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Community structure of deep-water decapod crustaceans below the oxygen minimum zone in the south-east Gulf of California and analysis of environmental drivers

Vanesa Papiol[A,B] *and Michel E. Hendrickx*[A]

[A]Unidad Académica Mazatlán, Instituto de Ciencias del Mar y Limnología,
Universidad Nacional Autónoma de México, PO Box 811, Mazatlán, Sinaloa 82000, Mexico.
[B]Corresponding author. Email: vpapioln@gmail.com

Abstract. Despite the ecological importance of decapod crustaceans in energy transfer in marine ecosystems, little is known on their distribution below oxygen minimum zones (OMZs). To understand the spatio-temporal dynamics of benthic and benthopelagic decapod crustaceans living below the OMZ cores, four seasonal oceanographic and sledge surveys were performed in the south-east Gulf of California at depths between 730 and 2250 m. Multivariate analyses indicate the existence of three major depth-related assemblages at: 800–1000, 1000–1200 and >1200 m (mean trawl depth). Benthic detritivores dominated between 800 and 1000 m and benthopelagic (i.e. swimming) predators dominated deeper, where dissolved oxygen (DO) values were higher. Assemblages comprised the same species throughout the year, but aggregations of smaller organisms were observed in June. DO significantly controlled the distribution of decapod crustaceans, likely through physiological exclusion of swimming species from hypoxic waters. Besides, the combined effects of DO and temperature contributed to defining the depth ranges occupied by each species. Food derived from surface-water production modulated changes in community parameters with different time lags in the different depth-related assemblages. These findings demonstrate the vulnerability of bathyal communities to the global pattern of OMZ expansion.

Additional keywords: benthos, deep sea, eastern tropical Pacific.

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Introduction

Oxygen minimum zones (OMZs) are large oceanic areas where dissolved oxygen (DO) concentration in the water falls persistently below 0.5 mL L^{-1} (22 μmol L^{-1}) (Levin 2003). They occur worldwide as a result of the combination of slow circulation of oxygen-poor source waters and great oxygen consumption in the process of decomposition of organic matter in areas with high surface productivity (Wyrtki 1962; Kamykowski and Zentara 1990). Where oxygen minima intercept the continental margin or seamounts, pronounced gradients in oxygen availability and organic matter flux are observed (Levin *et al.* 2000; Devol and Hartnett 2001), and fauna have characteristic patterns of distribution. Those patterns differ across size groups and, although meiofauna are not reduced within OMZ cores ($DO < 0.15$ mL L^{-1} or 6.6 μM: Levin 2003) (Wishner *et al.* 1990, 1998; Saltzman and Wishner 1997), macro- (Wishner *et al.* 1990; Hughes *et al.* 2009; Ingole *et al.* 2010) and megafauna (Mullins *et al.* 1985; Wishner *et al.* 1990; Murty *et al.* 2009; Gooday *et al.* 2009; Hunter *et al.* 2011) are virtually absent. Instead, in the lower OMZ boundary (0.15 mL L^{-1} or 6.6 $\mu M < DO < 0.5$ mL L^{-1} or 22 μM), large aggregations of macro- and megafauna take place (Diaz and Rosenberg 1995; Levin 2003; Murty *et al.* 2009; Hunter *et al.* 2011) where there is an abundant supply of organic matter and DO increases gradually (Devol and Hartnett 2001; Honjo *et al.* 2008; Roullier *et al.* 2013). Below the OMZ boundary, fauna densities usually decline. Although few of the studies provide exhaustive information with high taxonomic resolution (i.e. to species level) of meio- (essentially foraminiferans: e.g. Mullins *et al.* 1985; Gooday *et al.* 2009), macro- (e.g. benthic polychaetes: Méndez 2007, 2013) and megafauna (e.g. benthic molluscs: Zamorano *et al.* 2007), rapid bathymetric successions of large taxonomic groups have been described in the lower OMZ boundary at Volcano 7 seamount (Wishner *et al.* 1990, 1995) and in the southern Gulf of California (Zamorano *et al.* 2007; Méndez 2007), both in the eastern tropical Pacific, and off the Pakistan margin (Gooday *et al.* 2009; Murty *et al.* 2009) and the Indian margin (Hunter *et al.* 2011), both in the Arabian Sea.

The megafauna living below the OMZ core likely play an important role in structuring the marine benthos through the physical disturbance of sediment (e.g. Hunter *et al.* 2011), predation upon meio- and macrofauna (Jeffreys *et al.* 2009*a*), and selective removal of both suspended and sedimented labile organic matter (Wishner *et al.* 1995; Smallwood *et al.* 1999; Jeffreys *et al.* 2009*b*). Together with polychaetes and ophiuroids, decapod crustaceans usually dominate the peaks in

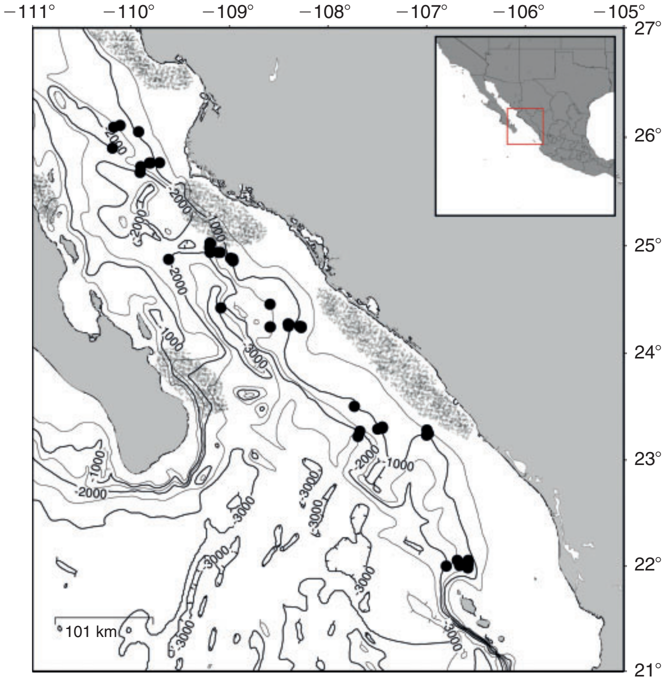

Fig. 1. Study area and sampling sites (black circles). Shaded areas indicate areas of upwelling (as indicated in Parker 1963).

megafauna abundance at lower OMZ boundaries (Wishner *et al.* 1990; Murty *et al.* 2009; Hunter *et al.* 2011). In these environments, they feed on multiple trophic levels (Jeffreys *et al.* 2009*a*) and participate in the reworking and mixing of surficial and deeper sediment layers (Hunter *et al.* 2011). Therefore, alterations in their distributions across OMZ-affected margins would translate to significant effects upon wider ecosystem processes, such as nutrient cycling and trophic structure. This is especially remarkable because of the high sensitivity of decapod crustaceans to changes in DO (Vaquer-Sunyer and Duarte 2008), which makes them particularly susceptible to the global pattern of spatial expansion of OMZs (Stramma *et al.* 2008). In deep waters (out of OMZs), it has been suggested that small declines of DO in water masses may provoke the drop in abundance of swimming species such as *Aristaeomorpha foliacea* (Cartes *et al.* 2011).

