



# Pelagic amphipod assemblage associated with subarctic water off the West Coast of the Baja California peninsula



Bertha E. Lavaniegos

Departamento de Oceanografía Biológica, Centro de Investigación Científica y Educación Superior de Ensenada, Carretera Ensenada-Tijuana No. 3918, Zona Playitas, Apdo, Postal 360, 22860 Ensenada, Baja California, Mexico

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## ABSTRACT

The California Current system is a large marine ecosystem with transition gradients between subarctic and tropical biomes containing diverse habitats. Biogeographic species groups must be carefully analyzed in order to detect tendencies shifting the ecosystem toward a more temperate or tropical state. Species composition of hyperiid amphipods was analyzed in July 2002 for evidence of subarctic water intrusion and for signals of the El Niño event developing in the equatorial Pacific. Multivariate analysis showed a dominance of “transition zone” species typical of the California Current. The main evidence of subarctic water intrusion was the extended distribution of *Themisto pacifica*, which reached as far south as 27°N, with particularly high abundances at 30–32°N. The intrusion of subarctic water took place despite evidence that an El Niño event was in progress. The zonal advection due to El Niño intersected the equatorward flow of the subarctic intrusion and probably produced a large cyclonic eddy off Baja California. This eddy maintained a limited El Niño influence at a few offshore stations near its southern boundary. The main environmental variables influencing the amphipod assemblage structure were water temperature and the abundance of salps. *T. pacifica*, a species with cool water affinity, was more sensitive to temperature, whereas subtropical species, such as *Vibilia armata*, were strongly correlated with the availability of salps.

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## 1. Introduction

The California Current system (CCS), a highly productive eastern boundary upwelling ecosystem (Fréon et al., 2009), extends from Vancouver, Canada, to the tip of the Baja California peninsula, Mexico (Mackas, 2006). The main stream of subarctic origin is characterized by low temperature, low salinity, and high oxygen content (Lynn and Simpson, 1987). This equatorward subarctic water flow is modified along its course by warmer and more saline subtropical water on the west side and by cooler upwelled water near the coast (Lynn and Simpson, 1987). The salinity of upwelled water depends on the depth of the upwelling cell (Chhak and Di Lorenzo, 2007). The end point of the California Current is difficult to establish because there is a paucity of data for the area adjacent to the tropics, but it is perceptible in the eastern tropical Pacific during February–July when the North Equatorial Countercurrent is weak (Kessler, 2006).

The CCS experiences high variability on different time scales (seasonal, interannual, decadal, etc.) with notable consequences for the zooplankton (Brinton and Townsend, 2003; Lavaniegos and Ohman, 1999, 2003). Interannual shifts have been mainly associated with El Niño (Durazo and Baumgartner, 2002; Lavaniegos et al., 2002), but other events also occur. For example, though subarctic water is the original

source of the California Current, an excessive volume of this water mass was recorded in July 2002 (Durazo et al., 2005; Huyer, 2003; Lavaniegos, 2009; Venrick et al., 2003). Freeland and Cummins (2005) attributed this intrusion of subarctic water to a southward shift of the North Pacific Current which bifurcates to form the California Current. This event had great biological consequences off the Baja California peninsula, resulting in an increase in chlorophyll but decrease in zooplankton volume during 2002 (Durazo et al., 2005; Lavaniegos, 2009). In the species level, there were some evidences of subarctic advection in July 2002 such as the increase in temperate euphausiids inhabiting off Baja California, *Euphausia pacifica* and *Thysanoessa spinifera* (Lavaniegos and Ambriz-Arreola, 2012). These temperate species usually dominate in the northern sector of the CCS, and off Oregon they showed high reproductive effort in July 2002 (Gómez-Gutiérrez et al., 2007); however, they were equally abundant off the Baja California peninsula in comparable amount, and similar to observations made in 2000 under La Niña conditions (Lavaniegos and Ambriz-Arreola, 2012).

Apart from euphausiids, other zooplankton taxa have not been studied off Baja California in relation to subarctic water intrusion. Lavaniegos and Hereu (2009) described seasonal changes in amphipod communities based on four cruises performed during 2005 in a wide area of the CCS comprised between 24 and 32°N. Strong seasonal changes were observed but four species (*Vibilia armata*, *Lestrigonus schizogeneios*, *Eupronoe minuta*, and *Primno brevidens*) characterized the main stream of the CCS year round. This region presents high mesoscale activity

E-mail address: [berlav@cicese.mx](mailto:berlav@cicese.mx).

(Parés-Sierra et al., 1993; Soto-Mardones et al., 2004), and multivariate analysis showed a close coupling between hyperiid species composition and mesoscale structures (Lavaniegos and Hereu, 2009). It is thus reasonable to hypothesize that the occurrence of subarctic intrusion would produce an increase in the abundance of the dominant species of the CCS and a probable extension in the distribution of species coming from the north. In the present study, hyperiid amphipods were analyzed for additional evidence of subarctic water intrusion. Hyperiid amphipods are remarkably diverse crustaceans compared to their relatively low abundance in the plankton, and they are highly sensitive to climate variability (Lavaniegos and Hereu, 2009; Lavaniegos and Ohman, 1999). They are a primarily oceanic group but a few species may have permanent local populations over the coastal shelf (Valencia et al., 2013; Zeidler, 1984). Conventionally, pelagic amphipods have been considered of little importance in marine food webs, receiving little attention from the scientific community; however, they may form dense aggregations (Lobel and Randall, 1986; Vinogradov, 1999) and are conspicuous prey items in stomach contents of fishes (Brodeur et al., 1987; Miller et al., 2010; Repelin, 1978; Schabetsberger et al., 2003) and birds (Gaston et al., 2009).

## 2. Methods

### 2.1. Sampling

The samples were obtained during IMECOCAL cruise 0207 conducted between July 12 and August 1, 2002 on board the RV *Francisco de Ulloa*, across a station grid of 12 transects perpendicular to the Baja California coast (Fig. 1a). At each station, conductivity, temperature and pressure measurements were taken using a Seabird CTD. Zooplankton was collected with a 71 cm diameter bongo net of 505  $\mu\text{m}$  mesh width. Oblique tows were done from 210 m (when bottom depth permitted) to the surface and from 10 m above the bottom to the surface at shallow stations. The volume of water strained was measured with a flowmeter in the mouth of the net. Samples were preserved with 4% formalin.

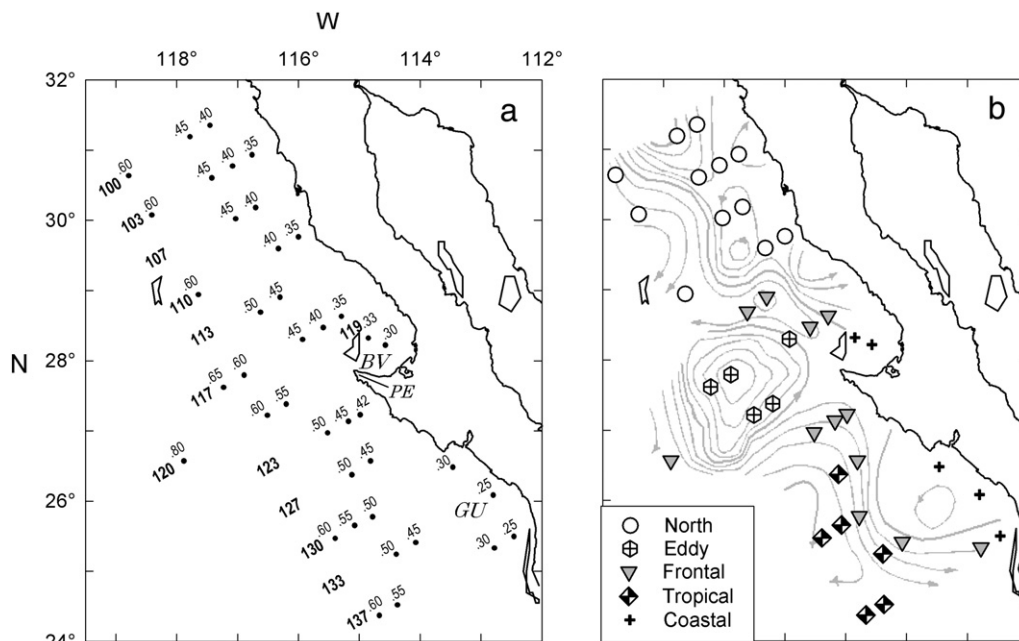
### 2.2. Taxonomic analysis

A total of 40 samples collected during the night were selected for the present study in order to reduce variability due to vertical migration. The hyperiid amphipods from the complete sample were counted and identified to species, using as reference Brusca (1981), Vinogradov et al. (1996), and Zeidler (2004).

