Effects of latitudinal changes in the oxygen minimum zone of the northeast Pacific on the distribution of bathyal benthic decapod crustaceans

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ABSTRACT

The presence of an Oxygen Minimum Zone (OMZ) is one of the major characteristics of the eastern Pacific. The OMZ changes strongly adjacent to Mexico in its thickness and intensity. The ecological impacts of those changes were studied by examining the community structures of bathyal benthic and bentho-pelagic decapod crustaceans, and their oceanographic contexts, on the Mexican Pacific slope along a wide latitudinal range (16–32°N). Decapod crustaceans were collected with a benthic sledge from 48 stations between 865 and 2165 m in three main areas: offshore of northern Baja California (NBC), off southern Baja California (SBC) and in the southern Mexican Pacific (SMP). Physical–chemical parameters were measured in the water column, and sediment composition was analyzed for each station. The narrowing and weakening of the OMZ north of ca. 26°N was confirmed. Water with dissolved oxygen < 0.5 ml l^{-1} occupied a stratum of 1231 m in the SMP vs. only 664 m off NBC. The strongest changes coincided with a region of surface, subsurface and intermediate water mass transitions, where less saline waters from the north extended to depths of ca. 1000 m. Sand proportions were higher in sediments to the south, whereas silt dominated offshore of NBC. A strong latitudinal shift in decapod community composition and bathymetric distribution occurred from off SBC to off NBC, coinciding with changes in oceanographic conditions. The dominant genera of decapod crustaceans at slope depths were cognate to those dominating slope areas in other tropical and subtropical regions of the world. In the SMP and off SBC, large aggregations of organisms were observed at 900–1300 m, with a sharp decrease in abundance at greater depth. Off NBC, the density of organisms was intermediate at all depths. The combined effects of dissolved oxygen concentration and characteristics of water masses affected the distribution of organisms. The faunal patterns were also related with sediment grain size.

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1. Introduction

Oxygen minimum zones (OMZs) are typically characterized by dissolved oxygen concentration (DO) < 0.5 ml l^{-1} (22 µmol l^{-1}) (Levin, 2003). The largest permanent OMZ on the planet (ca. 26 million km^2) occurs in the eastern Pacific (Helly and Levin, 2004; Paulmier and Ruiz-Pino, 2009). This OMZ is not homogenous, and its thickness, intensity, and vertical distribution vary with latitude (Helly and Levin, 2004). The most marked variations in these three parameters in the northeast Pacific take place around latitudes 24–26°N, off the Mexican Pacific coast. From the south to ca. 26°N the OMZ is vertically thickest and most intense, with DO < 0.5 ml l^{-1}

between depths of ca. 100 and 1000 m, and DO < 0.2 ml l^{-1} between ca. 100 and 800 m. North of 26°N (to ca. 32°N) the OMZ is narrower and moderate; water with DO < 0.5 ml l^{-1} only occupies a thin layer of 100 m at about 550–650 m, and values of DO < 0.2 ml l^{-1} are not recorded (Helly and Levin, 2004).

OMZs are often associated with eastern boundary current systems, such as the California and Humboldt currents in the eastern Pacific (Gutknecht et al., 2013). The massive surface production of these regions translates to large fluxes of labile organic material through the water column (Gutknecht et al., 2013; Rouiller et al., 2014). In OMZ areas, the magnitude of these fluxes is sustained downward by the low remineralization rates due to the low oxygen availability (Rouiller et al., 2014). As a result, slope sediments beneath the core of the OMZ (DO < 0.15 ml l^{-1} or 6.6 µM: Levin, 2003) are particularly rich in labile organic material (Cowie et al.,

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1999; Devol and Hartnett, 2001; Honjo et al., 2008). However, along the bottom below those strongest DO minima, a gradual increase in DO is accompanied by steep bathymetric gradients in organic-matter availability (Cowie, 2005). Although the little knowledge available of fauna distribution in areas under the influence of OMZs is mainly dedicated to meiofauna (Wishner et al., 1990, 1995; Saltzman and Wishner, 1997) and macrofauna (Levin et al., 2009, 2010; Hughes et al., 2009; Ingole et al., 2010), some studies on benthic megafauna have identified the linked patterns in DO and food quality as the main drivers of their patterns of distribution in highly productive, oxygen-depleted areas (Murty et al., 2009; Hunter et al., 2011; Papiol and Hendrickx, 2016). Low DO within the core of the OMZ prevents the survival of both macro- and megafaunal taxa, despite the large availability of food. Within the lower OMZ boundary (DO between 0.15 ml l^{-1} and 0.5 ml l^{-1}), the release in oxygen restriction and the large availability of labile organic material in the sediments favor large aggregations of macro- and megafaunal benthic and benthopelagic invertebrates (Diaz and Rosenberg, 1995; Levin, 2003; Murty et al., 2009; Hunter et al., 2011) and high levels of biological activity (Wishner et al., 1995). At greater depth, beneath the OMZ boundary (DO > 0.5 ml l^{-1}), the decrease in the availability of labile food sources is likely responsible for decreasing megafaunal abundance, despite a continuous increase in DO with depth. These faunal responses to environmental characteristics of OMZs have usually been described from bathymetric transect studies in which stations at the same depth along different transects are located within a latitudinally narrow and stable OMZ area (i.e., homogenous width, intensity and vertical distribution). However, it is expected that regional-scale variations in OMZ characteristics will influence faunal patterns. Changes in the distribution of DO in the water column and in the transfer of organic material to bathyal depths would be key factors driving such patterns. To the authors' knowledge, this issue has only been addressed in one study performed by Witte (2000) in the Arabian Sea. She detected spatial variations in macrofaunal biomass associated with variations in food availability. To date, no similar information is available for megafaunal taxonomic groups.

The megafauna of lower OMZ boundaries is dominated by polychaetes, ophiuroids and decapod crustaceans (Wishner et al., 1990; Murty et al., 2009; Hunter et al., 2011). Those play important roles in structuring the marine benthos through physical disturbance of sediment (e.g., Hunter et al., 2011), predation upon meio- and macrofauna (Jeffreys et al., 2009a) and selective removal of both suspended and sedimented labile organic matter (Wishner et al., 1995; Smallwood et al., 1999; Jeffreys et al., 2009b). Among these bathyal taxa, decapod crustaceans are the most sensitive to oxygen depletion (Vaquer-Sunyer and Duarte, 2008) and, although they feed at multiple trophic levels (Jeffreys et al., 2009a), their dynamics depend directly or indirectly on surface production and particle flux to bathyal depths (e.g., Cartes et al., 2008; Fanelli et al., 2013). Thus, crustaceans are expected to be highly susceptible to regional changes in OMZ characteristics.

We have examined the regional distribution patterns of the OMZ and of megafaunal decapod crustaceans below the OMZ core along the Mexican slope in the northeastern Pacific. The OMZ there features important changes in its main attributes, allowing us to analyze the influence of those changes on the faunal patterns. Beside providing baseline knowledge of the structure and function of the megafaunal communities of the region, the results may provide insights about the potential consequences of impending oxygen minima expansions (Stramma et al., 2008; 2010) and of changes in marine production and vertical export (Bopp et al., 2001; Doney et al., 2012) possibly associated with climate change.

2. Materials and methods

2.1. Sampling locations

Within the TALUD project, three multidisciplinary research cruises were carried out over the Pacific slopes off western Mexico (northeast Pacific: Fig. 1). Samplings aboard the R/V "El Puma" of the Universidad Nacional Autónoma de México (UNAM) were performed off both the northern (NBC) (TALUD
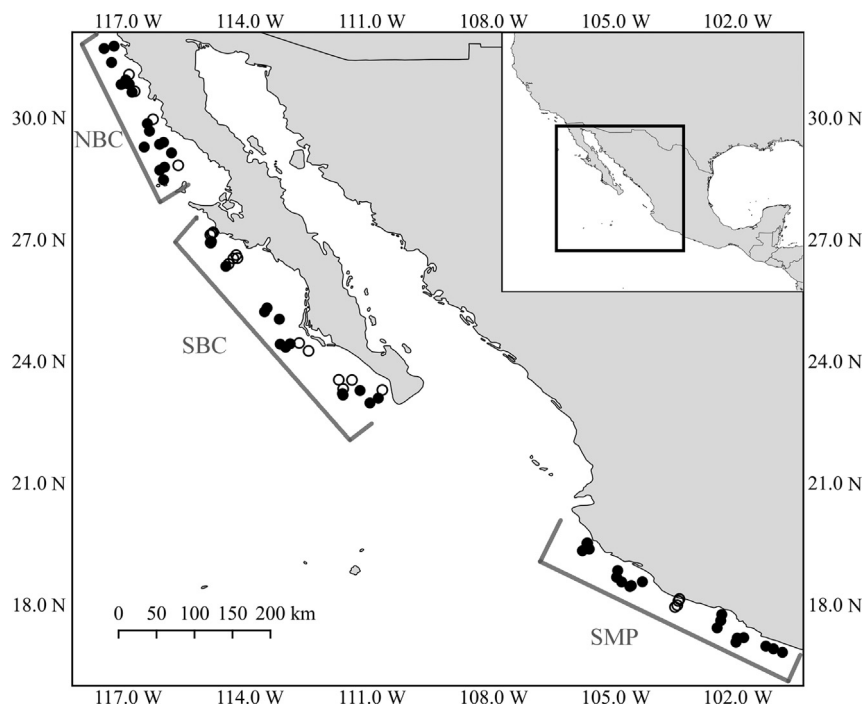

Fig. 1. Study area and sampling sites. Open symbols for stations with CTD casts only; solid symbols for stations with CTD casts and benthic sledge hauls.

XVI-B, May–June 2014) and southern (SBC) (TALUD XV, July–August 2012) Baja California peninsula's west coast and in the southern Mexican Pacific (SMP) (TALUD XII, March–April 2008).

2.2. Sampling of environmental data

Hydrographic data were obtained from 71 stations over depths between 270 and 2165 m (Fig. 1) using a CTD–O_2 (Seabird 19 with oxygen probe) and rosette-mounted 10 L Niskin bottles. The vertical sampling frequency was 2 Hz at a lowering speed of 1 m s^{-1}. Near-bottom temperature (T) and salinity (S) data and water samples were obtained $\sim$20 m above bottom (20mab). Dissolved oxygen near the bottom (20mab) was estimated from water samples with Winkler titrations (Strickland and Parsons, 1972). Additionally, oxygen, temperature and salinity profiles were obtained from the CTD–O_2 continuous records in the water column.

Phytoplankton pigment concentrations (PPC, mg Chla m^{-3}) were obtained from http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_month and used as indices of surface primary production in the area. This was used to assess the response of bathyal decapod crustaceans to surface production processes (Cartes et al., 2004). Monthly average PPC values recorded for each locality on the date of sampling (PPC$_{sim}$) and 1–6 months before (PPC$_{-1}$ to PPC$_{-6}$) were used to evaluate the time lag between surface processes and the faunal response.