Despite the magnitude of OMZs in the world (Stramma *et al.* 2008; Paulmier and Ruiz-Pino 2009) and the potential vulnerability of decapod crustaceans to DO variations, little is known of their community structure, dynamics and ecology below OMZ cores. This is especially true for the OMZ of the eastern Pacific, which is the largest OMZ of the world (Helly and Levin 2004; Paulmier and Ruiz-Pino 2009). In this region, such knowledge is available for latitudes where the OMZ core becomes narrower and more moderate (e.g. Quiroga *et al.* 2009) and therefore OMZ effects are expected to be milder. Conversely, studies in the widest and more intense sections of the OMZ (see Helly and Levin 2004) are almost non-existent. For this reason, the present study analyses the community ecology of decapod crustaceans of the continental slope off the west coast of Mexico, in an area where the OMZ is wide and intense. Specifically, the present paper aims to (1) analyse the main bathymetric and temporal patterns of distribution of the decapod crustacean community below the OMZ core in the south-east Gulf of California, Mexico, and to (2) identify the main environmental drivers of those patterns. With this, not only base knowledge for assessing potential future impacts can be established, but also new insights on the consequences of impending expansions of oxygen minima (Stramma *et al.* 2008, 2010) are to be gained.

Materials and methods

Study area

The study was conducted on the continental slope off the State of Sinaloa (south-east Gulf of California) (Fig. 1) at depths ranging from 730 to 2250 m (Appendix 1). The southern Gulf of California connects with the Pacific Ocean at its mouth, reaching depths of 3000 m (Álvarez-Borrego and Schwartzlose 1979). Near-bottom water temperature (T) decreases gradually with depth to values $<10°\text{C}$ at ~500 m and values $<2°\text{C}$ at ~2000 m (Hendrickx 2003). The area is characterised by the presence of an OMZ that is particularly wide (700–800-m width) and intense, with a core reaching microxic ($\text{DO} < 0.0024\ \text{mL}\ \text{L}^{-1}$ or 1 μM) or anoxic ($\text{DO} < 0.0227\ \text{mL}\ \text{L}^{-1}$ or 0.1 μM) conditions from ~150 m to 600–800 m (Hendrickx 2001; Hendrickx and Serrano 2013). DO increases gradually to values of ~1 $\text{mL}\ \text{L}^{-1}$ (44 μM) from 800 to 1500 m, and experiences a further steady increase to depth greater than 2000 m where oxygen concentration reaches values $>2\ \text{mL}\ \text{L}^{-1}$ (88 μM) (Hendrickx 2001). Below 200-m depth, the seabed in the study area is characterised by muddy bottoms, and laminated diatomaceous sediments are formed where the basin slopes intersect the oxygen minimum in the water column (Calvert 1966).

The depth range studied is influenced by the North Pacific Intermediate Water at 600–900 m, characterised by a minimum salinity (S) ($S = 34.5$, $t = 4–9°C$), and the Pacific Bottom Water ($S = 34.5$ psu, $t < 4°C$), found below the Pacific Intermediate Water. Both water masses show no seasonal variability in their T–S characteristics (Robles and Marinone 1987; Hendrickx and Serrano 2010).

Nutrient inputs to the southern Gulf of California are mainly driven by wind-induced upwelling. Wind-induced upwelling occurs off the mainland coast in winter conditions (December–May) (Álvarez-Borrego 2010). Most of the rain in the southern Gulf falls between June and October. Upwelling off the mainland in winter favours the increase in phytoplankton production, coinciding with periods of water column homogeneity. In summer conditions, phytoplankton production is lowest and the water column is stratified (Thunell 1998). Related to this, sedimentation in this region is dominated by two seasonally varying components: biogenic silica during late autumn–spring and lithogenic material during summer (Thunell 1998). Water exchange between the Gulf and the Pacific Ocean also fertilises the southern Gulf of California; less dense, warmer surface water (~0–200 m) leaves the Gulf into the Pacific, and deep (~200–600 m) colder water has a net flow into the Gulf (Marinone 2003). Nutrient inputs to the Gulf from rivers are very small due to extensive dam systems, and most of the terrigenous input to the Gulf is by eolian transport rather than from river runoff (Calvert 1966).

Biological data

Within the general frame of the TALUD project, four multidisciplinary surveys (TALUD IV, V, VI and VII) were carried out between August 2000 and June 2001 on a seasonal basis (August, December, March, and June respectively) (Appendix 1). Samples of benthic and benthopelagic decapod crustaceans were obtained from below the OMZ core using a benthic sledge with a 2.35-m horizontal opening and a 0.90-m vertical opening equipped with an outer collecting net of ~5.5 cm (2 1/4′) stretch mesh and an inner net of ~2.0 cm (3/4′) stretch mesh. A total of 51 trawls were performed from the oceanographic vessel *El Puma*, of the Universidad Nacional Autónoma de México (UNAM). Trawling generally lasted 30 min (time at bottom) at an average speed of 1.75 kn (~0.9 m s^{-1}). Swept area was estimated based on trawling speed and time at the bottom according to the formula: time at bottom × trawling speed × horizontal opening.

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

Environmental data

Conductivity, temperature and depth (CTD) casts (Seabird 19) and rosette-mounted 10-L Niskin bottles were deployed at each station (one cast per station). Near-bottom temperature data and water samples were obtained ~20 m above bottom (20 m AB). DO content was estimated with the Winkler Titration (Strickland and Parsons 1972). Salinity measures were not available due to malfunction of the recording system on board.

Phytoplankton pigment concentration (PPC, mg Chl-*a* m^{-3}) values were obtained from http://giovanni.gsfc.nasa.gov/giovanni/ (accessed 7 December 2014) and were used as an estimate 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 in order to evaluate the time lag between surface processes and the faunal response.

Sediment sampling and analysis

Sediment was sampled by means of a Smith–McIntyre dredge or a modified USNEL box core at each sampling station and samples of the top 3 cm were obtained and stored at 4–8°C. In the laboratory, sediments were dried to constant weight at 60°C. The total organic carbon (TOC) content was then determined by treating samples with an oxidant mixture of 1 N $K_2Cr_2O_7$+ concentrated H_2SO_4+Ag_2SO_4, and titrating with 0.5 N $Fe(NH_4)_2(SO_4)_2$ (Loring and Rantala 1992; Soto-Jiménez and Páez-Osuna 2001). Solutions of dextrose at known concentrations were used as standards for developing calibration curves. Organic carbon in the sediments was used as an indicator of food availability (Beaulieu 2002).