### 2.3. Data analysis

Abundance was standardized to 1000  $\text{m}^3$  of filtered water. Further data were transformed using the function  $\log_{10}(x + 1)$  to reduce the strong effect on the statistical analyses of the high abundance of some species. The surface circulation described by Soto-Mardones et al. (2004), complemented with information from Durazo et al. (2005), was used to identify mesoscale features (Fig. 1). Total hyperiid abundances among mesoscale structures were compared with the nonparametric Kruskal–Wallis test and when significant, the Mann–Whitney test was used to compare structures pair by pair. The latter test was also used to compare abundances of some individual species. Species richness and diversity in mesoscale structures (defined in Fig. 1b) were estimated using the Margalef index and the Shannon index, respectively.

Species present in five or more samples were selected to perform multivariate analysis and two stations lacking amphipods were excluded. Thus, the data matrix consisted of 38 stations  $\times$  41 species. A similarity matrix was calculated with the Bray–Curtis index and cluster analysis was performed taking into account both sampling units (stations) and species (on the transposed matrix). Data were previously standardized dividing for total abundance and then log-transformed. Further, a hierarchical agglomerative clustering strategy was used with the average group linkage method. Cluster dendrograms were cut where the resulting cluster groups were ecologically interpretable; the similarity cut off levels showed 55% of similarity for the station clusters and 36% for the species clusters. In addition, the non-metric multi-dimensional scaling (NMS) ordination method was used (Clarke and Warwick, 2001) to confirm the cluster analysis.



**Fig. 1.** Study area off Baja California (Mexico). (a) Stations numbers occupied at night during IMECOCAL cruise 0207 (transect line in bold); BV, Vizcaino Bay; GU, Gulf of Ulloa; PE, Punta Eugenia. (b) Surface circulation (gray lines) based on dynamic height anomalies (0/500 db); the symbols indicate the denomination of mesoscale structures used in the present study.

Principal component (PC) analysis was performed using log-abundance of the 41 common species. The scores of the main PC were then related to environmental variables by multiple regression analysis. The variables considered were temperature at 10 and 150 m depth, salinity at 10 and 150 m depth, and salp abundance. These depths were selected to detect the effects of warming due to El Niño or of cooling and freshening due to subarctic water intrusion. Organisms living in the upper layer are more affected by surface temperature in the mixed layer, whereas those remaining below the thermocline are more affected by subsurface warming. Durazo et al. (2005) determined that the main effects of subarctic intrusion are observed in the upper 100 m of the water column. As slight warming was recorded below 100 m, suggesting the presence of a weak El Niño, the temperature at 150 m depth may be useful to explore the effect of warming or freshening on non-migrating organisms living below the thermocline. For stations shallower than 150 m, the near-bottom temperature was used. Salp abundance was included because salps are the main host species of hyperiid amphipods.

### 3. Results

Eighty-three hyperiid species were recorded in Baja California waters during July 2002 (Table 1). One third of these species were rare, occurring in only one or two samples, while five species (*P. brevidens*, *V. armata*, *E. minuta*, *L. schizogeneios*, and *L. shoemakeri*) were strongly dominant, occurring in 82–90% of the samples. The geometric means (GM) for these dominant species ranged from 10 to 50 ind/1000 m<sup>3</sup> (Fig. 2). The other 17 common species presented GM between 1 and 10 ind/1000 m<sup>3</sup> and a regular incidence in the samples (35–70%). Some of these common species, however, could be considered regionally dominant because their high abundances were circumscribed to northern or southern stations. For example, *Themisto pacifica* was very abundant to the north of 30°N, *Anchylomera blossevillei* occurred only to the south of 26°N, and *Lycaeopsis themistoides* was distributed offshore (Supplemental Fig. 1).

Total hyperiid abundances differed with regard to mesoscale structures (defined in Fig. 1b) as shown by the Kruskal–Wallis test ( $p = 0.001$ ). The GM for coastal stations was 8 ind/1000 m<sup>3</sup>, contrasting with a GM two orders of magnitude higher for oceanic mesoscale structures. In the oceanic region, the abundance of hyperiids was highest in the north structure and lowest in the tropical structure (GM = 750 and 156 ind/1000 m<sup>3</sup> respectively), and the difference was significant ( $p < 0.002$ ). In the eddy and frontal structures, hyperiid abundances were similar (GM = 427 and 340 ind/1000 m<sup>3</sup> respectively), but only the frontal station results were significantly lower compared with the northern stations ( $p < 0.028$ ).

A similar contrast between coastal and oceanic waters was observed for species richness and diversity. The Margalef Index averaged between 2.8 (eddy) and 4.2 (tropical), compared to only 0.2 for the coastal group. Mean Shannon Index was from 0.78 to 1.05 for oceanic mesoscale structures and only 0.17 for coastal stations. Therefore, these indices were sensitive only to strong differences in richness and diversity between nearshore and offshore regions but not to mesoscale activity.

#### 3.1. Mesoscale faunal composition

Amphipods were not found at two coastal stations (130.30 and 137.25) and they were thus excluded from the similarity analysis. The other three coastal stations were well separated from the rest in the cluster analysis (Fig. 3). Three clusters resulted in cutting the dendrogram at 55% similarity level (Fig. 3a). The smallest cluster was group 3, consisting of a pair of Vizcaino Bay stations (119.33 and 120.30), and their similarity was due to the presence of a few specimens of *L. schizogeneios* and *L. shoemakeri* (Fig. 4).

Oceanic stations formed two clusters (Fig. 3a). The largest cluster (1) gathered together 28 stations that were split into two subgroups: all the

northern stations and the distant station 120.80 (1A), and a mixture of eddy and frontal stations (1B). The MDS plot (Fig. 3b) confirmed the solid relation among the stations inside the clusters and the correspondence with the mesoscale structures (Fig. 3b). The composition was similar among the three mesoscale structures included in cluster 1 (North, Eddy, and Frontal) with four species (*P. brevidens*, *V. armata*, *L. schizogeneios*, and *L. shoemakeri*) being the main contributors to the similarity (Fig. 4a). Though the percentage of similarity contributed by these four species was more than 50% (Fig. 4a), considering absolute abundance, the difference among the north, eddy and frontal structures was notable due to the large abundance of *P. brevidens* in the northern assemblage (Fig. 4b). The Mann–Whitney comparison between *P. brevidens* abundances in the north and frontal structures was highly significant ( $p < 0.001$ ). The abundance of this species in the eddy was midway between the north and frontal structures and there were no statistical differences. In effect, none of the 41 most abundant species had numeric differences between the eddy and frontal structures except *Phronima atlantica*, which was less abundant in the eddy ( $p = 0.043$ ). The most exclusive species at the northern stations (cluster 1A) were *T. pacifica*, *Paraphronima gracilis*, and *Phronimopsis spinifera*. Together these three species contributed to high dissimilarity between the north and the eddy (22.6%), frontal (17.7%), and tropical (14.2%) structures.

Cluster 2 comprised five offshore southern stations (Fig. 3) and was clearly tropical. The similarity was mainly due to *E. minuta*, followed by *V. armata* and *A. blossevillei* (Fig. 4a). This last species could be considered a good indicator of tropical water, because it contrasts the high similarity contribution at tropical stations (9.7%) and the low percentage for the other mesoscale structures (0% for north and eddy, and 0.03% for frontal). In terms of the abundance of total amphipods, it was notably low at the stations pertaining to the tropical cluster (Fig. 4b). Despite the low abundance, some species were present only in this structure, such as *Rhabdosoma whitei* and *Vibilia chuni*, and others were completely absent in the north (*A. blossevillei*, *Amphityrus sculpturatus*, *Phrosina semilunata*, *Lycaea serrata*). Combining these six species, the dissimilarity contribution between the tropical and other structures (north, eddy, and frontal) was 21–23%.

