SEASONAL VARIABILITY OF PELAGIC AMPHIPODS OFF BAJA CALIFORNIA DURING LA NIÑA 2011 AND COMPARISON WITH A "NEUTRAL YEAR" (2005)

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ABSTRACT

We describe the seasonal variation of hyperiid amphipods in oceanic waters between Punta Eugenia and Punta Abreojos, Baja California, during 2011, a cool year due to the influence of La Niña. Mean sea surface temperature in the study area was similar from January to July (16°–17°C) but cooler than usual, with anomalies of −1 to −3°C in the context of 1997–2013. Further, SST increased 3°C in October, restoring the typical temperature during this month (21°C). Vertical salinity profiles were also similar during January, April, and July, showing the influence of subarctic water in the upper layer (33.3–33.7 psu), while in October a range of higher values (33.5–33.8 psu) was observed due to the influence of subtropical water. We recorded 63 hyperiid amphipod species in 2011, the lowest number in January and the highest in October (17 and 54, respectively). Despite seasonal changes in diversity, few species (*Eupronoe minuta*, *Primno brevidens*, *Lestrigonus schizogeneios*, and *Simorhynchotus antennarius*) were the most abundant throughout the year. The exception was the warm-water species *Lestrigonus bengalensis*, which was the second most abundant in October, indicating the influence of subtropical oceanic water. Similarity analysis showed similar communities for spring and summer, while winter and autumn were very dissimilar from each other and differed from the spring–summer cluster. However, the species with highest contribution to similarity were the same (*E. minuta*, *L. schizogeneios*, and *P. brevidens*) but with different proportions. A matrix of environmental variables was correlated with the amphipod similarity matrix through a BIOENV analysis. The best combination of environmental variables ($\rho S = 0.644$) was the 10 m depth temperature, 10 m depth salinity, mixed layer depth, stratification in the upper 100 m, and zooplankton volume (this last used as a proxy for host availability). Finally, when the community structure was compared with data from a previous amphipod study (2005), we found that species composition was very similar, but seasonal differences in the abundance of 30 of the 52 common species persist possibly due to the effects of La Niña.

INTRODUCTION

Hyperiid amphipods are marine pelagic crustaceans. The ecology of hyperiids is better known in temperate and polar regions due to their importance in food webs (Dalpadado et al. 2001; Armstrong et al. 2005; Collins et al. 2008). They have been found in stomach contents of fishes and vertebrates from tropical and subtropical regions (Repelin 1978; Satoh 2004; Mostarda et al. 2007). Amphipods exhibit symbiotic or parasitoid relationships with gelatinous organisms such as salps, ctenophores, siphonophores, and medusae (Laval 1980). Amphipod species have been used as indicator organisms because they are diverse and respond rapidly to climate events like El Niño and La Niña (Gasca et al. 2012), to decadal changes (Lavaniegos and Ohman 1999), and to the influence of mesoscale circulation (Gasca 2004; Gasca and Suarez-Morales 2004; Lavaniegos and Hereu 2009).

Few studies describing species composition in tropical regions have addressed the effects of climate variability. Gasca et al. (2012) analyzed the seasonal and interannual variability of hyperiids off the Jalisco coast during 1995–98. They observed a seasonal pattern, with one period influenced by cool water from the California Current (February–June) and another period influenced by warm water from the North Equatorial Countercurrent (July–December). Species richness and evenness were higher in the first, whereas *Hyperioides sibaginis* and *Lestrigonus bengalensis* dominated in the second. These species were particularly abundant during El Niño 1997–98. Further, Valencia et al. (2013) compared amphipod assemblages in Panama Bay during the wet and dry seasons of 2007–08. The most abundant species were also *H. sibaginis* and *L. bengalensis*, with less diversity in the neritic zone during the rainy season.

Another eastern Pacific region analyzed for seasonal variability in hyperiid abundance is the California Current (CC). Studies have been conducted in the Santa Barbara Channel (Brusca 1967a,b), off the Oregon coast (Lorz and Pearcy 1975), and off Baja California (Lavaniegos and Hereu 2009). These studies showed a mainly oceanic distribution and increasing abundance during the course of the year. Brusca (1967a) performed stratified sampling between summer 1962 and spring

1963 that suggested vertical migration for *Streetsia challengeri*, *Lestrigonus schizogeneios*, and *Primno brevidens* (the latter two reported as *Hyperia bengalensis* and *Primno macropa*). Lorz and Pearcy (1975) did not find evidence of vertical migration off Oregon over a longer period (1963–67) though only two strata were sampled (0–150 y 150–450 m). They observed some interannual variability, which was associated with a warm year in 1963, some species (*Hyperia medusarum*, *Hyperoche medusarum*, *Paraphronima gracilis*, *S. challengeri*, and *Tryphana malmi*) presenting higher abundances in the offshore region.

The most recent study on seasonal variation in the CC covered an extended area off north and central Baja California in 2005, and found minimum abundance of total amphipods in January and maximum in October (Lavaniegos and Hereu 2009). Similarity analysis showed a group associated with the main flow of the CC (*Vibilia armata*, *Lestrigonus schizogeneios*, *Eupronoe minuta*, and *Primno brevidens*), and faunistic identity for some mesoscale structures. Based on that study, the objective of the present research is to characterize the seasonal variation in hyperiid amphipod abundance during 2011 and elucidate the influence of La Niña 2010–12. The selected study area, between Punta Eugenia and Punta Abreojos (fig. 1), has high presence of tropical species and is more vulnerable to cooling.

The 2010–12 La Niña event was intense and prolonged in the Pacific Ocean. It started in July 2010, enhanced at the end of 2010 (Nam et al. 2011; Boening et al. 2012; Feng et al. 2013), and subsequently decreased in June–July 2011, though a second pulse occurred from late 2011 to mid-2012 (Hu et al. 2014). In the California Current System (CCS), intense upwelling was recorded in summer 2010, with negative temperature anomalies (1˚–2˚C) and low oxygen levels at some locations (Nam et al. 2011). SST anomalies off Baja California reached more negative values during La Niña 2010–12 than during La Niña 1999–2000, particularly in October 2010 and January 2011 (Bjorkstedt et al. 2011). Chlorophyll concentration presented positive anomalies and the zooplankton contained abundant medusae year round (Bjorkstedt et al. 2012; Lavaniegos et al. 2015).

METHODS

Study Area

The CCS is one of the large marine eastern boundary upwelling ecosystems, and presents high variability at different time scales. The strength of the current and mixing of the water masses vary seasonally. In spring, intense northwestern winds induce coastal upwelling and the strength of the CC is maximal, transporting a higher volume of subarctic water. As the current advances to the equator the wind field weakens, and the

water is modified as a result of solar warming and mixing with subtropical water (Lynn and Simpson 1987). There is high mesoscale activity such as fronts, eddies, and squirts (Soto-Mardones et al. 2004; Jerónimo and Gómez-Valdés 2007).

The study area is located in the subtropical sector of the CCS between Punta Eugenia and Punta Abreojos (fig. 1). Punta Eugenia is considered the highest coastal prominence of the CCS and a zone of oceanographic transition (Durazo and Baumgartner 2002; Jerónimo and Gómez-Valdés 2006), with upwelling occurring year round (Zaytsev et al. 2003; Torres and Gómez-Valdés 2015). The equatorward flow prevails to the south of Punta Eugenia though the influence of the equatorial current system is perceived, mainly the North Equatorial Countercurrent, which flows eastward to the coasts of Central America and gains strength from August to January (Kessler 2006). This promotes the entrance of subtropical water off southern Baja California, slightly increasing surface salinity.

Sampling and Taxonomic Analysis

Zooplankton samples were taken during four IMECOCAL cruises performed in 2011 (fig. 1). The sampling dates for the selected study were January 1–2, April 22–25, July 14–17, and October 17–19. Oblique tows were performed at 0–200 m depth using a bongo net of 500 μm mesh width and 71 cm mouth diameter. Filtered water volume was recorded with a flowmeter in front of the net. The zooplankton samples were preserved with 4% formaldehyde buffered with sodium borate (Smith and Richardson 1977). Hydrocasts were made with a Seabird CTD in the upper 1000 m to obtain temperature and salinity data.

Thirty-five samples were analyzed for hyperiid amphipods. Two coastal shelf stations (bottom <200 m depth) where amphipods were scarce were excluded (fig. 1). All amphipods in the sample were counted and identified to species using the taxonomic keys given by Bowman (1973), Brusca (1981), and Vinogradov et al. (1996).

Data Analysis

Similarity of amphipod communities was analyzed using the Bray-Curtis index for the complete abundance database (35 samples x 63 species). We prepared a dendrogram based on the similarity matrix using the group average. Statistical significance of clusters was established with the SIMPROF test (PRIMER v.6; Clarke and Warwick 2001). Additionally, we performed a nonmetric multidimensional scaling (NMDS) analysis to supplement the ordination obtained in the dendrogram. The contribution to similarity by species in each cluster was estimated with SIMPER (Clarke and Warwick 2001).
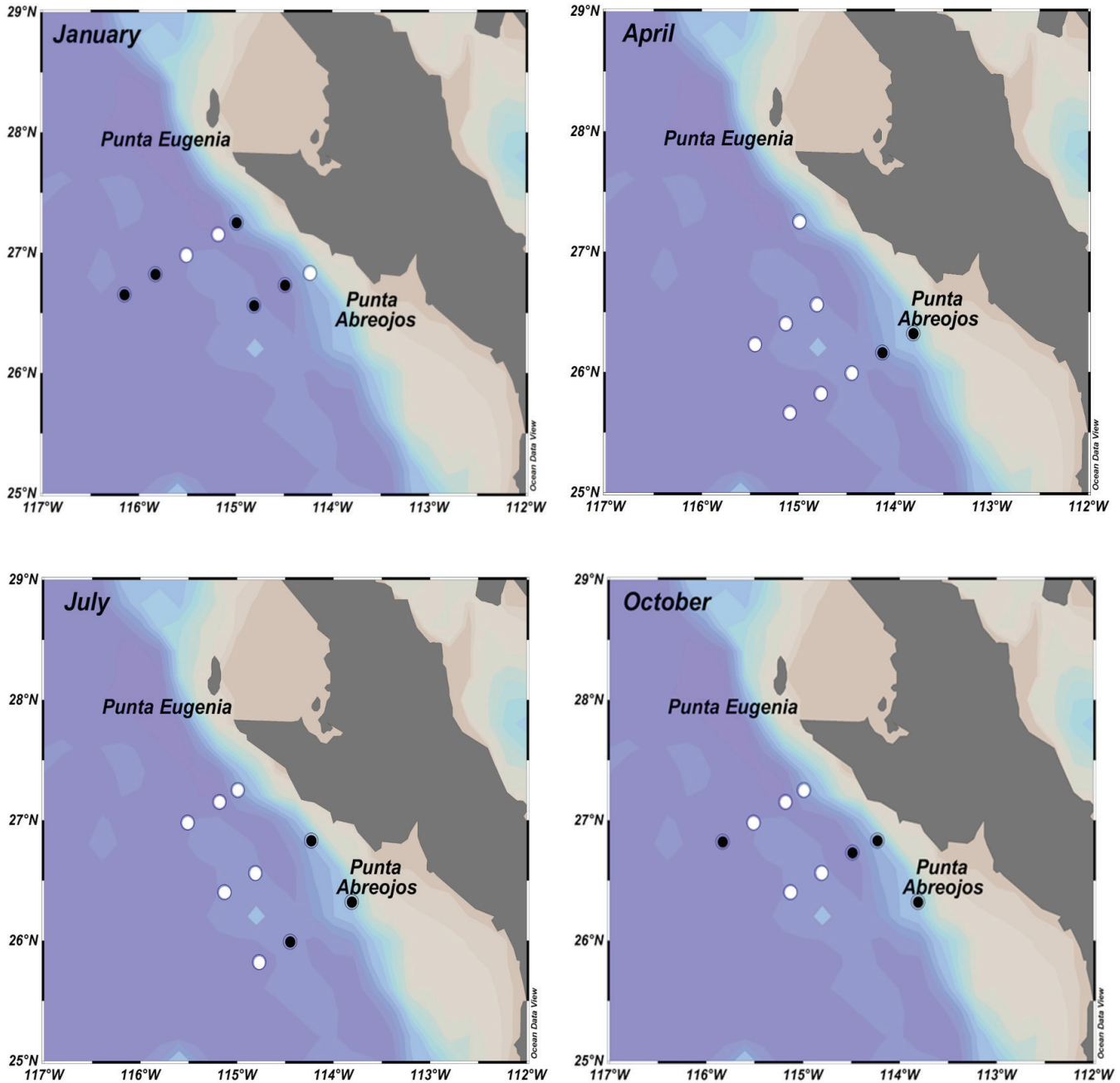
Figure 1.   Sampling stations during 2011. White (black) symbols indicate occupancy during daytime (nighttime). Gray area is the coastal shelf (<200 m depth).