2.3. Sediment sampling and analysis

Sediment was collected with a modified USNEL box core at each sampling station, and samples of the top 3 cm were stored at 4–8 °C. At the laboratory, sediments were dried to a constant weight at 60 °C. Organic carbon in the sediments is an indicator of food availability (Beaulieu, 2002). We determined organic carbon (OC$_{sed}$) content by treating samples with an oxidizing mixture of 1N $K_2Cr_2O_7$+concentrated H_2SO_4+Ag_2SO_4, and then titrating with 0.5 N Fe(NH$_4$)$_2$(SO$_4$)$_2$ (Loring and Rantala, 1992). Solutions of dextrose were used to develop calibration curves.

Grain size distribution was determined by laser dispersion (Malvern Mastersizer 2000E) on sediment samples, after treatment with 30% H_2O_2 to destroy organic matter.

2.4. Sampling of decapod crustaceans

Samples of benthic and bentho-pelagic decapod crustaceans were obtained from 48 trawls performed below the OMZ core, between 865 and 2165 m (Fig. 1; Appendix A), using a benthic sledge with an opening 2.35 m wide and 0.90 m high, equipped with an outer collecting net of ca. 5.5 cm (2 1/4″) stretch mesh, and an inner net of ca. 2.0 cm (3/4″) stretch mesh. Trawling generally lasted 30 min at an average speed of 1.75 knots. Swept area was estimated based on trawling speed and time at the bottom.

All benthic and bentho-pelagic decapod crustaceans collected were identified to species level, counted and weighed (wet weight), either on board or in the laboratory. Specimens were fixed in 4% formaldehyde seawater solution for at least one week, washed with tap water and preserved in 70% ethanol. Selected specimens were preserved directly into 70% ethanol. The majority of specimens were deposited in the Regional Collection of Marine Invertebrates (ICML-EMU) at the Instituto de Ciencias del Mar y Limnología, UNAM, in Mazatlán, Mexico.

2.5. Data analysis

2.5.1. Environmental data

A temperature vs. salinity (T–S) diagram composed of approximately 84,000 points was constructed to identify the water masses found in the study area. Vertical profiles (average and standard deviation) of T, S and DO were obtained for the three study areas. The CTD–O_2 values were linearly vertically interpolated to obtain one per meter. In addition, latitudinal sections of T, S and DO were obtained for each area. Sections were constructed using data from 8, 7 and 8 stations for the NBC, SBC and SMP regions, respectively. Interpolations between the profiles of T, S and DO at separated stations were made every 5 km using cubic Hermite interpolation.

Product-moment (r) correlations were calculated between the sediment variables measured (OC$_{sed}$ and grain size) and latitude and depth to characterize their relationships to location and bathymetry.

2.5.2. Decapod crustacean community structure

Megafaunal species recorded in fewer than 5% of the samples were omitted from the data set to prevent their undue influence on the results (Gauch, 1982). Abundance and biomass were standardized to a common swept area of 1 ha (N ha^{-1} and g ha^{-1}, respectively).

Using samples containing decapod crustaceans, Bray–Curtis similarity indices (Bray and Curtis, 1957) were calculated for square-root transformed species density per haul to define the similarity of the faunal compositions among the sampling sites (Clarke and Warwick, 2001). Megafaunal species groupings were evaluated by group-average linkage cluster analysis of the resemblance matrix. Sample relationships were also analyzed by nonmetric multidimensional scaling (nMDS: Clarke and Warwick, 2001) of resemblance matrix, producing a 2-dimensional ordination. To roughly quantify the spatial component of that ordination, Spearman's correlation coefficients were calculated between sample coordinates in dimensions 1 and 2 of the nMDS and sampling latitude and depth.

To evaluate whether assemblages differed among the three sampling areas and with depth, a distance-based Permutational Analysis of Variance (PERMANOVA: Anderson et al., 2008) was performed using a two-factor crossed design considering "depth range" (three levels grouping samples every 400 m; 900–1300, 1300–1700, 1700–2100) and "area" (three levels: NBC, SBC, and SMP) as factors. Pair-wise tests were performed when the interaction between the two factors was significant in order to evaluate more fully the effects of latitude in each depth stratum. Significance was set at $p=0.05$, and p-values were obtained using 9999 permutations of residuals under a reduced model. A SIMPER routine performed on the Bray–Curtis matrix (Clarke, 1993) was used to identify whether species typifying each depth interval differed among areas.

Species were classified into functional groups according to their feeding strategies (predators, P; predators/facultative deposit feeders, P/D; predators/facultative scavengers, P/S; and deposit feeders/facultative scavengers, D/S) based on the literature. The bathymetric and latitudinal patterns of density and biomass were analyzed by trophic group. Differences were tested by means of PERMANOVA, following the same two-factor design with "depth range" and "area" as factors after log-transformation of the raw data.

The turnover of taxa within each area and depth stratum was explored using a multivariate test for homogeneity of dispersion (PERMDISP) based on Jaccard dissimilarity measures (Anderson et al., 2006). Species diversity indices (S, number of species; H', Shannon index; and J', evenness) were also calculated per area and

per depth stratum within each area. To compare the depth distributions of the species among areas, the Center of Gravity (CoG) (Stefanescu et al., 1992; Cartes et al., 2011) in each area was calculated for the species that were collected in at least two hauls per area.

2.5.3. Effects of environmental factors on assemblages

The relationships between species density and environmental variables were explored by several univariate and multivariate techniques. The environmental variables explored were T_{20mab}, DO_{20mab}, S_{20mab}, OC_{sed}, PPC_{sim} and PPC_{-1-6} and percentages of sand, silt and clay in the sediments. Before the analyses, a Draftsman plot was performed on the environmental data set in order to identify correlations among the variables. Only variables that were not correlated (Pearson's correlation, $\rho \leq 0.75$) were used for the analyses. DISTLM (distance-based multivariate multiple regression based on a linear model: McArdle and Anderson, 2001) was performed to check which environmental variables drive assemblage species composition. DISTLM were generated with a forward permutation procedure, using an AIC selection scheme (Anderson et al., 2008). Canonical correspondence analysis (CCA) (ter Braak, 1986) was performed on density data for the dominant decapod species and the environmental variables to detect relationships between the species and those variables. Density data were log-transformed prior to CCA calculations and a permutation test (based on 1000 permutations) was performed to evaluate whether the set of environmental variables could significantly explain the observed shifts in species densities.

All statistical analyses were performed using PRIMER6 and PERMANOVA+(Clarke and Warwick, 2001; Anderson et al., 2008), STATISTICA 10 (StatSoft Inc.), and CANOCO (ter Braak and Smilauer, 2002) software.

3. Results

3.1. Environmental variables

3.1.1. T–S diagram

The T–S diagram (Fig. 2) shows clear differences between the NBC and the SMP areas in surface and subsurface waters, with Subarctic Water (SAW) at the surface off NBC and Subtropical Surface Water (StSW) in the SMP. Both water masses were present off SBC, with SAW at latitudes above 24°N, and StSW at lower latitudes. Deeper, some influence of low-salinity North Pacific Intermediate Water (NPIW) was recorded off NBC and Equatorial Subsurface Water (ESsW) was recorded farther south. Deeper than 1000 m (as estimated from the three profiles in Fig. 3), Pacific Deep Water (PDW) was detected in all three areas.

3.1.2. T, S, and DO profiles

The temperature (T) profiles (Fig. 3) were similar in the three regions, except for a weaker temperature change near the surface off NBC compared to the other regions. Below 900 m, temperature variance within each area was almost nil. Overall mean temperature of 2.22 ± 0.06 °C was recorded at 2000 m depth.

Salinity decreased near the surface and increased sharply in subsurface water (Fig. 3). Off NBC, S decreased from 33.56 g kg^{-1} at 8 m to 33.30 g kg^{-1} at 48 m, and then gradually increased with depth, reaching values of 34.61 g kg^{-1} at 2000 m. Salinity maxima of 34.72 g kg^{-1} were recorded at 200 m off SBC and of 34.80 g kg^{-1} at 125 m in the SMP. A second relative minimum was recorded between 600 and 800 m both off SBC and in the SMP. At 2050 m, S values were 34.67 g kg^{-1} off SBC and 34.63 g kg^{-1} in the SMP. Below 1100 m salinity profiles in the three regions behaved similarly. The greatest within-area variance in salinity profiles occurred
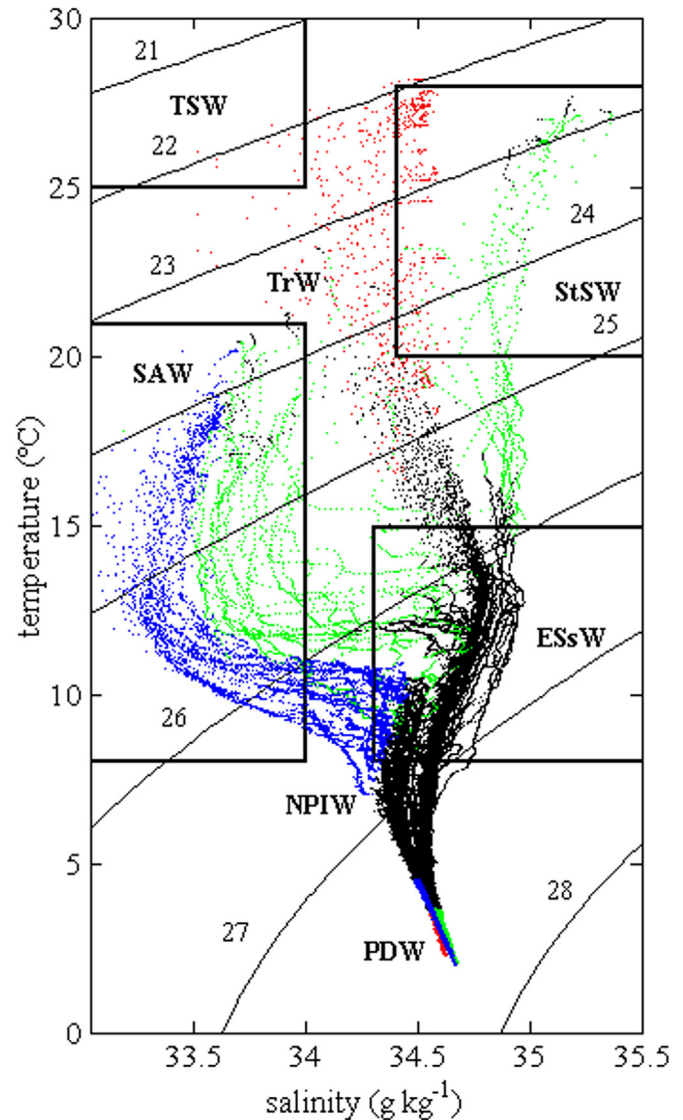

Fig. 2. T–S data pairs. The blue, green and red dots correspond to the NBC, SBC and SMP cruises, respectively, with DO ≥ 0.5 ml l^{-1}; the black dots correspond to the three cruises as a whole with DO < 0.5 ml l^{-1}. The thin lines represent the density anomaly σ_t and the thick lines represent the limits of the different water masses. TSW: Tropical surface water; TrW: Transitional water; StSW: Subtropical surface water; SAW: Subarctic water; ESsW: Equatorial subsurface water; NPIW: North Pacific intermediate water; PDW: Pacific deep water.

between the surface and 1000 m off SBC, indicating a saline transition.

