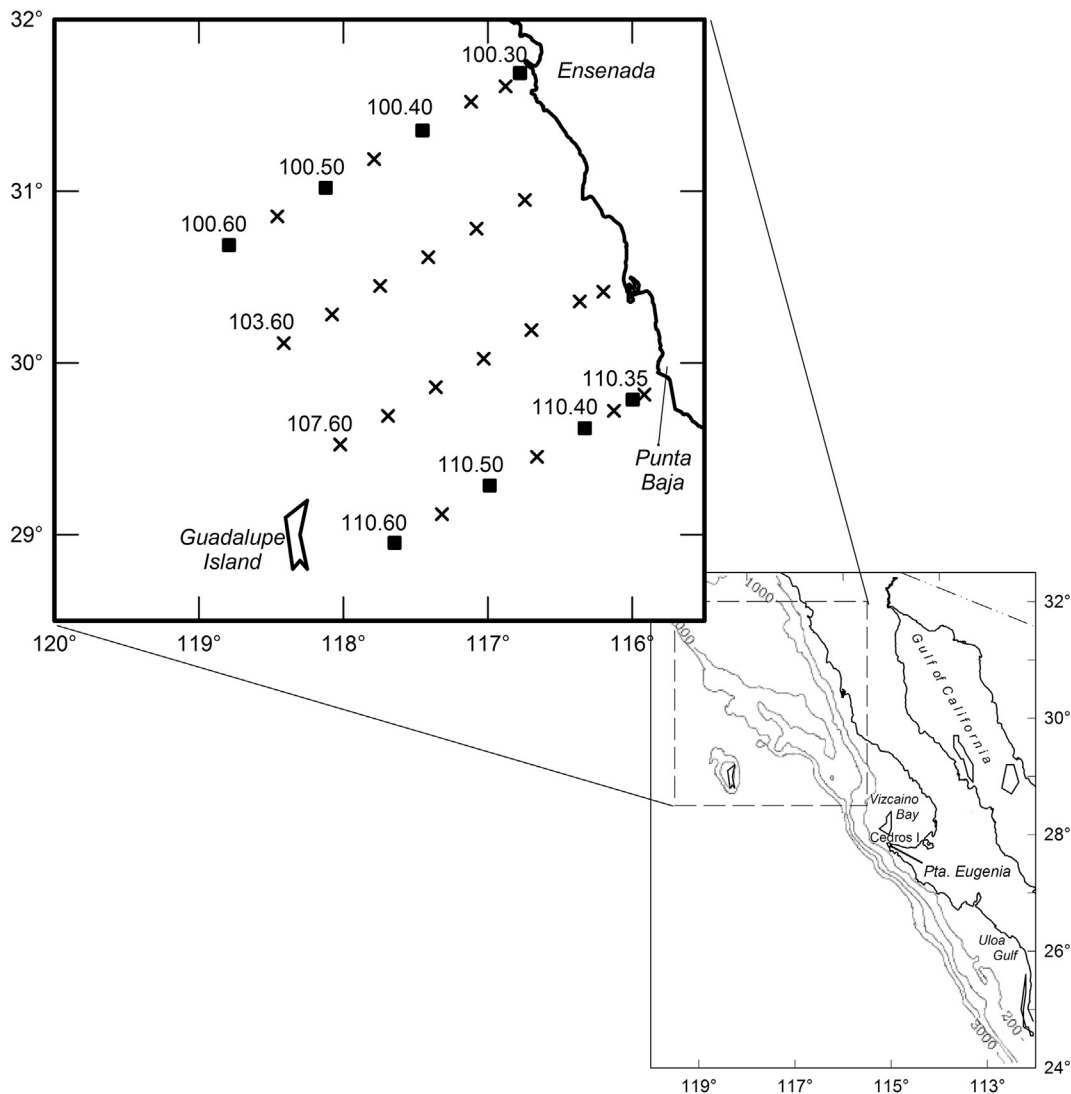
widow rockfish *Sebastes entomelas* (Phillips, 1964; Bosley, 2014). Bertram et al. (2009) also reported hyperiids in the diet of the Cassin's auklet (*Ptychoramphus aleuticus*). Records of gut contents from fish of the Baja California region are scarce (Pinkas et al., 1971), although hyperiid prey have been reported in flying fish from the Mexican tropical Pacific (van Noord et al., 2013). Therefore, hyperiid amphipods constitute an important trophic link and are also highly sensitive to temperature changes.

The main objective of the present study is to investigate the response of hyperiid species composition to interannual climate variability, based on a set of samples collected during the summer season over the period 2002 to 2008. Diverse interannual changes in climate were observed during this period. First, there was a subarctic water intrusion in 2002–2003 (Venrick et al., 2003; Durazo et al., 2005), attributed to the southward shift of the North Pacific Current which bifurcates to form the California Current and Alaska Current (Freeland and Cummins, 2005). Secondly, this period included the occurrence of three weak El Niño events (2002–2003, 2004–2005, and 2006–2007); the first two were considered a different type of El Niño event with maximum warm anomalies limited to the central equatorial Pacific (Ashok et al., 2007; Lee and McPhaden, 2010). Finally, during 2007–2008 conditions changed in the Pacific basin to give rise to a La Niña event. Biological

evidences of the subarctic water intrusion were analyzed by Lavaniegos (2014), showing the presence of the subarctic amphipod *Themisto pacifica* and increased abundances of *Primno brevidens*. However, the response of hyperiids to other interannual events during 2002–2008 has not been previously addressed, and is the objective of the present study. Only data from the summer were selected to highlight interannual differences. It is expected that a decrease or increase of the dominant species (*Vibilia armata*, *Lestrigonus schizogeneios*, *Eupronoe minuta*, and *Primno brevidens*) and changes in species diversity will occur as a function of warm and cold phases of the El Niño Southern Oscillation (ENSO).

## 2. Methods

The area sampled is located off the coast of northern Baja California, Mexico, between Ensenada and Punta Baja (Fig. 1). The region is characterized by temperate conditions influenced by the recirculation of the southern California eddy (Simpson et al., 1986; Haury et al., 1993). The sampling grid considered in the present study was delimited by the four northern lines of the oceanographic cruises undertaken as part of the “Investigaciones Mexicanas de la Corriente de California” (IMECOCAL) monitoring program. Transect-lines are perpendicular to



**Fig. 1.** Study area off northern Baja California, Mexico with bathymetry (m) showing sampling stations in the upper inset. Though the complete grid is shown, only stations occupied at nighttime were analyzed which are shown in Fig. 10 and Appendix 1. Squares indicate stations selected for vertical profiles. The transect line is indicated by 3-digit integer and the station position in transect by decimals.

**Table 1**

IMECOCAL cruise with dates and number of zooplankton night time samples used in taxonomic identification. The dates correspond only to the area considered in the present study (see Fig. 1).

Cruise	Date	Number of samples
0207	12–18 Jul. 2002	12
0307	7–15 Jul. 2003	12
0407	9–14 Jul. 2004	11
0507	14–21 Jul. 2005	14
0607	7–12 Jul. 2006	10
0708	25–31 Aug. 2007	15
0807	27 Jul.–2 Aug. 2008	13

the coast, separated by 40 n.m. and contained stations 20 n.m. apart (Fig. 1).

Conductivity, temperature and pressure measurements were obtained from CTD casts (Seabird model) performed at each station. Temperature and salinity from a 10 m depth were used as a proxy for surface values. Anomalies were estimated by removing monthly means from the period 1951–1966 (historical data from the California Cooperative Oceanic Fisheries Investigations program; [http://www.calcofi.org/new\\_data/index.php/publications/calcofi-data-reports/archived-data-reports](http://www.calcofi.org/new_data/index.php/publications/calcofi-data-reports/archived-data-reports)). This was preferred because the summer mean for 2002–2008 (18.37 °C) did not reflect a mean for July, as some cruises were conducted later in the season, particularly in 2007 (Table 1). The July mean for the period 1951–1966 was 17.75 °C and that for August was 18.80 °C. Therefore, to estimate anomalies the long-term mean for July was used for the summers 2002–2008, except for 2007 when the August mean was used. Some stations from transect-lines 100 and 110 (see Fig. 1) were selected to obtain vertical profiles of thermohaline conditions, and to compare with a typical profile based on the long-term means from July from 1950 to 1978 estimated by Lynn et al. (1982).

Zooplankton samples were collected with a 71 cm-diameter bongo net of 505-µm mesh width, towed obliquely between the surface and 210 m depth. A flowmeter attached to the mouth of the net measured the volume of water strained by the net. Zooplankton samples were preserved with 4% formalin. The samples selected for the present study were those collected during nighttime from summer cruises conducted over the period 2002–2008. These were conducted mainly during July, although in 2008 the cruise started in late July and the 2007 cruise was conducted in late August (Table 1). The number of samples per cruise was between 10 and 15; thus a total of 87 samples were analyzed (Table 1). Samples from the shallow stations (bottom <200 m depth) were discarded due to low presence of amphipods in coastal shelf waters. Station coordinates, bottom depth and sampling hour, are shown in Appendix 1.