Evaluation of biophysical coupling was done with the BIO–ENV procedure found in Primer (Clarke and Warwick 2001). This analysis performs Spearman correlation between two similarity matrices, one is the amphipod species matrix and the other is the explanatory matrix based on Euclidian distances among environmental variables (table 1). The community matrix is fixed and for the environmental matrix, all subsets of possible combinations of variables are examined to select the best combination, that is, the one that maximizes the Spearman correlation coefficient. The depth of the mixed layer was defined as the depth where temperature changed 0.5°C relative to SST. The stratification index, based on density, was calculated following Simpson et al. (1978) for layers of 0–50, 0–100, and 0–200 m depth.

The hyperiid community of 2011 was compared with previous data from 2005 using similarity analysis. The abundances of dominant amphipod species were compared by a two-factor analysis of variance between year and month, previous transformation of data to log–

TABLE 1
Environmental variables used in correlation analysis with the similarity matrix of amphipod species through the BIOENV analysis.

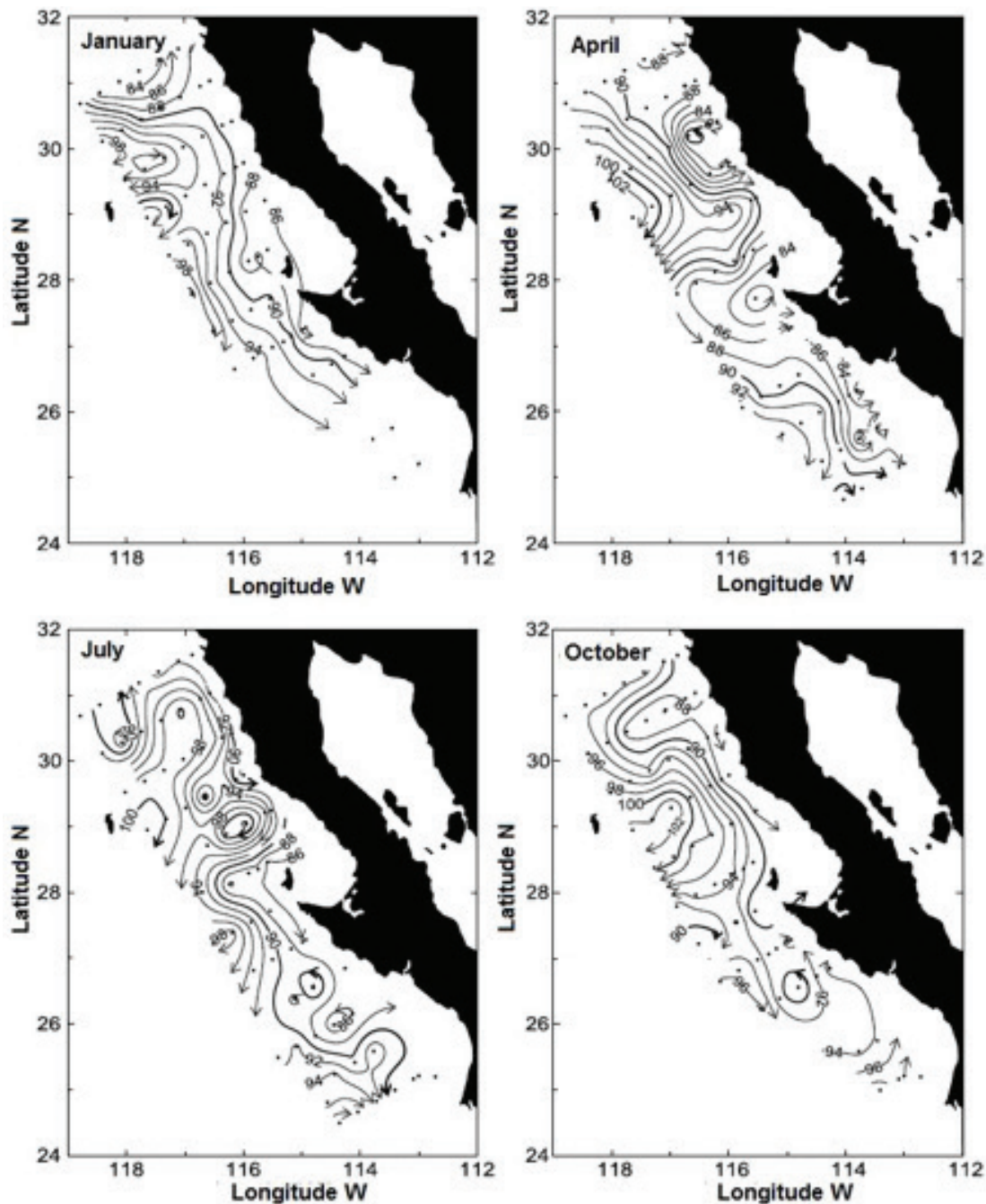| Variable	Abbreviation
Temperature at 10, 30, 50, and 200 m depth	T10, T30, T50, T200
Salinity at 10, 30, 50, and 200 m depth	S10, S30, S50, S200
Dissolved Oxygen at 10, 30, 50, and 200 m depth	DO10, DO30, DO50, DO200
Mixed Layer Depth	MLD
Stratification Index from surface to 50, 100, and 200 m	SI50, SI100, SI200
Integrated Chlorophyll *a*	Ch-*a*
Zooplankton Biomass	ZB

Figure 2. Geostrophic flow during 2011 estimated from 0/500 dbar dynamic height anomalies. Contour interval is 2 dynamic cm. Current direction is indicated by arrows.
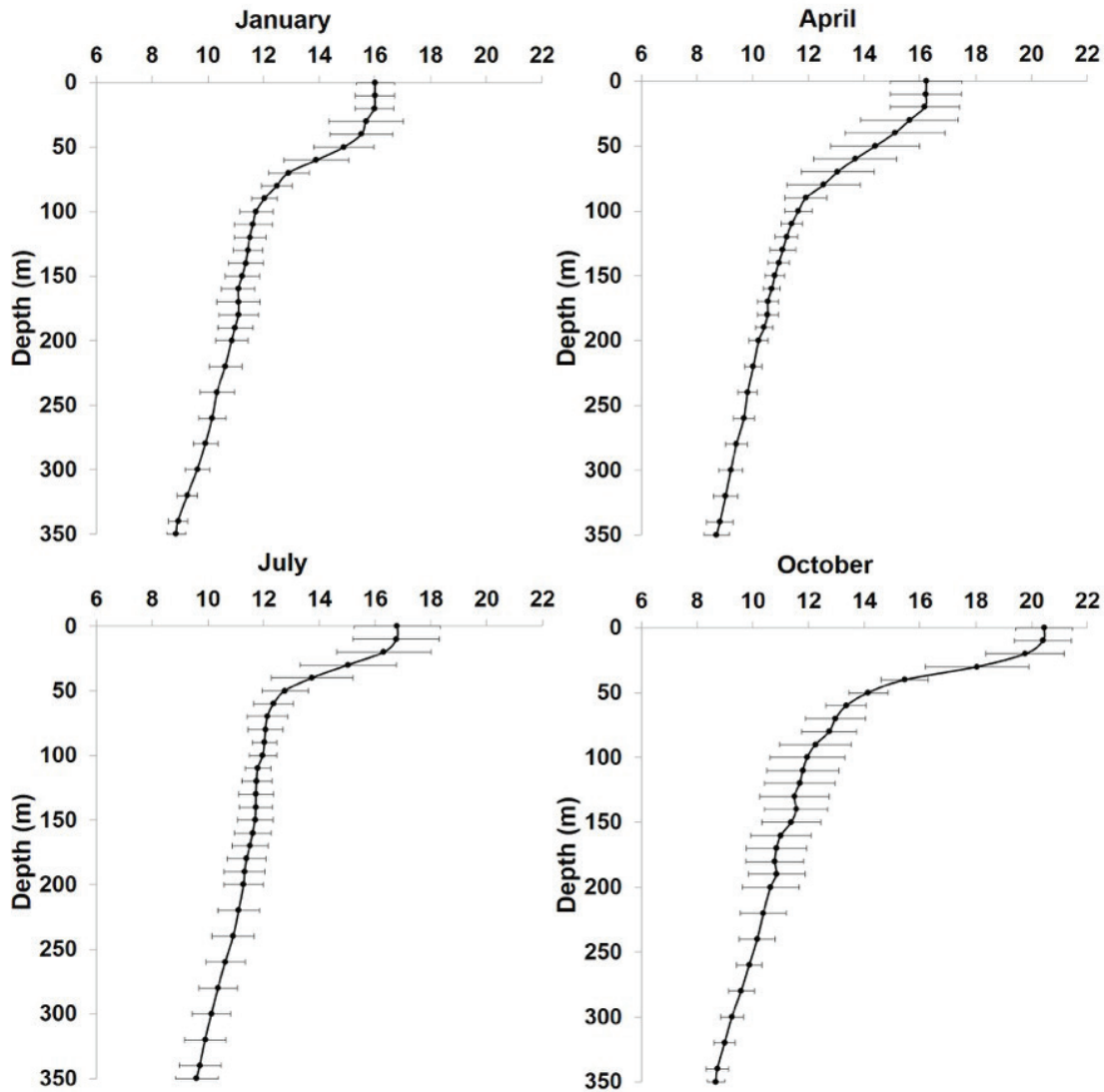
Figure 3.   Vertical profiles of mean temperature (˚C) and standard deviation during the four seasons in 2011.

arithms. Since the 2005 data were obtained exclusively at nighttime stations but the 2011 data combined both day and night stations, we first compared the 2011 day and night data in order to evaluate any possible influence of diel vertical migration of the organisms. Since most of the species did not present differences all samples were included for interannual comparisons.

RESULTS

Environmental Conditions

Surface circulation derived from dynamic height showed equatorward flow during the four seasons in 2011 (fig. 2). During spring and summer the flow was more intense to the north of Punta Eugenia, but there were no notable differences to the south. Mesoscale structures were minimal in January though deficient sampling in the southern part of the study area did not allow resolving the geostrophic flow. A cyclonic eddy was observed off Punta Eugenia during April but further south the flow normalized and enhanced in the study area. Small eddies were observed in July, with the main flow toward the equator. Finally, in October, a return flow from the south was observed introducing subtropical water into the study region (fig. 2).

Surface temperature (10 m) showed similar values from January to July, with mean temperature of 16°–17°C, and increased 3°C in October (fig. 3). However, below 50 m depth the temperature decreased to 14°C; therefore, in October, the thermocline was strong. Vertical salinity profiles were also similar from January to July, presenting two layers separated by a halocline (fig. 4). The upper low-salinity layer (33.3–33.7 psu) corresponding to subarctic water had variable thickness, reaching 60 m in January
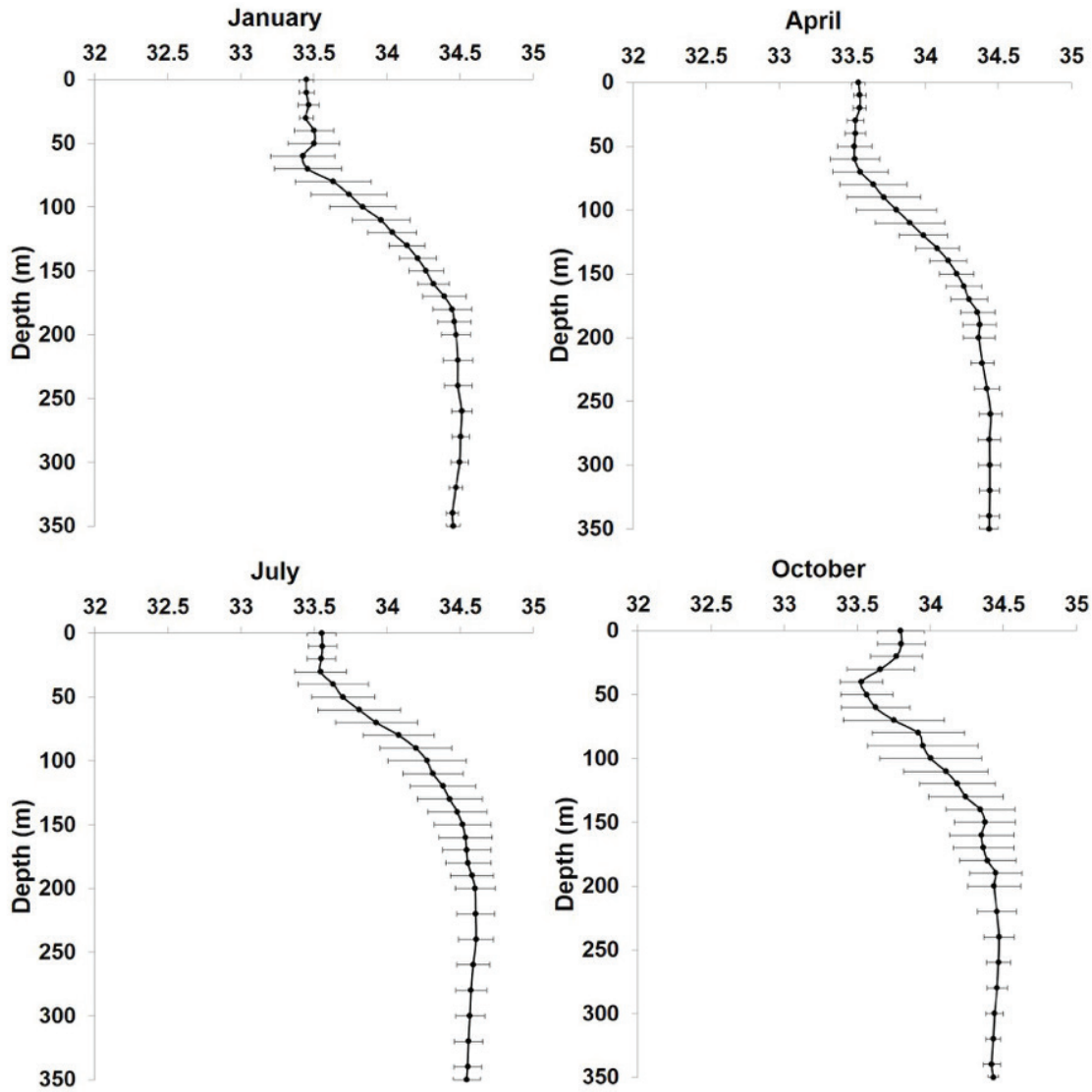
Figure 4.   Vertical profiles of mean salinity (psu) and standard deviation during the four seasons in 2011.