Data analysis

Assemblage structure and faunal composition

Megafauna species recorded in fewer than 5% of the samples were omitted from the dataset to prevent an undue influence on the results (Gauch 1982). Abundance and biomass were standardised to a common swept area of 1 ha (individuals ha^{-1} and g ha^{-1}).

First, zero-adjusted Bray–Curtis similarity indices (Bray and Curtis 1957; Clarke *et al.* 2006) were calculated on square-root-transformed species density per haul to define the relationships of the faunal composition among sampling sites (Clarke and Warwick 2001). The intralocation resemblance was subjected to group-average linkage cluster analysis. A similarity profile (SIMPROF) test was applied to check for statistical significance of the groups obtained by cluster analysis (Clarke and Warwick 2001).

In order to test for bathymetric and seasonal variations in assemblage structure, a two-factor distance-based Permutational Analysis of Variance (PERMANOVA) (Anderson *et al.* 2008) was performed on the composition matrix considering depth range and month of sampling (four levels: December, March, June, August) as factors. The depth groups considered were those obtained by cluster analysis. Significance was set at $P = 0.05$ and P-values were obtained using 9999 permutations, with permutation of residuals under a reduced model. A Similarity Percentage analysis (SIMPER) routine performed on the square-root-transformed matrix (Clarke 1993) was used to identify those species that most typify each of the groups identified. Species were classified according to their feeding strategy based on literature (see Appendix 2) and the percentage contribution of each trophic group in terms of density to each of the groups previously identified by cluster analysis was estimated. In most cases trophic data of the species were not available and information on taxonomically close species was used.

Patterns in density, biomass, mean individual weight and diversity

The spatio-temporal patterns of density and biomass were analysed for each depth and month of sampling. The patterns of mean individual weight per station were also explored as a function of depth and sampling period. Because some samples contained low numbers of decapod crustaceans, the overall mean individual weight per station could potentially be altered by the sporadic appearance of a significantly large or small organism. With the purpose of checking for this bias, the patterns of mean individual weight considering each species appearing at each station were plotted against its density.

Patterns were also explored for assemblage diversity using Hurlbert's expected species richness index ($ES(n)$: Hurlbert 1971). This index minimises the effects of sample size in diversity estimations by allowing reduction of data collection to a common size (n). However, Hurlbert's index can be affected by the distribution of specimens among species, so the Shannon diversity index (H') was also calculated.

Statistical differences for all these parameters were tested by means of PERMANOVA following the same two-factor design (with depth stratum and month as factors) after log-transformation of raw data.

Environmental variables

Differences between environmental variables corresponding to sledge samples containing and not containing decapod crustaceans were tested by means of one-way PERMANOVA. Spatial and temporal variations in environmental variables were tested by means of two-way PERMANOVA with a crossed design considering both depth and month of sampling as factors. Although permutational ANOVA was designed for multivariate analysis of distance matrices, it can be used for univariate ANOVA. Because we had only one dependent variable in the analysis, and used Euclidean distances, the resulting sums of squares and F-ratios are the same as Fisher's univariate F-statistic in traditional ANOVA. Significance was set at $P = 0.05$; P values were obtained using 9999 permutations of residuals under a reduced model (Anderson 2001).

Correlation of fauna distribution with environmental variables

The relationship between density, biomass and mean weight by station and environmental variables was explored by different univariate and multivariate techniques. The environmental variables explored were: depth, temperature at <20 m AB ($T_{20\ \mathrm{m\ AB}}$), oxygen at <20 m AB ($DO_{20\ \mathrm{m\ AB}}$), total organic carbon (TOC) in sediments, and PPC simultaneous and 1–6 months before sampling (PPC_{sim} and PPC-1–6). Before the analyses a Draftsman plot was performed on the environmental dataset in order to identify whether any of the variables were correlated. Only data that were not autocorrelated (Pearson's correlation, $\rho < 0.75$) were retained for the analysis. First, DISTLM (distance-based multivariate multiple regression based on a linear model: McArdle and Anderson 2001) was used to check which environmental variables drive assemblage species composition. DISTLM was generated with forward permutation procedure, using AIC selection scheme (Anderson *et al.* 2008). These models were performed both considering all samples and considering only samples containing decapod crustaceans. After that, canonical correspondence analysis (CCA) (Ter Braak 1986) was performed on biomass data for the dominant decapod species and the set of variables previously mentioned in order to detect any relationship between the species and those variables. Biomass data were log-transformed before 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 species biomass patterns. Finally, Generalised Linear Models (GLMs) were used to identify which variables explain the patterns of mean weight of the whole decapod crustacean community. The GLM is a flexible generalisation of ordinary least-squares regression. The dependent variables were normalised by log-transformation and distribution family used was Gaussian with identity link. Model selection was based on minimising Akaike Information Criterion (AIC) values.

All statistical analyses were carried out with PRIMER 6 and PERMANOVA + (Clarke and Warwick 2001; Anderson *et al.* 2008), STATISTICA 10 (StatSoft Inc.), XLSTAT (Addinsoft) and R ver. 2.14.2 (see http://www.r-project.org/, accessed 10 October 2015).

Results

In total, 1475 specimens belonging to 28 species grouped in 18 families were collected (see Appendix 2); 16% of the samples did not contain any decapod crustacean species.

Assemblage structure and faunal composition

The cluster analysis performed on density data showed that depth is the main assemblage-structuring factor (Fig. 2). We distinguish two main groups at 15% similarity and three main groups at 20% similarity. One group mainly contained samples obtained on the lower OMZ transition zone (LTZ) of the OMZ core, between ~800 and 1000-m depth (the sample obtained at mean depth of 789 m included in this group), where mean oxygen concentration was 0.18 ± 0.09 mL L^{-1} (8 ± 4 μM); a second group mostly comprised samples collected in the lower boundary of the OMZ (LB) between 1000 and 1200 m, where mean oxygen was 0.48 ± 0.17 mL L^{-1} (21 ± 7 μM); and a third group primarily comprised samples obtained well below the OMZ (OW = oxic waters) at depths greater than 1200 m, where oxygen concentration was greater than 0.75 mL L^{-1} or 33 μM (mean $O_2 = 1.26 \pm 0.52$ mL L^{-1} or 55 ± 23 μM). Samples not containing decapod crustaceans also clustered with this last group, notwithstanding their depth of collection. The SIMPROF test shows that the groups obtained by cluster analysis differ significantly in their multivariate structure ($P < 0.01$).

The two-way PERMANOVA performed on the same matrix indicated significant values for the factor 'depth range', which was set at three levels: LTZ, LB and OW (pseudo-$F_{2,50} = 6.61$, $P = 0.0001$). There was no significant difference for either factor 'month' (pseudo-$F_{3,50} = 0.94$, $P > 0.05$) or for the interaction of depth with month (pseudo-$F_{6,50} = 1.07$, $P > 0.05$). All the assemblages identified by depth differed significantly (LTZ *v.* LB: $t = 1.65$, $P < 0.05$; LB *v.* OW: $t = 2.30$, $P < 0.001$; LTZ *v.* OW: $t = 2.40$, $P < 0.001$). Instead, no significant changes were detected between any of the consecutive samplings (all $P > 0.05$).