Oxygen concentration profiles were typical of the eastern subtropical Pacific: an abrupt decrease near the surface, lowest values in a layer at intermediate depths, followed by a gradual increase with increasing depth (Fig. 3). The thickness of the OMZ (water with DO < 0.5 ml l^{-1}) was notably reduced northwards, occupying 290–954 m off NBC, 136–1205 m off SBC and 38–1269 m in the SMP. The DO increase rate between 1000 and 2000 m was greater off NBC (0.19 ml l^{-1} 100 m^{-1}) than off SBC (0.12 ml l^{-1} 100 m^{-1}) or in the SMP (0.13 ml l^{-1} 100 m^{-1}). Linked to this, DO at 2000 m was much higher off NBC (2.35 ml l^{-1}) compared to off SBC (1.53 ml l^{-1}) or in the SMP (1.42 ml l^{-1}).

3.1.3. Latitudinal T, S and DO sections

Three sections covering 395 (NBC), 588 (SBC) and 590 (SMP) km, were obtained (Fig. 4). The NBC and SBC sections were 220 km apart, and the SBC and SMP sections 640 km apart.
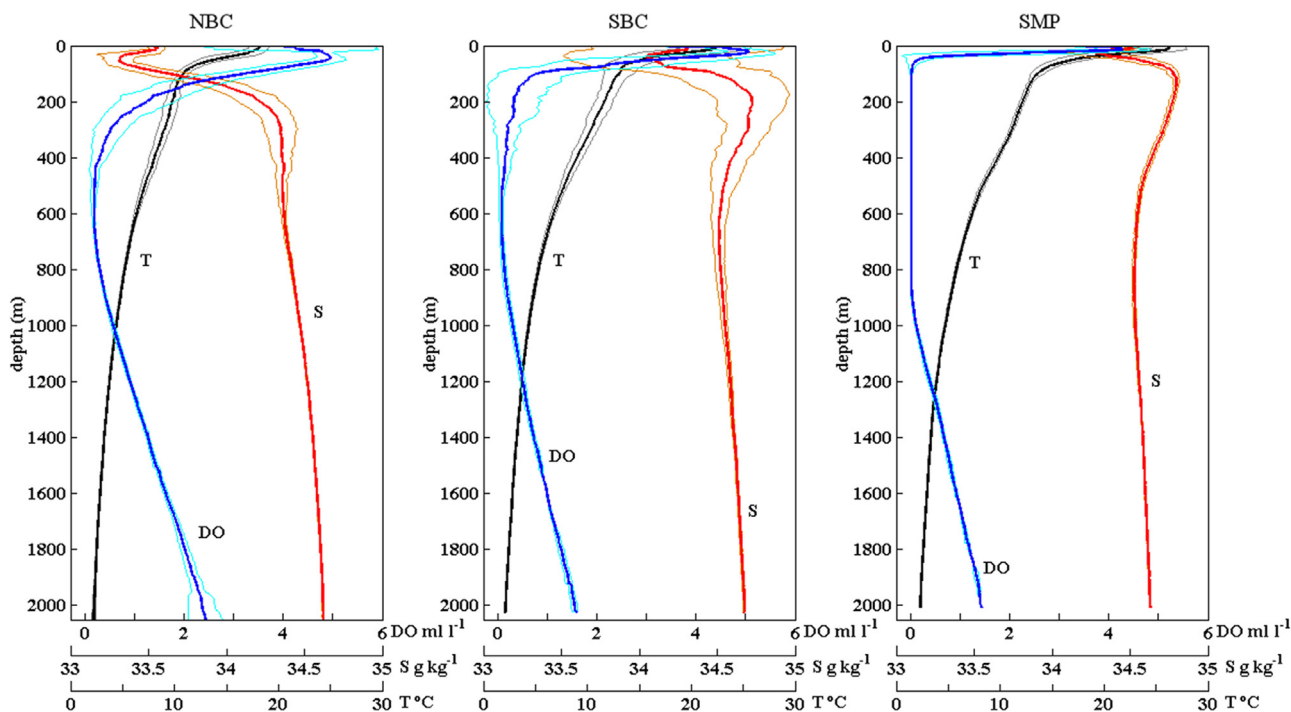
Fig. 3. Bathymetric profiles of average (and standard deviation) temperature (T), salinity (S) and oxygen (DO) measured for the three sampling regions.

Surface temperature was lower at higher latitudes (Fig. 4a), averaging 18.1, 22.6 and 25.1 °C for the NBC, SBC and SMP sections. The 10 °C isotherm was shallower to the north, 180 m vs. 281 and 382 m on the two southern sections. This contrasts with the nearly constant depth of the 5 °C isotherm among latitudes at ca. 870 m. Below 800 m the temperature decreased steadily on all three sections.

Salinity was distinctly lower in the north: average overall values for each section were 34.31, 34.53 and 34.60 g kg^{-1} at NBC, SBC and SMP, respectively (Fig. 4b). These differences were greater at the surface, with average S values of 33.52, 34.20 and 34.54 g kg^{-1}. Related to this, a surface salinity front was observed off SBC, between 23.15°N (TALUD XV, St. 3) and 24.33°N (TALUD XV, St. 10), with a maximum gradient (increasing southward) at approximately 24°N of 0.10 (g kg^{-1}) km^{-1}. This front, but with a weakening gradient below the surface, was recorded to a depth of 850 m. Also off SBC and in the SMP, an intrusion of water with higher salinity was recorded between 100 and 350 m. In all three sections, a monotonic increase in salinity was recorded below 850 m.

As mentioned above, the thickness of the OMZ decreased toward higher latitudes (Fig. 4c). This was the most marked for the depth intervals with DO ≤ 0.2 ml l^{-1}, which averaged thicknesses of 261, 631 and 1026 m for the NBC, SBC and SMP sections, respectively. The centers of those intervals were located at 562, 590, and 559 m. The upper 0.5 ml l^{-1} oxygen isopleth was located shallower southwards, above 60 m in the SMP vs. about 190 m off NBC. The 0.5 ml l^{-1} oxygen isopleth below the OMZ was deeper toward the south, at 960, 1204 and 1270 m. By fitting straight lines to the upper 0.5 ml l^{-1} isopleths along the sections, the slopes obtained were -0.30 (NBC), -0.24 (SBC) and 0.04 m km^{-1} (SMP), indicating that major changes of DO with respect to depth occur in the northern sections, while isopleth remains at almost constant depth in the southern area (SMP).

Off both NBC and SBC there were negative correlations (NBC $r = -0.61$; SBC $r = -0.91$) along the sections between the depths of the shallow 0.5 ml l^{-1} oxygen isopleths and the depths of the 10 °C isotherms. By contrast, the isopleths of 0.5 ml l^{-1} DO below

the OMZ were positively correlated with the 5 °C isotherms in all three sections (NBC $r = 0.86$; SBC $r = 0.83$; SMP$=0.54$), showing almost parallel trends. This result is reflected in the thickness of the OMZ, which increases as the 10 °C isotherm rises at lower latitudes.

3.1.4. Sediment composition

Product-moment correlations between sediment characteristics and latitude were all significant ($p < 0.05$): silt ($r = 0.74$) and organic carbon ($r = 0.37$) contents in the sediments increased from south to north (Fig. 5; Appendix A). Conversely, sand ($r = -0.46$) and clay ($r = -0.67$) proportions in the sediments were negatively correlated with latitude. Correlations between sediment characteristics and depth were only significant for sand ($r = -0.36$) and clay ($r = 0.33$).

3.2. Decapod crustacean community structure

A total of 3050 crustacean specimens belonging to 58 species representing 17 families was collected (Appendix B). Two new species, *Glyphocrangon taludensis* and *Bresilia pacifica*, have been described (Hendrickx, 2010, 2014a), and two additional species are new to science but are still being described (*Glyphocrangon* sp. A and *Munidopsis* sp. A). Eight species were recorded for the first time from the Mexican Pacific, and 14 more represented new records within sub-regions of the Mexican Pacific, of which 11 were collected off the west coast of Baja California (see Appendix B). Of the total of 48 samples available, only four (8%) did not contain any decapod crustacean species.