and April, and 40 m in July. The halocline presented a progressive salinity increase by mixing with subsurface equatorial water, reaching 34.5 psu around 170 m depth.

In contrast, October presented a three-layer structure due to the presence of more saline subtropical water (33.8–34.0 psu) in the upper 30 m. Beneath this layer, the nucleus of low-salinity subarctic water was evident at 40–70 m depth, and below, salinity increased again, with maximum salinity around 200 m depth. Note that in October there was higher subsurface variability with higher standard deviation values (fig. 4), possibly linked to the cyclonic eddy affecting the study area (fig. 2).

Amphipod Community

A total of 63 species were found over the entire study period, but their presence varied seasonally (appendix 1). The most common species throughout the year were *E. minuta*, *L. schizogeneios*, and *P. brevidens*. *S. antennarius* was also common except in January 2011, when it was present in only two samples. In contrast, some species such as *Eupronoe maculata*, *Hyperietta vosseleri*, and *Scina similis*, among others, occurred at only one station during the entire period and were therefore considered rare.

The number of species as well as cumulative abundance increased during the course of the year (fig. 5). In January, 17 species were recorded with a cumulative geometric mean (GM) of 31 ind/1000 m³. By April the number of species was twice as high and the cumulative GM increased fourfold (133 ind/1000 m³). The number of species decreased slightly in July (from 32 to 28) but the cumulative GM increased (245 ind/1000 m³), indicating higher dominance of certain species. Finally, the highest number of species (54) and cumulative GM (327 ind/1000 m³) occurred in October.
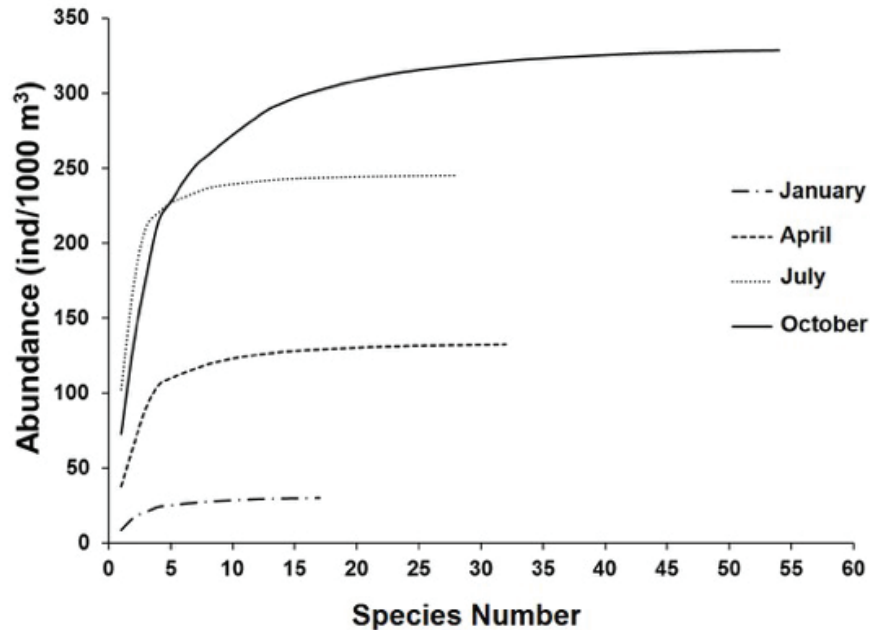
137

Figure 5.   Cumulative abundances of amphipod species based on geometric means in decreasing order during the four seasons in 2011.

The dominant hyperiids during winter were *E. minuta*, *L. schizogeneios*, *P. brevidens*, and *V. armata*. They presented a GM ranging from 3.5 to 8.7 ind/1000 m³, whereas the rest of species were below 2 ind/1000 m³ (appendix 1). Other small juvenile organisms could not be identified to species but most of them belonged to the genera *Lestrigonus* and *Scina* (GM of 1.1 and 1.0 ind/1000 m³, respectively).

In April, three dominant species (*E. minuta*, *L. schizogeneios*, and *P. brevidens*) presented GM = 38, 25, and 27 ind/1000 m³ respectively, increasing between 240 and 525% in relation to January (appendix 1). In contrast, the abundance of *V. armata* increased moderately (32%) and it was displaced from fourth place by *S. antennarius*. Of the remaining species, one third ranged from 1 to 4.7 ind/1000 m³ and the rest were below 0.6 ind/1000 m³. A large number of juvenile *Lestrigonus* were found, probably pertaining to the dominant species (*L. schizogeneios*), with a GM = 36 ind/1000 m³.

During summer, the three most abundant species continued to be *E. minuta*, *L. schizogeneios*, and *P. brevidens* but the abundance of only the last two increased (GM = 103 and 69 ind/1000 m³, respectively), while that of *E. minuta* was similar to spring (appendix 1). Five other species showed abundances of 3 to 9.8 ind/1000 m³, and the rest were below 2 ind/1000 m³. As in spring, abundant juvenile *Lestrigonus* were recorded (GM = 47 ind/1000 m³).

The most remarkable changes in composition occurred in October. The four most abundant species were *L. bengalensis*, *L. schizogenios*, *P. brevidens*, and *S. antennarius* (GM =

60, 73, 44, and 38 ind/1000 m³, respectively). The abundances of *E. minuta* and *L. schizogeneios* decreased 65% and 29%, respectively, from July to October, whereas the population of *S. antennarius* increased 280%. Many common species observed in previous months increased in abundance during October, and other species not previously observed were recorded (*Anchylomera blossevillei*, *Tetrathyrus arafurae*, *T. forcipatus*, among others).

Cluster Analysis

Similarity analysis among stations produced four clusters (Simprof p < 0.05) that evidenced structural seasonal differences in the amphipod community during 2011 (fig. 6A). Most of the stations sampled in winter and autumn fell into separate clusters (2 and 1, respectively), while spring and summer presented a strong similarity and shared cluster 4. The NMDS analysis confirmed the separation of the clusters (fig. 6B).

The amphipod assemblage from the autumn cluster (1) had the maximal mean similarity (68.9%) of all clusters. The main species contributing to similarity were *L. schizogeneios* and *P. brevidens* with 8.5% each (fig. 7). However, three other species (*L. bengalensis*, *Platyscelus ovoides/serratulus*, and *S. antennarius*) had equally high percentages (7.2%–8.1%). This, in addition to the higher contribution of species in the "others" category, denoted a more diverse community compared to the rest of the clusters, with greater equitability in abundances per species.

The winter cluster (2) presented the minimal mean similarity (53.7%). *E. minuta*, *L. schizogeneios*, and *P. brevi-*
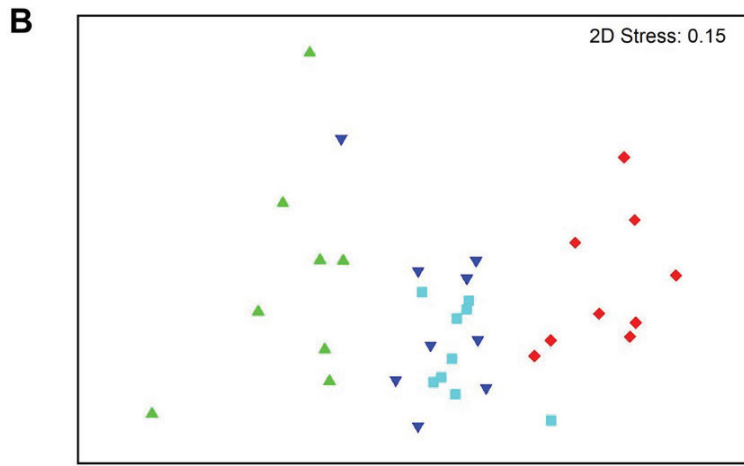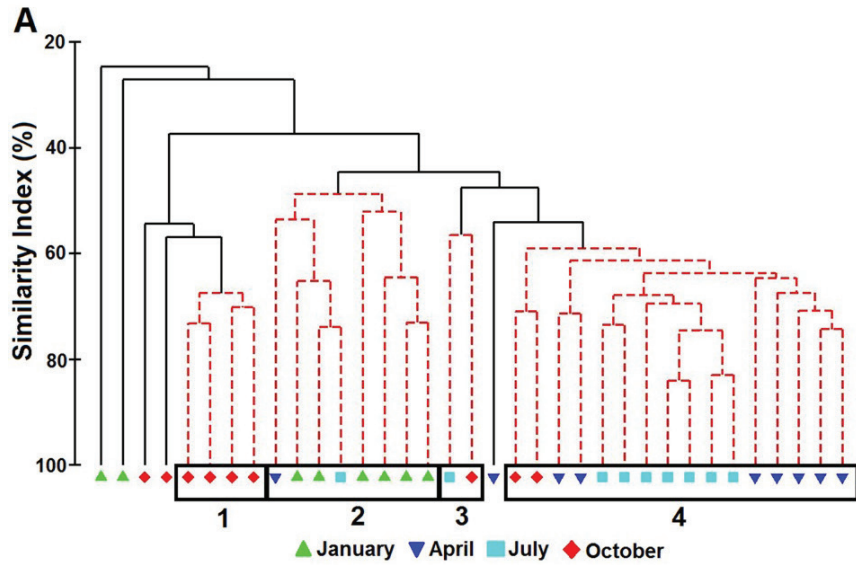
Figure 6. Cluster analysis based on the Bray-Curtis similarity matrix among stations: (A) Dendrogram showing the significant differences among clusters (black lines) using the Simprof test (p < 0.05). (B) Nonmetric multidimensional scaling (symbols indicate the months in 2011).
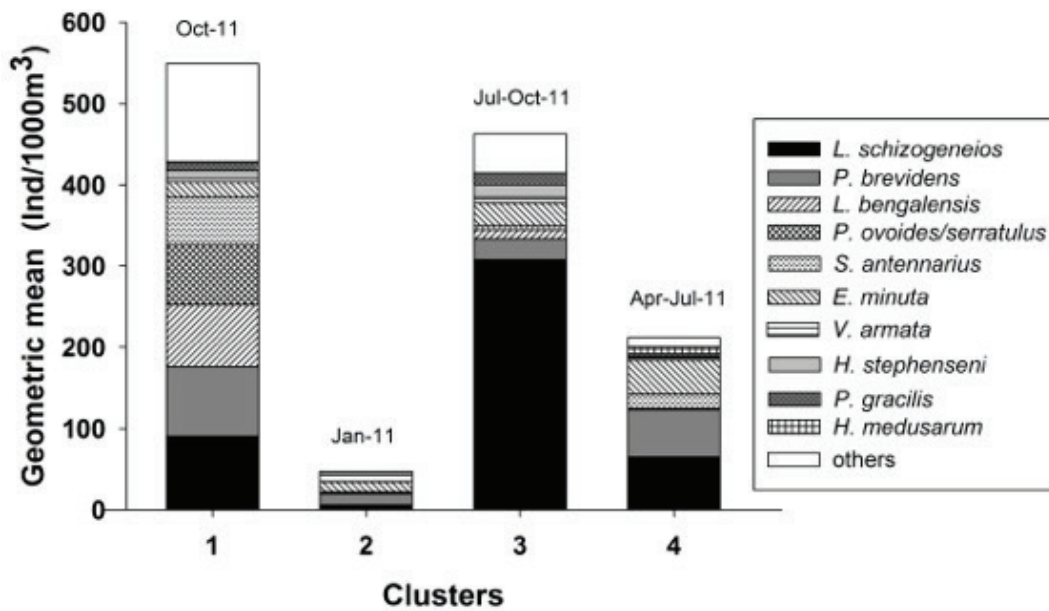
Figure 7. Stacked geometric means for the main species contributing to similarity in the clusters shown in Figure 6. The selected species are a combination of the five species with the highest contribution in each cluster obtained by SIMPER analysis. The "others" category indicates the sum of the remaining species.