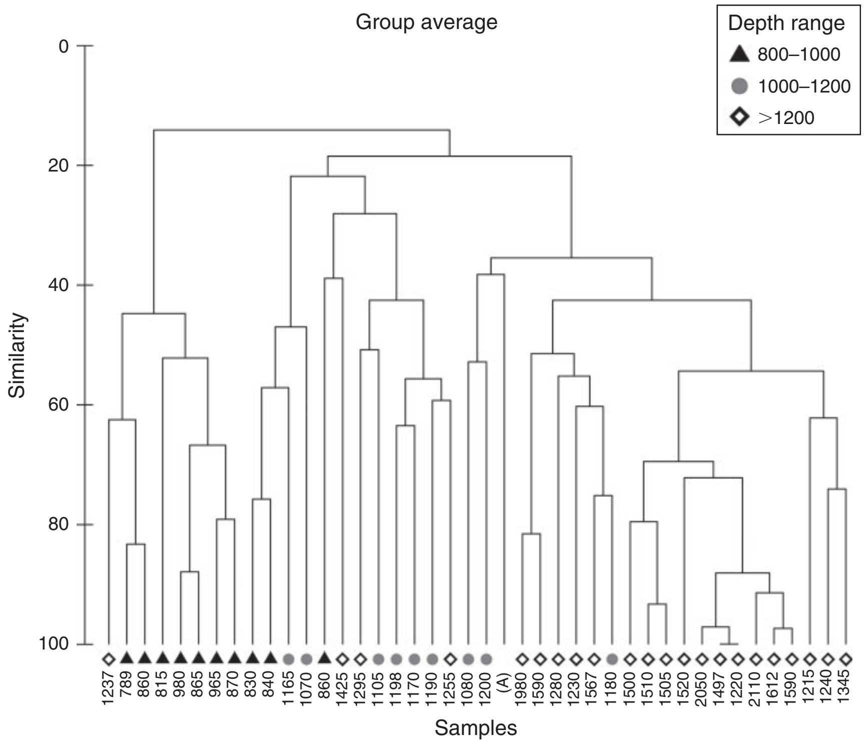

Fig. 2. Cluster analysis of density data from benthic sledge catches based on zero-adjusted Bray–Curtis resemblance matrix. (A) corresponds to samples not containing decapod crustaceans.

Table 1. Results of SIMPER analysis carried out for decapod crustaceans to show average similarities within each depth range
Cut-off at cumulative contributions of 60%

	Average abundance	Average similarity	Percentage contribution	Cumulative percentage
Lower transition zone (LTZ; 800–1000 m)				
Average similarity = 16.96				
Munidopsis depressa	6.78	14.53	85.65	85.65
Lower boundary (LB; 1000–1200 m)				
Average similarity = 24.85				
Heterocarpus affinis	2.25	8.19	32.96	32.96
Glyphocrangon spinulosa	1.83	5.85	23.54	56.5
Benthesicymus tanneri	1.62	3.16	12.73	69.23
Oxic waters (OW; >1200 m)				
Average similarity = 23.48				
Acanthephyra brevicarinata	1.6	19.51	83.08	83.08

The SIMPER routine was consequently made only for these three bathymetric groups. In the LTZ assemblage, only one species, the squat lobster *Munidopsis depressa*, accumulated 86% of the average similarity (Table 1). The LB assemblage was typified by the pandalid shrimp *Heterocarpus affinis*, the glyphocrangonid *Glyphocrangon spinulosa* and the benthesicymid *Benthesicymus tanneri*, those three species accumulating 69% of the average similarity. Finally, below 1200 m only *Acanthephyra brevicarinata* accumulated 83% of the average similarity. Dissimilarity between assemblages was always high (>85%), and was greater between the two shallow assemblages (LTZ *v.* LB = 94%) than between the two deep ones (LB *v.* OW = 87%) (Table 2). Whereas *M. depressa* was very abundant in the LTZ, it was virtually absent in the LB. The opposite occurred with *G. spinulosa* and another caridean shrimp (*Nematocarcinus faxoni*). *Heterocarpus affinis* was the species that accumulated most dissimilarity between the LB and the OW, its presence being restricted to the LTZ and the LB.

Three main feeding strategies (detritivores, predators and scavengers) were identified, with some species having mixed strategies (Appendix 2; Fig. 3). In terms of density, detritivores and organisms with mixed feeding strategies of predation and detritus feeding dominated the LTZ assemblage (98%), whereas predators were predominant at greater depths (Fig. 3).

Table 2. Results of SIMPER analysis carried out for decapod crustaceans to show average dissimilarities between depth ranges
Cut-off at cumulative contributions of 60%

	Average abundance			Average dissimilarity	Percentage contribution	Cumulative %
	LTZ	LB	OW			
Average dissimilarity = 93.69						
Munidopsis depressa	6.78	0.62		25.78	27.51	27.51
Heterocarpus affinis	1.38	2.25		16.07	17.15	44.67
Glyphocrangon spinulosa	0	1.83		10.69	11.41	56.08
Nematocarcinus faxoni	0.26	1.77		7.47	7.97	64.05
Average dissimilarity = 97.69						
Munidopsis depressa	6.78		0.78	36.02	36.87	36.87
Acanthephyra brevicarinata	0		1.6	20.92	21.41	58.28
Heterocarpus affinis	1.38		0.14	9.27	9.49	67.77
Average dissimilarity = 87.08						
Heterocarpus affinis		2.25	0.14	14.07	16.16	16.16
Acanthephyra brevicarinata		1.22	1.6	13.83	15.88	32.04
Glyphocrangon spinulosa		1.83	0.75	12.63	14.5	46.54
Nematocarcinus faxoni		1.77	1.15	9.51	10.92	57.46
Benthesicymus tanneri		1.62	0.85	8.92	10.24	67.7

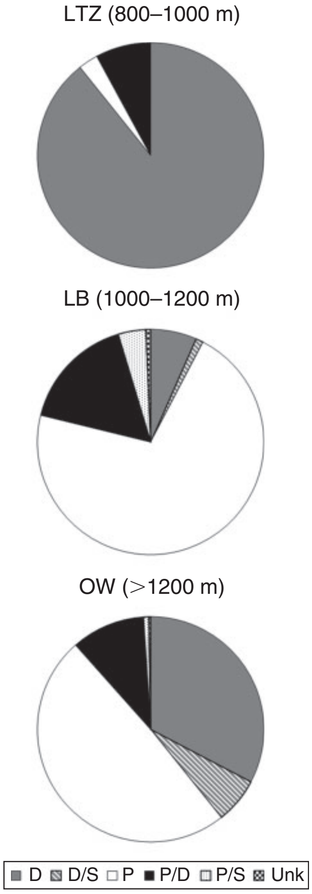

Fig. 3. Percentage contribution of the different feeding strategies identified in terms of density by depth range. D, detritivores; S, scavengers; P, predators; Unk, unknown; LTZ, lower oxygen minimum zone (OMZ) transitional zone assemblage; LB, lower OMZ boundary assemblage; OW, oxic waters assemblage.