Cluster analysis and MDS showed that latitude and depth are the main factors driving assemblage structure. On the MDS, there is a strong latitudinal gradient from left to right, with the SMP stations located at the right of the plot and those from off NBC at the left (Fig. 6). The samples collected at 1300–1700 m and 1700–2100 m are typically at the top of the plot, and those collected at 900–1300 m are at the bottom. In agreement, dimension 1 of the MDS was correlated with latitude ($r = -0.77$; $p < 0.001$) and longitude ($r = 0.76$; $p < 0.001$) and dimension 2 was correlated
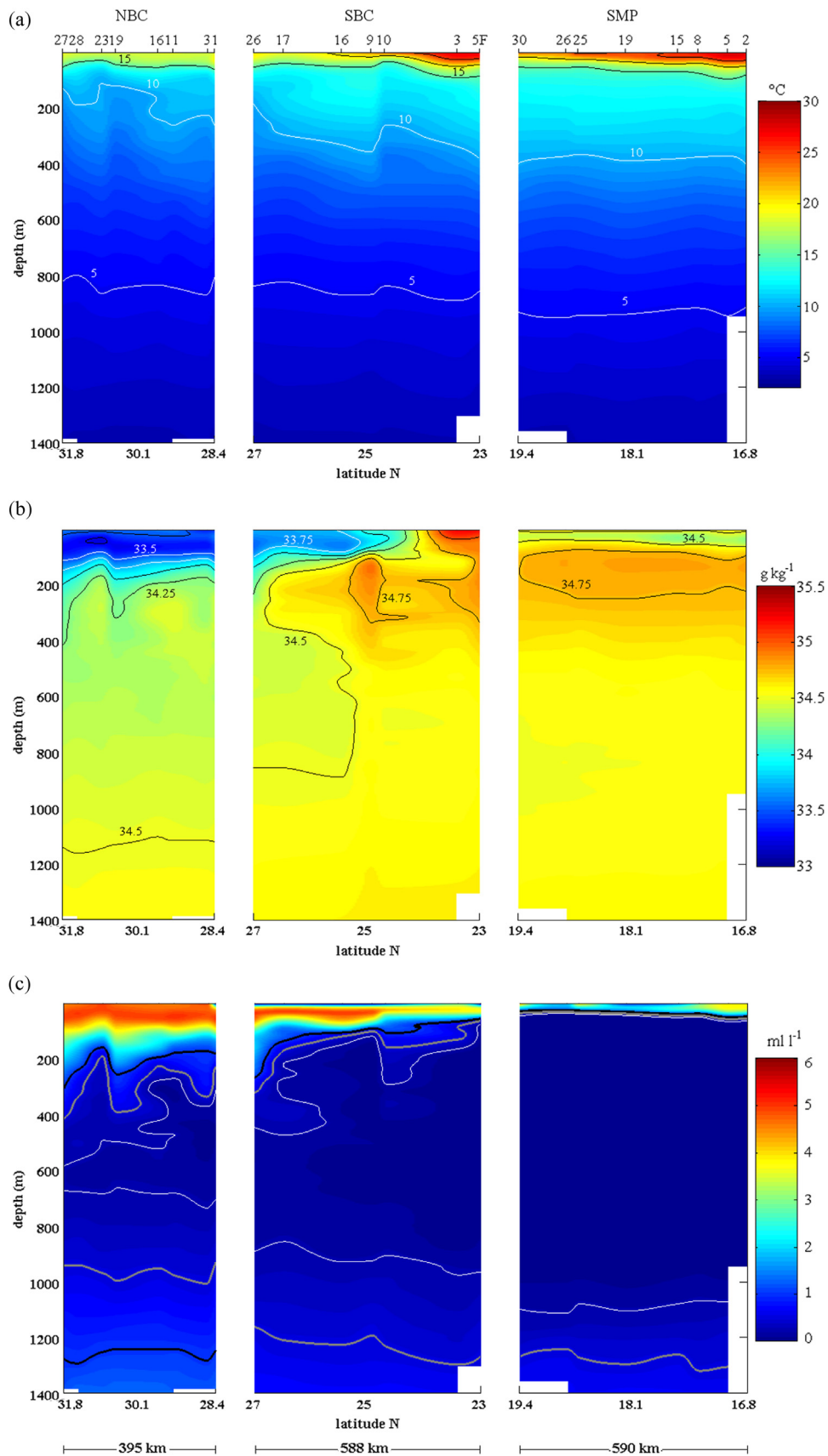
Fig. 4. Vertical sections of (top) temperature (°C), () salinity (g kg^{-1}), and (c) oxygen (ml l^{-1}) along a north–south transect parallel to the coastline for each sampling region. The numbers at the top indicate the stations.
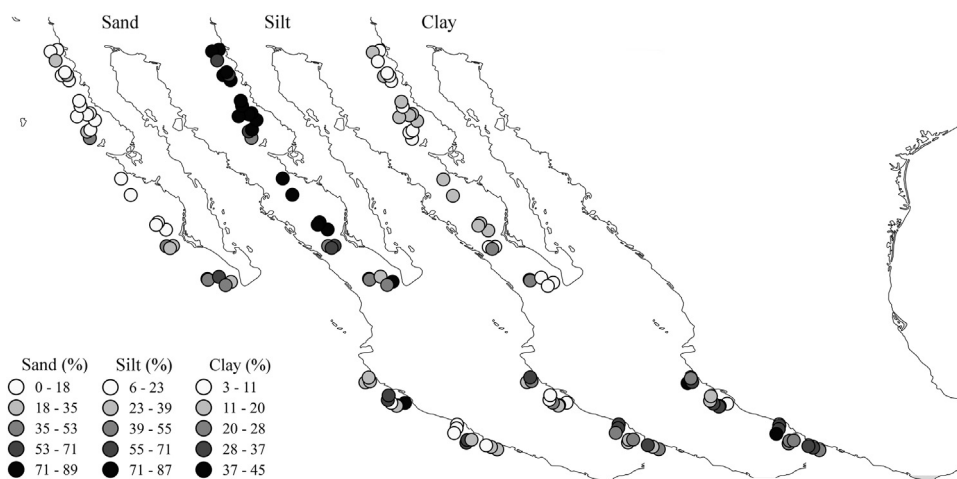
Fig. 5. Grain size distribution over the study area, considering the proportions of sand, silt and clay.
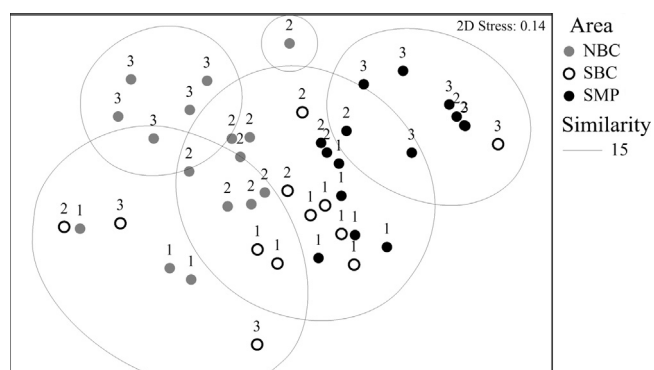

Fig. 6. MDS ordination plot of abundance data from benthic sledge catches based on a Bray–Curtis resemblance matrix. Circles define clusters at the 15% level of similarity. Numbers indicate the depth intervals:

with depth ($r=0.69$; $p<0.001$). Four main groups were obtained by clustering at 15% similarity (Fig. 6). One group consists of samples obtained at 1700–2100 m off NBC. A second group comprises primarily samples collected at 900–1300 m off NBC and at 1700–2100 m off SBC, and it also includes some intermediate depth samples from both areas. A third group mainly includes samples collected in the SMP at 1700–2100 m. The fourth group consists of samples obtained at intermediate depths in all three areas and at the shallowest off SBC and SMP stations.

The two-way PERMANOVA indicated significant differences among areas ($pseudo\text{-}F_{2,42}=6.79$; $p<0.001$) and depth strata ($pseudo\text{-}F_{2,42}=4.29$; $p<0.001$), and for the interaction between area and depth ($pseudo\text{-}F_{4,42}=2.60$; $p<0.001$). Pair-wise comparisons for the factor "area" showed that the three areas differed significantly (Table 1). For the interaction, both at 900–1300 m and deeper than 1700 m, the decapod-crustacean assemblages were similar in the SMP and off SBC but different when those were compared to assemblages off NBC (Table 1). At 1300–1700 m, changes in the assemblage composition were not significant between adjacent sampling areas, but the assemblages recorded in the SMP and off NBC were significantly different. The implication is that the change in the assemblage composition in respect to latitude at 1300–1700 m is gradual.

The SIMPER analysis showed that *Glyphocrangon spinulosa* and *Nematocarcinus faxoni* typified both the SMP and SBC assemblages at 900–1300 m (Table 2). In the SMP, *Acanthephyra brevicarinata*, *Lebbeus scrippsi*, *Nephropsis occidentalis* and *Munidopsis quadrata* were also major components of the 900–1300 m assemblage. Off

Table 1
Results of PERMANOVA pairwise comparisons for the factor "area" and for the interaction term "area x depth range" for decapod crustaceans. Probability estimates for significant results are in boldface.

Variable	t	P (perm)
Area		
NBC vs. SBC	1.76	**0.0004**
NBC vs. SMP	3.70	**0.0001**
SBC vs. SMP	2.06	**0.0004**
Depth range × area		
900–1300 m		
NBC vs. SBC	2.29	**0.0135**
NBC vs. SMP	2.29	**0.0184**
SBC vs. SMP	1.23	0.1515
1300–1700 m		
NBC vs. SBC	1.07	0.3214
NBC vs. SMP	2.32	**0.0010**
SBC vs. SMP	1.39	0.1079
1700–2100 m		
NBC vs. SBC	1.87	**0.0181**
NBC vs. SMP	3.73	**0.0070**
SBC vs. SMP	1.48	0.0905

SBC, *Benthesicymus tanneri* and *N. occidentalis* were also important members of the community in that stratum. The 900–1300 m assemblage off NBC was characterized by the pandalid *Plesionika sanctaecatalinae*. At 1300–1700 m, *A. brevicarinata* and *N. faxoni* typified the decapod crustacean assemblage in the SMP, and the latter also typified the group in SBC and NBC samples from this stratum. Additionally, *Galacantha diomedeae*, *B. tanneri* and *G. spinulosa* were important off NBC. At 1700–2100 m, *A. brevicarinata* was again the most typifying species in the SMP. The species collected at 1700–2100 m off SBC differed among samples. Those were: *A. brevicarinata*, *B. tanneri*, and *P. sanctaecatalinae* (Appendix B). Off NBC, the assemblage below 1700 m was characterized by the benthic shrimps *Paraponthopilus occidentalis* and *Glyphocrangon* sp. A. Within each area, similarity within each depth stratum increased with depth both off NBC (from 32.23% at 900–1300 m to 51.60% at 1700–2100 m) and in the SMP (from 38.55% at 900–1300 m to 49.24% at 1700–2100 m). In sharp contrast, off SBC intra-group similarity decreased with increasing depth, from 40.26% to 0.

The standardized mean densities of each of the 58 species are in Appendix B. Density and biomass values by depth stratum and area had high intra-sample variances (Fig. 7), which likely led to the lack of statistical significance of the two-way PERMANOVA main tests and their interaction. Off SBC and in the SMP, peak densities of

Table 2
Average abundances of species (Av. Ab), similarities of species abundance (Av. Sim) and cumulative contributions to the similarity (Cum. %) obtained by SIMPER analysis carried out for decapod crustaceans by area within each depth range. Cut-off at cumulative contributions of 80%.

| Northwestern Baja California (NBC)				Southwestern Baja California (SBC)				Southern Mexican Pacific (SMP)			
	Av.Ab	Av.Sim	Cum.%		Av.Ab	Av.Sim	Cum.%		Av.Ab	Av.Sim	Cum.%
900–1300 m											
Average similarity: 32.23				Average similarity: 40.26				Average similarity: 38.55			
Plesionika sanctaecatalinae	2.24	26.30	81.59	*Glyphocrangon spinulosa*	6.28	14.94	37.10	*Nematocarcinus faxoni*	12.67	13.03	33.81
				Nematocarcinus faxoni	10.95	8.79	58.93	*Acanthephyra brevicarinata*	3.06	4.89	46.51
				Benthesicymus tanneri	3.71	4.85	70.98	*Glyphocrangon spinulosa*	5.54	4.36	57.81
				Nephropsis occidentalis	2.44	3.38	79.38	*Lebbeus scrippsi*	3.81	4.17	68.64
				Stereomastis pacifica	1.78	2.14	84.70	*Nephropsis occidentalis*	2.13	3.75	78.36
								Munidopsis quadrata	3.87	2.65	85.24
1300–1700 m											
Average similarity: 36.07				Average similarity: 13.38				Average similarity: 43.39			
Nematocarcinus faxoni	3.17	14.46	40.08	*Nematocarcinus faxoni*	4.21	13.38	100.00	*Acanthephyra brevicarinata*	3.79	32.51	74.94
Galacantha diomedeae	3.46	9.58	66.63					*Nematocarcinus faxoni*	3.89	8.81	95.24
Benthesicymus tanneri	1.56	3.25	75.63								
Glyphocrangon spinulosa	2.71	2.37	82.21								
1700–2100 m											
Average similarity: 51.60				Average similarity:				Average similarity: 49.24			
Parapontophilus occidentalis	5.90	24.21	46.93	All similarities are 0				*Acanthephyra brevicarinata*	4.05	41.04	83.33
Glyphocrangon sp. nov	6.87	19.35	84.44								
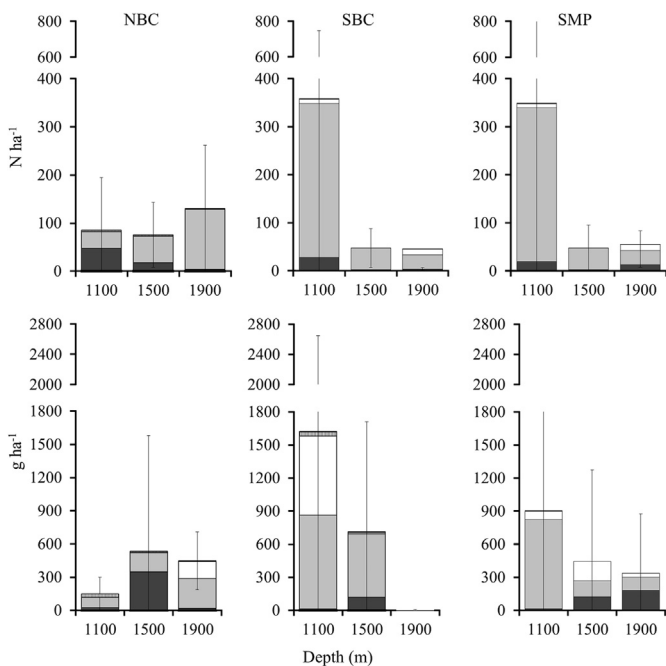
Fig. 7. Standardized mean abundance (N ha^{-1}) and biomass (g ha^{-1}) of decapod crustaceans by feeding strategy, by area and by depth interval. Deposit feeders (dark grey), predators (light grey), predators/facultative scavengers (striped), predators/facultative deposit feeders (white). Bars indicate ± standard deviations. NBC=northwestern coast of the Baja California peninsula; SBC=southwestern coast of the Baja California peninsula; SMP=southern Mexican Pacific.