TABLE 2
The best variable combinations obtained with BIOENV correlation analysis between the hyperiid amphipod community and environmental variables. Number of variables (k), Spearman rank correlation (ρS), Temperature (T10), Salinity (S10), and Dissolved Oxygen at 10 m depth (DO10), Mixed Layer Depth (MLD), Stratification Index 0–50 m (SI50), Stratification Index 0–100 m (SI100), and Zooplankton Biomass (ZB).

k	Best Variable Combinations	ρS
4	ZB, MLD, S10, T10	0.644
	ZB, MLD, S10, SI100	0.643
	ZB, MLD, S10, DO10	0.628
	ZB, MLD, T10, SI100	0.620
5	ZB, MLD, S10, T10, SI100	0.644
	ZB, MLD, S10, SI100, DO10	0.637
	ZB, MLD, S10, T10, SI50	0.623
	ZB, MLD, S10, T10, DO10	0.621
6	ZB, MLD, S10, T10, SI100, DO10	0.620
	ZB, MLD, S10, T10, SI100, SI50	0.620

dens made the highest contribution with a pooled similarity of 74% (fig. 7). However, the absolute abundance of amphipods was very low, with GM of 6, 14, and 13 ind/1000 m³ for each one of these three species.

A pair of stations, one from July and another from October formed cluster 3, with a pooled similarity of 56.5%. The main contribution came from *L. schizogeneios* (21%), which was strongly dominant (GM of 308 ind/1000 m³).

The highest number of stations joined in cluster 4, mainly from spring and summer, with global similarity of 63.9%. *E. minuta*, *L. schizogeneios*, and *P. brevidens* contributed the most to similarity (57.6%). These species were the same as in cluster 2, but in cluster 4 the cumulative percentage was lower. However, absolute abundance of them was considerably higher, with GMs of 42, 65, and 58 ind/1000 m³, respectively (fig. 7).

Relation between the amphipod community and hydrography

Correlation analysis between the similarity matrix (amphipod community) and environmental conditions matrix (table 1) produced several combinations with four to six more influential variables (table 2). Spearman correlation (ρS) had similar values in all the selected combinations, and a global coefficient of 0.644, with a significance of 1% in 99 permutations. The suite of variables that best explained the community structure was a combination of temperature and salinity at 10 m depth, mixed layer depth, and the zooplankton biomass. The addition of a fifth variable (0–100 m stratification index) did not add more value to ρS, which means that increased stratification and a narrower mixed layer depth are strongly correlated.

If the environmental variables are shown with the coordinates of the NMDS plot (fig. 6B), a characteristic

pattern emerges (fig. 8). Temperature at 10 m depth was similar in January and April, and the stations are positioned on the left side of the NMDS plot. It increased slightly in July and strongly in October and the stations are on the right side of the NMDS plot (fig. 8A). Salinity at 10 m depth showed a similar trend (fig. 8B). This incrementing pattern illustrates the influence of subtropical oceanic water in autumn. Furthermore, the mixed layer depth was wider during January–April but became shallower during July–October (fig. 8C). In concordance, stratification increased during the year, reaching maximal values in October (fig. 8D) as denoted by a strong thermocline (fig. 4).

Zooplankton biomass was low in winter but high from April to October, and there was high variability among stations (fig. 8E). Considering zooplankton biomass as indicator of gelatinous organisms, which contributed strongly to the volume, it is clear why amphipod abundance was so poor in January. The increase in amphipod abundance in subsequent months is consistent with greater availability of gelatinous substrate that is used by hyperiids for reproduction and feeding.

Comparison of the 2011 and 2005 amphipod communities

Before comparing amphipod communities between years, we compared abundances between sampling hours (day and night) for the year 2011 in order to discard the possible influence of diel vertical migration. Significant differences were found only for two species: *E. minuta* (U = 80, p = 0.031) and *V. armata* (U = 74, p = 0.017). The first presented higher abundance in daylight samples and the inverse occurred with the second. Due to the low number of nighttime samples for 2011 (n = 13), and since most of the species did not present significant day-night differences, all data from 2011 were used to compare a "cool" year (2011) with a "neutral" year (2005). However, one should keep in mind that the 2005 data based exclusively on nighttime samples may overestimate the abundance of *V. armata* and underestimate the abundance of *E. minuta* in relation to 2011, and that both are influential species due to their abundances.

Analysis of variance with year and month as factors showed significant interannual differences for several dominant species (table 3). The abundance of the preponderant species *L. schizogeneios* and *P. brevidens* was higher in 2011 than in 2005. The abundance of these species and that of *S. antennarius* tripled in 2011, and *T. malmi*, a rare species in 2005, was more common in 2011. However, the abundances of a large number of species declined during the cool year. The most notable was *V. armata* that in 2005 had a GM = 23 ind/1000 m³ but only 20% of this amount during the cool year of 2011. A similar decrease was also observed for *P. curvi-*
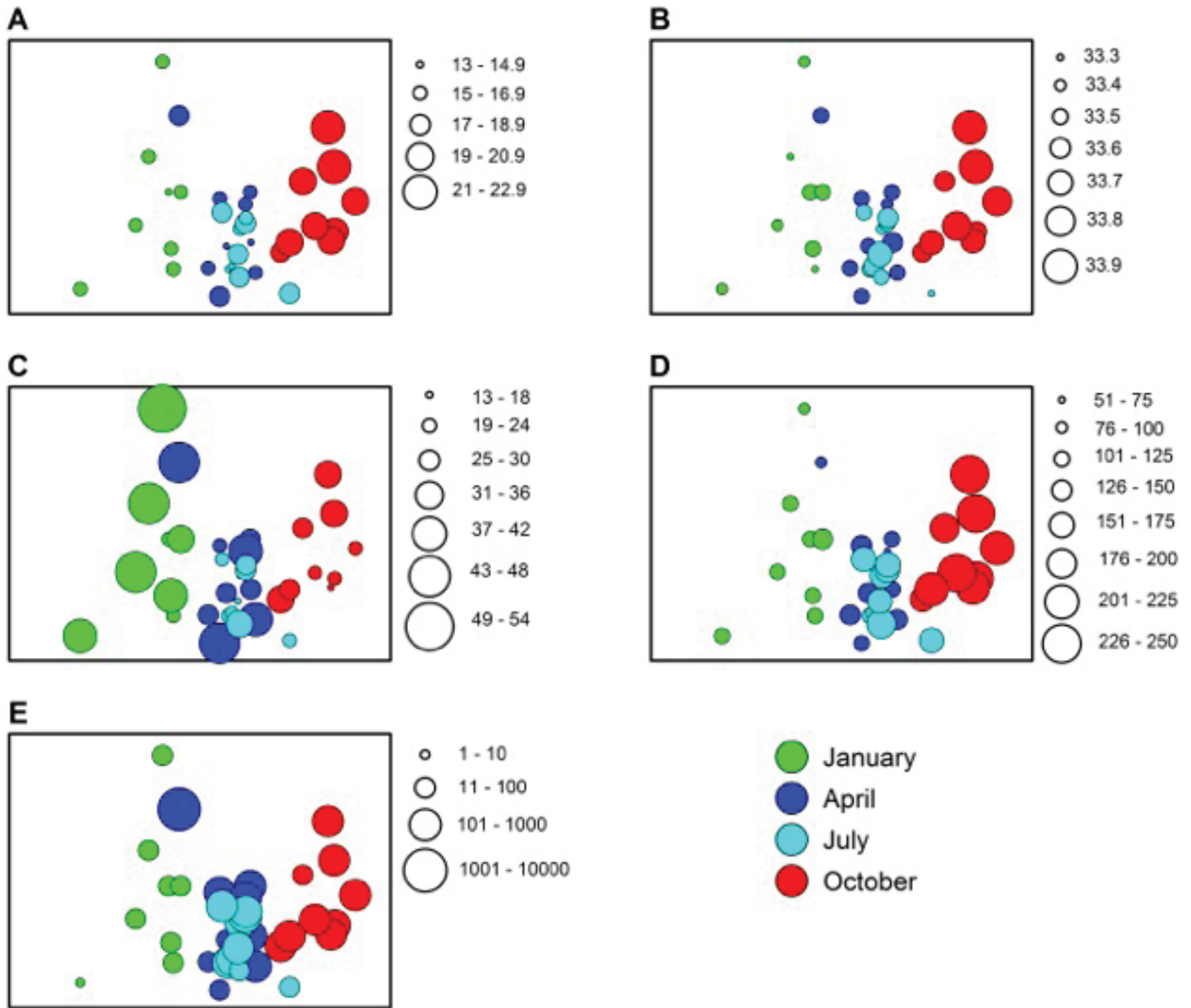
Figure 8.   NMDS as in Figure 6 but varying the symbol sizes as a function of the environmental variables: (A) 10 m depth temperature, (B) 10 m depth salinity, (C) mixed layer depth (m), (D) stratification index of 0–100 m, and (E) zooplankton biomass (µl m⁻³).

pes, P. semilunata, S. borealis, and *V. asutralis.* Other species were completely absent in the study region during 2011, such as *A. sculpturatus, V. gibbosa,* and *V. viatrix,* among others of certain importance in 2005. The ANOVA also indicated interaction between seasonal and interannual effects. *A. blossevillei, E. maculata, L. bengalensis, L. shoemakeri, L. pulex, P. atlantica,* and *R. whitei* presented interannual differences limited to some part of the year (table 3). For example, *A. blossevillei* and *L. bengalensis* were absent from January to July of 2011 but in October had similar abundances in both years. Finally, several other species did not show interannual differences but only the expected seasonal variability (table 3).

The similarity analysis combining data from 2005 and 2011 produced twelve clusters (Simprof p < 0.05).

Four of them were identical to the clusters obtained using only 2011 data, and the numeration of clusters (1–4) was retained (fig. 9A). The rest of the conglomerates exclusively presented stations from 2005, configuring two for winter (clusters 5 and 7), two for spring (clusters 6 and 12), one for summer (cluster 11), and three for autumn (clusters 8–10). The formation of separate clusters for each year denoted interannual dissimilarity. However, the NMDS showed proximity between points of the same seasons in July and October, but not in January and April (fig. 9B). In the NMDS the stress was moderately high (0.19), indicating difficulties in establishing a two-dimensional arrangement. Therefore, we decided to maintain the arrangement obtained in the dendrogram.