Patterns in density, biomass and mean individual weight

The interaction between the factors depth and month obtained from two-way PERMANOVA was not significant for any of the variables explored (density, biomass and mean individual weight). Main tests for bathymetric and temporal variations in density and biomass were not significant either, the lack of statistical significance probably owing to a generalised high intra-samples variance (Fig. 4). In general, density decreased with depth (Fig. 4*a*). However, in March density was greatest in the OW, the peak attributable to a very abundant sample obtained from 1255 m (close to the LB). Although not significant, we observed a pattern of greatest density in August and lowest density in March, variations being larger at the LTZ assemblage. Biomass was somewhat higher at the LB compared with the LTZ, although not significantly, and a significant minimum ($t = 2.52$, $P < 0.05$) was found at deeper stations (the OW) (Fig. 4*b*). At a seasonal scale, biomass was greatest in December and lowest in June at the shallowest assemblages (LTZ). At the LB biomass was also greatest in December. A peak in the deepest assemblage (OW) in March again corresponded to the sample collected at 1255 m (as observed for density).

Mean individual weight changed significantly both with depth (pseudo-$F_{2,42} = 9.03$, $P < 0.001$) and across seasons (pseudo-$F_{2,42} = 3.24$, $P < 0.05$), and the interaction between the two factors was not significant ($P > 0.05$). Mean individual weights of organisms were statistically similar at the LTZ and OW assemblages ($P > 0.05$), and differed from those at the LB (LTZ *v.* LB: $t = 3.25$, $P < 0.01$; LB *v.* OW: $t = 4.32$, $P < 0.001$). In general, samples consisting of small decapod crustaceans (<6 g individual^{-1}) predominated at the LTZ (800–1000 m) and OW (>1200 m) assemblages (Fig. 5), but not at intermediate sampling depths (LB; 1000–1200 m). Seasonally, mean weight of animals found in December and March significantly (or almost) differed from those observed in June and in August (August *v.* December: $t = 2.03$, $P = 0.06$; March *v.* June: $t = 2.35$, $P < 0.05$). In general, organisms were smaller in June

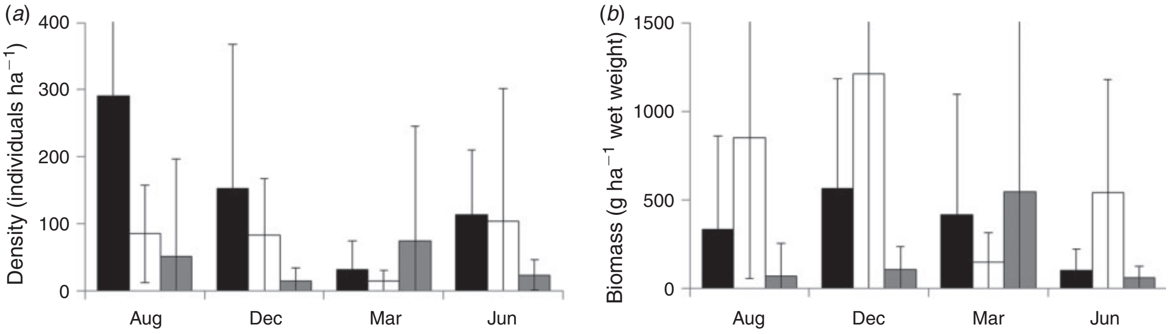

Fig. 4. Standardised mean (*a*) density (number of individuals ha^{-1}) and (*b*) biomass (g ha^{-1} wet weight) of decapod crustaceans by depth range and sampling period. Black columns indicate samples from the LTZ (800–1000 m), white columns indicate samples from the LB (1000–1200 m) and grey columns indicate samples from the OW ($>$1200 m). Bars indicate ±standard deviation.

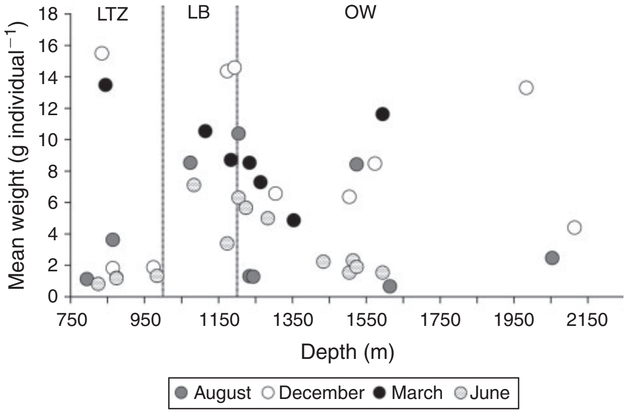

Fig. 5. Bathymetric patterns in mean individual wet weight (g individual^{-1}) of decapods per haul and sampling period. The different bathymetric groups obtained by cluster analysis are signalled.

and larger in December at all depths, with few exceptions. Consistently with such bathymetric and temporal patterns, results of the plots of mean individual weight per species at each station *v.* density showed that there were higher densities of small organisms ($<$5 g individual^{-1}) at the LTZ (800–1000 m) and that larger animals ($>$15 g individual^{-1}) were recorded at deeper assemblages, especially at the LB (1000–1200 m) (Fig. 6). Seasonally, within each depth stratum, the maximum values of mean individual weight were lower in June than in the other months and, except for the deeper stations, considerably greater densities (and greater proportions) of small organisms ($<$5 g individual^{-1}) were also observed in June.

Patterns in diversity

Expected richness, as measured by the Hurlbert index ES(*n*), varied across depth strata (pseudo-$F_{2,50} = 4.53$, $P < 0.05$) but neither across seasons nor for the interaction between depth and season. Expected richness was significantly greatest in the LB assemblage (ES(*100*) = 5.17 ± 4.07), and was statistically similar at the LTZ (ES(*100*) = 1.76 ± 1.41) and the OW (ES (*100*) = 2.56 ± 2.80). Expected richness did not vary across any consecutive seasons. H' followed bathymetric patterns similar to those of ES(*n*), with greatest values in the LB (H': LTZ = 0.40 ± 0.51; LB = 1.62 ± 1.17; OW = 0.74 ± 0.86). Seasonal variations were again not significant.

Environmental variables

None of the environmental variables explored varied between samples containing and not containing decapods.

Near-bottom temperature varied both across depth strata (pseudo-$F_{2,50} = 21.41$, $P < 0.001$) and across surveys (pseudo-$F_{3,50} = 3.46$, $P < 0.05$), and the interaction between the two terms was not significant ($P > 0.05$). $T_{20\ \mathrm{m\ AB}}$ decreased with depth (LTZ = 5.07 ± 0.90°C; LB = 3.70 ± 0.40°C; OW = 3.01 ± 0.57°C) and changes were significant from the LTZ to the LB ($t = 4.66$, $P < 0.001$) (Fig. 7*a*). $T_{20\ \mathrm{m\ AB}}$ was statistically lower in August (3.9 ± 1.6°C) than in consecutive (December: 5.5 ± 0.5°C; $t = 2.52$, $P < 0.05$) and previous (considering a composite year, June: 5.6 ± 0.8°C; $t = 3.03$, $P < 0.01$) samplings.