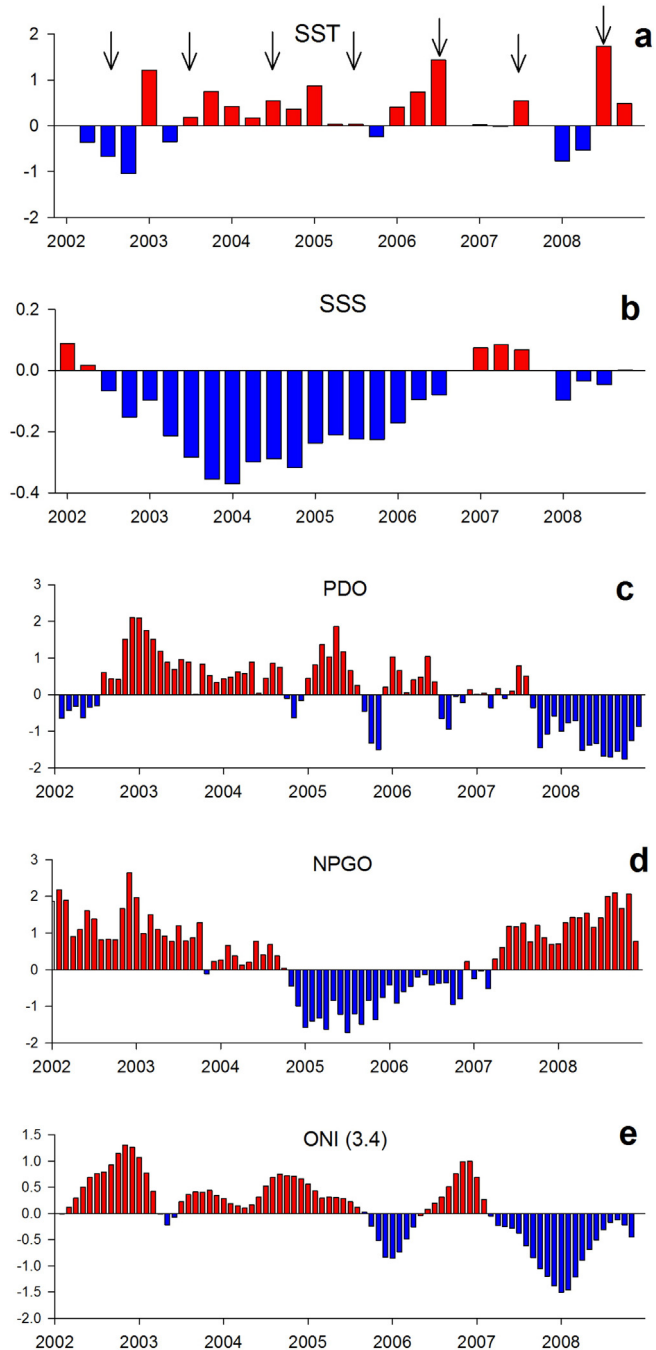
Hyperiid amphipods from the whole sample were counted and identified to species, using as reference the key of Hyperiid Amphipods of the World Oceans (Vinogradov et al., 1996), and modifications for the superfamily Phronimoidea proposed by Zeidler (2004). Due to some limited erroneous identification of *Lestrigrionus schizogeneios* as *L. shomakeri*, the data for these two species were pooled. However, *L. schizogeneios* was by far the more abundant of the two species, comprising ~95% of the organisms in this two species. Juveniles that were identified only to genera level due to their small size were not used in statistical analysis. The total length of all amphipods was measured to the nearest mm using a square Petri dish with a grid.

In the present study, two abundance parameters were considered: 1) the abundance in the samples, used for rarefaction analysis, and size-frequency and carbon biomass estimates; 2) standardized abundance (individuals per 1000 m<sup>3</sup>), which was used for the rest of analysis, after log-transformation. Therefore, in the present study either the log-mean (transformed data average) or the geometric mean (retransformed mean) were used. Abundance data were converted to

dry weight (DW) using the weight-length function of *Primno abyssalis* from the Oyashio Current (Yamada et al., 2002):

$$DW (mg) = 0.006 (L)^{2.71}$$

where L is the body length expressed in mm. The carbon content was taken as 54.3% of the DW based on Yamada and Ikeda (2003).



**Fig. 2.** Environmental conditions during 2002–2008 in the study area (a–b) and large scale Pacific indicators (c–e). (a) Sea surface temperature (SST) anomalies, (b) sea surface salinity (SSS) anomalies, (c), Pacific Decadal Oscillation (PDO), (d) North Pacific Gyre Oscillation (NPGO), and (e) Oceanic El Niño Index (ONI) in the Region 3.4 (5°N–5°S, 120°–170°W). Arrows indicate anomalies of the summer cruises analyzed in the present study.

## 2.1. Statistical analysis

Interannual differences in abundance were evaluated with the Kruskal-Wallis test for total amphipods and selected species, followed by *a posteriori* comparisons of average ranks to identify specific differences. Diversity analysis was conducted using rarefaction curves based on non-standardized abundance and pooling data of all samples from each cruise.

Differences in species composition were determined with multivariate similarity analyses, based on the Bray-Curtis index and using the software PRIMER 6 (Clarke and Gorley, 2006). Abundance data of 88 species and 86 stations were log-transformed prior to calculating a similarity matrix, used to build a dendrogram and a non-metric Multi-Dimensional Scaling (MDS) ordination. One station was excluded (number 100.30 from July 2005) due to overall poor abundance. Sixteen very rare species (occurring in one sample) were also excluded.

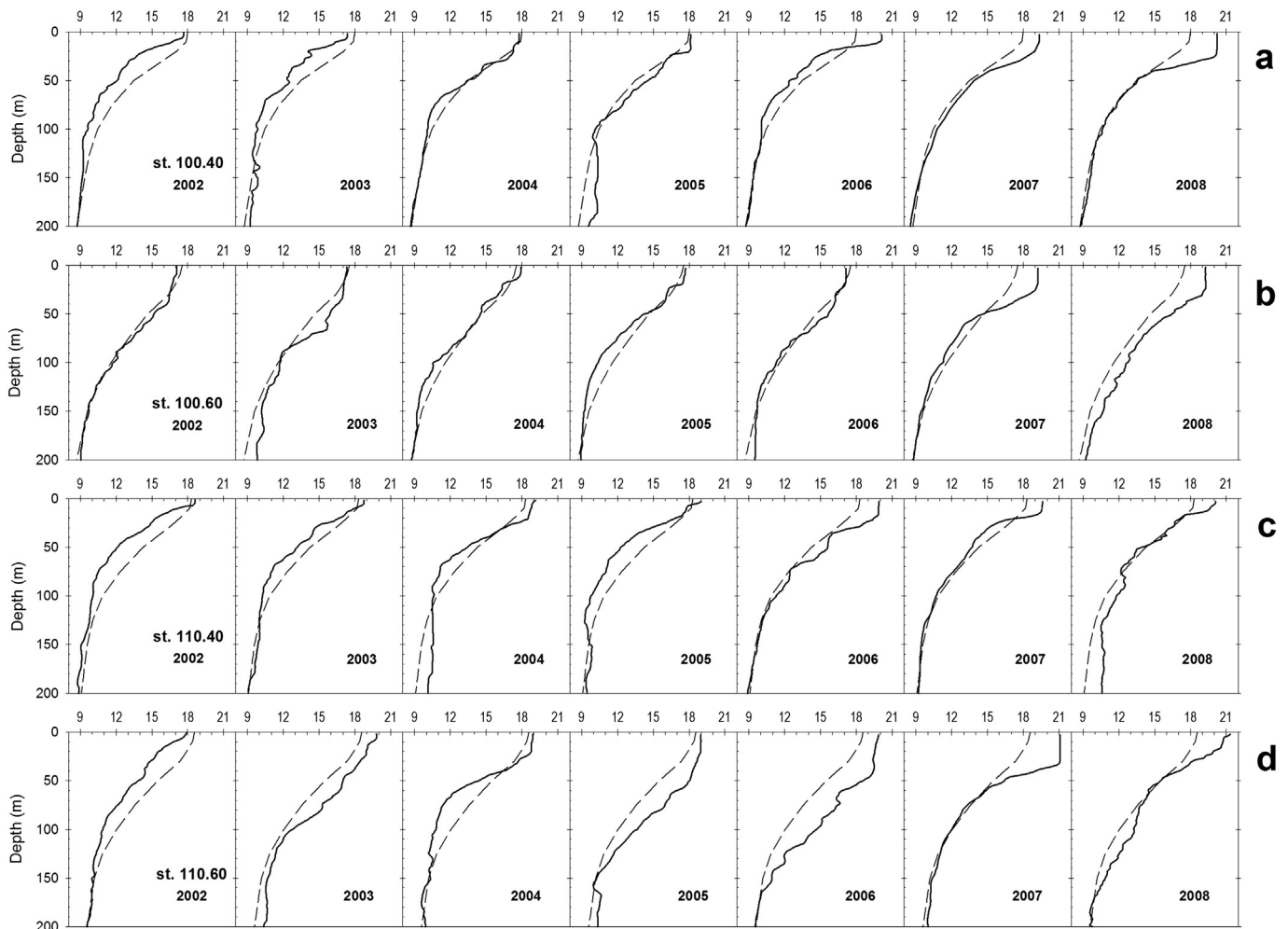
## 3. Results

### 3.1. Thermohaline conditions

Sea surface temperature (SST) in the study area was relatively high during most of the period 2002–2008, with positive anomalies except in the year 2002 and the first half of 2008 (Fig. 2a). The positive SST anomalies between 2003 and 2006 were associated with weak El Niño

events (Fig. 2e). Considering exclusively the summer season, the highest positive SST anomalies (1–2 °C) occurred in 2006 and 2008, while moderate anomalies (0.5 °C) occurred in 2004 and 2007 (Fig. 2a). The positive SST anomalies of July 2004 and July 2006 may be associated to El Niño Modoki events (2004–2005 and 2006–2007, respectively). However, the positive SST anomalies in August 2007 and July 2008 are not consistent with the occurrence of the La Niña 2007–2008 event. The only summer with a negative SST anomaly was July 2002, showing an inverse pattern to that of the Oceanic Niño Index (ONI) (Fig. 2e). This cooling was associated with a subarctic water intrusion in the CCS, from July 2002 to July 2003. The intrusion of subarctic water was more evident in sea surface salinity (SSS) anomalies, showing that low salinity in the upper layer persisted until 2006 (Fig. 2b). This extra-tropical forcing during 2002 did not show a clear relation with the Pacific Decadal Oscillation (PDO) (Fig. 2c). Excluding 2007–2008, however, there was agreement between the SSS (Fig. 2b) and the North Pacific Gyre Oscillation (NPGO). The intensification of negative SSS anomalies was gradual during 2002 and 2003, reaching the most negative value in the winter of 2003–2004, coinciding with positive NPGO values (Fig. 2d). Later, during 2004–2006, SSS anomalies gradually decreased coinciding with a decrease of the NPGO in 2004 until a shift to negative values occurred during 2005–2006, indicating the weakening of the north Pacific gyre during 2004–2006.