TABLE 3
**Dominant amphipod species from the Punta Eugenia–Punta Abreojos region. The geometric mean (GM) abundance
during a "neutral year" (2005) and a cool year (2011) is shown, and the associated probability of two-way ANOVA
with factors year and month. Significant values are highlighted in bold for $\alpha = 0.001$.**

| Species | GM (ind/1000 m³) | | Year | Month | Year*Month |
	2005	2011			
Amphithyrus sculpturatus	1.0	—			
Anchylomera blossevillei	1.6	0.2	**<0.001**	0.115	**0.001**
Eupronoe maculata	1.0	<0.1	**0.001**	**<0.001**	**<0.001**
Eupronoe minuta	14.5	21.0	0.259	**<0.001**	0.043
Hyperoche medusarum	1.5	2.1	0.746	**<0.001**	0.567
Hyperioides longipes	0.9	0.3	0.112	0.034	0.388
H. sibaginis	1.4	0.9	0.546	**<0.001**	0.272
Hyperietta stephenseni	1.1	1.5	0.469	**<0.001**	0.344
Laxohyperia vespuliformes	1.3	0.8	0.126	**<0.001**	0.019
Lestrigonus bengalensis	7.8	1.9	**<0.001**	**<0.001**	**0.001**
L. schizogeneios	10.6	31.9	0.001	**<0.001**	0.537
L. shoemakeri	3.2	0.6	**<0.001**	0.003	**<0.001**
Lycaa pulex	2.7	0.5	**<0.001**	**<0.001**	0.001
Lycaeopsis themistoides	0.9	0.6	0.258	0.004	0.471
Oxycephalus clausi	1.8	0.7	0.017	**<0.001**	0.009
Paraphronima gracilis	2.9	2.8	0.534	**<0.001**	0.154
Phronima atlantica	1.5	0.7	0.011	0.024	**<0.001**
P. curvipes	1.2	0.1	**<0.001**	0.327	0.058
P. sedentaria	1.0	0.7	0.366	0.940	0.143
P. stebbingi	0.8	0.7	0.611	0.233	0.013
Phronimopsis spinifera	0.2	0.8	0.005	0.083	0.009
Phrosina semilunata	2.9	0.8	**<0.001**	**<0.001**	0.050
Platyscelus ovoides / P. serratulus	4.5	2.7	0.181	0.003	0.059
Primno brevidens	9.3	30.1	**<0.001**	**<0.001**	0.036
Rhabdosoma whitei	1.4	0.4	0.007	0.050	**0.001**
Scina borealis	0.8	0.1	**<0.001**	0.118	0.087
S. tullbergi	2.0	1.2	0.040	**<0.001**	0.105
Simorynchotus antennarius	2.4	9.4	**<0.001**	**<0.001**	0.002
Streetsia challengeri	0.7	0.2	0.003	0.157	0.036
Themistella fusca	0.6	0.4	0.501	**<0.001**	0.224
Tryphana malmi	0.1	1.9	**<0.001**	0.014	0.005
Vibilia armata	22.8	4.4	**<0.001**	0.103	0.097
V. australis	1.5	0.2	**<0.001**	0.053	0.289
V. gibbosa	1.0	—			
V. stebbingi	0.6	0.5	0.871	**<0.001**	0.846
V. viatrix	2.4	—			

The two clusters from January 2005 had low internal similarity, averaging 41.9% and 55.2% for clusters 5 and 7, respectively. The main species contributing to the similarity differed in each winter group (fig. 10). Group 5 included mainly nearshore stations with sparse hyperiids, *E. minuta*, *P. sedentaria*, and *Platyscelus ovoides/ serratulus* being the main contributors with a pooled similarity of 51%. Hyperiid abundance was slightly higher in cluster 7 containing offshore stations (fig. 11), with *R. whitei*, *V. armata*, and *V. viatrix* as the most influential species (38% of cumulative similarity). The winter clusters from 2005 contrasted with the winter 2011 cluster 2, in which *E. minuta* and *P. brevidens* contributed 58% of the similarity (fig. 10) and did not present separation between nearshore and offshore stations (fig 11). *E. minuta* and *P. brevidens* had GMs of 13 and 14 ind/1000 m³, respectively, compared to lower GMs in cluster 5 (8 and 2 ind/1000 m³) and cluster 7 (3 and 1 ind/1000 m³).

In April 2005, the two assemblages (clusters 6 and 12) contrasted strongly both in abundance and species composition (figs. 10 and 11). The cumulative sum of GMs from all species amounted to 84 ind/1000 m³ in cluster 6 formed by offshore stations and to 337 ind/1000 m³ in cluster 12 with nearshore stations. Mean similarity was relatively high in both (61.1% and 65.8%, respectively). The main species contributing to similarity in cluster 6 were *P. semilunata*, *P. ovoides/serratulus*, and *V. armata* (46%), while *E. minuta* and *P. brevidens*, characteristic of the CCS were absent. Cluster 12 contributed strongly to similarity due to *V. armata* (12.5%), followed by *E. minuta* (10.1%) and *V. gibbosa* (9.6%), all them with high GMs (113, 44, and 42 ind/1000 m³, respectively). Compared to the 2011 spring–summer cluster 4, cluster 6 had high dissimilarity in dominant CCS species (*E. minuta*, *L. schizogeneios*, and *P. brevidens*). The differences between clusters 4 and 12 were due to three *Vibilia* species, with *V. gibbosa* and *V. viatrix* absent in 2011 and *V. armata* hav-
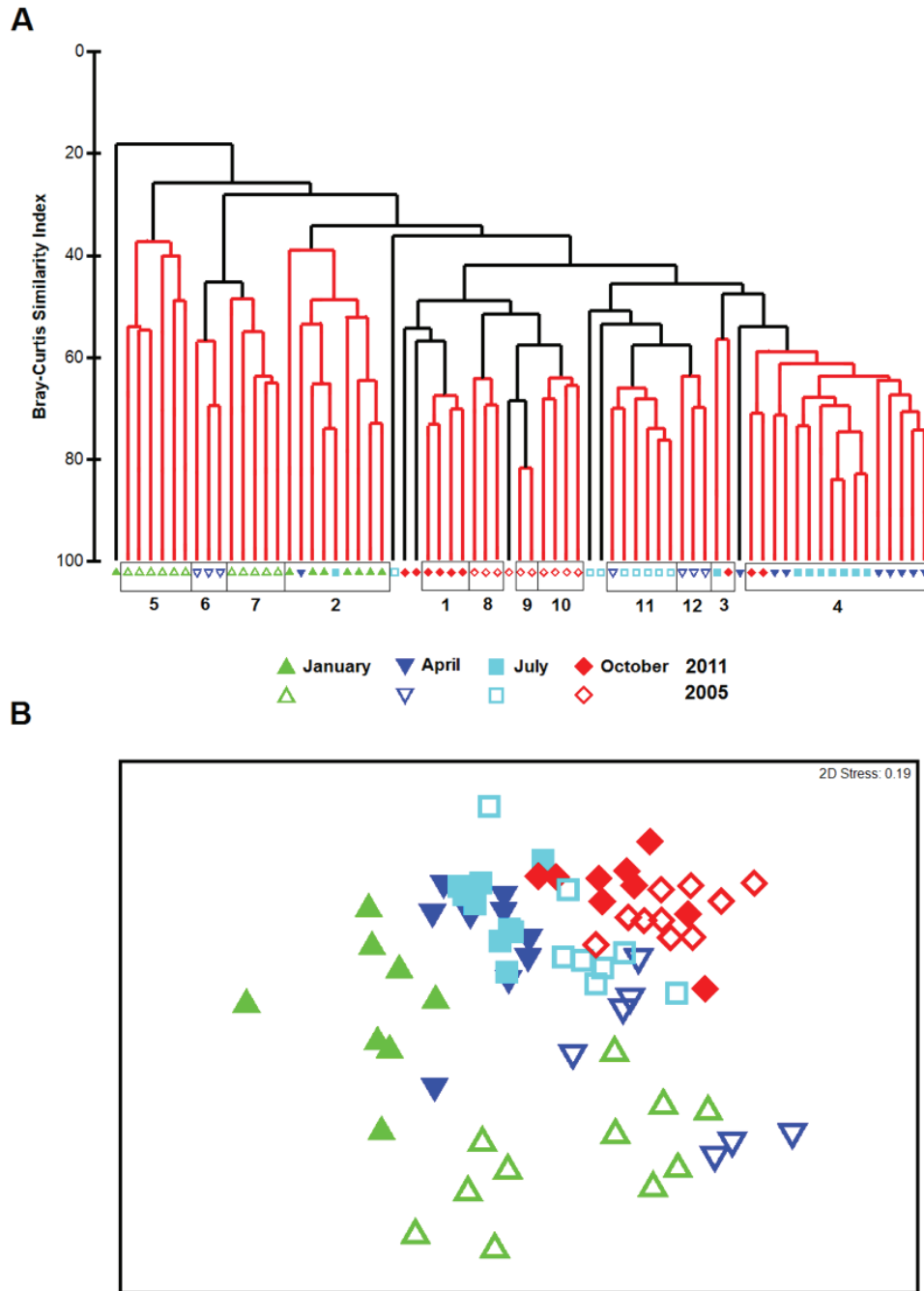
Figure 9. Cluster analysis based on the Bray-Curtis similarity combining stations from 2005 and 2011: (A) Dendrogram showing, with black lines, the significant differences among clusters using the Simprof test (p < 0.05). (B) Nonmetric multidimensional scaling with symbols indicating the months from 2005 (open) and 2011 (closed).

ing a GM of only 2 ind/1000 m³, though this low esti–mate may not be reliable because of the inclusion of daytime samples in 2011.

The 2005 summer amphipod community only formed cluster 11, which included nearshore stations, and the only offshore station was excluded from this cluster (fig. 11). It presented strong dominance of *V. armata* (GM = 173 ind/1000 m³) and other CC species (*E. minuta*,

L. schizogeneios, and *P. brevidens*), which overall embraced a similarity of 37%. Cluster 11 was close to cluster 12 (from April 2005) in the dendrogram (fig. 9) and both were relatively close to cluster 4 (April–July 2011). The dissimilarity between clusters 11 and 4 is attributed mainly to *L. bengalensis* and *V. armata* (fig. 10).

October 2005 had a varied assortment of groups. The two main ones (clusters 8 and 10) show a north–
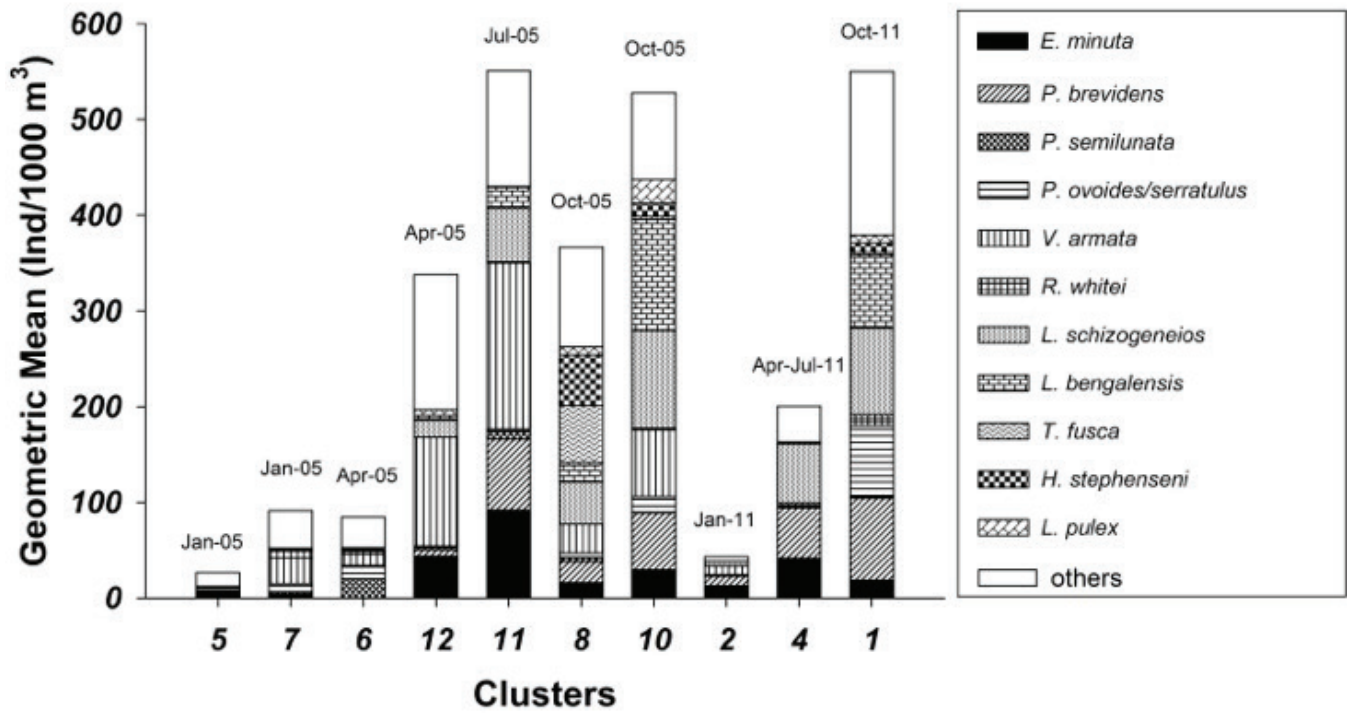
Figure 10.   Stacked geometric means from species with strong contribution to similarity in the clusters shown in Figure 9A. Clusters 3 and 9 formed by a pair of stations were omitted. The selected species are a combination of the two species with the highest contribution in each cluster obtained by SIMPER analysis. The "others" category indicates the sum of the remaining species. Conglomerates are ordered as they appear in the dendrogram, excluding conglomerates 3 and 9 formed by two stations.
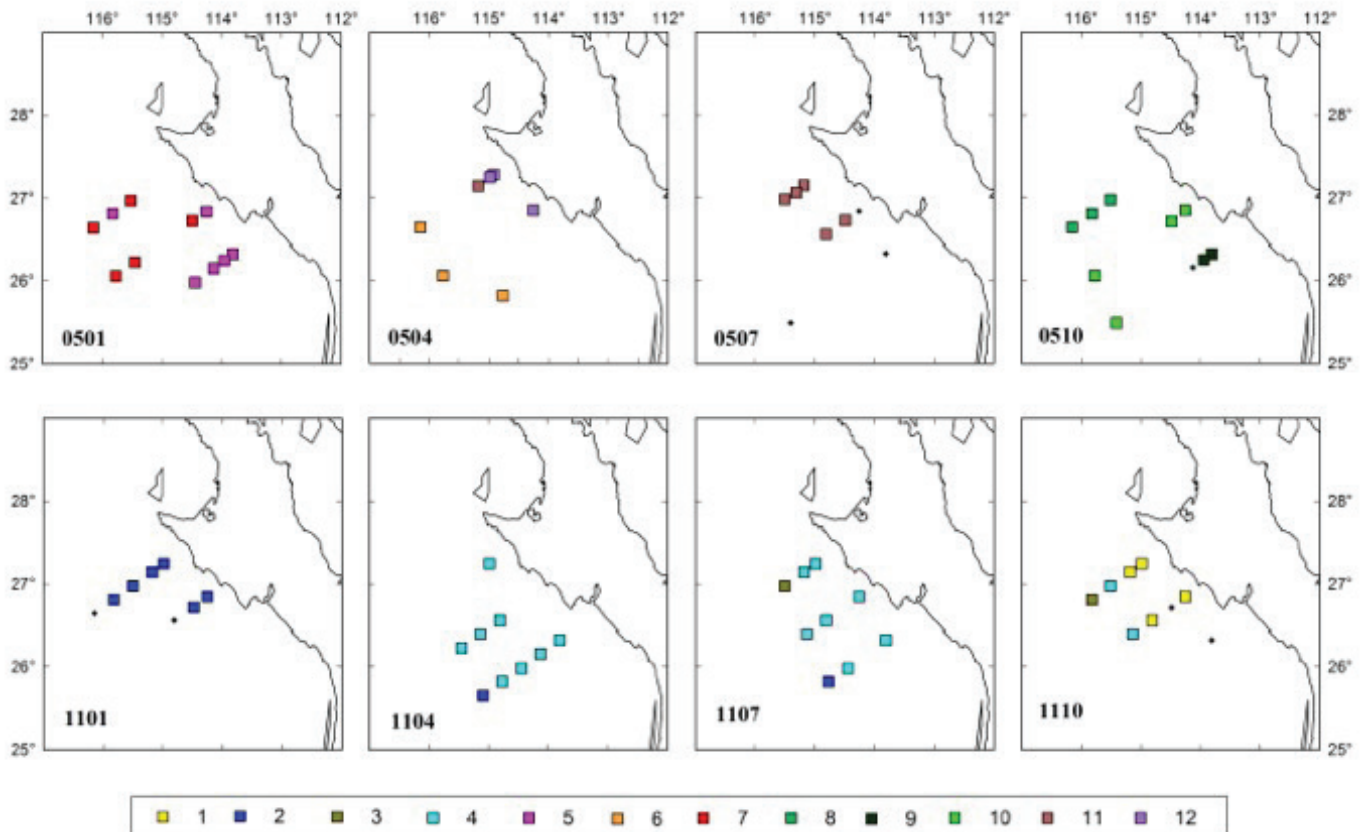