$DO_{20\ \mathrm{m\ AB}}$ changed with depth (pseudo-$F_{2,50} = 89.85$, $P < 0.001$) and seasonally (pseudo-$F_{2,50} = 9.92$, $P < 0.001$), but the interaction between the two factors was not significant ($P > 0.05$). $DO_{20\ \mathrm{m\ AB}}$ increased with depth (LTZ = 0.18 ± 0.09 mL L^{-1} or 8 ± 4 µM; LB = 0.48 ± 0.17 mL L^{-1} or 21 ± 7 µM; OW = 1.26 ± 0.52 mL L^{-1} or 55 ± 23 µM) (Fig. 7*b*), with significant changes across all depth strata (LTZ *v.* LB: $t = 6.26$, $P < 0.001$; and LB *v.* OW: $t = 6.30$, $P < 0.001$). Seasonally, $DO_{20\ \mathrm{m\ AB}}$ decreased almost significantly ($P = 0.06$) from March (0.84 ± 0.49 mL L^{-1} or 37 ± 22 µM) to June (0.64 ± 0.57 mL L^{-1} or 28 ± 25 µM), but no significant differences were observed between other sampling periods.

Sedimentary TOC (Fig. 7*c*) did not vary significantly throughout the bathymetric range ($P > 0.05$), and the interaction between depth and survey was not significant either ($P > 0.05$). Instead, TOC varied significantly across sampling periods (pseudo-$F_{3,50} = 14.75$, $P < 0.001$). Organic carbon in sediments measured in December (5.19 ± 0.75%) and March (5.20 ± 0.75%) was higher than that measured in June (3.76 ± 0.71%) and August (3.70 ± 0.58%).

Phytoplankton pigment concentration increased from November to March and remained high until May, decreasing to minimum levels from July through November (Fig. 8). PPC was much higher in 2000 than in 2001. An unusual secondary peak in PPC was observed in August 2000.

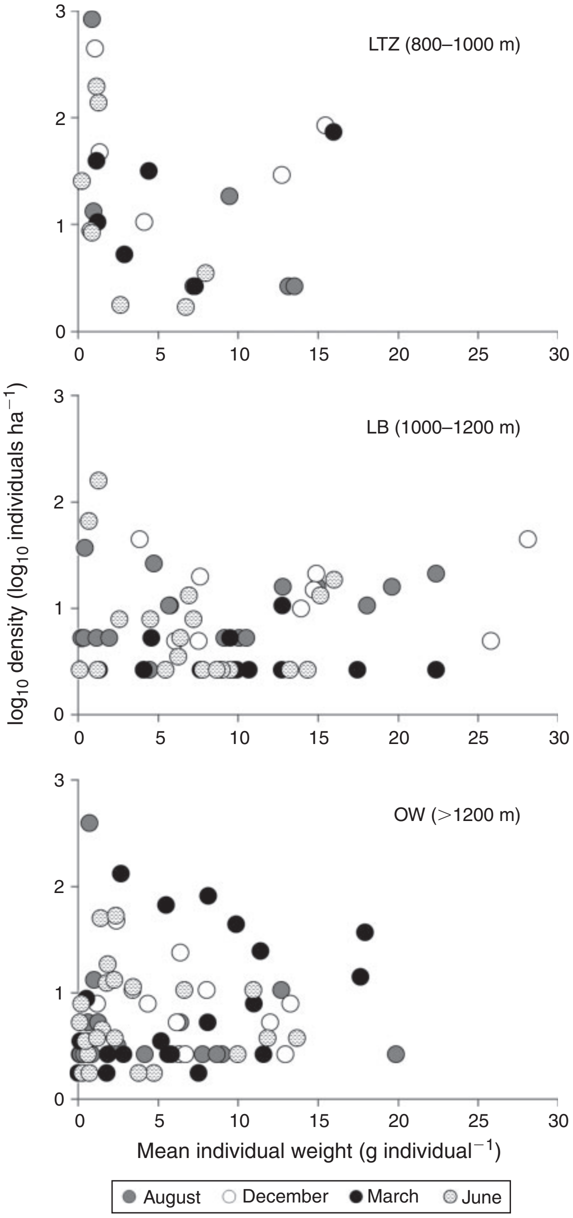

Fig. 6. Plots of mean individual weight considering the species appearing at each station *v.* their density by depth assemblage and sampling period. LTZ, lower oxygen minimum zone (OMZ) transitional zone assemblage; LB, lower OMZ boundary assemblage; OW, oxic waters assemblage.

Correlation of fauna distribution with environmental variables

A draftsman plot showed high degrees of correlation between several pairs of environmental variables, thus for analysis we retained: $T_{20\ \mathrm{m\ AB}}$, $O_{20\ \mathrm{m\ AB}}$ (positively correlated with depth), sedimentary TOC, PPC_{sim} and PPC-1, PPC-2, PPC-4–6 (PPC-5 was positively correlated with PPC-3).

DISTLM performed on the density matrix considering both samples containing and not containing decapod crustaceans explained 14% of the total variance, with only oxygen being included in the model (Table 3). When only samples containing decapod crustaceans were considered, DISTLM explained 29% of the total variance, including $T_{20\ \mathrm{m\ AB}}$ and $O_{20\ \mathrm{m\ AB}}$ as explanatory variables.

CCA ordination significantly ($P < 0.0001$) explained a total of 70.31% of the variance with the first two axes (Fig. 9). The biomass of the two *Munidopsis* species sampled at shallower stations (i.e. *M. depressa* and *M. hystrix*) were located at the right side of the plot in association with samples collected shallower than 1000 m, and were linked to higher temperatures and greater PPC recorded between 3 and 6 months before the sampling. The biomass of species associated with samples collected deeper than 1000 m were located at the left side of the plot and were linked to greater oxygen concentrations and higher PPC-2.

GLM performed on mean individual weight explained 28% of the total deviance. Greater PPC-5 enhanced the presence of smaller organisms (Table 4).

Discussion

The present study analysed the structure of the community of benthic and benthopelagic decapod crustaceans below the core of the OMZ in the south-east Gulf of California over a wide bathymetric range (730–2250 m). Also, it explored intra-annual patterns of the decapod crustaceans' community structure under OMZ areas for the first time and investigated the influence of environmental variables sampled simultaneously on those patterns. Below the OMZ core, the decapod crustaceans' community structured in three major depth-related assemblages. Edge effects (Mullins *et al.* 1985) consisting in a fairly rapid taxonomic substitution of dominant species with depth and in high densities of decapod crustaceans over a narrow bathymetric range were observed. Composition of assemblages remained constant throughout the year, but some changes in mean individual weight of organisms were observed. The patterns in community structure (i.e. community composition, biomass and mean individual weight) were significantly correlated with oxygen, temperature and surface production before the samplings. These results are consistent with previous studies on megafauna under OMZ areas (Murty *et al.* 2009; Quiroga *et al.* 2009; Sellanes *et al.* 2010; Hunter *et al.* 2011).