#### 3.2. Biogeographic groups

The cluster analysis applied to the transposed matrix resulted in one strong faunal group (cluster I) with 64% of similarity and other faunal groups resulted if the cut off level was maintained at 36% of similarity (Fig. 5a). The corresponding MDS plot (Fig. 5b) shows that only clusters I and II are completely separated from the rest. These clusters are closely linked, corresponding to species typical of the California Current, also named ‘transition zone’ species (Bowman, 1973). Transition zone species were defined by Brinton (1962) based on exclusive or dominant euphausiids in the region “between Subarctic Water and Central Water in the mid-Pacific and between Subarctic Water and Equatorial Water in the California Current”. The species grouped in cluster I (*L. schizogeneios*, *L. shoemakeri*, *V. armata*, *P. brevidens*, *E. minuta*, and *P. gracilis*) were extensively distributed in the study area but had the highest abundances in the northern part. The species in cluster II were quite abundant in the northern part but were scarce toward the south. Three species (*T. pacifica*, *P. spinifera* and *Tryphana malmi*) were particularly rare to the south of 30°N.

Cluster III had low similarity (38%) but showed a wide separation from clusters I and II in the MDS plot (Fig. 5b). The seven species in cluster III were scarce or absent at the northern stations and some of them (*Platyscelus ovooides*, *A. blossevillei*, and *A. sculpturatus*) had high abundances to the south of the cyclonic eddy in the frontal area parallel to the coast, between 28° and 25°N; this indicates tropical fauna.

Cluster III was related to three other clusters that were defined as subgroups a, b, and c of one weak cluster IV (amalgamating at 31% similarity level). Twelve species are involved in the complete cluster IV

**Table 1**  
Hyperiid amphipod species collected off the western coast of Baja California in July 2002. Classification and biogeography based on Vinogradov et al. (1996) with modifications from Zeidler (2004). (NS) is the number of samples with presence of the species (total number of samples = 40). Gelatinous hosts reported in Laval (1980) are shown: (Ct) ctenophores, (Do) doliolids, (He) heteropods, (Me) medusae, (Py) pyrosomes, (Ra) radiolarian colonies, (Sa) salps, and (Si) siphonophores. (\*) indicates the “transition zone species” typical of the CCS and (♦) species abundant in the oligotrophic waters of the central North Pacific gyre (Shulenberg, 1977). Other references used for the biogeography and hosts are denoted with a number in parentheses: (1) Bowman, 1960; (2) Bowman, 1973; (3) Brusca, 1981; (4) Nair, 1995; (5) Lavaniegos and Ohman (1999); (6) Gasca and Haddock, 2004; (7) Gasca et al., 2007; (8) Aoki et al., 2013.

Species	NS	Biogeography	Host
<b>Family Lanceolidae</b>			
<i>Lanceola clausi</i> Bovallius, 1885	2	Warm-temperate cosmopolite	
<i>Lanceola loveni</i> Bovallius, 1885	1	Warm-temperate cosmopolite	
<i>Lanceola sayana</i> Bovallius, 1885	1	Warm-temperate cosmopolite	Me
<b>Family Scinidae</b>			
<i>Scina borealis</i> (G.O. Sars, 1882)	23	Warm-temperate cosmopolite*	
<i>Scina crassicornis</i> (Fabricius, 1775)	1	Warm-temperate cosmopolite♦	
<i>Scina curvicaudata</i> Chevreux, 1914	2	Tropical	
<i>Scina tullbergi</i> (Bovallius, 1885)	20	Subtropical (3)*	Si
<b>Family Vibiliidae</b>			
<i>Vibilia armata</i> Bovallius, 1887	33	Temperate-subtropical (3)*	Sa
<i>Vibilia australis</i> Stebbing, 1888	21	Temperate-subtropical (3)*	Si (5), Sa (6)
<i>Vibilia chuni</i> Behning & Woltereck, 1912	8	Warm-temperate cosmopolite	Sa
<i>Vibilia cultripes</i> Vosseler, 1901	4	Subtropical-tropical	
<i>Vibilia gibbosa</i> Bovallius, 1887	3	Subtropical-tropical	
<i>Vibilia robusta</i> Bovallius, 1887	3	Subtropical-tropical	Sa
<i>Vibilia stebbingi</i> Behning & Woltereck, 1912	2	Subtropical-tropical	Sa
<i>Vibilia viatrix</i> Bovallius, 1887	18	Warm-temperate cosmopolite	Sa
<b>Family Paraphronimidae</b>			
<i>Paraphronima crassipes</i> Claus, 1879	13	Warm-temperate cosmopolite	Si
<i>Paraphronima gracilis</i> Claus, 1879	28	Warm-temperate cosmopolite*	Si, Sa (5)
<b>Family Phronimidae</b>			
<i>Phronima atlantica</i> Guérin-Méneville, 1836	17	Temperate-subtropical (3)	Sa (8)
<i>Phronima bucephala</i> Giles, 1887	1	Subtropical (3)	Sa (8)
<i>Phronima colletti</i> Bovallius, 1887	1	Tropical	Si, Sa
<i>Phronima curvipes</i> Vosseler, 1909	18	Subtropical-tropical	Si
<i>Phronima dunbari</i> Shih, 1991	1	Tropical	Sa (8)
<i>Phronima pacifica</i> Streets, 1877	2	Tropical	Si, Sa
<i>Phronima sedentaria</i> (Forsskål, 1775)	10	Warm-temperate cosmopolite	Sa, Py (8)
<i>Phronima stebbingii</i> Vosseler 1901	4	Warm-temperate cosmopolite	
<i>Phronimella elongata</i> (Claus, 1862)	2	Subtropical-tropical	Sa (8)
<b>Family Phrosinidae</b>			
<i>Anchylomera blossevillei</i> Milne-Edwards, 1830	7	Warm-temperate cosmopolite	Py
<i>Phrosina semilunata</i> Risso, 1822	11	Warm-temperate cosmopolite	
<i>Primno brevidens</i> Bowman, 1978	35	Temperate-subtropical (3)*	Si (6)
<i>Primno latreillei</i> Stebbing, 1888	2	Subtropical-tropical♦	
<b>Family Hyperiididae</b>			
<i>Hyperia spinigera</i> Bovallius, 1889	1	Warm-water cosmopolite (2)	
<i>Hyperoche cryptodactylus</i> Stebbing, 1888	3	Subtropical?	
<i>Hyperoche medusarum</i> (Krøyer, 1838)	20	Temperate-subtropical (2, 3)*	Ct, Me
<i>Hyperoche picta</i> Bovallius, 1889	2	Temperate-subtropical (3)	Ct, Me, Si, Sa
<i>Laxohyperia vespuliformes</i> Vinogradov & Volkov, 1882	3	Tropical	
<i>Themisto pacifica</i> Stebbing, 1888	23	Subarctic Pacific (1)*	Sa (3), Me
<b>Family Lestrigonidae</b>			
<i>Hyperietta luzoni</i> (Stebbing, 1888)	2	Subtropical (2)	
<i>Hyperietta parviceps</i> Bowman, 1973	16	Subtropical (2)	
<i>Hyperietta stebbingi</i> Bowman, 1973	5	Subtropical (2)	Ra
<i>Hyperietta stephensi</i> Bowman, 1973	6	Subtropical (2)	Ra
<i>Hyperietta vosseleri</i> (Stebbing, 1904)	6	Subtropical-tropical♦	
<i>Hyperioides longipes</i> Chevreux, 1900	2	Subtropical (2)*	
<i>Lestrigonus bengalensis</i> Giles, 1887	1	Subtropical-tropical♦	Me
<i>Lestrigonus macrophthalmus</i> (Vosseler, 1901)	2	Tropical (2)	
<i>Lestrigonus schizogeneios</i> (Stebbing, 1888)	36	Subtropical (2)*	Do (5), Ct, Me
<i>Lestrigonus shoemakeri</i> Bowman, 1973	34	Subtropical (2)	
<i>Phronimopsis spinifera</i> Claus, 1879	16	Subtropical (3)	
<b>Family Iulopididae</b>			
<i>Iulopsis loveni</i> Bovallius, 1887	1	Tropical	Me
<i>Iulopsis mirabilis</i> Bovallius, 1887	9	Subtropical (3)	
<b>Family Lyceopsidae</b>			
<i>Lycaeopsis themistoides</i> Claus, 1879	11	Tropical	Si
<b>Family Pronoidae</b>			
<i>Eupronoe armata</i> Claus, 1879	1	Subtropical-tropical	
<i>Eupronoe maculata</i> Claus, 1879	14	Subtropical-tropical	Sap
<i>Eupronoe minuta</i> Claus, 1879	34	Subtropical-tropical	Si
<i>Paralycaea gracilis</i> Claus, 1880	1	Subtropical	Me
<i>Parapronoe cambelli</i> Stebbing, 1888	1	Subtropical-tropical	
<i>Parapronoe crustulum</i> Claus, 1879	2	Subtropical-tropical	
<i>Parapronoe parva</i> Claus, 1879	2	Subtropical-tropical	
<i>Pronoe capito</i> Guérin-Méneville, 1836	4	Tropical	