326 ind. ha^{-1} and 358 ind. ha^{-1} were observed at 900–1300 m, and a sharp decrease to 48 ind. ha^{-1} occurred in both areas at 1300–1700 m (Fig. 7). At greater depth in the SMP, density remained similar to values observed at 1300–1700 m (46 ind. ha^{-1}), while off SBC density below 1700 m decreased sharply (4 ind. ha^{-1}). Off NBC, density was lowest at 1300–1700 m (76 ind. ha^{-1}) and highest at 1700–2100 m (130 ind. ha^{-1}). Biomass patterns paralleled density patterns both in the SMP and off SBC. Off NBC, however, they were different: biomass was lowest at 900–1300 m and highest at 1300–1700 m, with a slight decrease at greater depth (Fig. 7). Among trophic functional groups, predators were more abundant than the other functional groups in all areas and depth intervals, except off NBC at 900–1300 m. In fact, deposit feeders represented less than 15% of the density of decapods in all areas, except in samples from 900 to 1700 m off NBC. Predator biomasses were in general higher than those of the other functional groups. However, considerable contributions to biomass by deposit feeders at 1300–1700 m in all areas and also in the deepest stratum in the SMP were associated with captures of large specimens of the crab *Neolithodes diomedeae*.

PERMDISP results revealed greatest dissimilarities within the samples from off SBC (average distance to centroid=56.24 ± 3.40), although differences among the areas were not significant (average distance to centroid: NBC=52.35 ± 2.20; SMP=51.52 ± 1.62). Considering each depth stratum, at 900–1300 m dispersion was similar in all three areas (Table 3). Both at 1300–1700 m and 1700–2100 m, greatest dissimilarity was within the off SBC samples, the differences being significant ($p < 0.05$) between the SMP and the off SBC samples from 1300–1700 m and among all areas at 1700–2100 m.

Overall, all three diversity indices, S, H′ and J′, were lowest off SBC. Values of S and H′ were greatest from the shallowest depth stratum (900–1300 m) in the SMP and off SBC (Table 3), with a marked minimum deeper than 1700 m off SBC. Off NBC, S and H′ slightly increased from 900–1300 m to a maximum at 1300–1700 m. Bathymetric patterns of J′ were in most cases opposed to those of S and H′. Latitudinal patterns of S and H′ were almost parallel, and both parameters clearly tended to decrease northwards at 900–1300 m but to increase northwards at 1300–1700 m. At 1700–2100 m, both S and H′ were greatest off NBC and lowest off SBC. J′ was lowest off SBC and greatest off NBC both at 900–1300 m and 1300–1700 m, as opposed to values from deeper samples.

Only six species were distributed in all three areas. For three of those species (i.e., *Glyphocrangon spinulosa*, *Nematocarcinus faxoni*, and *Pandalopsis ampla*), the CoG was deepest off NBC (between 1350 and 1450 m) and shallower (between 1000 and 1200 m) off SBC and in the SMP (Fig. 8). The latitudinal pattern of the CoG of *B. tanneri* was the opposite, and it was distributed between ca. 1100 and 1200 m in the northern areas and at 1383 m in the SMP. The CoG of *Parapagurus foraminosus* was deeper both off NBC (1970 m) and in the SMP (1720 m) than at mid latitudes. For *G. diomedeae*, the CoG did not vary so widely and was located between 1280 and 1400 m in all areas, being shallowest (1281 m) off SBC.

3.2.1. Effects of environmental factors on assemblages

Positive correlations were detected among depth, oxygen and salinity recorded near the bottom, which all were negatively correlated with temperature. Percentages of sand were negatively correlated with percentages of silt, and PPC_{-4} was positively correlated with PPC_{-3} and PPC_{-5}.

DISTLM performed on the density matrix accounted for 30% of the total variance, and identified sand and clay contributions (%) to sediment composition and oxygen as explanatory variables (Table 4).

For the CCA ordination plot, percentages of sand and clay were discarded as their variance-inflation factor was greater than 20. The remaining explanatory variables significantly ($p = 0.002$) accounted for 42.13% of the variance, with 27% of the total explained from the first two CCA axes (Fig. 9). Samples were distributed along axis 1 according to depth. Samples from 900–1300 m were at the left and those collected at depths > 1700 m were at the right of the plot. Samples were ordinated according to latitude along axis 2, with samples from off NBC at the top of the plot and those from the SMP at the bottom. Axis 1 was mainly correlated with near-bottom temperature ($r = -0.88$) and oxygen ($r = 0.94$), and also with silt in the sediments ($r = 0.68$) and PPC_{-1} ($r = 0.52$). Axis 2 was correlated with near-bottom salinity ($r = 0.62$) and again with silt ($r = 0.47$). Most crangonoid species (i.e., *Parapontophilus occidentalis*, *Glyphocrangon* sp. A, and *G. taludensis*), *Parapagurus foraminosus* and

Acanthephyra brevicarinata were associated with greater depths and higher DO. The rest of the species were more abundant when temperature was higher. The density of the species associated with NBC samples (i.e., *Munidopsis alfredolaguardae*, *Plesionika sanctaecatalinae*, *Parapontophilus occidentalis* and *Glyphocrangon* sp. A) was enhanced by greater proportions of silt and of organic carbon in the sediments. Densities of species collected at southern stations (SMP) were more associated with surface production.

4. Discussion

This is the first attempt to describe the composition and structure of the benthic and bentho-pelagic decapod crustacean community simultaneously with its oceanographic context over wide latitudinal (16–32°N; 1573 km) and bathymetric (865–2165 m) ranges in an area featuring substantial changes in the main characteristics of the world's largest OMZ (Paulmier and Ruiz-Pino, 2009). Furthermore, it is one of the first studies providing detailed ecological information of benthic decapod crustaceans under OMZs including data of high taxonomic resolution (Quiroga et al., 2009; Papiol and Hendrickx, 2016). The considerable numbers of new species and of distribution expansions of decapod crustaceans described from this survey emphasize the lack of knowledge of bathyal megafauna in the eastern Pacific off Mexico. Because samplings in the three areas comprised in this study were performed in different years, interannual variations in the environmental characteristics and in the structure of the community cannot be discarded. However, the main large-scale environmental processes potentially affecting the deep Mexican Pacific (i.e. El Niño-Southern Oscillation) were homogenous in the three years of the samplings, and values of the Oceanic Niño Index were negative during most of the period of the study (from 2008 to 2014) (http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml). Besides, the results obtained agree with the findings reported in previous studies in the region. Therefore, we believe that the results obtained in the present study reflect the existence of stable, long-term patterns of community structure on the mesoscale, that are linked to a permanent latitudinal gradient of environmental conditions.

Table 3
Decapod crustacean within-group Jaccard dissimilarity (JD), species richness (S) and diversity (J′, H′) at each area in each depth stratum.

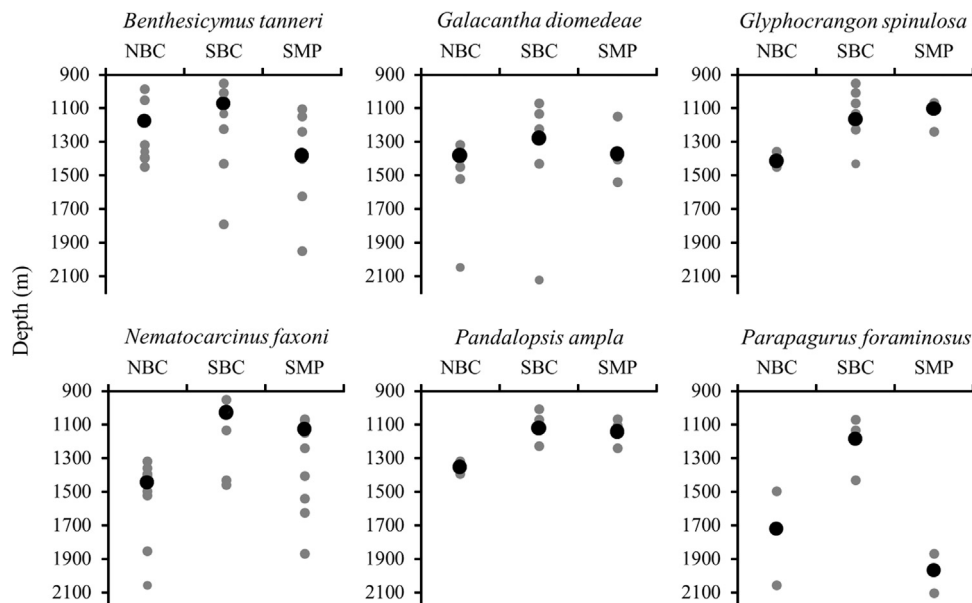|	JD	S	J′	H′
Northwestern Baja California (NBC)				
900–1300 m	37.85	4.33	0.79	1.08
1300–1700 m	43.52	6.38	0.79	1.39
1700–2100 m	31.40	6.20	0.69	1.23
Southwestern Baja California (SBC)				
900–1300 m	40.54	8.00	0.62	1.27
1300–1700 m	55.60	4.00	0.61	0.70
1700–2100 m	57.74	1.33	0.81	0.19
Southern Mexican Pacific (SMP)				
900–1300 m	38.24	10.00	0.64	1.26
1300–1700 m	41.02	3.60	0.74	0.75
1700–2100 m	41.40	3.80	0.71	0.82

Fig. 8. Optimal depth habitat (CoG, center of gravity, black) and depths of capture (grey) of the six species captured over the entire latitudinal interval of each area.