Temperature profiles at selected stations showed spatial variability depending on whether we examine the nucleus of the CC (sta. 100.40,



**Fig. 3.** Vertical temperature profiles during summer of 2002–2008 at oceanographic stations 100.40 (a), 100.60 (b), 110.40 (c), and 110.60 (d). Dashed line indicates a typical profile based in the 1950–1978 long-term mean (Lynn et al., 1982).

and 110.40), or the offshore stations (100.60 and 110.60). Temperatures were lower than the long-term mean of 1950–1978 (Lynn et al., 1982) in the upper 125 m for stations 100.40 (Fig. 3a) and 110.40 (Fig. 3c) during 2002–2003. In subsequent summers, the temperature in station 100.40 approximated the normal profile, except for the upper 20–40 m during 2006–2008 temperatures were 1.5–2 °C higher (Fig. 3a). At station 110.40 (Fig. 3c), the temperature in the upper layer showed cooling from 2002 to 2005. Below a depth of 100 m, some years showed higher temperatures, as in July 2008. Conditions offshore exhibited greater north–south latitudinal differences: at station 100.60 temperature profiles were more or less typical during 2002–2006 (Fig. 3b), while at station 110.60 the upper 125 m showed cooling during July 2002, and subsurface cooling in 2004, but warming during the rest of study period (Fig. 3d). At this station, subsurface warming was important in July 2005 and July 2006, while in 2007–2008 it was more restricted to the upper layer of the water column (Fig. 3d).

Salinity profiles during the first part of the study period (2002–2005) revealed strong stratification due to low values in the upper layer compared to the long-term mean derived from 1950 to 1978 (Fig. 4). The lowest salinity corresponded to the period 2003–2005 and affected mainly the upper 100 m, but at station 110.60 (Fig. 4d) low salinities were observed below 100 m throughout most of this period. Along the transect 100 (Fig. 4a, b), the anomalous low values started to disappear in 2006 and disappeared completely in 2007, suggesting mixing of water masses. In general, below 100 m the salinity showed

values slightly higher than those of a typical profile, intensifying water column stratification. In the upper 50 m the only values higher than the long-term mean occurred in 2007 (Fig. 4a, d). This may be an artifact because sampling was conducted in late August when the seasonal influence of subtropical water occur (Lynn and Simpson, 1987), while the long-term salinities for the period 1950–1978 were estimated during July (Lynn et al., 1982).

### 3.2. Species composition of the hyperiid amphipod assemblage

The total abundance of hyperiid amphipods found in the samples remained relatively constant through the study period, with geometric means (GM) values between 557 and 867 individuals (ind) per 1000 m<sup>3</sup>, except for the summer of 2005 when there were only 212 ind per 1000 m<sup>3</sup> (Fig. 5). This difference was statistically significant and due to the scarcity of *Lestrignus schizogeneios* (Table 2). These calculations are conservative because they did not include the smallest *Lestrignus* juveniles (1 mm), which had summer GM values of 34–80 ind per 1000 m<sup>3</sup> (and were even lower in 2005 with only 4 ind per 1000 m<sup>3</sup>), and comprised 52–74% of all juvenile amphipods identified to genera. Other small juveniles that were frequently observed were *Vibilia* (1–2 mm), *Phronima* (1–5 mm), *Hyperietta* (1 mm), *Scina* (1–2 mm), *Brachyscelus* (1–2.5 mm), and *Paraphronima* (2–3 mm). Some small juveniles observed inside nectophores of siphonophores indicated

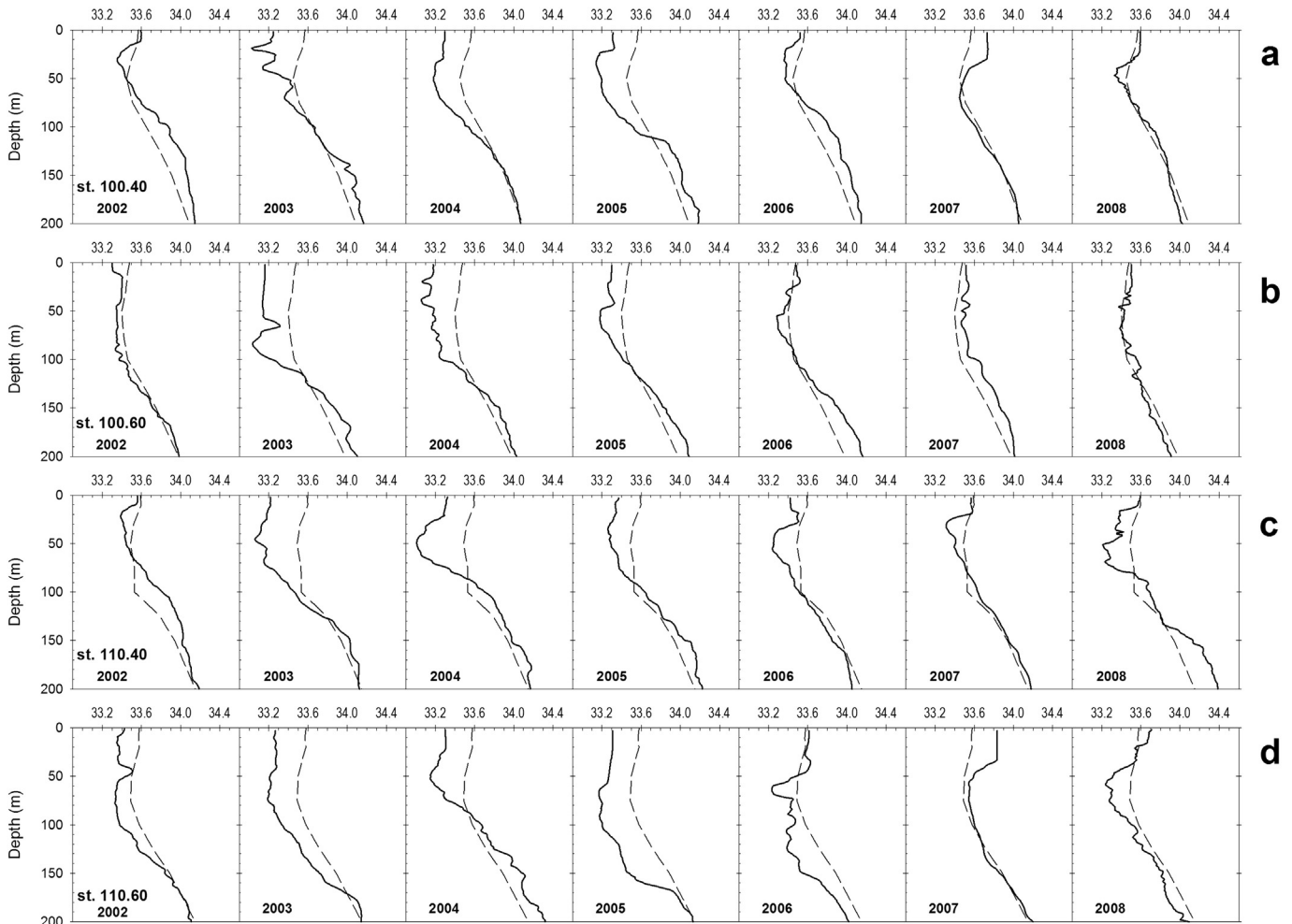
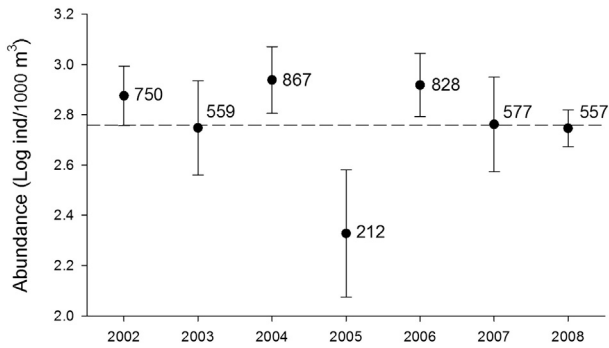


Fig. 4. Vertical salinity profiles during summer of 2002–2008 at oceanographic stations 100.40 (a), 100.60 (b), 110.40 (c), and 110.60 (d). Dashed line indicates a typical profile based in the 1950–1978 long-term mean (Lynn et al., 1982).



**Fig. 5.** Mean abundance and 95% confidence interval of total hyperiid amphipods during summer off the coast of northern Baja California, Mexico, with log-transformed data. The dashed line is the long-term mean and numbers indicate geometric means.

active reproduction but no exhaustive analysis of these records was undertaken.

There were 104 species identified during the entire study period, but 50% were infrequent, occurring in 1–10% of the samples (Appendix 1). Rarefaction curves, pooling the amphipods from the whole study area, showed the lowest diversity in July 2002, with only 32 species in 1000 individuals (Fig. 6). In contrast, in summer 2008 there were 53 species in 1000 individuals. Diversity was also high during 2005 with 51 species in 1000 individuals, despite the low abundance of amphipods during that summer (Fig. 5). The rest of the years yielded intermediate values, with 39–48 species in 1000 individuals.