Table 1 (continued)

Species	NS	Biogeography	Host
Family Lycaeidae			
<i>Lycaea pachypoda</i> (Claus, 1879)	6	Subtropical–tropical	Me, Sa, Py
<i>Lycaea pauli</i> Stebbing, 1888	9	Tropical?	
<i>Lycaea pulex</i> Marion, 1874	21	Temperate–subtropical (3)	Sa, Py
<i>Lycaea serrata</i> Claus, 1879	9	Tropical	
<i>Simorhynchotus antennarius</i> (Claus, 1871)	8	Subtropical–tropical	Me
Family Tryphanidae			
<i>Tryphana malmi</i> Boeck, 1870	11	Temperate–subtropical (3)	Me (7), Si
Family Brachyscelidae			
<i>Euthamneus rostratus</i> (Bovallius, 1887)	1	Warm–temperate cosmopolite	Me (6)
Family Oxycephalidae			
<i>Calamorrhynchus pellucidus</i> Streets, 1878	17	Subtropical–tropical	
<i>Oxycephalus clausi</i> Bovallius, 1887	3	Warm–temperate cosmopolite (4)	Ra, Ct, Me, He, Sa
<i>Oxycephalus piscator</i> Milne-Edwards, 1830	3	Subtropical–tropical (4)	Ct
<i>Rhabdosoma brevicaudatum</i> Stebbing, 1888	1	Subtropical–tropical	
<i>Rhabdosoma minor</i> Fage, 1954	1	Subtropical–tropical	
<i>Rhabdosoma whitei</i> Bate, 1862	5	Warm–temperate cosmopolite	Ct
<i>Streetsia challengeri</i> Stebbing, 1888	21	Warm–temperate cosmopolite*	
<i>Streetsia porcella</i> (Claus, 1879)	1	Tropical	Ra, Ct
<i>Streetsia steenstrupi</i> (Bovallius, 1887)	11	Subtropical–tropical	
Family Platyscelidae			
<i>Amphithyrus sculpturatus</i> Claus, 1879	15	Subtropical–tropical	
<i>Hemityphis tenuimanus</i> Claus, 1879	2	Subtropical–tropical	
<i>Paratyphis promontori</i> Stebbing, 1888	1	Tropical	
<i>Paratyphis spinosus</i> Spandl, 1924	1	Subtropical	
<i>Platyscelus ovoides</i> (Risso, 1816)	22	Tropical	Me
<i>Platyscelus serratulus</i> Stebbing, 1888	4	Subtropical–tropical	
Family Parascelidae			
<i>Hemiscelus diplochelatus</i> Stewart, 1913	4	Tropical?	
<i>Parascelus edwardsi</i> Claus, 1879	11	Subtropical–tropical	Si
<i>Parascelus typhoides</i> Claus, 1879	8	Subtropical–tropical	Si (6)

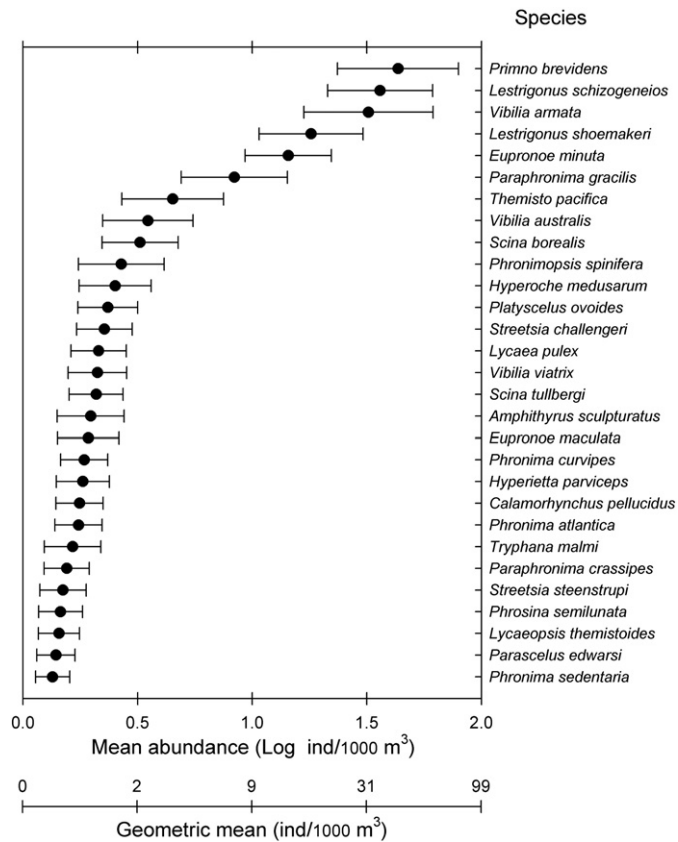
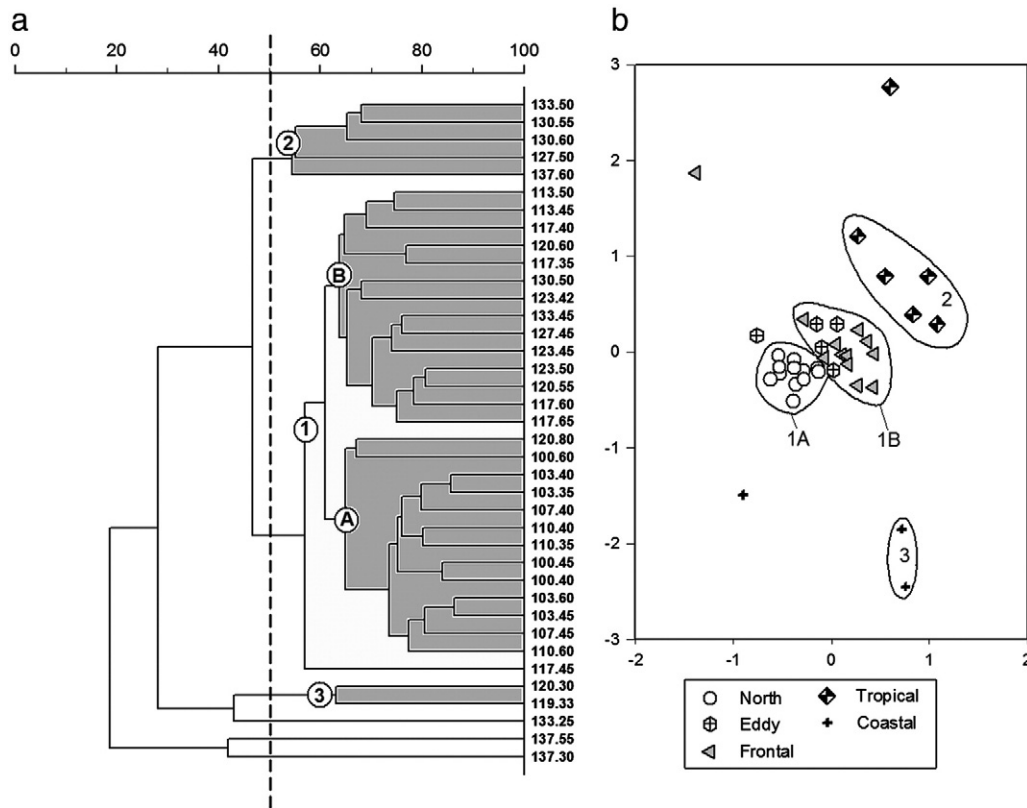


Fig. 2. Mean abundance and 95% confidence interval of hyperiid species during July 2002 off Baja California. Only the common species occurring in at least 25% of the samples are shown. Data were log-transformed. Additional axis at the bottom shows the retransformed mean: (antilogarithm  $\bar{x}$ ) - 1.

(Fig. 5a) with midway position in the MDS between tropical and transition zone groups (Fig. 5b). Species in these subgroups had variable distribution patterns. Some were abundant in the cyclonic eddy and frontal structures (*Vibilia australis*, *Vibilia viatrix*, *Lycaea pulex*), whereas others were absent in the eddy (*Lycaeopsis themistoides*, *Parascelus edwardsi*) or scattered in the oceanic zone (*Calamorrhynchus pellucidus*, *Phronima atlantica*).