Figure 11.   Geographic distribution of clusters defined in the dendrogram with combined stations from 2005 and 2011 (fig. 9A).

south arrangement and cluster 9 is formed by a pair of nearshore stations (fig. 11). These groups as well as cluster 1 from October 2011 had high hyperiid abundance and species richness (fig. 10). Though the October conglomerates appeared close to each other in the NMDS plot (fig. 9B), the most important species contributing to the similarity were different in each one of them: *H. stephenseni*, *H. vosseleri*, and *T. fusca* (summing 26%) in cluster 8; *A. sculpturatus*, *L. bengalensis*, and *L. pulex* (26%) in cluster 9; *L. bengalensis*, *L. schizogeneios*, and *V. armata* (29%) in cluster 10; and *L. schizogeneios*, *P. ovoides/serratulus*, and *P. brevidens* (25%) in cluster 1. Dissimilarity between the 2005 and 2011 October clusters was mainly due to the absence of *A. sculpturatus*, *E. maculata*, and *H. vosseleri* in cluster 1. In contrast, the GM of *P. ovoides/serratulus* was high in cluster 1 (74 ind/1000 m³) but between 5 and 16 ind/1000 m³ in clusters 8–10. The abundance of *S. antennarius* was also high in cluster 1 (MG = 59 ind/1000 m³), but below 10 ind/1000 m³ in clusters 8–10.

DISCUSSION

Climatic conditions during 2011 were associated with the cool phase of ENSO (La Niña), which lasted from summer 2010 to the beginning of 2012. This was one of the coldest events on record, characterized by a relaxation between May and July of 2011, and further resurgence of cooler conditions during autumn in the central equatorial Pacific (Thorne et al. 2012; Hu et al. 2014). In the CCS, cool SST was evident from spring 2010 until summer 2011, with enhanced upwelling activity (Bjorkstedt et al. 2011). However, in the study region, SST experienced a remarkable increase in October 2011, which affected the pelagic ecosystem. The strength of La Niña 2010–12 also affected the surface circulation. Usually, the flow of the CC is strongest from late winter (February–March) to early summer, in concordance with the seasonality of the winds (Huyer 1983; Lynn and Simpson 1987; Zaitsev 2003). However, in January 2011 the CC flow was relatively strong off Baja California (fig. 2) compared to the typical circulation for this month (see Figure 4 in Strub and James 2000). Thermohaline conditions in the study area were not entirely typical because low salinity and temperature occurred since winter instead of only at spring but the warmest water occurred in autumn as usual (Durazo 2015).

The biological consequences of La Niña included high integrated chlorophyll (>40 mg/m²) in the Baja California region throughout most of the year, decreasing at the end of 2011, a pattern not completely consistent with observations elsewhere in the CCS (Bjorkstedt et al. 2012). Moreover, the zooplankton volume was high in 2011, above the long-term mean, with preponderance of gelatinous organisms such as hydromedusae and salps. Crustaceans responded differently. The abundance of copepods was high from January to July and decreased in October, while euphausiids had negative anomalies all year round, contrasting with the pattern observed for amphipods in the present study (Lavaniegos et al. 2015). Here we confirm the low diversity of amphipods in cold months, whether by the absence of some species or the decreased abundances of others (table 3).

Comparison of the 2011 and 2005 amphipod communities

The composition, abundance, and diversity of hyperiid amphipods off Baja California during 2011 showed a seasonal pattern as described for 2005 by Lavaniegos and Hereu (2009). In both years, both amphipod abundance and species diversity were poor in winter. The abundance of total amphipods increased from April to October but more strongly in October. Some differences in the composition and abundance of particular species reflected the cool climate during 2011 in contrast with 2005. The climate in 2005 could be considered neutral for the second part of the year but not the beginning, because El Niño conditions still prevailed in January of that year (Lyon and Barnston 2005). Therefore, it is not surprising that the winters of 2005 and 2011 had included the most dissimilar hyperiid assemblages in the cluster analysis (fig. 9).

Some species were present in 2005 but were absent in 2011, probably affected by the cooling caused by La Niña. Most notably, *A. blossevillei*, *O. clausi*, and *P. curvipes* were absent from January to July 2011, and *V. gibbosa* and *V. viatrix* were absent from January to April 2011. These species were moderately abundant in 2005 (GMs between 1 and 13 ind/1000 m³, table 3). *A. blossevillei* in particular could be an indicator of warm conditions because it was one of the frequent species during El Niño 1997–98 in the Mexican tropical Pacific (Gasca et al. 2012). However, it is also found at subtropical latitudes as in the Canary Current (Thurston 1976), the Sargasso Sea (Gasca 2007), and the Tasman Sea (Zeidler 1992). On the other hand, *O. clausi* appears to be a species capable of tolerating wide temperature ranges because it has been recorded from subarctic (Lorz and Pearcy 1975) to tropical latitudes (Gasca et al. 2012; Valencia et al. 2013). However, it was not present during the cool months of 2011 in the present study.

The dominant species also differed between 2005 and 2011. The typical species in the CCS during 2005 were *E. minuta*, *L. schizogeneios*, *P. brevidens*, and *V. armata* (Lavaniegos and Hereu 2009). These species, except for *V. armata*, were also abundant in 2011. Our findings for *V. armata* are not those expected for the subtropical region of the CC, because though its frequency of occurrence was high during 2011, it was not abundant;

however, its abundance in 2011 may have been underestimated due to the sampling depth (0–200 m) and hour (most of the samples were collected during daylight hours). There is evidence that *V. armata* undertakes vertical migration (Brusca 1967a; Thurston 1976; Tranter 1977). According to Cornet and Gili (1993), this species presents a wide range of vertical migration, remaining between 200 and 1000 m depth during daytime. The other species with significant day–night differences was *E. minuta* but in this case, diurnal abundances were higher. Though *E. minuta* did not present interannual differences, this could be a failed result due to a possible overestimation of the 2011 abundances (excess of daytime samples). This is consistent with studies from the Gulf of California (Siegel-Causey 1982) and Canary Current (Thurston 1976), where *E. minuta* apparently exhibited reverse migration. However, in the Indian Ocean, it showed a tendency to migrate during nighttime above 200 m (Tranter 1977).

Significant interannual differences for *L. schizogeneios* and *P. brevidens* were due to substantially higher abundances in 2011, probably favored by low temperatures. According to Xu (2009), *L. schizogeneios* is able to tolerate a wide range of temperatures, but the higher abundance found during 2011 in the present study suggests a preference for temperate conditions. *P. brevidens* also shows a preference for temperate conditions defined by the 15°–18°C isotherms at 30 m depth, demarcating its southern limit of distribution in the CCS during March–July (Bowman 1978).

In the present study, *S. antennarius* was among the dominant species, but during 2005 it had low abundance. Gasca et al. (2012) recorded this species during the period influenced by the CC in the Mexican tropical Pacific, and Zeidler (1984) observed it only from March to June when temperature was decreasing and the salinity was stable off Queensland, Australia.

Comparison with other regions

The subtropical region of the CC has a high diversity of hyperiid amphipods (Lavaniegos and Ohman 1999; Lavaniegos and Hereu 2009). The influence of this current permeates even in the eastern tropical Pacific (ETP) as observed by Gasca et al. (2012) off the coast of Colima and Jalisco, where the diversity of these crustaceans showed a seasonal fluctuation despite the occurrence of El Niño 1997–98, with high diversity but low abundances during the season influenced by the CC (February–June). In contrast, during July–December the North Equatorial Countercurrent influences the region and there is low hyperiid diversity. In this region, the species *H. sibaginis* and *L. bengalensis* prevailed as the most frequent and abundant (Gasca et al. 2012). However, in the present study, these species occurred exclusively in

October, and *L. bengalensis* was the second most abundant amphipod species in the study area. The tropical affinity of this species has also been confirmed in diverse tropical regions such as Banderas Bay (Gasca and Franco-Gordo 2008), Panama Bay (Valencia et al. 2013), the Australian coast (Zeidler 1984), the Caribbean Sea (Gasca and Suarez-Morales 2004), Gulf of Mexico (Gasca 2004; Gasca et al. 2009), and the Brazilian coast (Lima and Valentin 2001). Therefore, in this study *L. bengalensisis* was considered a tropical species, typical of autumn conditions when there is influence of subtropical water off Baja California. In October 2011, *H. sibaginis* was also abundant though its contribution to similarity was not as high as that of *L. bengalensis*. The latter and four other species (*L. schizogeneios*, *P. ovoides*, *P. brevidens*, and *S. antennarius*) contributed the maximal similarity percentages (fig. 7).

In the assemblage of species present in the Mexican tropical Pacific during periods influenced by the CC, one of the species that contributed strongly to similarity was *V. armata* (Gasca et al. 2012). However, the abundance of this species is low in the ETP compared with the CCS (Brusca 1981; Lorz and Pearcy 1975; Lavaniegos and Ohman 1999, 2003; Lavaniegos and Hereu 2009; Lavaniegos 2014), and with other eastern boundary upwelling ecosystems (Thurston 1976; Cornet and Gili 1993) and the Indian Ocean (Tranter 1977). In the Gulf of California, the abundance of *V. armata* was related to upwelled water derived from the mixing of subtropical surface and subsurface water (Siegel-Causey 1982). Valencia-Ramírez (2010) reported the occurrence of this species in a tongue of cool and saline water associated with the Colombia Current.