Despite the diversity trend observed, the dominance of a few species was a salient feature during the study period, with only twelve species presenting geometric means of 10–300 ind per 1000 m<sup>3</sup> during one or more summers (Fig. 7). At the beginning of the study period (July 2002) the dominant species was *Primno brevidens* with 37% of the total abundance based on the GM. In subsequent years, this species never reached >22% and the minimum attained was 6% during July 2006. The absolute abundance of this species showed significant inter-annual differences (Table 2, Fig. 8g). July 2005 witnessed the lowest abundance of *P. brevidens* (GM = 11 ind per 1000 m<sup>3</sup>), a value significantly lower than that obtained for the rest of the years, when it ranged from 36 to 221 ind per 1000 m<sup>3</sup>. The second most abundant species

during July 2002 was *L. schizogeneios* with a similar relative abundance in 2003, 2007, and 2008 (22–26%). Extreme changes occurred during the middle of the study period, with the highest relative abundance occurring in 2004 (47%), decreasing to 2% in 2005, and increasing again to 35% in 2006 (Fig. 7). However, the statistical comparison was only significant between 2005 and the rest of the years, with a GM of only 2 ind per 1000 m<sup>3</sup> in July 2005 and 75–308 ind per 1000 m<sup>3</sup> during the remaining summers (Fig. 8d).

The dominance of *P. brevidens* and *L. schizogeneios* during July 2002 was reflected by their combined contribution of 62% of the total hyperiids (Fig. 7). These two species were also co-dominant in August 2007 with a value slightly lower than in July 2002 (56%). However, during other summers the pattern of species dominance showed significant differences: in July 2003 co-dominance of three species occurred with similar relative abundances for *Paraphronima gracilis*, *P. brevidens* and *L. schizogeneios*. The high abundance of *P. gracilis* (GM = 77 ind per 1000 m<sup>3</sup>) observed in 2003 was significantly higher than four other summers (2004, 2005, 2007, and 2008), when MG values were between 6 and 22 ind per 1000 m<sup>3</sup> (Table 2; Fig. 8e).

Furthermore, during the period 2004–2006 the hyperiid community showed high dominance of one species, with *L. schizogeneios* dominating in July 2004 and July 2006 while *Vibilia armata* dominated in July 2005. *Eupronoe minuta* also showed an increase in its relative abundance in 2004–2006, thus rivaling that of *P. brevidens* in July 2004 or even surpassing it in 2005–2006. Despite the high proportion of *V. armata* in July 2005, the absolute abundance did not show significant differences with other years (Table 2; Fig. 8k). The only significant difference for this species was detected between July 2003 (GM = 12 ind per 1000 m<sup>3</sup>) and the summers of 2002 and 2006 (GM of 75 and 111 ind per 1000 m<sup>3</sup>, respectively). The GM of *E. minuta* during the summer of 2005 (28 ind per 1000 m<sup>3</sup>), however, was significantly lower than in 2004 and 2006 (89 and 97 ind per 1000 m<sup>3</sup>, respectively), despite a similar relative abundance of this species during the three years (Fig. 7). Low abundances of *E. minuta* were also found during other summers (2002, 2003, and 2007 (Table 2; Fig. 8a).

In July 2008 co-dominance of four species was observed (Fig. 7). Although the relative abundance of *L. schizogeneios* was higher (26%), three other species (*P. brevidens*, *V. armata*, and *E. minuta*) were present in similar proportions and jointly contributed 42% of the total abundance.

**Table 2**

Interannual comparison of the abundance of dominant species of hyperiid amphipods using the Kruskal-Wallis test (H) and associated probability (p). The last column shows the results of a *posteriori* multiple comparisons of average ranks to identify specific differences.

Species	Kruskal-Wallis		Specific differences
	H	p	
<i>Eupronoe minuta</i>	27.2	<0.001	(2002, 2003) < (2004, 2006)
<i>Hyperietta stephenseni</i>	21.5	0.002	2005 < (2004, 2006)
<i>Lestrigonus bengalensis</i>	28.2	<0.001	Missing in 2002 2005 < (2004, 2006–2007) 2008 < 2004
<i>Lestrigonus schizogeneios/L. shoemakeri</i>	38.3	<0.001	2005 < (2002, 2004, 2006–2007) 2003 < 2004
<i>Paraphronima gracilis</i>	39.0	<0.001	2005 < (2002–2003) 2004 < (2003, 2007)
<i>Phronimopsis spinifera</i>	37.9	<0.001	(2003, 2005, 2007–2008) < 2002
<i>Primno brevidens</i>	30.3	<0.001	2005 < (2002–2004, 2007) 2006 < 2002
<i>Scina tullbergi</i>	38.8	<0.001	(2002–2004) < 2008 2003 < 2005
<i>Simorhynchotus antennarius</i>	31.1	<0.001	2002 < (2004, 2006–2008) 2005 < 2007
<i>Themisto pacifica</i>	24.4	<0.001	Missing in 2004–2007 (2003, 2008) < 2002
<i>Vibilia armata</i>	19.5	0.003	2003 < 2006
<i>Vibilia chuni</i>	40.0	<0.001	Missing in 2002 (2005–2006, 2008) < (2003, 2007)
Total hyperiids	28.8	<0.001	2005 < (2002, 2004, 2006–2007)

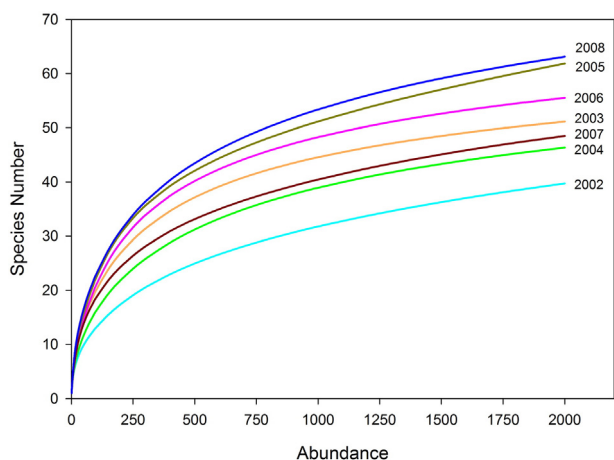


Fig. 6. Rarefaction curves based on the cumulative abundance of amphipods aggregated by year, from 2002 to 2008.

### 3.3. Similarity analysis of summer amphipod assemblages

Cluster analysis allowed a deeper understanding of the structure of amphipod assemblages, as it used a higher number of species (88). The dendrogram based on the similarity index (Fig. 9) resulted in four large clusters (A, B, C, E) of 9–43 samples, and three minor clusters (D, F, G) of 3 samples. Cluster A had the highest similarity (69%), and grouped with all stations from July 2002 suggesting a specific identity associated to the lowest SST of the study period (Fig. 10). In this assemblage, *P. brevidens* made the highest contribution to the similarity among sampling points (15%). However, this species was not the main contributor to the dissimilarity of Cluster A with the rest of clusters, but rather this was made by *Themisto pacifica* and *Phronimopsis spinifera* which although moderately abundant in July 2002, were scarce during the rest of the study period.

Another two clusters (C and E) could be identified, with most of the stations belonging to a particular year. Cluster C grouped stations

relatively near the coast, seven from 2005 and three from 2007 (Fig. 10). This group was dominated by *Vibilia armata* and *E. minuta* (summed similarity = 37%) while *L. schizogeneios* was a rare species. Cluster E was an assemblage with a higher species diversity associated to warm conditions (Fig. 10). Thus, during July 2006 the sampling points were in a tongue of warm water, while the rest of the samples in the cluster, from different years, were always at offshore stations (110.60, 110.55 or 103.55), and therefore could be associated to the incursion of central equatorial water. *Lestrigomus schizogeneios* was dominant in this group but contributed only 10% to the similarity in the cluster. Species with moderate abundance such as *Lycaeopsis zamboangae*, *Phronima curvipes*, *Lestrigonus begalensis*, and *Phrosina semilunata* made a high contribution to the similarity in this group (sum = 20%) and marked dissimilarity with other clusters.

The large cluster B included 43 samples organized in three subgroups: B1) nine stations from July 2003; B2) nine stations from July 2004; and B3) a combination of samples from 2006 to 2008 (Figs. 9–10). Stations from subgroups B1 and B2 occurred in waters with a lower SST (17–19 °C) compared to subgroup B3 (18–21 °C; Fig. 10). In general, *L. schizogeneios* and *P. brevidens* (summing 24%) made the main contribution to the similarity. Nevertheless, the abundances of these species, particularly *L. schizogeneios*, contrasted among subgroups. The species contributing to the highest dissimilarity among the subgroups were *Vibilia chuni*, *L. bengalensis*, *Phrosina semilunata*, *Vibilia australis*, and *Scina tullbergi*. Abundances of *V. chuni* were maximal in B1, those of *L. bengalensis* and *P. semilunata* in B2, and that of *Scina tullbergi* in B3, while *V. australis* showed similar abundances in B1 and B3.

The MDS (Appendix 3) confirmed the separation of large clusters defined in the dendrogram (Fig. 9). The tridimensional MDS was selected since it had a stress lower than the bi-dimensional MDS (0.14 and 0.19, respectively). However, the small clusters (D, F, and G) did not show a clear separation in the MDS. Samples included in these minor clusters shared a common feature, i.e., were located at offshore stations (Fig. 10) in 2005 (D), 2008 (F), and 2003–2005 (G). In the MDS, samples from clusters D and F appear embodied in cluster B, while those from cluster G are mixed with those from cluster E.