### 3.3. Relation with environmental factors

The 41 common hyperiid species submitted to principal component analysis contributed 72.6% of the variance explained by five principal components (Table 2). Approximately half of this variance was extracted by the first component (PC1), which reflected the latitudinal distribution of species, showing negative values for transition zone species dominant in the north and positive values for tropical species with a southern tendency (Supplemental Table 1). Multiple regression using the PC1 scores with five predictor variables (temperature at 10 and 150 m, salinity at 10 and 150 m, and salp abundance) was highly significant with  $R^2$  relatively elevated (Table 3). Of the five coefficients, only temperature at 150 m depth and salp abundance were significant. Transition zone species had negative PC1 loadings (Supplemental Table 1) and, therefore, a correspondence exists with low 150-m-temperatures typical of subarctic water. Positive loadings were associated with warm water. The inverse relationship between PC1 and salp availability indicated a higher abundance of salps with negative PC1 loadings (i.e., transition zone species). Thus, in the area where transition zone species predominated, the subsurface temperature was low and numerous salps were available as substrate for the amphipods. However, the variability of salp abundance was high and had a low correlation with subsurface temperature ( $R^2 = 0.196$ ). Except for two stations that recorded 13 °C and had no salps, the rest of the stations had temperatures of 9–12 °C and a variable amount of salps, which tended to be more abundant in the northern part and the eddy.



**Fig. 3.** Similarity among sampling stations: (a) dendrogram with dashed line indicating the cutoff level and resultant clusters; (b) non-metric multidimensional scaling ordination (stress = 0.13). Symbols correspond to mesoscale structures and the clusters defined in the dendrogram (1A, 1B, 2, 3) are encircled.

The second principal component (PC2) explained 16.5% of the variance (Table 2), with high negative loadings for the most northern species (*P. spinifera*, *T. pacifica*, and *T. malmi*). Positive loadings corresponded to three species of *Vibilia* and *Eupronoe maculata*. Influential variables in the multiple regression analysis were temperature at 10 m depth and salp abundance, both with positive coefficients in the regression equation. Once again, the relationship between salps and temperature presented low correlation ( $R^2 = 0.110$ ). Salp abundance varied regardless of the surface temperatures and also varied within the mesoscale structures, tropical stations presenting a slight tendency to low salp values. Only two stations had temperatures around 23 °C; at most of the stations temperature ranged from 16 to 21 °C. Salps and total amphipod abundances were strongly correlated (Fig. 6).

Three principal components (PC3, PC4, and PC5) contributed individually less than 10% of the variance (Table 2). Species loadings are difficult to interpret in PC3, but a tendency to high positive loadings was observed for tropical species. Multiple regression of PC3 with the ecosystem variables was significant but had a low  $R^2$  and no coefficient was significant (Table 3).

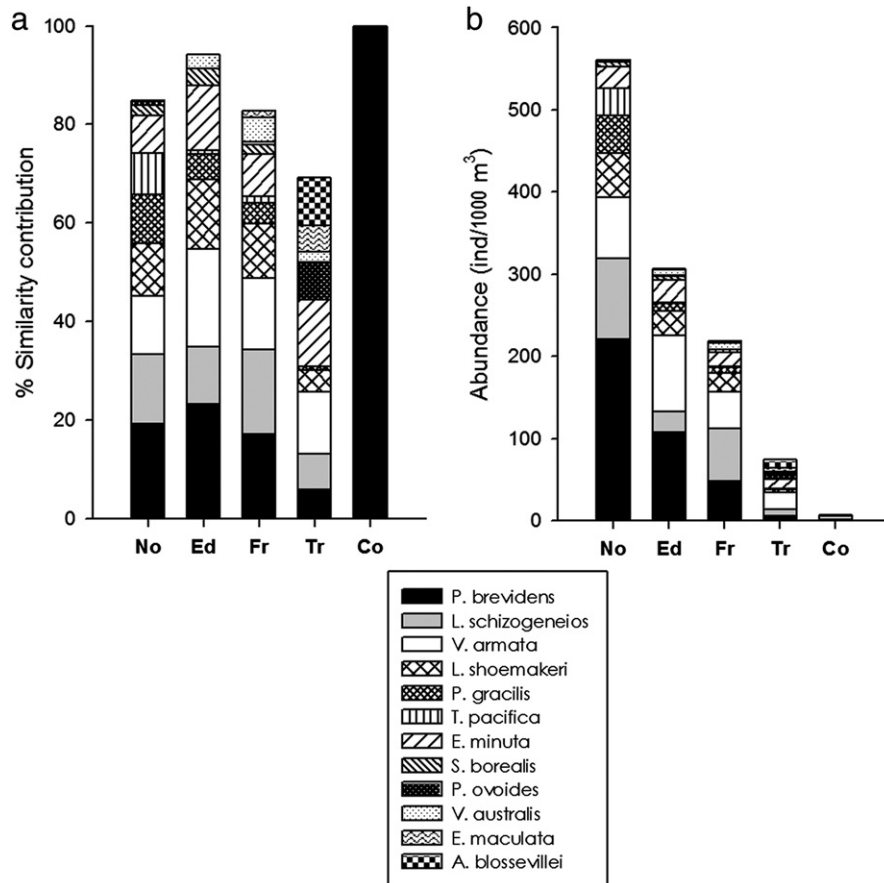
The biogeographic assemblages (clusters I and II) obtained revealed the different types of response among species. Stenotherm species such as *T. pacifica* were associated with the coldest water (Fig. 7a–b) but presented weak correlation with salp availability ( $R^2 = 0.203$ ). On the other hand, subtropical species such as *V. armata* presented low correlation with temperature at 150 m ( $R^2 = 0.149$ ) and 10 m depth ( $R^2 = 0.051$ ) but strong correlation with salp availability (Fig. 7c).

#### 4. Discussion

The CCS is a large marine ecosystem with transition conditions between subarctic and tropical biomes containing diverse habitats. Marine

biota has been intensively studied from the northern sectors to southern California waters, but the region off Baja California, clearly subtropical, has received less attention. At Point Conception (35°N) the coastline bends toward the southeast and from this point to the tip of the Baja California peninsula (23°N) subtropical species are the dominant fauna, the presence of tropical species increasing progressively southward. In the present study, it was evident that a high abundance of total hyperiids occurred off northern Baja California, as would be expected in temperate regions at subarctic latitudes (Vinogradov et al., 1996).

The importance of understanding the subtropical communities of the Baja California sector is not exclusively local but necessary to understand the CCS as a whole. In this sense, the influence of the subarctic water intrusion that occurred in July 2002 affected not only the current upstream but reached Baja California waters as indicated by the biological evidence obtained in the present study. The main evidence of subarctic water advection was the extended distribution of *T. pacifica*, reaching as far south as 27°N, with particularly high abundances at 30–32°N. This outcome contrasts with the previous study by Lavaniegos and Hereu (2009) in which *T. pacifica* was scarcely recorded during the four seasons of 2005. This species was found scarcely in two samples collected in January and one in April, and was absent the rest of the year; therefore, its presence during July 2002 was probably due to advection of subarctic water in the region (Durazo et al., 2005). The distribution of *T. pacifica* was described by Bowman (1960) based on cruises performed off the western coast of the United States and Baja California. This author reported an area of large abundances of this species to the north of Point Conception and that it became sparse further south until disappearing near Punta Eugenia (28°N). *T. pacifica* also occurs in other subarctic locations and is clearly associated with subarctic water (Mackas et al., 2005; Yamada et al., 2004). This species forms large aggregations as has also been



**Fig. 4.** Main species of hyperiid amphipods from different mesoscale structures identified in Fig. 1: (a) mean similarity contribution; (b) geometric mean abundance. The species shown are a combination of the seven with highest similarity percentage in one or more of the mesoscale structures: No, North; Ed, Eddy; Fr, Frontal; Tr, Tropical; and Co, Coastal.

observed for other *Themisto* species in the cooler part of oceans (Auel and Ekau, 2009; Kraft et al., 2012; Marion et al., 2008; Padovani et al., 2012; Vinogradov et al., 1996).