The study revealed that strong transitions in terms of both oceanographic characteristics and community composition and structure take place in the eastern Pacific off Mexico. The study area is a region of confluence of different surface and intermediate water masses and is characterized by narrowing and shallowing of the OMZ to the north. Beside the usual role of depth in shaping the near-bottom fauna, this community also changes significantly with latitude. Many of the changes occurred in the middle part of the Baja California Peninsula, coinciding with the narrowing and attenuation of the OMZ. The changes were related with oceanographic (mainly salinity and dissolved oxygen concentration) and geological (mainly sediment composition) features. The particular oceanographic context of the study area favors the prediction of the potential effects of climate-driven changes, such as the decrease in dissolved oxygen concentration in the sea (Matear and Hirst, 2003; Joos et al., 2003) and changes in the thermohaline circulation (Bryden et al., 2005; Hughes and Narayanaswamy, 2013).

Table 4
Results of DISTLM models carried out for the decapod crustacean community. df=degrees of freedom; %Clay, %Silt=proportions in the sediments; DO_{20mab}=dissolved oxygen 20 m above the bottom.

Variable	AIC	Pseudo-F	P	Prop.	Cum.
%Clay	347.93	6.69	0.0001	0.14	0.14
DO_{20mab}	343.80	6.13	0.0001	0.11	0.25
%Silt	342.84	2.78	0.0025	0.05	0.30
df=41					

4.1. Oceanographic context

The strong salinity gradients recorded off SBC have already been reported (Miranda-Bojórquez et al., 2014) and are linked to the presence of various surface, subsurface and intermediate water masses in the northeast Pacific (see Fiedler and Talley, 2006 for a review). The SAW and StSW converge in surface waters (Durazo and Baumgartner, 2002), and the presence of the NPIW is detected at intermediate depths in the north by a low salinity signature observed to 1000 m. Consistent with our results, significant salinity differences exceeding 1.0 g kg^{-1} to a depth of 10 m between two stations, for example, at 26°50.03′N and 23°11.63′N, have been reported from off the west coast of the Baja California Peninsula (Miranda-Bojórquez et al., 2014).

The northward narrowing of the OMZ reported in this study for the Mexican Pacific is consistent with analyses provided by Helly and Levin (2004) and Hendrickx and Serrano (2010). Results obtained from this survey indicate that the vertical center of the OMZ remained almost constant for the three cruises at around 600 m, a depth consistent with observations by Miranda-Bojórquez et al. (2013) off NBC. The supply of oxygenated water off NBC above 200 m is associated with the influence of SAW, which belongs to the California Current system (Durazo, 2014). This combination of high DO, low temperatures and low salinity has long been recognized (Sverdrup et al., 1942). Also, the NPIW supplies oxygen-rich water to ca. 600 m off NBC. Conversely, the smaller thickness of the subsurface tier with DO > 0.2 ml l^{-1} in the SMP is linked to the intrusion there of the StSW, reportedly characterized by high temperature and

Fig. 9. CCA of benthic sledge hauls based on abundance data for the dominant species of decapod crustaceans. The first two factors (F) are plotted together with explanatory variables. Species codes: *Abrev*: Acantephyra brevicarinata; *Btan*: Benthesicymus tanneri; *Gdio*: Galacantha diomedeae; *Gspi*: Glyphocrangon spinulosa; *Gtal*: Glyphocrangon taludensis; *GlyA*: Glyphocrangon sp. A; *Lscr*: Lebbeus scrippsi; *Malf*: Munidopsis alfredolaguardae; *Mqua*: Munidopsis quadrata; *Nfax*: Nematocarcinus faxoni; *Nocc*: Nephropsis occidentalis; *Pamp*: Pandalus amplus; *Pfor*: Parapagurus foraminosus; *Psan*: Plesionika sanctaecatalinae; *Spac*: Stereomastis pacifica. Environmental variable codes: DO_{20mab}: oxygen concentration 20 m above the bottom; T_{20mab}: temperature 20 m above the bottom; PPC_{-1-6}: phytoplankton pigment concentration at surface 1–6 months before the sampling; OC_{sed}: percentage total organic carbon in sediments; % Silt: silt proportions in the sediments. (1) 900–1300 m; (2) 1300–1700 m; (3) 1700–2100 m.

salinity (Wyrtki, 1967; Durazo and Baumgartner, 2002; Fiedler and Talley, 2006). The subsurface saline maximum detected off SBC and in the SMP may constitute an obstacle to the diffusion of oxygen from the surface to greater depth, likely favoring the presence of oxygen depleted water. That is because the salinity and temperature changes enhance the presence of a picnocline, which inhibits vertical mixing and prevents local ventilation of subsurface water (Fiedler and Talley, 2006). Moreover, the lower salinity in the water column recorded off NBC likely favors highest concentration of DO below 1000 m (Millero et al., 2002; Millero, 2005). Nevertheless, DO is a non-conservative variable, and its concentration is a function of surface dissolution from the atmosphere, photosynthesis, inorganic oxidation and metabolic demand (Gutknecht et al., 2013).

The observed sediment-type patterns fit the typical inverse relationship between distance from the coast (or depth) and grain size (Guilcher, 1958), that is, coarser sediments were found at shallower stations. Probably owing to the presence of a wider continental shelf to the north, slope sediments had greater proportions of silt and lower proportions of sand off NBC. However, submarine topographic structures and a wide range of sediment transport processes may account for some of the grain-size patterns observed (Stow and Mayall, 2000). Greater proportions of coarser sediments to the south were linked with a likely more oligotrophic benthic system (i.e. with lower contents of organic carbon).

4.2. Decapod crustacean community structure

Although some of the dominant species (i.e., *Nematocarcinus faxoni*, *Benthesicymus tanneri*, *Glyphocrangon spinulosa*, and *Galacantha diomedeae*) were distributed along the entire survey area, strong latitudinal changes in faunal composition occurred at around 26°N. This faunal transition has been reported previously for decapod crustaceans by Wicksten (1989), but without the present, substantially increased knowledge of deep-sea species in the region. A considerable number of bathyal decapod crustaceans have their northern (e.g., *Acantephyra brevicarinata*, *Glyphocrangon alata*, *Heterocarpus affinis*, *Nephropsis occidentalis*, *Paracrangon areolata*) or southern (e.g., *Munidopsis alfredolaguardae*, *Spirontocaris sica*, *Chorilia turgida*) distribution limits close to 26°N (Wicksten, 1989; Hendrickx and Ríos-Elósegui, 2014; Hendrickx, 2014b, 2015; Papiol et al., in press). Moreover, in her study, Wicksten (1989) also found that "there is a sharp break in faunal distributions between waters off northern Baja California and all areas to the south" in shallow water (50–500 m) decapod communities. The distribution of pandalid shrimps is characteristically associated with this faunal shift. Species of *Pandalus* are typically associated with northern latitudes, including off NBC, whereas *Heterocarpus* is a predominantly tropical-southern genus distributed from off SBC southward (Hendrickx and Wicksten, 1989; Hendrickx, 1995; Wicksten, 2012). Representatives of both *Heterocarpus* (i.e., *H. affinis*) and *Plesionika* (i.e., *P. trispinus*) are present in the southern Gulf of California between ca. 22 and 26°N (Papiol and Hendrickx, 2016), across the peninsula from our SBC study area.

A large part of the dominant genera in the study area (i.e., *Nematocarcinus*, *Plesionika* and *Acanthephyra*) are common to the typical decapod crustacean genera dominating slope areas from tropical and subtropical regions both in the Pacific (e.g., Wicksten, 1989; Quiroga et al., 2009) and the Atlantic oceans (to 45°N; see Cartes, 1993a and references cited therein; Pajuelo et al., 2015), and in the Mediterranean Sea (e.g., Cartes and Sardà, 1992; Fanelli et al., 2013). The genus *Glyphocrangon* (Glyphocrangonidae), which was one of the most diversified groups after the Galatheidae and the Lithodidae, is dominant in tropical and subtropical regions of the northeastern Pacific. Besides, four species (*G. alata*, *G. loricata*, *G. rimapes*, and *G. wagini*) have also been reported off Chile (SE Pacific), although this genus is not dominant in slope assemblages there

(Andrade and Baéz, 1980; Retamal and Jara, 2002; Quiroga et al., 2009; Hendrickx, 2012). In the Atlantic, one species of *Glyphocrangon* (*G. longleyi*) was also dominant in the tropical southwestern Gulf of Mexico, in the northwestern Atlantic (Escobar-Briones et al., 2008), but this genus is uncommon in the tropics and subtropics of the eastern Atlantic, where it is mostly restricted to more northern areas (see Cartes, 1993a and references cited therein). However, *G. longirostris* dominated along the northern wall of the Galicia Bank (ca. 42.5°N, NE Atlantic) likely due to the influence of the northerly sourced Labrador Sea Water (Cartes et al., 2014). In the deep Mediterranean Sea, *Glyphocrangon* spp. are absent (Cartes and Sardà, 1992; Follesa et al., 2009; Capezzuto et al., 2010; Fanelli et al., 2013), likely due to paleoecological reasons (Cartes, 1993a). Species of *Parapontophilus* have been reported in the tropics and subtropics of the Atlantic and Pacific oceans, but the dominance of this genus has not been established (Komai, 2008; De Grave and Fransen, 2011).

In the southern areas sampled during our survey (i.e., SBC and SMP), *Nematocarcinus faxoni* was replaced along the depth gradient by the oplophorid shrimp *Acanthephyra brevicarinata*. Preponderance of species of *Acanthephyra* in deeper, less productive areas has already been reported (e.g., north-western Mediterranean: Cartes and Sardà, 1992; Fanelli et al., 2013; central-western Mediterranean: Follesa et al., 2009; north-eastern Atlantic: Cartes et al., 2014; Gulf of California: Papiol and Hendrickx, 2016). In fact, *Acanthephyra* is one of the few genera of decapod crustaceans that have been reported from the hadal zone (Jamieson et al., 2009). In the NW Mediterranean, *A. eximia* and *Plesionika* spp. have similar diets (Cartes, 1998), but *A. eximia* has lower feeding intensity (Cartes, 1993b, 1993c) and consistently dominates the more oligotrophic lower slope assemblage (Cartes and Sardà, 1992). Off NBC, *A. brevicarinata* was not collected, and at 1700–2100 m the decapod crustacean assemblage was dominated by *Glyphocrangon* sp. A and another species of the Crangonoidea, *Parapontophilus occidentalis*. While *Acanthephyra* spp. are nektobenthic or meso-bathypelagic, mainly feeding on macroplankton (Cartes, 1998), the Crangonoidea are burrowers (Komai, 2008; Li et al., 2011) that feed rather strictly on benthos (Rice, 1981; Van Dover et al., 1992; Cartes et al., 2007; Papiol et al., 2013). Therefore, their association with the seafloor is strong, as shown by the positive correlations between the biomass of *P. occidentalis* and silt proportions in the study area sediments (Hendrickx and Papiol, 2015).