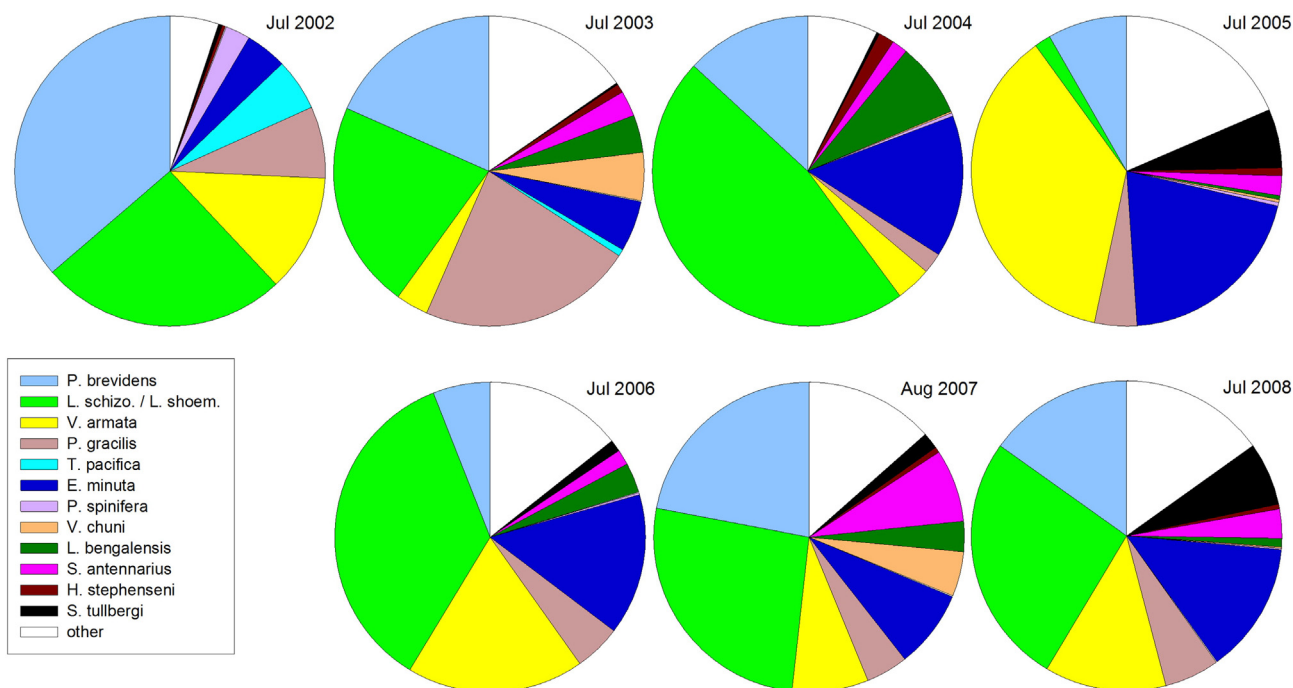
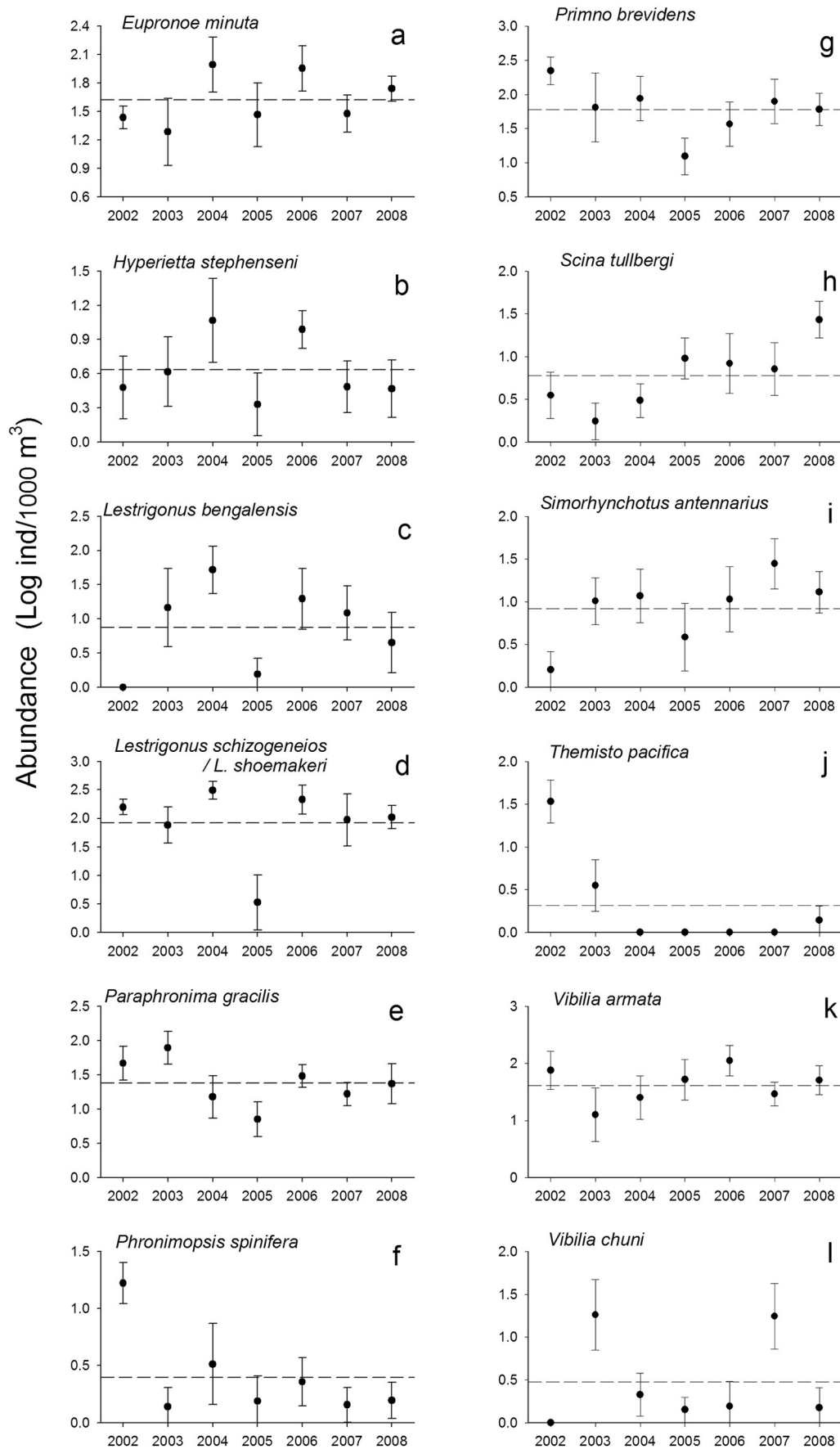


Fig. 7. Species composition of summer hyperiid amphipods identified off the northern coast of Baja California, showing those species with geometric mean > 10 individuals per 1000 m<sup>3</sup> in one or more years. The rest of the species are contained in the category "other". The species appear in the same order during all summers.



**Fig. 8.** Mean abundance and 95% confidence interval of dominant summer amphipod species off northern Baja California, with log-transformed data. The horizontal dashed line is the long-term mean.



Therefore, considering only the results of large clusters and sub-groups, two periods were evident, one during 2002–2005 when the amphipod assemblages showed some important fluctuations in the abundance or identity of dominant species. The second period in 2006–2008 showed a relatively constant species assemblage that coincided with the higher SST, except for a tongue with the highest SST in 2006 that revealed a high diversity probably associated to the 2006–2007 El Niño event. Differences in composition from nearshore to offshore stations also were detected in some years (2005, 2007, and 2008), suggesting a likely influence of upwelling fronts, evidenced by isotherms parallel to the coastline (Fig. 10). This nearshore-offshore contrast in SST was more conspicuous in 2005 and 2007, with the appearance of a nearshore community poor in amphipods (cluster C) in 2007.

### 3.4. Amphipod size and biomass

Hyperiid amphipods had a wide size range, from 1 to 60 mm body length, with most of the specimens ranging from 1 to 16 mm. Adults of some species reached body lengths of up to 30–35 mm, and these belonged to genera of Phronimidae (*Phronima*, *Phronimella*), Phrosinidae (*Phrosina semilunata*) and Oxycephalidae (*Calamorrhynchus*, *Oxycephalus*, *Rhabdosoma*, *Streetsia*). The largest size was recorded for *Rhabdosoma whitei* (9–60 mm), which has an extremely slim body. Excluding *Rhabdosoma* and considering amphipods in the range of 1–20 mm, summer frequency histograms presented three modal classes (Fig. 11).

The first mode occurred at 2–3 mm and reflected the high abundance of *L. schizogeneios* females in combination with young *P. brevidens*. The 2 mm size was dominated by other species (*L. bengalensis*) only in 2003. In 2005, due to the low abundance of *L. schizogeneios*, the 2–3 mm mode was negligible (Fig. 11). Although this is the main mode in terms of abundance, the magnitude of the mode diminished when expressed in terms of carbon biomass (Fig. 12).

The second peak in abundance was the 5–6 mm size class which made a variable contribution of species throughout the study period (Fig. 11). *Primno brevidens* was one of the amphipod species

contributing to this size class but was dominant strictly in 2002 (in combination with *Vibilia armata*). The mode shows displacement relative to the 7 mm size class when biomass instead of abundance is considered, highlighting the importance of *V. armata* (Fig. 12). In other years, the abundance of *L. schizogeneios* males made an important contribution to the 5 mm size class, and *E. minuta* to the 6 mm size class (Fig. 11). However, the biomass contribution of these species appears moderately important in some years compared with *V. armata* (Fig. 12). The composition of the 6 mm size class differed the most during 2007, when *Vibilia chuni* dominated in terms of both abundance and biomass (Figs. 11–12).