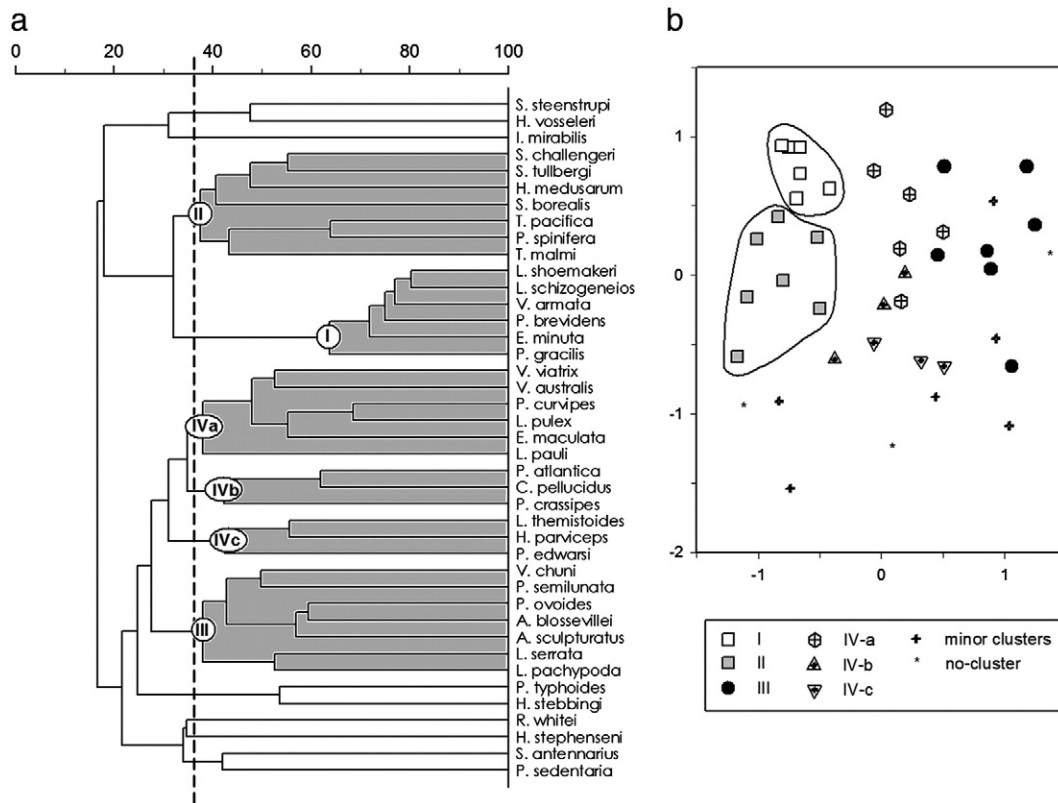
#### 4.1. Biogeographic assemblages

Species assemblages may be analyzed in two ways, either as areas containing common fauna or as groups of covariant species. The cluster analysis among species performed produced four clusters separating the biogeographic groups. Cluster I was a subtropical assemblage of six abundant and well-distributed species in the study area, joined by high similarity percentage: *V. armata*, *P. gracilis*, *L. schizogeneios*, *L. shoemakeri*, *P. brevidens*, and *E. minuta* (Fig. 5). These species are dominant in Baja California waters (Lavaniegos and Hereu, 2009), and some of them are also well represented in other regions of the CCS. *V. armata* was observed in large numbers in the Santa Barbara Passage, southern California (Brusca, 1967a), but was less common in northern regions off Oregon where it contributed only 10% of the hyperiids, while *P. gracilis* was the second most abundant with 56% (Lorz and Percy, 1975). Data from these authors were not standardized for filtered water, making it impossible to compare absolute abundances with the present study. Similar observations have been made for *P. brevidens* by Bowman (1978), who described this species as subtropical and considered its northern distribution limit to be Point Conception, becoming scarce north of this prominence where it is replaced by *Primno macropa*. Another species not recorded off Oregon (Lorz and Percy, 1975) but present in the Santa Barbara Passage was *E. minuta*, though less abundant than *V. armata* (Brusca, 1967a). Two cluster I species (*L. schizogeneios* and *L. shoemakeri*) were absent off Oregon and in southern California waters, though Brusca (1967a) reported *Lestrigonus bengalensis* in low

abundance. Species of the genus *Lestrigonus* are difficult to identify, and Bowman (1973) considered that it was a misidentification of *L. schizogeneios*. This species was found to be the second most abundant in California and Baja California waters and was replaced in the southernmost part of the CCS by the closely related *L. shoemakeri* (Bowman, 1973). Therefore, the correspondence of species in cluster I for southern sectors of the CCS indicates that the area may be considered subtropical and confirms the main assemblage for the Baja California region found in a previous study by Lavaniegos and Hereu (2009).

Cluster II was composed of temperate species headed by *T. pacifica* (Fig. 5) with moderate to high abundance in northern Baja California waters but with low presence in the south. Four species in cluster II (*T. pacifica*, *Streetsia challengerii*, *T. malmi*, and *Hyperoche medusarum*) were reported by Lorz and Percy (1975) as among the most common off New Port, Oregon, reinforcing the evidence of subarctic water intrusion off Baja California. Hyperiid species from cluster II (July 2002) were also common in the previous study by Lavaniegos and Hereu (2009), except for *T. pacifica*, and the tendency of *S. challengerii*, *T. malmi*, *H. medusarum*, and *Scina tullbergi* to increase in spring denoted the temperate affinity of these species. Both *Phronomopsis spinifera* and *Scina borealis* were equally abundant in the winter and spring of 2005 (Lavaniegos and Hereu, 2009). Low surface salinity (<33.3) was observed at the northern transects, limited to 30–32°N in the winter of 2005 but covering 50% of the Baja California area in the spring of 2005 (Durazo, 2009; Peterson et al., 2006). The presence of organisms carried from the north to Baja California during the subarctic intrusion was also documented for euphausiids as a result of the high abundance of *E. pacifica* (Lavaniegos and Ambriz-Arreola, 2012).

Cluster III species are primarily tropical (Fig. 5), although Vinogradov et al. (1996) described three of them (*V. chuni*, *A. blossevilliei*, and



**Fig. 5.** Similarity among 41 common species: (a) dendrogram with dashed line indicating the cutoff level and resultant clusters; (b) non-metric multidimensional scaling ordination (stress = 0.21). Symbols correspond to the main clusters defined in the dendrogram and the clusters separated from the rest are encircled.

*P. semilunata*) as warm-temperate cosmopolites. They were absent in the temperate waters off Oregon (Lorz and Percy, 1975), though Brusca (1981) referred to some records of *A. blossevillei* off Washington in his revision of the northeast Pacific hyperiids, while *P. semilunata* was found exclusively in California waters. The latter two species are regular inhabitants of the North Pacific Gyre (Shulenberg, 1977), and off Baja California they were associated with oligotrophic waters during the winter of 2005 (Lavaniegos and Hereu, 2009). In the present study, *A. blossevillei* had high abundances only in the southern part of the area.

Two other species in cluster III (*Lycaea pachypoda* and *Amphithyrus sculpturatus*) were designated as subtropical-tropical by Vinogradov et al. (1996) based on sparse [few] records, but Brusca (1981) only reported *A. sculpturatus* in Baja California waters. The rest of the cluster III species (*Lycaea serrata*, and *P. ovoides*) are considered tropical (Vinogradov et al., 1996). *P. ovoides* is a regular inhabitant of the central equatorial Pacific (Repelin, 1978) and was abundant in the present study at the southern stations. In contrast, dominant species from the Subtropical Pacific Gyre such as *Scina crassicornis*, *Hyperitta vosseleri*, *Lestrigonus bengalensis*, and *Primno latreillei* (Shulenberg, 1977) were rare (Table 1). Also scarce were species recorded in high abundance in the eastern tropical Pacific, such as *Hyperioides sibaginis* and *L. bengalensis* (Gasca and Franco-Gordo, 2008; Gasca et al., 2012; Valencia and Giraldo, 2009, 2012; Valencia et al., 2013). However,

**Table 2**  
Principal component analysis of hyperiid amphipods off Baja California during July 2002. Data matrix included abundances of 41 species transformed to logarithms.

PC	Eigenvalues	% Variation	Cum % variation
1	15.50	32.3	32.3
2	6.86	16.5	53.8
3	3.21	7.7	61.6
4	2.39	5.7	67.3
5	2.19	5.3	72.6

those studies are biased to small amphipods due to sampling near the coast (Gasca and Franco-Gordo, 2008; Gasca et al., 2012; Valencia and Giraldo, 2009) and, in the case of the Colombian studies (Valencia and Giraldo, 2009, 2012; Valencia et al., 2013), a different net type (30 cm mouth diameter, 250  $\mu$ m mesh width) was used.