Relation between the amphipod community and environmental variables

The correlation between environmental variables and amphipod community coincided with that observed in other regions. Xu and Mei (2006) found a correlation between amphipod abundance and SST in the China Sea but exclusively in spring, explained by an oceanic tendency in amphipod distribution where SST was higher. On the contrary, off Baja California, an inverse relation between SST and amphipod abundance was found during July 2002, associated with the intrusion of subarctic water (Lavaniegos 2014). However, the correlation was stronger for *T. pacifica* compared with the subtropical species *V. armata* (Lavaniegos 2014). In 2011, the positive correlation between amphipods and temperature appeared to be related to a good reproductive season or survival during spring–summer as well as to a massive intrusion of tropical species in autumn.

Surface salinity was another variable included in the correlation analysis. In the CCS low temperature and

salinity values are indicative of subarctic water, whereas high values are associated with subtropical water (Lynn and Simpson 1987). However, in other eastern Pacific regions with high precipitation, low salinity is associated with warm tropical water, as occurs in Panama Bay, where Valencia et al. (2013) found a neritic-oceanic contrast in hyperiid assemblages explained by a plume of low salinity. In the Gulf of California, with another water mass regime, surface salinity was also the best predictor of amphipod abundance (Siegel-Causey 1982).

The tolerance of amphipods to thermohaline variability depends on the species. For example, *L. schizogeneios* is an abundant species in diverse regions, classified by Xu (2009) as eurythermal and euryhaline, supporting wide ranges of surface temperature (13.5°–28.3°C) and salinity (27.2–34.8). However, this species is not so abundant in the ETP (Gasca et al. 2012), and though persistent during all phases of ENSO 1997–98, its contribution was linked to the CC influence. Its cosmopolite tendency in warm-temperate waters and wide thermohaline tolerance may explain why *L. schizogeneios* is one of the most frequent and abundant species off Baja California.

A species with low tolerance to temperature was *T. forcipatus*, found exclusively in October 2011 with low abundance in the study area. This species could be a good indicator of alteration under local environmental conditions. It is abundant in coastal zones (Zeidler 1984; Cornet and Gili 1993) and limited to the upper 20 m (Gasca and Suarez-Morales 2004). Gasca et al. (2012) reported similar findings during ENSO 1997–98. This explains the absence of *T. forcipatus* during January–July 2011 off Baja California when SST was cool (16°–17°C), and its low abundance in October despite appropriate SST; however, its preference for the coastal shelf prevent us from finding in the present study in which only oceanic stations were analyzed.

Stratification of the water column influenced the amphipod assemblages observed in 2011 (table 2). Cornet and Gili (1993) also highlighted the influence of stratification on the amphipod community in the Benguela Current, which was compressed in the upper 40 m because of a strong thermocline and the presence of gelatinous zooplankton. Under these conditions, the organisms did not migrate vertically despite reports of migration and wide vertical distribution ranges from other regions (Brusca 1967a; Thurston 1976; Roe 1984).

Finally, with this study it was possible to establish the seasonal variability of pelagic amphipods in the CCS and that La Niña conditions had a greater effect on the surface layer during the first part of 2011. The relaxation of this event in autumn produced an extreme seasonal change, with massive intrusion of tropical species in the region off central Baja California. That extreme seasonal change could be comparable to the effect of a warm-ing event (for example, a weak El Niño). Since different species are linked to varying environmental factors, which may not be exactly the same from event to event, it is necessary to analyze more years of rigorous analysis of species specific abundance anomalies. This will aid to a better appreciation of the scope, not just of La Nina events in general, but individual La Nina event effects. Ultimately, this will increase the robustness of year-to-year comparisons and the potential for critical comparable time series data.

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LITERATURE CITED

Armstrong, J. L., J. L. Boldt, A. D. Cross, J. H. Moss, N. D. Davis, K. W. Myers, R. V. Walker, D. A. Beauchamp, and L. J. Haldorson. 2005. Distribution, size, and interannual, seasonal and diel food habits of northern Gulf of Alaska juvenile pink salmon, *Oncorhynchus gorbuscha*. Deep Sea Res. Part II 52:247–265.

Bjorkstedt, E. P., R. Goericke, S. McClatchie, E. Weber, W. Watson, N. Lo, B. Peterson, B. Emmett, R. Brodeur, J. Peterson, M. Litz, J. Gomez-Valdez, G. Gaxiola-Castro, B. Lavaniegos, F. Chavez, C. A. Collins, J. Field, K. Sakuma, P. Warzybok, R. Bradley, J. Jahncke, S. Bograd, F. Schwing, G. S. Campbell, J. Hildebrand, W. Sydeman, S.A. Thompson, J. Largier, C. Halle, S. Y. Kim, and J. Abell. 2011. State of the California Current 2010–11: Regionally variable responses to a strong (but fleeting?) La Niña. Calif. Coop. Oceanic Fish. Invest. Rep. 52:36–68.

Bjorkstedt, E. P., R. Goericke, S. McClatchie, E. Weber, W. Watson, N. Lo, W. Peterson, R. Brodeur, S. Bograd, T. Auth, J. Fisher, C. Morgan, J. Peterson, R. Durazo, G. Gaxiola-Castro, B. Lavaniegos, F. Chavez, C.A. Collins, B. Hannah, J. Field, K. Sakuma, W. Satterthwaite, M.O'Farrell, S. Hayes, J. Harding, W. Sydeman, S. A. Thompson, P. Warzybok, R. Bradley, J. Jahncke, R. Golightly, S. Schneider, J. Largier, R.M. Suryan, A. J. Gladics, C.A. Horton, S.Y. Kim, S. Melin, R. De Long, and J. Abell. 2012. State of the California Current 2011–12: Ecosystems respond to local forcing as La Niña wavers and wanes. Calif. Coop. Oceanic Fish. Invest. Rep. 53:41–76.

Boening, C., J. K. Willis, F. W. Landerer, R. S. Nerem, and J. Fasullo. 2012. The 2011 La Niña: So strong, the oceans fell. Geophysical Res. Lett. 39, L19602, doi: 10.1029/2012GL053055.

Bowman, T. E. 1973. Pelagic amphipods of the genus *Hyperia* and closely related genera (Hyperiidea: Hyperiidae). Smithsonian C. Zool. 136:1–76.

Bowman, T. E. 1978. Revision of the pelagic amphipod genus *Primno* (Hyperiidea: Phrosinidae). Smithsonian C. Zoology 275:1–23.

Brusca, G. J. 1967a. The ecology of pelagic Amphipoda, I. Species accounts, vertical zonation and migration of Amphipoda from the waters off southern California. Pac. Sci. 21:382–393.

Brusca, G. J. 1967b. The ecology of pelagic Amphipoda, II: Observations on the reproductive cycles of several pelagic Amphipods from the waters off southern California. Pac. Sci. 21:449–456.

Brusca, G. J. 1981. Annotated keys to the Hyperiidea (Crustacea: Amphipoda) of North American coastal waters. Allan Hancock Found. Tech. Rep. 5:1–76.

Clarke, K. R. and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Natural Laboratory, 172 p.

Collins, M., R. Shreeve, S. Fielding, and M. Thurston. 2008. Distribution, growth, diet and foraging behaviour of the yellow-fin notothen *Patagonotothen guntheri* (Norman) on the Shag Rocks shelf (Southern Ocean). J. Fish Biol. 72:271–286.

Cornet, C., and J. M. Gili. 1993. Vertical distribution and daily migrations of hyperiid amphipods in the northern Benguela in relation to water column stratification. Deep-Sea Res. I 40:2295–2306.

Dalpadado, P., N. Borkner, B. Bogstad, and S. Mehl. 2001. Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES J. Mar. Sci. 58:876–895.

Durazo, R. 2015. Seasonality of the transitional region of the California Current System off Baja California. J. Geophys. Res., Oceans 120:1173–1196, doi: 10.1002/2014JC010405.

Durazo, R., and T. Baumgartner. 2002. Evolution of oceanographic conditions off Baja California: 1997–99. Prog. Oceanogr. 54:7–31.

Feng, M., M. J. McPhaden, S. Xie, and J. Hafner. 2013. La Niña forces unprecedented Leeuwin Current warming in 2011. Sci. Rep. 3, 1277, doi: 10.1038/srep01277.

Gasca, R. 2004. Distribution and abundance of hyperiid amphipods in relation to summer mesoscale features in the southern Gulf of Mexico. J. Plankton Res. 26:993–1003.

Gasca, R. 2007. Hyperiid amhipods of the Sargasso Sea. Bull. Mar. Sci. 81:115–125.

Gasca, R., and C. Franco-Gordo. 2008. Hyperiid amphipods (Peracarida) from Banderas Bay, Mexican Tropical Pacific. Crustaceana 81:63–575.

Gasca, R., C. Franco-Gordo, E. Godínez-Domínguez, and E. Suárez-Morales. 2012. Hyperiid amphipod community in the eastern tropical Pacific before, during, and after El Niño 1997–98. Mar. Ecol. Prog. Ser. 455:123–139.

Gasca, R., H. Manzanilla, and E. Suárez-Morales. 2009. Distribution of hyperiid amphipods (Crustacea) of the southern Gulf of Mexico, summer and winter, 1991. J. Plankton Res. 31:1493–1504.

Gasca, R. and E. Suárez-Morales. 2004. Distribution and abundance of hyperiid amphipods (Crustacea: Peracarida) of the Mexican Caribbean Sea, (August 1986). Caribb. J. Sci. 40:23–30.

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

Huyer, A. 1983. Coastal upwelling in the California Current system. Prog. Oceanogr. 12:259–284.

Jerónimo, G., and J. Gómez-Valdés. 2006. Mean temperature and salinity along an isopycnal surface in the upper ocean off Baja California. Cienc. Mar. 32:663–671.

Jerónimo, G., and J. Gómez-Valdés. 2007 A subsurface warm-eddy off northern Baja California in July 2004. Geophys. Res. Lett. 34, L06610, doi: 10.1029/2006GL028851.

Kessler, W. S. 2006. The circulation of the eastern tropical Pacific: A review. Prog. Oceanogr. 69:181–217.

Laval, P. 1980. Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. Oceanogr. Mar. Biol. 18:11–56.

Lavaniegos, B. E. 2014. Pelagic amphipod assemblage associated with subarctic water off the West Coast of the Baja California peninsula. J. Marine Syst. 132:1–12.

Lavaniegos, B. E., and C. M. Hereu. 2009. Seasonal variation in hyperiid amphipod abundance and diversity and influence of mesoscale structures off Baja California. Mar. Ecol. Prog. Ser. 394:137–152.

Lavaniegos, B. E., L. C. Jiménez-Pérez, and G. Gaxiola-Castro. 2002. Plankton response to El Niño 1997–98 and La Niña 1999 in the southern region of the California Current. Prog. Oceanogr. 54:33–58.

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

Lavaniegos, B. E., and M. D. Ohman. 1999. Hyperiid amphipods as indicators of climate change in the California Current. *In* Crustaceans and the Biodiversity Crisis. Proceedings of the 4th International Crustacean Congress, Vol. 1, F. R. Schram and J. von Vaupel Klein, eds., Brill, Leiden, pp. 489–509.

Lavaniegos, B. E., and M. D. Ohman. 2003. Long-term changes in pelagic tunicates of the California Current. Deep Sea Res. II 50:2473–2498.

Lima, M., and J. Valentin. 2001. Preliminary results to the holistic knowledge of the Amphipoda Hyperiidea faunal composition off the Brazilian coast. J. Plankton Res. 23:469–480.

Lorz, H., and W. Pearcy. 1975. Distribution of hyperiid amphipods off the Oregon coast. J. Fish. Res. Board Can. 32:1442–1447.

Lynn, R., and J. Simpson. 1987. The California Current System: The seasonal variability of its physical characteristics. J. Geophys. Res. 92(C12):12947–12966, doi: 10.1029/JC092iC12p12947.

Lyon, B., and A. G. Barnston. 2005. The evolution of the weak El Niño of 2004–05. US CLIVAR Variations 3(2):1–4.

Mostarda E., D. Campo, L. Castriota, V. Esposito, M. P. Scarabello, and F. Andaloro. 2007. Feeding habits of the bullet tuna *Auxisrochei* in the southern Tyrrhenian Sea. J. Mar. Biol. Assoc. UK 87:1007–1012.

Nam, S., H. J. Kim, and U. Send. 2011. Amplification of hypoxic and acidic events by La Niña conditions on the continental shelf off California. Geophys. Res. Lett. 38, L22602, doi: 10.1029/2011GL049549.