The 11 mm size class yielded the third mode and was extremely high in 2003 due to the high abundance of *Paraphronima gracilis* (Fig. 11). It was even more conspicuous when abundance was converted to carbon biomass (Fig. 12). The biomass peak of *P. gracilis* was important in 2002 and 2006–2008, although to a lesser extent than in 2003, while it was negligible in 2004–2005. As a result the summer of 2004–2005 showed the lowest total amphipod biomass during the study period. These calculations should be treated with caution since they are based on only one weight-length function (estimated for *Primno abyssalis* by Yamada et al., 2002), and the diversity of body shapes is considerable within the group of hyperiid amphipods.

### 4. Discussion

Local conditions of temperature and salinity described during 2002–2008 resulted from a combination of ENSO and extra-tropical influences. The short duration of El Niño events during the study period, make it particularly difficult to identify the peak of these events, especially if only the summer season is considered as in the present study. Therefore, in order to guide the discussion, Table 3 compares climatic events between the equatorial Pacific and regions of the CCS. The exact timing of ENSO during the summer (following the ONI mean of May–June–July), indicated that between 2002 and 2006 the study system was found most of the time under El Niño conditions, while during the summers of 2007–2008 La Niña was present. There are some inconsistencies in determining how much the ENSO is reflected in the SST anomalies of the CCS. The first one occurred in the summer of 2002

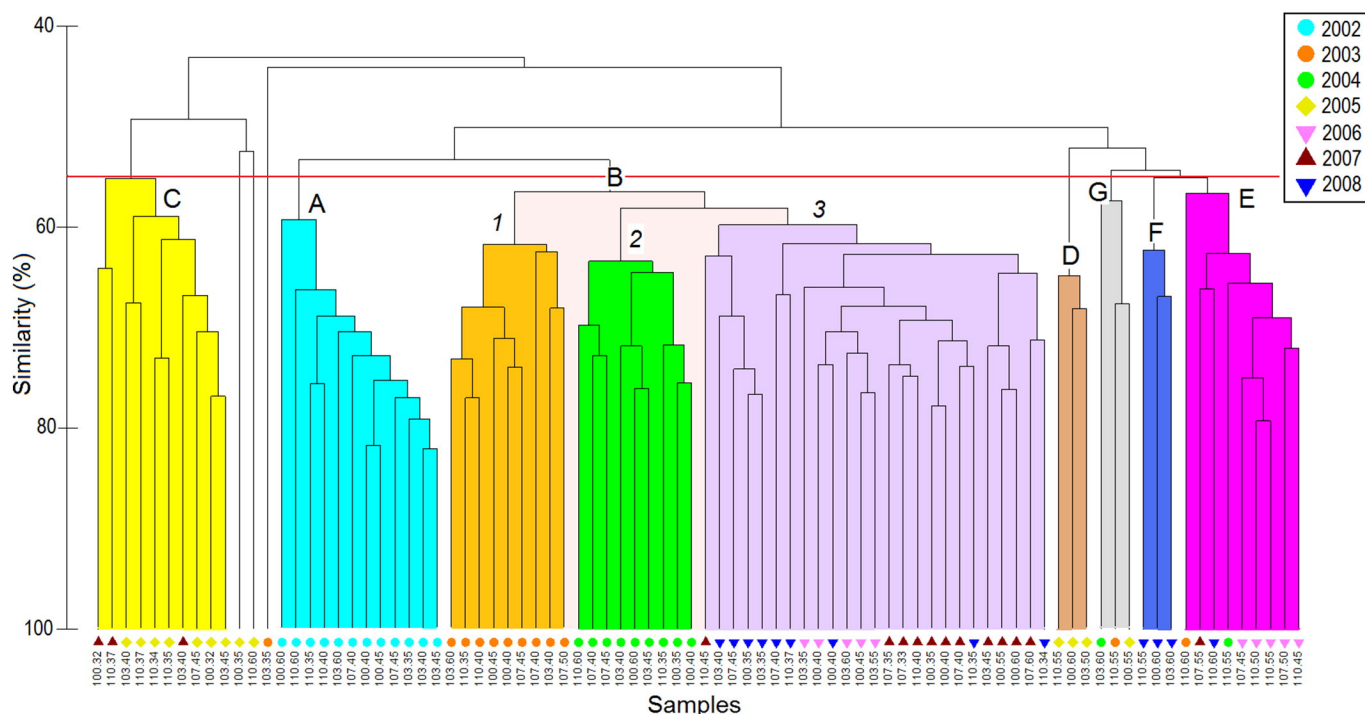


Fig. 9. Results of cluster analysis based on the composition of hyperiid amphipod species in sampling stations from seven summers during the period 2002–2008.

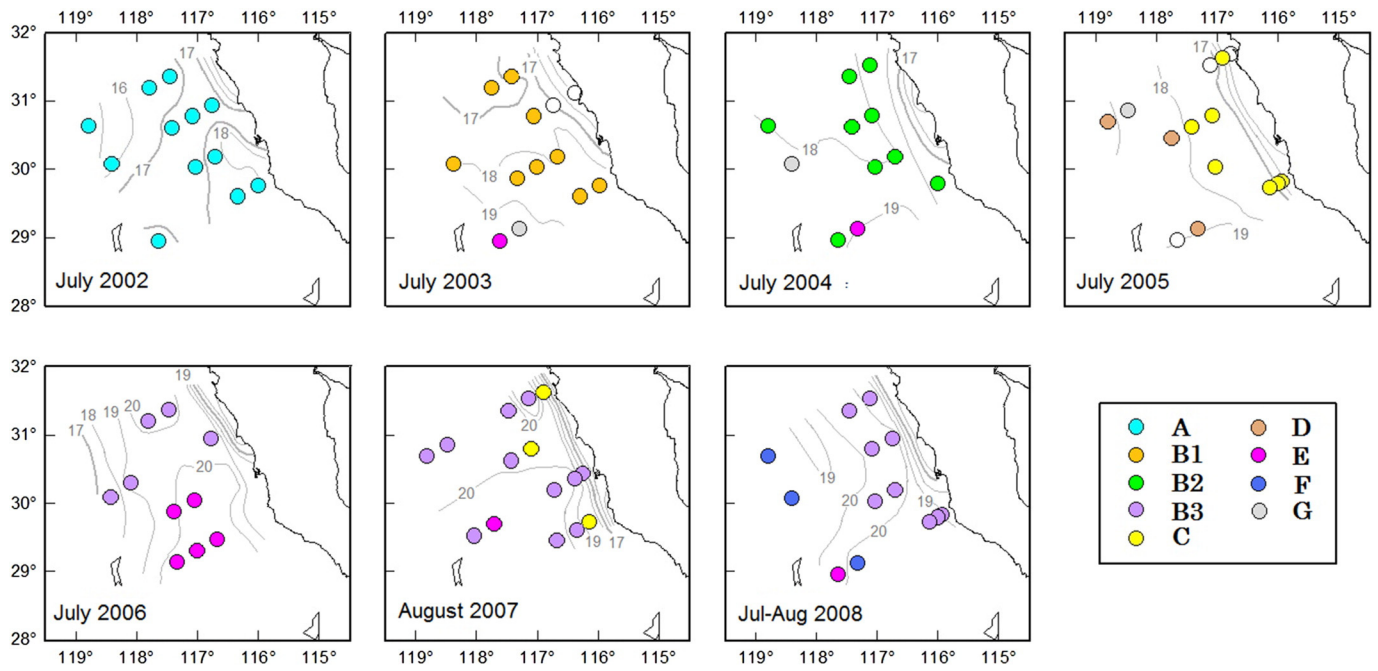


Fig. 10. Geographic distribution of clusters defined in the similarity analysis (see Fig. 9). Contour lines show surface isotherms (°C).