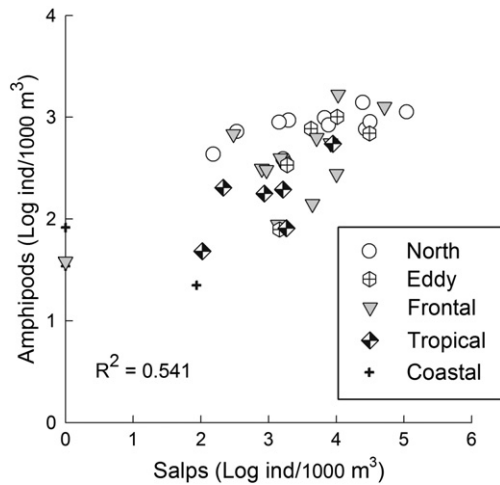
Other species of lesser abundance and variable distribution patterns (Table 1) were grouped in cluster IV, which may be considered of minor importance due to weak similarity (Fig. 5). Only *V. australis* had relevant similarity at the frontal stations and *E. maculata* in the south (Fig. 4). Therefore, compared to the southern stations (tropical and frontal mesoscale structures), hyperiids were more abundant in the northern part of the study area and consisted mainly of subtropical species (cluster II). The geometric mean for the northern stations was 750 ind/1000 m<sup>3</sup>, which is 254% higher than that observed in July 2005. This means that the subarctic intrusion resulted in an enrichment of hyperiid amphipods.

The ecological relevance of clusters 1 and 2 that contain species with high abundances may be better appreciated when compared with data

**Table 3**  
Multiple regression analysis between principal components (PC) and ecosystem variables: PC = a + b<sub>1</sub>(T<sub>10</sub>) + b<sub>2</sub>(S<sub>10</sub>) + b<sub>3</sub>(T<sub>150</sub>) + b<sub>4</sub>(S<sub>150</sub>) + b<sub>5</sub>(SA). Standard error is shown and significance of the model and each coefficient is indicated: (\*) p < 0.05, (\*\*) p < 0.01, and (\*\*\*) p < 0.001. Predictor variables are 10 m temperature (T<sub>10</sub>), 10 m salinity (S<sub>10</sub>), 150 m temperature (T<sub>150</sub>), 150 m salinity (S<sub>150</sub>), and salp abundance (SA) transformed to logarithms (Log ind/m<sup>3</sup>). N = 38.

Parameters	PC1	PC2	PC3
R <sup>2</sup>	0.709***	0.546***	0.364**
a	-8.1 ± 97.6	92.3 ± 81.2	-160.8 ± 65.7*
b <sub>1</sub> (T <sub>10</sub> )	0.24 ± 0.48	0.90 ± 0.40*	0.63 ± 0.33
b <sub>2</sub> (S <sub>10</sub> )	3.71 ± 4.34	-4.82 ± 3.61	-1.38 ± 2.92
b <sub>3</sub> (T <sub>150</sub> )	1.91 ± 0.76*	1.06 ± 0.63	0.04 ± 0.52
b <sub>4</sub> (S <sub>150</sub> )	-4.02 ± 3.07	1.13 ± 2.55	-3.71 ± 2.06
b <sub>5</sub> (SA)	-1.25 ± 0.43**	1.13 ± 0.36**	0.20 ± 0.29



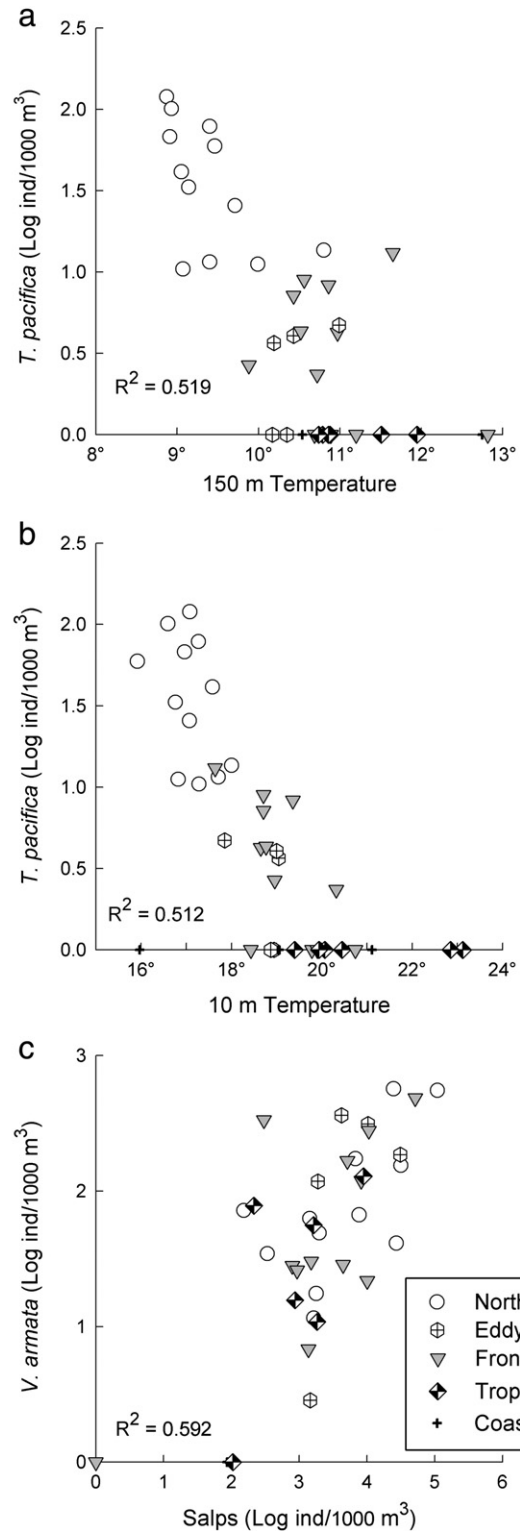


**Fig. 6.** Amphipod abundance as a function of salp abundance. Symbols correspond to the mesoscale structures.

from the summer of 2005 (Table 4). The abundances of four of the subtropical species and one subarctic species differed significantly in northern Baja California waters. How much biomass does this abundance represent? Recently, Ikeda (2013) reviewed proximal and metabolic parameters of pelagic amphipod species pertaining mainly to subarctic and arctic biomes. Applying information on *Primno abyssalis* and *Themisto japonica* from the Japan Sea to the congeners *P. brevidens* and *T. pacifica*, the carbon mass resulted in values of 16 and 4 mg/1000 m<sup>3</sup> for the geometric means of July 2002 respectively, in the northern Baja California region (Table 4). In contrast, in July 2005, the value for *P. brevidens* was only 1 mg/1000 m<sup>3</sup> and for *T. pacifica* was zero. These figures may appear unimpressive but they represent an increment in amphipod biomass available for planktivorous fishes and other predators in the oceanic zone. In cool regions the importance of hyperiids linking herbivorous mesozooplankton and higher trophic levels is well known (Dalpadado, 2002; Naydenko, 2009; Pinchuk et al., 2013), but they also play a similar role in temperate regions like the CCS particularly during summer and fall (Schabetsberger et al., 2003; Suntsov and Brodeur, 2008).