Latitudinal changes in the community structure from off NBC to the south not only occur in terms of species composition but also consist of changes in the abundance, diversity and depth distribution patterns of decapod crustaceans. South of the NBC area, under the thick and intense OMZ, organisms aggregated massively at the lower OMZ boundary, at 900–1300 m, a pattern parallel to that observed under OMZs elsewhere (Mullins et al., 1985; Murty et al., 2009; Hunter et al., 2011; Papiol and Hendrickx, 2016). In contrast, such aggregations were not observed off NBC, where the OMZ is less intense. In the same sense, observations of maximal diversity just below the intense OMZ core south of NBC are consistent with previous studies (Murty et al., 2009; Sellanes et al., 2010; Papiol and Hendrickx, 2016) and confirm the variable character of the OMZ lower boundary (Sellanes et al., 2010). While studying macrofauna communities in the Arabian Sea, Levin et al. (2000) found similar edge effects in terms of peak densities in the lower OMZ boundary but did not find similar diversity bathymetric patterns. The diversity of macrofauna is predominantly regulated by food availability rather than by oxygen levels (Levin, 2003), and high dominance is recorded within the OMZ where few low-oxygen tolerant species take advantage of enriched food conditions. Besides, models of productivity/diversity interactions generally predict a parabolic relationship, with added food availability increasing diversity at low levels but decreasing diversity at high levels (Rosenzweig, 1995; Huston, 1979). The stations analyzed by Levin et al. (2000) appear to

fall on the right half of the food-diversity parabola (Levin et al., 2001). Despite the patterns of diversity of macrofauna, diversity megafauna in the Arabian Sea peaked in the OMZ lower boundary (Murty et al., 2009), patterns similar to those observed in the present study. The center of gravity of most species distributed along all the survey area was shallower in the southern sampling areas. In areas without strong oxygen deficiencies, regional variations in the depth distributions of species have been observed and are defined by the environmental conditions (Cartes et al., 2004; Guijarro et al., 2012; Fanelli et al., 2013) and by species–species interactions (i.e. trophic relationships: Cartes, 1998; Cartes and Carrassón, 2004).

4.3. Drivers of community structure

Grain size partially explained the latitudinal patterns in community composition. Greater silt proportions in the sediments off NBC favored the presence of deposit and benthic feeders, such as *Munidopsis alfredolaguardae*, *Galacantha diomedeae*, *P. occidentalis* and *Glyphocrangon* sp. A. Those rely for nutrition directly or indirectly (i.e., through their prey) on the organic content in the sediments, so their distributions should be affected by the sediment's character. Sediment size and organic content are usually negatively correlated (Bergamaschi et al., 1997; Secrieru and Oaie, 2009), and the CCA showed that both high silt proportions and more organic carbon in the sediments enhanced the abundance of deposit and benthic feeders in the northern study area. The probable burrowing behavior of most of these organisms (Auster et al., 1995; Hudson and Wigham, 2003; Komai, 2008) would also benefit from medium- to fine-grained sediments, which require less energy for burrowing (Grow, 1982; Qureshi and Saher, 2012) and allow for larger, more complex burrows because of their stronger cohesion (Morrisey et al., 1999; Rudnick et al., 2005).

Because the thickness and intensity of the OMZ change along the survey area from south to north, most markedly at around 26°N, the relationship between community structure and oxygen obtained in our models has an obvious latitudinal component. South of the NBC area, the release in oxygen limitation under a thick and intense OMZ combined with the typical large flux of labile organic material in these areas enhance massive aggregations of organisms in the OMZ lower boundary (Diaz and Rosenberg 1995; Levin, 2003; Murty et al., 2009; Hunter et al., 2011; Papiol and Hendrickx, 2016). However, the impacts of food availability on the patterns of distribution of the biota were not fully elucidated in our study, probably due to the lack of more informative and specific measures of food quality (e.g., $\delta^{13}C$ or pigment concentrations in the sediments). The plenty availability of food in the lower OMZ boundary may also promote the shallower distribution of species below the severe OMZ, and organisms seem to be able to live in water as shallow as allowed by their oxygen requirements. As mentioned earlier, the regional variations in the depth distribution of many animals are not only defined by the effects of environmental conditions, but also depend on species–species interactions (Cartes, 1998; Cartes and Carrassón, 2004). In the OMZ lower boundary, the minimum depth of occurrence of the species is not restricted by the presence of competitors because most of these are effectively excluded from the OMZ core. In contrast, off NBC the lack of a severe oxygen limitation in the water column may allow for the presence of organisms at all depths, and interspecific competition phenomena may be important in the exclusion of "lower boundary species" from shallower areas (Cartes et al., 2004). The presence of organisms throughout the water column is associated with greater consumption of sinking particles and a lower flux of particles to the sea-bottom. As a consequence, no opportunistic aggregations take place off NBC.

The oxygen concentration is partially modulated by water mass circulation and vertical position, and both depend upon temperature and salinity (Millero et al., 2002; Millero, 2005). The waters off SBC involve transitions among surface, subsurface and intermediate water masses, so those may play some role in the observed oxygen and faunal shifts. Beside topographic barriers and biological factors (e.g., dispersal abilities, predator–prey relationships, competitive interactions), the physical–chemical gradients, such as the observed salinity fronts or the change in oxygen availability below 1700 m, can also act to limit species distributions (Briggs, 1974; Vermeij, 1978; Wicksten, 1989). Although the strongest environmental gradients were observed at depths shallower than those effectively sampled, they could still have affected the distribution of, for example, planktonic eggs or larvae (Lindley, 1986; Scheltema, 1988; Torres et al., 2014). Furthermore, even small environmental changes at great depths likely affect deep-sea species distributions, given the overall stability of the deep-sea physical environment (Fanelli et al., 2013).

The correlations among faunal composition, species distributions and oxygen concentration also have bathymetric components. Although it is widely recognized that depth is a main gradient structuring deep-sea megafaunal communities, it is a proxy for a combination of several environmental variables affecting deep-sea organisms more directly than depth *per se*. Among those variables, water mass characteristics and variables associated with depth (T, S, and DO) have consistently been identified as crucial drivers of the distribution of bathyal megafauna species in areas subjected (Murty et al., 2009; Quiroga et al., 2009; Papiol and Hendrickx, 2016) or not subjected (e.g., Fanelli et al., 2013; Cartes et al., 2014; Pajuelo et al., 2015) to the influence of OMZs. Steep bathymetric gradients of T and DO occur beneath OMZs, and may restrict some decapod crustaceans to specific depth intervals. That would involve the interdependence between their aerobic capacity and their temperature tolerance, as observed in most metazoans (Frederich and Pörtner, 2000; Ekau et al., 2010).

We conclude that the structure of the decapod crustacean community below the OMZ core off the Pacific coasts of Mexico changed parallel to variations in the OMZ characteristics: the decrease in intensity of the OMZ off Northern Baja California was accompanied by the disappearance of the so-called "edge effects" (Mullins et al., 1985) associated with OMZ areas. The surface, subsurface and intermediate water mass transitions in the region favored changes in both the OMZ and the decapod crustacean community, indicating a potential susceptibility of bathyal decapod crustaceans to predicted climate-driven environmental variations, particularly more intense reduction in midwater oxygen availability and changes in the thermohaline circulation. Sediment composition was also important in defining the community composition. However, the expected role of food could not be detected by the approximation used.

Appendix A. Sampling locations, environmental parameters and details of benthic sledge hauls performed off the Pacific coast of Mexico during the oceanographic cruises TALUD XII, XV and XVIB. Listed parameters measured at 20 m above the bottom (20mab) were; T=temperature; S=salinity; DO=dissolved oxygen concentration; OC_{sed}=total organic carbon in the sediments, %Sand, %Silt and %Clay=sand, silt and clay proportions in the sediments

Station	Date	Location	Depth range (m)	T_{20mab} (°C)	S_{20mab} (g kg^{-1})	DO_{20mab} (ml l^{-1})	% OC_{sed}	% Sand	%Silt	%Clay
Southern Mexican Pacific - TALUD XII										
2	28-mar-08	16°49′18″ N 100°30′52″ W	990–1088	5.00	34.54	0.20	3.63	29.48	42.44	28.07
3	28-mar-08	16°54′35″ N 100°44′10″ W	1380–1456	3.31	34.58	0.80	3.96	34.89	36.20	28.91
5	28-mar-08	16°58′28″ N 100°55′20″ W	1977–1925	2.30	34.63	1.48	3.03	1.85	66.22	31.93
8	29-mar-08	17°04′16″ N 101°39′28″ W	1880–1940	2.34	34.63	1.49	1.37	53.54	25.91	20.55
9	29-mar-08	17°10′26″ N 101°37′37″ W	1392–1420	3.29	34.58	0.75	1.70	56.89	23.51	19.60
10	28-mar-08	17°11′03″ N 101°28′05″ W	1180–1299	3.66	34.56	0.51	3.30	29.37	43.36	27.26
13	30-mar-08	17°45′16″ N 102°00′29″ W	1199–1100	3.96	34.55	0.36	1.74	1.49	67.15	31.37
14	30-mar-08	17°36′20″ N 102°01′59″ W	1415–1476	3.24	34.59	0.80	2.09	0.73	66.78	32.49
15	30-mar-08	17°25′33″ N 102°07′20″ W	2080–2125	2.12	34.63	1.61	1.80	0.41	54.49	45.09
23	01-abr-08	18°33′43″ N 103°57′45″ W	1058–1088	4.39	34.54	0.22	–	88.51	6.44	5.05
24	01-abr-08	18°28′00″ N 104°14′10″ W	1535–1542	3.10	34.59	0.95	1.34	57.67	22.41	19.91
25	01-abr-08	18°26′45″ N 104°16′10″ W	1858–1879	2.46	34.62	1.39	2.40	34.28	33.29	32.44
26	01-abr-08	18°33′27″ N 104°28′21″ W	2125–2165	2.06	34.64	1.59	2.17	17.16	50.21	32.63
27	02-abr-08	18°40′28″ N 104°35′51″ W	1040–1095	5.10	34.53	0.26	1.96	69.85	12.41	17.74
28	02-abr-08	18°50′19″ N 104°34′14″ W	1101–1106	4.11	34.53	0.27	2.13	63.55	17.84	18.61
29	02-abr-08	19°19′37″ N 105°26′20″ W	1609–1643	2.82	34.60	1.03	4.54	25.30	36.30	39.40
30	26-mar-08	19°22′05″ N 105°16′18″ W	1350–1380	3.35	34.58	0.71	4.07	17.77	49.59	32.64
30B	26-mar-08	19°30′37″ N 105°19′16″ W	865–1045	6.00	34.52	0.11	3.02	22.34	55.38	22.29
Southwestern Baja California - TALUD XV										
2	04-ago-12	23°12′02″ N 111°20′50″ W	1118–1150	3.75	34.59	0.50	1.20	74.81	21.59	3.61
3	04-ago-12	23°09′55″ N 111°20′0″ W	1395–1465	3.02	34.63	0.90	–	–	–	–
8	30-jul-12	24°25′48″ N 112°38′06″ W	1212–1235	3.44	34.60	0.65	3.54	29.59	61.92	8.48
9	30-jul-12	24°25′12″ N 112°52′48″ W	1425–1494	2.93	34.63	0.97	2.05	36.18	54.82	9.00
10	29-jul-12	24°20′42″ N 112°44′48″ W	2088–2125	2.06	34.68	1.73	–	–	–	–
13	30-jul-12	25°02′12″ N 112°54′06″ W	1210–1245	3.98	34.57	0.44	5.06	8.36	80.31	11.33
15	02-ago-12	25°18′50″ N 113°12′17″ W	1246–1309	3.51	34.59	0.62	5.44	3.08	82.92	14.00
16	03-ago-12	25°13′11″ N 113°15′56″ W	1770–1810	2.77	34.63	1.07	3.80	3.53	82.17	14.30
17	31-jul-12	26°20′24″ N 114°13′07″ W	2111–2136	2.15	34.67	1.62	4.44	2.82	80.97	16.21
25	01-ago-12	24°25′12″ N 112°52′48″ W	1370–1518	2.81	34.63	1.02	4.94	5.39	79.14	15.47
5C	05-ago-12	23°16′42″ N 110°54′55″ W	980–1036	4.71	34.56	0.22	1.21	60.56	33.72	5.73
5E	05-ago-12	23°05′22″ N 110°27′54″ W	948–954	4.36	34.57	0.29	–	–	–	–
5F	05-ago-12	22°58′15″ N 110°40′17″ W	1035–1108	3.50	34.61	0.61	2.36	46.96	45.61	7.43
Northwestern Baja California - TALUD XVIB										
1	23-may-14	28°28′18″ N 115°45′12″ W	2038–2054	2.10	34.63	1.83	3.66	37.38	52.11	10.51
3	23-may-14	28°42′36″ N 115°50′42″ W	1350–1365	3.40	34.54	0.78	1.82	32.69	64.72	2.59
4	23-may-14	28°47′05″ N 115°43′47″ W	1237–1284	3.40	34.53	0.76	5.68	9.53	87.08	3.39
6	24-may-14	29°08′09″ N 115°33′26″ W	1004–1102	4.38	34.47	0.40	4.33	5.34	82.58	12.08
8	31-may-14	29°23′48″ N 115°45′12″ W	1416–1480	3.14	34.55	0.90	5.38	3.32	84.89	11.79
9	30-may-14	29°20′53″ N 115°51′00″ W	1848–1860	2.31	34.61	1.52	4.16	0.00	84.50	15.50
11	30-may-14	29°16′48″ N 116°13′46″ W	1679–1698	2.62	34.59	1.26	3.47	0.46	85.63	13.91
15	29-may-14	29°40′24″ N 116°06′00″ W	2010–2046	2.26	34.62	1.60	4.57	2.16	86.97	10.87
16	29-may-14	29°51′24″ N 116°09′06″ W	1425–1360	3.14	34.56	0.97	4.08	5.45	82.61	11.94
19	25-may-14	30°39′00″ N 116°31′40″ W	1385–1433	3.16	34.55	0.90	3.96	4.31	84.62	11.07
20	26-may-14	30°51′16″ N 116°42′11″ W	2075–2090	2.37	34.61	1.47	2.60	1.18	86.29	12.53
21	28-may-14	30°49′24″ N 116°47′48″ W	2018–2093	2.43	34.60	1.43	2.21	1.08	86.38	12.54
22	28-may-14	30°49′47″ N 116°35′54″ W	1480–1560	3.05	34.56	0.96	1.34	34.47	59.97	5.56
23	27-may-14	30°56′02″ N 116°40′55″ W	1296–1340	3.15	34.54	0.76	3.28	9.47	79.46	11.07
26	26-may-14	31°46′06″ N 116°58′21″ W	982–989	4.17	34.48	0.48	3.70	7.27	83.26	9.47
27	27-may-14	31°42′36″ N 117°13′00″ W	1394–1397	3.32	34.54	0.78	3.68	2.44	84.99	12.58
28	27-may-14	31°22′00″ N 117°02′00″ W	1461–1532	3.11	34.55	0.93	–	–	–	–