Repelin, R. 1978. Les amphipodes pélagiques du Pacifique occidental et central: Biologie, écologie et relations trophiques avec la faune ichthyologique. Travaux et documents de l'ORSTOM, Paris 86:1–381.

Roe, H. S. J. 1974. Observations on the diurnal vertical migrations of an oceanic animal community. Mar. Biol. 28:99–113.

Satoh, K. 2004. Occurrence of *Phronima sedentaria* (Forskål, 1775) (Amphipoda, Hyperiidea) in the stomach of the longnose lancet fish, *Alepisaurus ferox* (Lowe, 1833) (Aulopiformes, Alepisauroidei) in the North and Tropical Atlantic Ocean. Crustaceana 77:729–739.

Siegel-Causey, D. 1982. Factors determining the distribution of hyperiid amphipoda in the Gulf of California. Ph.D. Thesis, University of Arizona, Tucson, 535 p.

Simpson J. H., C. M. Allen, and N. C. G. Morris. 1978. Fronts on the continental shelf. J. Geophys. Res. 83:4607–4614, doi: 10.1029/JC083iC09p04607.

Smith, P. and S. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fisheries Technical Paper, No. 175.

Soto-Mardones, L., A. Parés-Sierra, J. Garcia, R. Durazo, and S. Hormazabal. 2004. Analysis of the mesoscale structure in the IMECOCAL region (off Baja California) from hydrographic, ADCP and altimetry data. Deep-Sea Res. II 51:785–798.

Strub, P. T., and C. James. 2000. Altimeter-derived variability of surface velocities in the California Current System: 2. Seasonal circulation and eddy statistics. Deep-Sea Res. II47:831–870.

Thorne, P. W., K. M. Willett, A. J. Dolman, and B. D. Hall. 2012. [State of the Climate in 2011. Global Climate.] Overview. Bull. Amer. Meteor. Soc. Spec. Suppl. 93(7):S7–S11.

Thurston, M. H. 1976. The vertical distribution and diurnal migration of the Crustacea Amphipoda collected during the SOND cruise, 1965 II. J. Mar. Biol. Assoc. U.K. 56:383–470.

Torres, H. S., and J. Gómez-Valdés. 2015. Coastal circulation driven by short-period upwelling-favorable winds in the northern Baja California region. Deep-Sea Res. Part I 98:31–42.

Tranter, H. A. 1977. Further studies of plankton ecosystems in the Eastern Indian Ocean VII. Ecology of the Amphipoda. Mar. Freshwat. Res. 28:645–662.

Valencia, B., B. Lavaniegos, A. Giraldo, and E. Rodríguez-Rubio. 2013. Temporal and spatial variation of hyperiid amphipod assemblages in response to hydrographic processes in the Panama Bight, eastern tropical Pacific. Deep-Sea Res. I 73:46–61.

Valencia-Ramírez, B. 2010. Seasonal variation of hyperiid amphipod assemblages in the Colombian Pacific. Ms. Thesis, Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California, México. 95 p. [In Spanish]

Vinogradov, M., A. Volkov, and T. Semenova. 1996. Hyperiid amphipods (Amphipoda, Hyperiidea) of the world oceans. Science Publishers, New Delhi, 632 p.

Xu, Z. 2009. Statistical analysis on ecological adaptation of pelagic Amphipoda in the East China Sea. Acta Oceanol. Sin. 28:61–69.

Xu, Z., and J. Mei. 2006. Study on relation between distribution and environment of pelagic amphipods. Acta Oceanol. Sin. 25:112–120.

Zaytsev, O., R. Cervantes-Duarte, O. Montante, and A. Gallegos-García. 2003. Coastal upwelling activity on the Pacific shelf of the Baja California Peninsula. J. Oceanogr. 59:489–502.

Zeidler, W. 1984. Distribution and abundance of some Hyperiidea (Crustacea : Amphipoda) in northern Queensland waters. Aust. J. Mar. Fresh. Res. 35:285–305.

Zeidler, W. 1992. Hyperiid amphipods (Crustacea: Amphipoda: Hyperiidae) collected recently from eastern Australian waters. Rec. Aust. Museum 44:85–133.

APPENDIX 1

Hyperiid amphipod species found during four seasons of 2011. The geometric mean (GM) of abundance (ind/1000 m³) and number of samples with presence (N) are shown by month. Small juvenile organisms difficult for identification are recorded only to genus. Total number of analyzed samples is indicated in parenthesis.

	January (8)		April (9)		July (9)		October (9)	
Species	GM	N	GM	N	GM	N	GM	N
Infraorder Physosomata								
Family Scinidae								
Scina borealis (G.O. Sars,1882)	—	0	—	0	—	0	0.22	2
Scina similis Stebbing,1895	—	0	—	0	—	0	0.10	1
Scina tullbergi (Bovallius, 1885)	—	0	1.97	5	0.97	4	2.44	8
Scina spp.	0.95	5		2	—	0	—	0
Infraorder Physocephalata								
Family Vibilidae								
Vibilia armata Bovallius, 1887	3.57	4	4.70	5	3.45	4	6.15	5
Vibilia australis Stebbing, 1888	—	0	—	0	0.14	1	0.50	3
Vibilia chuni Behning & Woltereck, 1912	—	0	0.18	1	0.11	1	0.29	2
Vibilia propinqua Stebbing, 1888	—	0	—	0	—	0	0.45	2
Vibilia stebbingi Behning & Woltereck, 1912	0.13	1	—	0	—	0	3.50	7
Vibilia spp.	—	0	0.87	4	0.27	2	1.48	5
Family Paraphronimidae								
Paraphronima crassipes Claus, 1879	—	0	—	0	—	0	0.22	2
Paraphronima gracilis Claus, 1879	0.45	2	3.02	6	3.02	7	7.10	8
Paraphronima spp.	0.13	1	—	0	0.13	1	0.17	1
Family Phronimidae								
Phronima atlantica Guérin-Méneville, 1836	—	0	1.01	5	0.16	1	2.25	6
Phronima colleti Bovallius, 1887	—	0	—	0	0.13	1	0.33	1
Phronima curvipes Vosseler, 1901	—	0	—	0	—	0	0.22	2
Phronima pacifica Streets, 1877	—	0	—	0	—	0	0.46	2
Phronima sedentaria (Forskål, 1775)	0.93	4	0.42	3	0.33	3	1.47	5
Phronima solitaria Guérin-Méneville, 1836	—	0	0.11	1	—	0	—	0
Phronima stebbingi Vosseler, 1901								
Phronima dunbari Shih, 1991	—	0	0.11	1	0.73	2	2.68	7
Phronima spp.	0.19	1	1.39	5	0.23	1	1.42	5
Phronimella elongata (Claus,1862)	—	0	—	0	—	0	0.73	2
Family Phrosinidae								
Anchylomera blossevillei Milne-Edwards, 1830	—	0	—	0	—	0	0.89	4
Phrosina semilunata Risso, 1822	0.13	1	1.45	6	0.89	3	0.77	4
Primno brevidens Bowman, 1978	8.17	7	27.35	9	69.12	9	43.70	9
Family Hyperiidae								
Hyperoche medusarum (Krøyer, 1838)	—	0	2.94	7	6.68	8	1.76	4
Laxohyperia vespuliformes Vinogradov & Volkov, 1982	—	0	0.11	1	0.11	1	6.13	8
Family Lestrigonidae								
Hyperietta luzoni (Stebbing, 1888)	—	0	—	0	—	0	0.80	3
Hyperietta parviceps Bowman, 1973	—	0	0.13	1	—	0	—	0
Hyperietta stebbingi Bowman, 1973	—	0	—	0	0.27	1	0.97	4
Hyperietta stephenseni Bowman, 1973	—	0	1.04	5	1.62	6	5.33	6
Hyperietta vosseleri (Stebbing, 1904)	0.13	1	—	0	—	0	—	0
Hyperietta spp.	—	0	0.14	1	0.19	1	—	0
Hyperioides longipes Chevreux, 1900	—	0	0.24	2	—	0	1.12	3
Hyperioides sibaginis (Stebbing, 1888)	—	0	—	0		1	10.99	7
Lestrigonus bengalensis Giles, 1887	—	0	—	0	—	0	59.77	9
Lestrigonus schizogeneios (Stebbing, 1888)	3.80	7	24.72	8	102.72	9	72.83	9
Lestrigonus shoemakeri Bowman, 1973	0.44	2	3.37	7	—	0	—	0
Lestrigonus spp.	1.08	3	35.61	9	46.74	9	42.77	9
Phronimopsis spinifera Claus, 1879	0.81	4	1.78	6	—	0	0.86	4
Themistella fusca (Dana, 1853)	—	0	—	0	0.33	2	1.59	4
Family Lycaeopsidae								
Lycaeopsis themistoides Claus, 1879	0.13	1	0.40	3	0.76	3	1.17	5
Lycaeopsis zambongae (Stebbing, 1888)	—	0	—	0	—	0	0.42	2
Lycaeopsis spp.	0.13	1	—	0	—	0	0.11	1
Family Pronoidae								
Eupronoe maculata Claus, 1879	—	0	0.11	1	—	0	—	0
Eupronoe minuta Claus, 1879	8.77	7	37.84	9	38.51	9	13.34	9
Parapronoe cambelli Stebbing, 1888	—	0	0.33	2	—	0	—	0
Parapronoe crustulum Claus, 1879	—	0	0.41	3	0.22	2	—	0
Parapronoe spp.	—	0	0.17	1	—	0	—	0
Pronoe capito Guérin-Méneville, 1836	—	0	0.56	4	0.23	2	0.55	3

(continued)

APPENDIX 1, continued

Hyperiid amphipod species found during four seasons of 2011. The geometric mean (GM) of abundance (ind/1000 m³) and number of samples with presence (N) are shown by month. Small juvenile organisms difficult for identification are recorded only to genus. Total number of analyzed samples is indicated in parenthesis.

Species	January (8) GM	N	April (9) GM	N	July (9) GM	N	October (9) GM	N
Family Lycaeidae								
Lycaea nasuta Claus, 1879	—	0	—	0	—	0	0.30	2
Lycaea pachypoda (Claus, 1879)	0.45	2	—	0	—	0	—	0
Lycaea pauli Stebbing, 1888	—	0	—	0	—	0	0.21	2
Lycaea pulex Marion, 1874	—	0	—	0	0.11	1	3.55	7
Lycaea serrata Claus, 1879	—	0	—	0	—	0	0.21	2
Lycaea spp.	—	0	—	0	—	0	0.55	3
Simorhynchotus antennarius (Claus, 1871)	0.36	2	15.36	9	9.84	9	37.92	9
Family Tryphaneidae								
Tryphana malmi Boeck, 1870	1.03	4	1.11	4	0.91	3	6.85	8
Family Brachyscelidae								
Brachyscelus crusculum Bate, 1861	—	0	0.31	2	—	0	0.42	3
Brachyscelus globiceps (Claus, 1879)	—	0	0.42	3	—	0	—	0
Brachyscelus spp.	—	0	—	0	0.10	1	—	0
Family Oxycephalidae								
Glossocephalus milneedwardsi Bovallius, 1887	—	0	—	0	—	0	0.11	1
Oxycephalus clausi Bovallius, 1887	—	0	0.11	1	—	0	6.59	6
Oxycephalus piscator Milne-Edwards, 1830	—	0	—	0	—	0	0.44	3
Oxycephalus spp.	—	0	—	0	—	0	0.43	2
Rhabdosoma minor Fage, 1954	—	0	—	0	—	0	0.22	1
Rhabdosoma whitei Bate, 1862	—	0	0.11	1	—	0	2.27	5
Rhabdosoma spp.	—	0	—	0	—	0	0.30	2
Streetsia challengeri Stebbing, 1888	0.28	2	0.26	2	—	0	0.12	1
Streetsia mindanaonis (Stebbing, 1888)	—	0	—	0	—	0	0.11	1
Family Platyscelidae								
Platyscelus ovoides (Risso, 1816)								
Platyscelus serratulus Stebbing, 1888	0.67	3	0.58	3	3.44	6	13.13	7
Tetrathyrus arafurae Stebbing, 1888	—	0	—	0	—	0	0.71	3
Tetrathyrus forcipatus Claus, 1879	—	0	—	0	—	0	1.90	7
Tetrathyrus spp.	—	0	—	0	—	0	0.28	1
Family Parascelidae								
Parascelus edwardsi Claus, 1879	—	0	—	0	0.11	1	0.92	3
Parascelus typhoides Claus, 1879	—	0	—	0	0.10	1	0.42	3
Parascelus spp.	—	0	—	0	—	0	0.19	1