#### 4.2. Limited influence of the 2002–2003 El Niño

It should be noted that the intrusion of subarctic water took place even though an El Niño event was in progress (McPhaden, 2004; Mosquera-Vásquez et al., 2013). Equatorial surface current fields computed from satellite measurements moved eastward from July 2002 and the sea surface temperature anomalies peaked in November 2002 (Lagerloef et al., 2003). Thus, zonal advection due to El Niño intersected the equatorward flow of the subarctic intrusion during July 2002 and probably produced the large cyclonic eddy off Baja California. Venrick et al. (2003) commented that subarctic intrusion was not evident in the Baja California region. Certainly the low salinity values affecting the CCS during July 2002 were less notable off Baja California compared to the upstream northern regions, but two points must be considered: 1) the subarctic water mass suffered a slight but gradual modification during its course from Canada to Baja California, and 2) the mesoscale activity could have masked in part the subarctic origin of the water. In regard to latitudinal differences, Lynn and Simpson (1987) reported a salinity minimum of 33.0 for the upper 100 m layer off Point Reyes (38°N, CALCOFI line 60) and of 33.5 off Punta Baja (30°N, CALCOFI line 110). In July 2002, the presence offshore of a cyclonic eddy of large dimensions (~200 km in diameter) also contributed to a slight increase in salinity. In the present study, faunal evidence suggested a mixing of subarctic and subtropical water reflected both in total hyperiid abundance (Fig. 4b) and species composition (Fig. 3). The hyperiid



**Fig. 7.** Relationship between selected variables and abundances of *Themisto pacifica* and temperature at 150 m (a) and 10 m depth (b), and between abundances of *Vibilia armata* and salps (c). Symbols correspond to the mesoscale structures.

assemblage in the cyclonic eddy was similar to that of the frontal stations and both had a blended structure between the north and tropical community. Therefore, the results of the present study are consistent with the interpretation of subarctic water trapped by the subtropical water flowing from the southwest (Venrick et al., 2003). The presence of species conforming different faunal assemblages in latitudinal extremes is expected due to the thermal gradient characteristic of the

**Table 4**  
Geometric mean nighttime abundance (ind/1000 m<sup>3</sup>) for selected species from oceanic and coastal regions off Baja California during July 2002 and July 2005. Resultant probability from the nonparametric comparison (Mann–Whitney) is shown highlighting values <0.05. The species were grouped in the three strongest clusters derived from the similarity analysis in July 2002. Numbers in brackets are the geometric mean of carbon biomass (mg/1000 m<sup>3</sup>).

Cluster/species	North (29.5–32°N)			Central (25–29.5°N)			Coastal	
	2002	2005	p	2002	2005	p	2002	2005
	n = 12	n = 14		n = 23	n = 23		n = 5	n = 4
Cluster 1 (subtropical)								
<i>Vibilia armata</i>	75	51	0.631	43	52	0.811	–	–
<i>Paraphronima gracilis</i>	46	6	<0.001	4	4	0.711	–	–
<i>Lestrigonus schizogeneios</i>	98	2	<0.001	31	13	0.130	5	–
<i>Lestrigonus shoemakeri</i>	53	2	<0.001	16	5	0.021	1	–
<i>Primno brevidens</i> <sup>a</sup>	221	12	<0.001	34	36	0.459	1	21
	[16]	[1]	<0.001	[4]	[4]	0.744	[1]	[3]
<i>Eupronoe minuta</i>	26	28	0.820	17	31	0.095	–	1
Cluster 2 (subarctic)								
<i>Scina borealis</i>	5	1	0.046	2	1	0.079	–	1
<i>Scina tullbergi</i>	3	9	0.015	1	5	<0.001	–	1
<i>Hyperoche medusarum</i>	2	2	0.860	2	4	0.155	–	2
<i>Phronimopsis spinifera</i>	16	1	<0.001	<1	1	0.305	–	–
<i>Themisto pacifica</i> <sup>b</sup>	33	–		1	–		–	–
	[4]			[<1]				
<i>Tryphana malmi</i>	4	2	0.212	<1	<1	0.777	–	–
<i>Streetsia challengerii</i>	4	2	0.118	1	1	0.256	–	–
Cluster 3 (tropical)								
<i>Vibilia chuni</i>	–	<1		1	–		–	–
<i>Anchylomera blossevillei</i>	–	<1		1	2	0.238	–	–
<i>Phrosina semilunata</i>	–	1		1	4	0.001	–	–
<i>Lycaea pachypoda</i>	<1	<1	0.297	<1	<1	0.433	–	–
<i>Lycaea serrata</i>	–	–		1	1	0.433	–	–
<i>Amphithyrus sculpturatus</i>	–	–		2	1	0.021	–	2
<i>Platyscelus ovooides</i>	2	1	0.297	2	2	0.744	–	–

<sup>a</sup> Body length was converted to dry weight based on the function DW ( $\mu\text{g}$ ) = 3.24 BL<sup>2.99</sup> of *Primno abyssalis* from the Japan Sea (Ikeda, 1995). Carbon = 39.0% DW estimated for *P. abyssalis* from the Japan Sea by Ikeda and Hirakawa (1998).

<sup>b</sup> Using DW ( $\mu\text{g}$ ) = 4.9 BL<sup>2.957</sup> of *Themisto japonica* from the Japan Sea (Ikeda, 1990). Carbon = 47.9% DW as estimated for *T. pacifica* (Yamada et al., 2004).

California Current. The eddy, however, deformed this thermal gradient during July 2002 and appears to have worked as a barrier to the displacement of the species coming into the area from the north, maintaining the influence of tropical species limited to the southern offshore stations. The constrained distribution of tropical species to the southern transects is unexpected for El Niño; on the contrary, a widespread presence of these species should be the scenario as occurred with copepods (Jimenez-Pérez and Lavaniegos, 2004), euphausiids (Lavaniegos and Ambríz-Arreola, 2012) and salps (Hereu et al., 2006) during the 1997–1998 El Niño.

#### 4.3. Relation with environmental factors

In the present study, the ‘transition zone species’ species, typical of the California Current, had negative PC1 loadings (Supplemental Table 1), corresponding to the lowest 150-m-temperatures of subarctic water. In contrast, the positive PC1 loadings corresponded to tropical species associated with warm water, and this warm water affected only two stations in the southwestern part of the study area. Though both low temperature and low salinity are characteristic of subarctic water in the present study, temperature was primarily responsible for structuring the hyperiid amphipod assemblages. Subsurface temperature (150 m) showed the influence of subarctic water in the Baja California region better. Lynn and Simpson (1987), in their extensive study of the CCS, showed that off central California (38°N) salinity is lowest at the surface and that in Baja California the subsurface core occurred/occurs at 50–100 m depth. This subarctic water blocked the progress of El Niño, and the strong relationship between species composition and temperature corroborates the advection of that water mass entering from the north.

Epipelagic species are more susceptible to changes in upper layer temperatures and are good indicators of water advection. This apparently occurred with *T. pacifica*, which showed a strong relation with

temperature (Fig. 7a–b). This species mainly inhabits the upper 200 m though it may be observed in small numbers down to 900 m depth (Yamada et al., 2004). Many hyperiid species are distributed in broad vertical ranges but are more abundant in the upper layer at least during the night (Macquart-Moulin, 1993; Vinogradov et al., 1996). There is limited research addressing the vertical distribution of hyperiid amphipods, particularly in subtropical and tropical regions. Brusca (1967b) found evidence of extensive vertical migration for *V. armata* in the Santa Barbara Passage, southern California, which disappears from the upper 200 m during daytime. Similar observations have been made for *V. armata* in the Canary Current (Thurston, 1976), the Benguela Current (Cornet and Gili, 1993), and the Mediterranean (Macquart-Moulin, 1993); however, Siegel-Causey (1982) found differences among stations in the Gulf of California. This species may change its behavior in the presence of salps as they give shelter (Laval, 1980), and a strong correlation between the abundances of *V. armata* and salps was found in the present study (Fig. 7C) and in a previous study in the Baja California region (Lavaniegos and Hereu, 2009).

In contrast, *Themisto* species are considered to be ‘free living’ species (Vinogradov, 1999; Vinogradov et al., 1996). Ikeda (2013) analyzed the metabolic rates of different species of hyperiid amphipods and determined a respiration rate value for *T. pacifica* (1.71  $\mu\text{O}_2 \text{ ind}^{-1} \text{ h}^{-1}$ ) similar to that of other free living crustaceans. The absence of correlation between *T. pacifica* and salps in the present study also suggests that it is a free living species. Some hyperiid species such as *Phronima* and *Phronimella* depend on gelatinous substrates for extended maternal care (Aoki et al., 2013). Other species like *Hyperoche mediterranea* (Hoogenboom and Hennen, 1985), *V. armata* and *L. schizogeneios* (Laval, 1980) deposit embryos with variable stages of development in a gelatinous host. However, the parasitoid condition of other hyperiid species is less known though some authors consider that most of the hyperiids show some type of parasitism and could even be responsible for the end of some salp blooms (Deibel and Paffenhöfer, 2009).

## 5. Conclusions

In the present paper, evidence has been presented of subarctic water intrusion affecting the terminal portion of the California Current, as previously shown for northern sectors. El Niño signals such as high surface temperature and abundance of tropical species were constrained to a small section in the southwestern part of the study area. The best indicator species was the subarctic species *T. pacifica*, which was apparently carried into the region by surface waters. These findings support the explanation given by Freeland and Cummins (2005) of a southward shift of the North Pacific Current that bifurcates to form the California Current. The main factors influencing the amphipod assemblage structure were temperature and the availability of salps.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jmarsys.2013.12.012>.

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