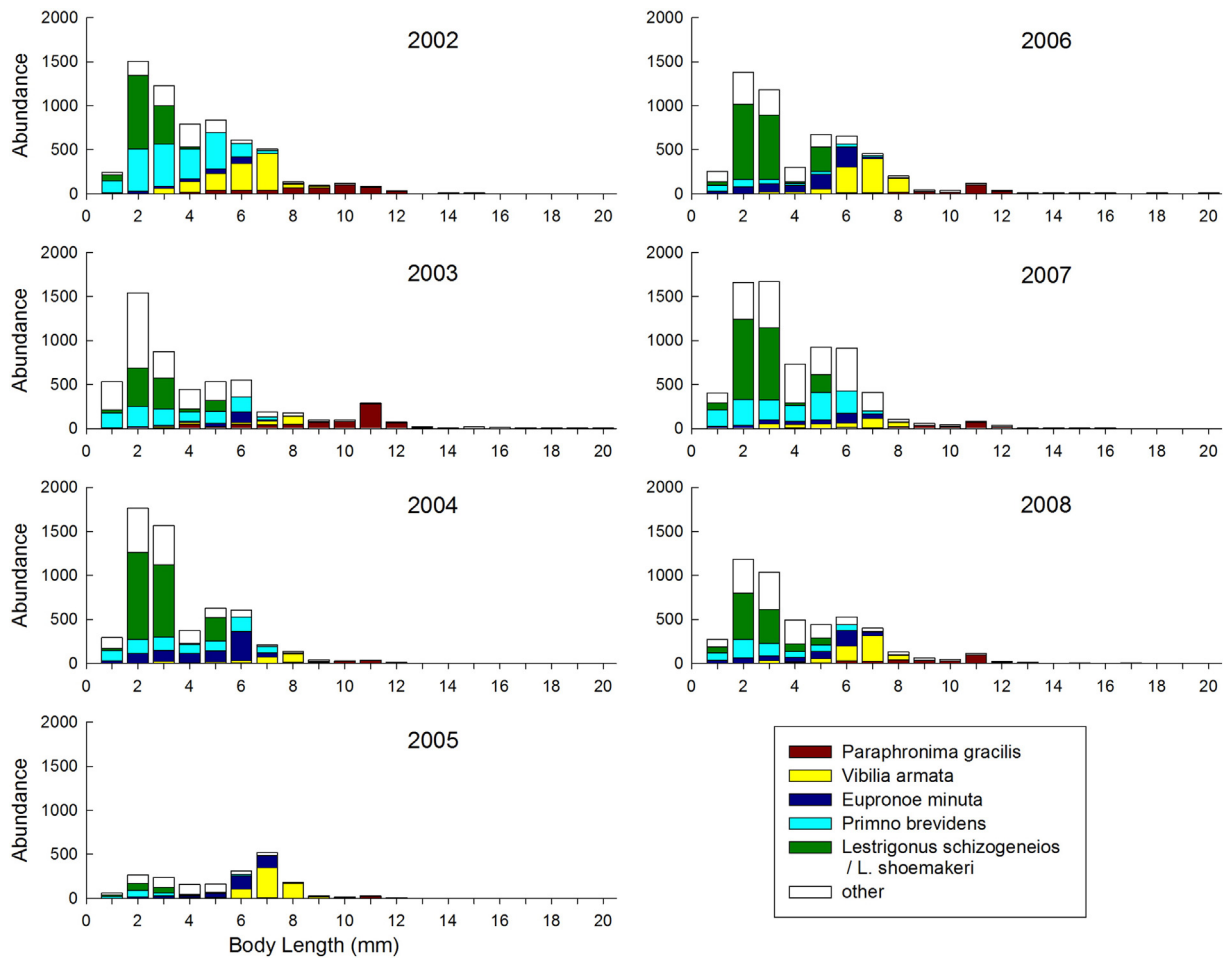
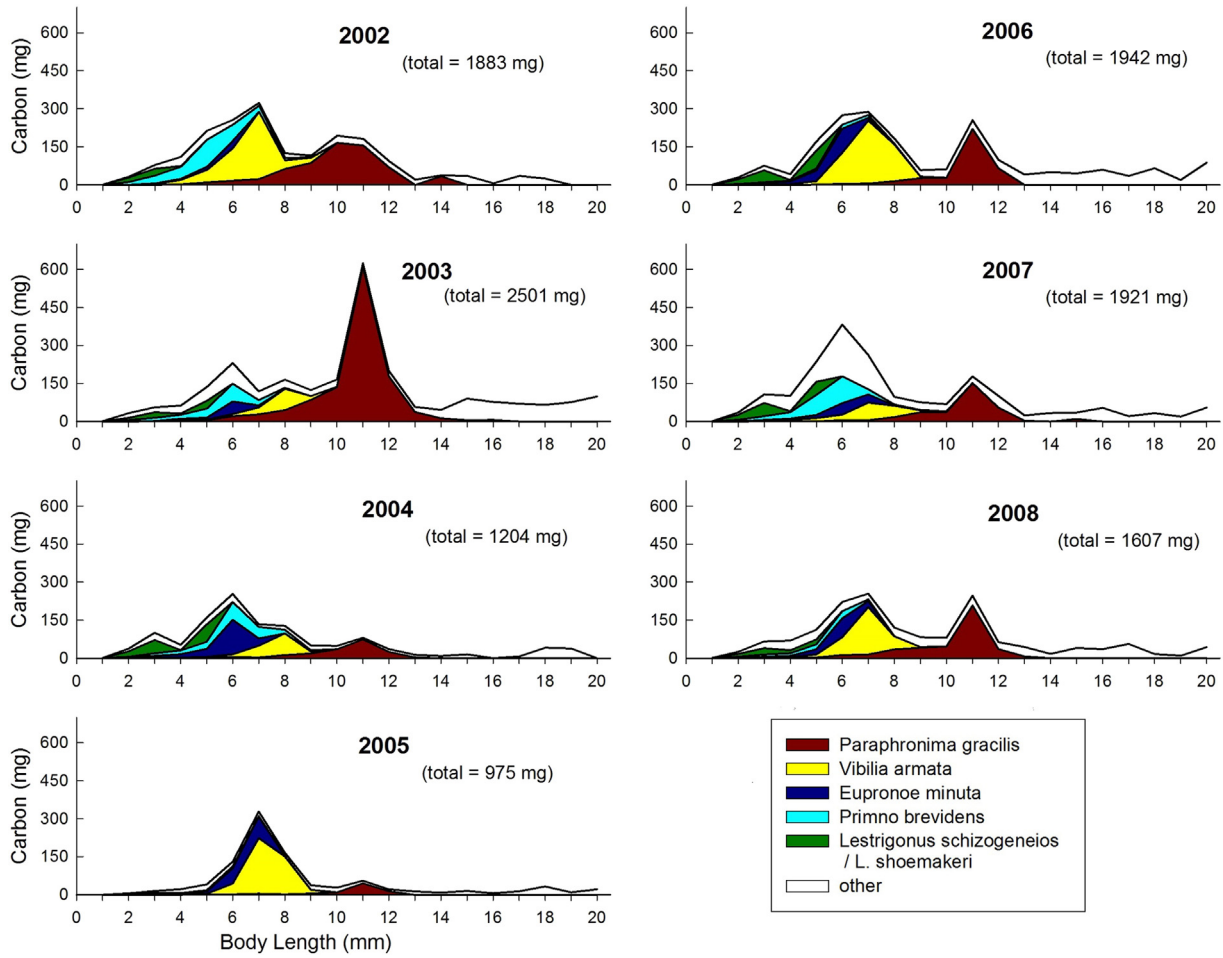


Fig. 11. Abundance by size class and year taking all hyperiid amphipods identified in the samples during the period 2002–2008. Colors indicate the relative contribution of dominant species.



**Fig. 12.** Carbon biomass (mg) by size class and year taking all hyperiid amphipods identified in the samples during the period 2002–2008. Colors indicate the contribution of dominant species.

when all regions of the CCS presented negative instead of positive anomalies as would correspond to El Niño 2002–2003 (Table 3). Extra-tropical processes altered surface circulation bringing a subarctic

water intrusion to the CCS (Freeland and Cummins, 2005) and resulting in records of negative SST anomalies from the north (Oregon, USA) to the south (Baja California, Mexico), although the latter was of a lesser

**Table 3**

Oceanic El Niño Index (ONI) from region 3.4 (5°N–5°S, 120°–170°W) and SST anomalies (°C) from regions of the California Current system (CCS) during summer 2002 to 2008. Values are the mean of May–June–July (MJJ) for ONI, and for the CCS regions the mean of July for SST anomalies except where indicated in parenthesis. In some regions the mean SST was not available and therefore the SST range was reported. SWI = Subarctic Water Intrusion, PSDCU = Preceded by a Spring Delay in Coastal Upwelling.

Year	ONI	SST Anomalies in the CCS			
	Region 3.4 (MJJ)	Northern Baja California	Southern California	Monterey Bay	Newport, Oregon
2002	+0.7	−0.7	−1 to −3 <sup>a</sup>	−1 <sup>b</sup>	−1.8 <sup>c</sup>
2003	<i>El Niño</i>	SWI	SWI	SWI	SWI
	−0.1	+0.2	~0 <sup>d</sup>	−0.5 <sup>b</sup>	+0.2 <sup>c</sup>
2004	<i>neutral</i>				
	+0.3	+0.5	+0.1 <sup>d</sup>	0 to −0.5 <sup>b</sup>	+0.9 <sup>c</sup>
2005	<i>El Niño (starting)</i>				
	+0.3	0	−0.6 <sup>d</sup>	+0.5 <sup>b</sup>	+0.8 to −1.3 <sup>c</sup>
2006	<i>El Niño (ending)</i>				
	+0.1	+1.4	+0.4 <sup>d</sup>	+0.5 <sup>b</sup>	PSDCU −0.7 <sup>c</sup>
2007	<i>El Niño (starting)</i>				
	−0.3	+0.5 (Aug)	−0.5 <sup>d</sup>	−1 (Aug) <sup>b</sup>	+1.3 (Aug) <sup>c</sup>
2008	<i>La Niña</i>				
	−0.5	+1.7 (Jul–Aug)	−0.1 (Aug) <sup>d</sup>	−0.5 <sup>b</sup>	−2.2 <sup>c</sup>
	<i>La Niña</i>				

<sup>a</sup> SST anomalies calculated using the climatologic mean of 1950–1999 (Bograd and Lynn, 2003).

<sup>b</sup> SST anomalies relative to 1988–2008 from the M1 mooring (Chavez, 2008).

<sup>c</sup> SST anomalies relative to 1996–2014 from the NOAA Buoy 46,050 (20 miles west of Newport (<http://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/da-sea-surface-temp.cfm>)).

<sup>d</sup> Mixed layer temperature anomalies relative to 1984–2008 (McClatchie et al., 2009).

magnitude during July 2002 (Bograd and Lynn, 2003; Venrick et al., 2003). The low diversity in 2002 is consistent with a more temperate community influenced by the subarctic water intrusion.