Appendix B. Standardized mean abundance (N ha^{-1}) of each species collected with the benthic sledge along the Pacific coast of Mexico by area and depth stratum. Depth distribution range in each area and main feeding strategies (D=detritivore; P=predator; P/D=predator/facultative deposit feeder; P/S=predator/facultative scavenger; D/S=deposit feeder/facultative scavenger) are also indicated for each species. Distribution records: FRM=first record for the Pacific off Mexico; NRM=new record for the Pacific off Mexico; FBCR=first record for west coast of Baja California; NBCR=new record for west coast of Baja California. Published sources indicated by number in brackets (see foot notes)

	Feeding strategy	NBC				SBC				SMP				Distribution records
		900–1300	1300–1700	1700–2100	Depth range (m)	900–1300	1300–1700	1700–2100	Depth range (m)	900–1300	1300–1700	1700–2100	Depth range (m)	
Suborder Dendrobranchiata Superfamily Penaeoidea Family Benthesicymidae														
Benthesicymus tanneri	P	17.51	3.60		982–1532	19.51	1.75	0.88	948–1810	1.88	3.06	0.53	1101–1977	
Family Solenoceridae														
Hymenopenaeus doris	D/S										1.40		1858–2165	
Suborder Pleocyemata Infraorder Stenopodidea Family Steopodidae														
Odontozona foresti	Unk.					0.38			1035–1108	0.27			1058–1088	FBCR (1)
Infraorder Caridea Superfamily Oplophoroidea Family Acanthephyridae														
Acanthephyra brevicarinata	P					0.75	0.58	0.88	1118–2125	8.84	13.57	17.14	1058–2165	NRM (2)
Acanthephyra brevirostris	P											1.05	1977–1925	
Acanthephyra curtirrostris	P		0.29	0.53	1461–2046									
Acanthephyra sp.	P		0.29	0.53	1409–2082									
Superfamily Bresilioidea Family Bresiliidae														
Bresilia pacifica	Unk.					0.38			1210–1245					New species (3)
Superfamily Nematocarcinoidea Family Nematocarcinidae														
Nematocarcinus agassizii	P		0.88		1296–1340									NRM (4)
Nematocarcinus faxoni	P		9.92	1.75	1296–2093	195.44	26.55	0.00	948–1494	207.54	23.20	1.58	1040–1879	NRM (4)
Superfamily Alpheoidea														

Species	Type													
Family Thoridae														
Lebbeus bidentatus	P									1.88	0.44		1040–1643	FRM
Lebbeus curvirostris	P		2.98		2010–2093					1.75			1040–1095	FRM
Lebbeus scrippsi	P					3.00			980–1245	16.45			1058–1299	NBCR
Lebbeus sp.	P									0.25			1040–1095	
Spirontocaris sica	P	10.50			1004–1102									
Superfamily Pandaloidea														
Family Pandalidae														
Heterocarpus affinis	P/D					37.51			948–1036	4.75			1040–1106	
Heterocarpus hostilis	P/D					0.38			980–1036	1.30			1040–1095	FRM
Pandalopsis ampla	P/D		0.58		1296–1425	8.63			980–1245	1.00			1040–1299	
Pandalus cf. *tridens*	P/D			0.35	2038–2054									
Plesionika sanctaecatalinae	P	5.25	1.26	4.38	982–2090		1.75	1.75	1370–2136					
Superfamily Crangonoidea														
Family Crangonidae														
Metacrangon procax	P		2.33		1394–1480					0.80	3.50		1058–1643	
Paracrangon areolata	P					0.38			980–1036	11.52			1040–1106	NBCR (5)
Parapontophilus occidentalis	P		10.41	39.56	1296–2093		1.75		1425–1494					NBCR (6)
Sclerocrangon atrox	P					0.38			1035–1108	6.02			1040–1106	NBCR (5)
Family Glyphocrangonidae														
Glyphocrangon alata	P					0.75			980–1245	13.25			1040–1299	NBCR (5)
Glyphocrangon spinulosa	P		19.84		1350–1480	40.51	9.63		948–1465	40.51			1040–1299	
Glyphocrangon taludensis	P		0.29		1425–1360					0.25	1.31	8.93	1040–2125	New species (7)
Glyphocrangon cf. *taludensis*	P									0.50			1040–1095	
Glyphocrangon cf. *sicaria*	P			1.05	2075–2090									
Glyphocrangon sp. A	P		2.63	68.80	1296–2093									New species
Infraorder Anomura														
Superfamily Galatheoidea														
Family Munidopsidae														
Galacantha diomedeae	D/S		16.44	1.05	1296–2054	1.88	0.88	0.58	1035–2136	0.38	1.31		1100–1542	
Munidopsis alfredolaguardae	D/S	45.52			982–1102	0.75			1035–1108					FBCR
Munidopsis bairdii	D/S			2.45	2018–2093									NBCR
Munidopsis bracteosa	D/S			0.53	2075–2090									FRM
Munidopsis depressa	D/S									4.13			865–1088	
Munidopsis hamata	D/S					0.38			980–1036					
	D/S									0.38			1101–1106	FRM

Species	Type												Ref
Munidopsis hendersoniana													
Munidopsis hystrix	D/S								0.80			1058–1088	
Munidopsis latirostris	D/S			0.53	2075–2090								FRM
Munidopsis cf. *lignaria*	D/S										1.58	1858–1879	
Munidopsis palmatus	D/S								1.61	0.44		1058–1380	NBCR
Munidopsis quadrata	D/S	1.75			982–989				19.42			1040–1106	
Munidopsis scabra	D/S					0.75		1118–1150	1.75			1040–1095	
Munidopsis sp. A	D/S	0.88	0.29		982–1560								New species
Superfamily Lithodoidea			0.58			0.58				0.44	0.53		
Family Lithodidae													
Lithodes couesi	P					0.58		1425–1494					
Neolithodes diomedeae	D/S		0.58		1416–1480	0.58		1425–1494		0.44	0.53	1609–1879	
Paralomis aspera	P/D		0.29		1394–1397				1.50			1040–1095	FRM
Paralomis otsuae	P/D									0.44		1609–1643	FBCR
Paralomis sp. 1	P			0.35	2038–2054								
Lithodidade sp. 1	P										0.53	1858–1879	
Lithodidade sp. 2	P	0.58	3.21	4.55	1237–1860								
Lithodidade sp. 3	P	0.88			1004–1102				4.75			1040–1095	
Superfamily Paguroidea													
Family Parapaguridae													
Parapagurus foraminosus	P/D		0.29	0.35	1461–2093	2.63	2.63	1035–1465			12.08	1858–2125	NBCR
Infraorder Astacidea													
Superfamily Nephropoidea													
Family Nephropidae													
Nephropsis occidentalis	P					7.88		980–1245	4.07			1058–1299	
Infraorder Axiidea													
Family Axiidae													
Calocarides sp. 2	D/S		0.29		1416–1480								
Infraorder Polychelida													
Family Polychelidae													
Stereomastis pacifica	P/S	2.63	1.65	0.35	982–1860	4.50	0.88	980–1465	0.54			1058–1088	
Infraorder Brachyura													
Superfamily Dorippoidea													
Family Ethusidae													
Ethusina robusta	Unk.										0.53	1858–1879	
Ethusina smithiana	Unk.								0.25			1040–1095	FRM

(1) Hendrickx (2002), (2) Hendrickx and Ríos-Elósegui (2014), (3) Hendrickx (2014a), (4) Hernández-Payán and Hendrickx (in press), (5) Hendrickx (2014b), (6) Hendrickx and Papiol (2015) and (7) Hendrickx (2010).

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