Bathymetric and seasonal trends

Where OMZs reach lowest DO concentration (i.e. anoxic and severely hypoxic fringes), homogenous benthic assemblages are usually observed (Jumars and Eckman 1983; Levin 2003; Hunter *et al.* 2011). However, below the OMZ core, the progressive increase of DO in an environment where food is not a limiting factor allows proliferation of deposit feeders and burrowers (Smith *et al.* 2000; Levin *et al.* 2009; Jeffreys *et al.* 2012; Méndez 2013). These organisms create considerable environmental patchiness in the deep-sea floor (Grassle and Sanders 1973; Jumars and Eckman 1983) and could be responsible for the patchy distribution observed below the OMZ core in the Gulf of California for small benthic megafauna (Méndez 2007; Zamorano *et al.* 2007) and for benthic and benthopelagic decapod crustaceans (in this study). Indeed, results indicate that populations within the depth range of a species were not spread uniformly but were segregated in areas of high density, which is a common characteristic of deep-sea ecosystems (Maynou *et al.* 1996; Carney 2005).

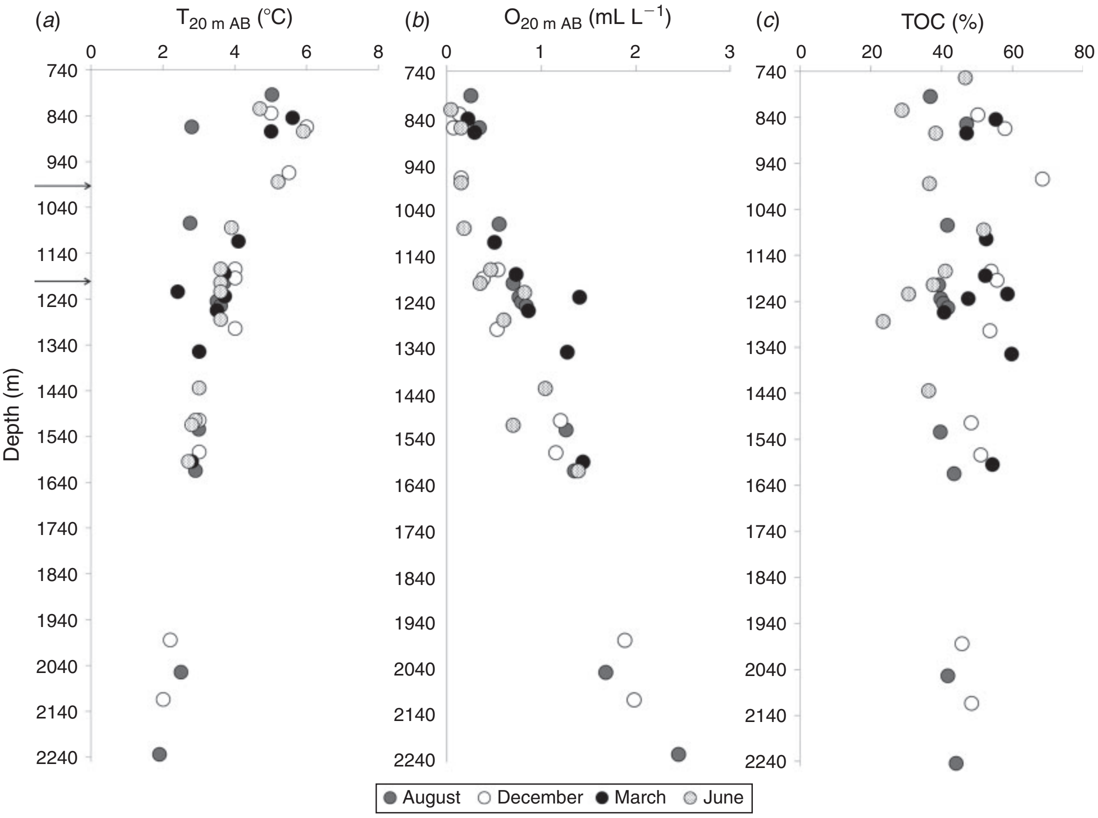

Fig. 7. Values of (*a*) temperature ($T_{20\,m\,AB}$) and (*b*) oxygen ($DO_{20\,m\,AB}$) recorded 20 m above the bottom, and (*c*) percentage of total organic carbon (TOC) measured in sediments by depth and sampling period. Arrows indicate depth boundaries between the fauna assemblages identified by cluster analysis.

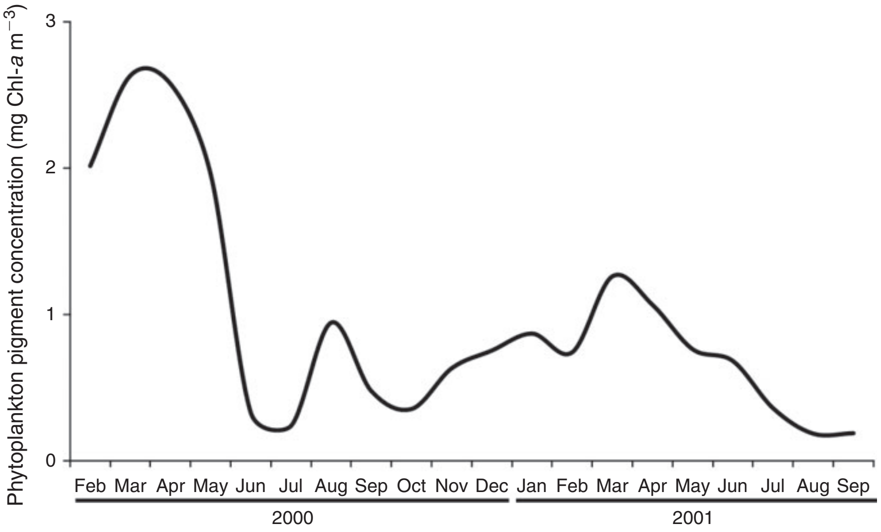

Fig. 8. Mean monthly phytoplankton pigment concentration (PPC) values in the study area during 2000 and 2001.