There was a better agreement between temperatures in the equatorial Pacific and local temperatures during 2003 and 2004 (Table 3). The summer of 2003 exhibited neutral conditions and the CCS presented SST anomalies close to zero in July 2003, while in the summer of 2004 a new El Niño was starting as reflected in the positive SST anomalies in the CCS during July 2004, except in Monterey Bay that was slightly cooler than other regions (Chavez, 2008; McClatchie et al., 2009). In the present study, amphipod communities in 2003 and 2004 were comparable, appearing as subgroups within a common cluster (Fig. 9). However, large amphipods (*Paraphronima gracilis*) were more abundant in 2003, and made a high contribution to the total biomass compared to 2004 when smaller amphipods (*L. schizogeneios* and *E. minuta*) dominated the community (Figs. 11–12). It is difficult to determine whether these changes observed in July 2004 were due to a rapid response to the El Niño 2004–2005, or a delayed effect of El Niño 2002–2003, or the sum of both events. Fisher et al. (2015) have argued that during Modoki Central Pacific (CP) El Niños the response of the zooplankton, specifically copepods, showed a time lag of 2–8 months. They used this argument to explain differences in anomalies of northern copepods (*Calanus marshallae*, *Pseudocalanus mimus*, and *Acartia longiremis*) off the Oregon coast, which were positive during the second half of the year 2002 but were negative during the second half of 2004, despite the fact that both time-intervals were under the influence of El Niño (2002–2003 and 2004–2005). Additionally, the most negative anomalies were observed after the time interval spanned by El Niño 2004–2005. They attributed the time lag to slower warming of deep water during a CP El Niño (Fisher et al., 2015). A possible lag in the response to El Niño cannot be excluded, although more than three months seems too long for zooplanktonic organisms. Positive anomalies of northern copepods off Oregon during 2002 may well be just the result of subarctic water advection, and this is also consistent with the presence of the subarctic amphipod *Themisto pacifica* downstream off north Baja California during July 2002 as well as the increased abundance of *Euphausia pacifica* (Lavaniegos and Ambriz-Arreola, 2012). Lavaniegos (2014) found that during July 2002 the subarctic intrusion neutralized the influence of El Niño, which was restricted to the south of Punta Eugenia, Baja California, where some tropical species such as *Anchylomera blossevillei*, *Amphithyrus sculpturatus* and *Phrosina semilunata* were observed.

Other taxonomic animal groups showed evidence of a strong and rapid response to El Niño 2004–2005. Felix et al. (2007) reported the presence of Galapagos fur seals (*Arctocephalus galapagoensis*) off the coast of Ecuador, and along the northern Chilean coast, a lower dietary richness was recorded in the black urchin (*Tetrapygus niger*) (Navarrete et al., 2008). In the CCS, Brodeur et al. (2006) reported the anomalous distribution of nekton as shown by the occurrence of larval Pacific hake and jack mackerel from Oregon to British Columbia, fish species that usually spawn in southern California Bight, as well as the presence of Humboldt squid, *Dosidicus gigas*, from Oregon to Alaska. Marked disruptions in trophic structure, particularly the decline of anchovies off central California, had a significant impact on large predators such as the California sea lion, which spent more time at sea and offshore searching for food (Weise et al., 2006). However, the changes observed in distribution in the northern sector of the CCS were probably related to local conditions such as a long delay in coastal upwelling north of Cape Mendocino (40°N), with consequences to biological productivity (Schwing et al., 2006; Barth et al., 2007). This could also explain why south of Point Conception (34.5°N) negative zooplankton anomalies were of lesser magnitude and even became positive off the Baja California coast (Mackas et al., 2006).

In agreement with findings made by Lavaniegos and Hereu (2009) off Baja California during 2005, the amphipod assemblage analyzed in the present study showed great diversity, and at the same time strong dominance of the species *Lestrigonus schizogeneios*, *Primno brevidens*,

*Vibilia armata*, and *Eupronoe minuta*. In light of results from the period 2002–2008 it is evident that July 2005 was the summer with the lowest abundance of hyperiid amphipods, and the reduction in *L. schizogeneios*, that become a rare species, is a highly anomalous condition. This raises the question of why during July 2005 the response observed in amphipods and euphausiids was so different, since euphausiids off Baja California exhibited a marked increase in April and July 2005 (Lavaniegos and Ambriz-Arreola, 2012). This increase in euphausiid abundance during 2005 was explained by advection from the north combined with active swimming of the organisms escaping from severe conditions of low productivity recorded in coastal waters of the northern CCS (Lavaniegos and Ambriz-Arreola, 2012), due to delayed spring upwelling (Schwing et al., 2006; Barth et al., 2007). Large euphausiid aggregations observed in spring and summer of 2005 could have affected amphipods via competition or predation on the small *Lestrigonus* juveniles. It is well known that euphausiids present opportunistic omnivory (Ohman, 1984; Barange et al., 1991), and are thus able to ingest small crustaceans such as copepod nauplii (Nakagawa et al., 2002). However, although the smallest *Lestrigonus* in the samples had sizes of 0.5–1 mm, which appear too large to be preyed by euphausiids, this hypothesis cannot be ruled out, considering the demand of food supply generated by large aggregations of euphausiids in 2005 (Lavaniegos and Ambriz-Arreola, 2012). It is also possible that other larger predators such as squid (Bazzino et al., 2010) and fish consumed the amphipods.

#### 4.1. Contrasting CP and EP El Niños

A peculiar characteristic of the study period was the occurrence of three consecutive El Niño events. The first two (2002–2003 and 2004–2005), were considered Modoki or Central Pacific (CP) El Niño events, whereas the third occurring in 2006–2007 was a weak Eastern Pacific (EP) El Niño (Lee and McPhaden, 2010). Salinity profiles off Baja California confirm the difference of El Niño types, showing high stratification during the summers of 2003 to 2005 under the influence of CP El Niño, but that this condition diminished in July 2006 and disappeared by July 2007 (Fig. 4). Stratification of the water column could explain in part the low chlorophyll concentrations observed in 2003–2005 off Baja California (Gaxiola-Castro et al., 2008), because more energy would be required to lift the isopycnals and bring nutrients to the upper layer (Kosro et al., 2006). The return to typical salinity profiles in 2006–2007 suggests the mixing of water masses, reflected by increased chlorophyll in the study region (Gaxiola-Castro et al., 2008).

During the summer of 2006 the ONI indicated the start of El Niño coinciding with positive SST anomalies in southern regions of the CCS (Table 3), and high diversity of amphipods was associated to a warm tongue east of Guadalupe Island (Fig. 10). In this parcel of warm water *Lycaeopsis zamboangae*, *Phronima curvipes*, *Lestrigonus begalensis*, and *Phrosina semilunata* appeared as important species during July 2006. In particular, the presence of *L. zamboangae* is a sign of influence of subtropical oceanic water as this species was primarily found at offshore stations. There are few studies about the effects of El Niño 2006–2007 on the plankton. In the southeastern Pacific, Criales-Hernández et al. (2008) reported a dominance of warm water copepods off Peru during summer 2006, while Gajardo et al. (2013) found high species richness of Foraminifera collected in sediment traps off Concepcion, Chile, with increased relative abundance of *Globigerina bulloides*, which according to Field et al. (2006) is a species with preference for near-surface stratification.

Thus, irrespective of the type of El Niño, during the summers of 2003–2006 the outstanding feature in the amphipod community was the strong fluctuation in dominant species (Fig. 7), and total carbon biomass (Fig. 12). It is possible that distributional changes in the nektonic community occurred in the CCS during 2004–2005 and that these resulted in compensatory changes in the trophic structure of this ecosystem (Brodeur et al., 2006), as suggested by the increased predation

pressure on *L. schizogeneios* by krill during July 2005 in the present study.

#### 4.2. La Niña 2007–2008

After this documented period of three consecutive El Niño events, the ecosystem changed to cooler conditions. La Niña 2007–2008 marked the last two summers of the study period (Table 3). This was an event of two year duration, with an intermediate stage between two cool pulses: one longer and cooler from March 2007 to June 2008, and the second from September 2008 to April 2009 (Hu et al., 2014). Thus, the summer did not capture the most intense conditions of La Niña, which occurred from October 2007 to February 2008 when temperature anomalies of  $-1.5$  to  $-2$  °C were attained. Not all regions of the CCS showed negative anomalies, neither in July 2007 nor in July 2008 (Table 3). Off Baja California positive anomalies were observed during August 2007 and July 2008, and were particularly high in 2008 (1.7 °C), contrasting with negative anomalies in other CCS regions (Table 3). In the Baja California region, the positive temperature anomaly in July 2008 was marked by high amphipod diversity (Fig. 6). This high diversity in 2008 suggests a mixture of temperate and tropical species, which would not be expected under the influence of La Niña. Alternatively, it may indicate the relaxation of La Niña as inferred from temperature profiles (Fig. 3). Diversity increase could result from relaxation of La Niña that may have brought tropical species from offshore to onshore waters. Warm anomalies off north Baja California are also consistent with the report of high capture of Pacific sardines in this region (Cota-Villavicencio et al., 2010).

However, the similarity analysis conducted in the present study (Fig. 9), highlighted the similarity in amphipod assemblages during 2006–2008 (except for the stations in the warm tongue during 2006), which in turn were closely related to assemblages occurring in 2003 and 2004. The similarity analysis revealed a key contribution of the characteristic subtropical CCS species (*L. schizogeneios*, *P. brevidens*, *V. armata*, and *E. minuta*), indicating the resilience of these target species to climatic change.

Apart from ENSO, larger-scale climatic influences might be operating in explaining changes observed in the pelagic ecosystem. It is noteworthy that the NPGO, which diminished in 2004 and changed to a negative sign in 2005–2006, coincided with a high stratification of the water column (Lavaniegos et al., 2015), when the main fluctuations in amphipod community were documented in the present study. However, the time-series of amphipod abundances are too short to attempt a correlation with decadal indices or to detect longer time-scale processes such as global warming.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jmarsys.2016.09.001>.

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