Notwithstanding the patchy distribution, some bathymetric patterns in community composition and structure were identified. Community composition changed over narrow bathymetric ranges, changes related both with the swimming capacities and the feeding strategies of the species. Benthic detritivores, mainly the galatheid *Munidopsis depressa*, dominated at the shallowest depths sampled (800–1000 m; LTZ), in an environment characterised by hypoxic conditions ($O_2 \leq 0.18$ mL L^{-1} or

Table 3. Summary results of distance-based permutational multivariate regression analysis (DISTLM) for density data of decapod crustaceans with environmental variables
20 m AB, 20 m above the bottom

	AIC	Pseudo-*F*	*P*	Proportion	Cumulative proportion
All samples					
Oxygen$_{20\ \mathrm{m\ AB}}$	391.47	7.68	0.0001	0.14	0.14
Without denuded samples					
Temperature$_{20\ \mathrm{m\ AB}}$	324.89	12.98	0.0001	0.25	0.25
Oxygen$_{20\ \mathrm{m\ AB}}$	324.58	2.20	0.04	0.04	0.29

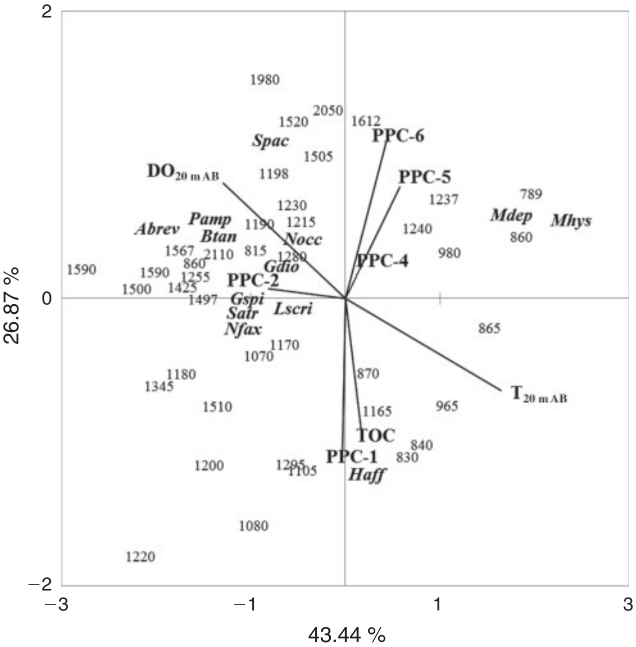

Fig. 9. CCA of seasonally obtained benthic sledge hauls based on biomass of dominant species of decapod crustaceans. Individual samples indicated with their corresponding mean depth. Species codes: *Abrev*, *Acantephyra brevicarinata*; *Btan*, *Benthesicymus tanneri*; *Gdio*, *Galacantha diomedeae*; *Gspi*, *Glyphocrangon spinulosa*; *Haff*, *Heterocarpus affinis*; *Lscr*, *Lebbeus scrippsi*; *Mdep*, *Munidopsis depressa*; *Mhys*, *Munidopsis hystrix*; *Nfax*, *Nematocarcinus faxoni*; *Nocc*, *Nephropsis occidentalis*; *Pamp*, *Pandalus amplus*; *Satr*, *Sclerocrangon atrox*; *Spac*, *Stereomastis pacifica*. Codes for environmental variables: DO$_{20\ \mathrm{m\ AB}}$, near-bottom oxygen concentration; T$_{20\ \mathrm{m\ AB}}$, near-bottom temperature; PPC$_{\mathrm{sim}}$, phytoplankton pigment concentration at surface simultaneous to sampling; PPC$_{1\text{–}6\mathrm{mo}}$, phytoplankton pigment concentration at surface 1–6 months before the sampling; TOC, percentage total organic carbon in sediments.

Table 4. Results of generalised linear models performed on mean individual weights of decapod crustaceans with environmental variables
PPC-5, phytoplankton pigment concentration at surface 5 months before sampling

	Percentage explained	d.f.	*F*	Sign of correlation	*P*	AIC
PPC-5	28.28	40	15.380	–	<0.001	79.69

8 µm: Kamykowski and Zentara 1990). Benthopelagic predators (i.e. *Acantephyra brevicarinata*, *Heterocarpus affinis*, *Glyphocrangon spinulosa* and *Benthesicymus tanneri*) dominated at depths greater than 1000 m (the LB and OW), where DO concentration was higher. Similar bathymetric patterns, with galatheids or crabs found at shallower depths than shrimps, were documented over Volcano 7, eastern tropical Pacific (Wishner *et al.* 1990, 1995). Instead, such patterns were not so clear in the Chilean margin (Quiroga *et al.* 2009), where the eastern tropical Pacific OMZ becomes narrower and milder (Helly and Levin 2004), and were opposite in the Pakistan margin (Arabian Sea) (Murty *et al.* 2009). However, the lack of a more precise taxonomic resolution of studies in the Pakistan margin does not allow sound conclusions in this respect.

High densities were observed below the OMZ core (DO < 0.15 mL L^{-1} or 6.6 µM) and constitute further evidence of the ability of benthic megafaunal organisms to proliferate at DO lower than 0.2 mL L^{-1} (9 µM) (see Hendrickx 2001; Murty *et al.* 2009; Hunter *et al.* 2011; Hendrickx and Serrano 2013). Organisms living in environments with low oxygen levels present adaptations that enhance their capacity for oxygen extraction and transport (Childress and Seibel 1998; Seibel *et al.* 1999; Jeffreys *et al.* 2012), enabling them to inhabit severely hypoxic environments such as the LTZ (Drazen and Seibel 2007). A maximum in biomass mainly consisting of the above-mentioned benthopelagic predators was recorded at 1000–1200 m (LB), below the maximum in density. Deep peaks in biomass have been documented at similar depths in the western Mediterranean (Stefanescu *et al.* 1993; Follesa *et al.* 2009, 2011; Cartes *et al.* 2013) and in the Atlantic (Marshall and Merrett 1977; Gordon and Duncan 1985; Gordon 1986) for near-bottom zooplankton and for benthopelagic fish and decapods. In the deep Mediterranean Sea, high biomasses consisting of large zooplankton feeder fish have been recorded between 1000 and 1300 m in association with an increase in biomass of their prey (i.e. zooplankton) (Cartes *et al.* 2013; Fanelli *et al.* 2013). Therefore, it is plausible that the peak biomass of decapod crustaceans observed in this study is sustained by the peaks of macrofauna occurring below OMZ cores (Wishner *et al.* 1990, 1995; Levin 2003; Levin *et al.* 2009). In the same sense, the expected drop in abundance of such macrofauna with depth (Levin 2003; Levin *et al.* 2009; Hughes *et al.* 2009) may be responsible for the decrease in density and biomass of benthopelagic decapod crustaceans observed below ~1200 m.

Highest diversity was recorded at the LB, as observed by Zamorano *et al.* (2007) for molluscs and by Méndez (2007) for polychaetes in the same area. This pattern coincides with that reported in the Chilean margin (Sellanes *et al.* 2010) and consistently suggests that OMZ boundaries constitute highly heterogeneous environments. Lowest diversities above and below the LB appear to be related to the influence of oxygen depletion on species richness, and of food availability on the abundance and dominance of particular species (Levin and Gage 1998; Levin *et al.* 2009; Gooday *et al.* 2009). Among decapod crustaceans, it is likely that only some galatheids can tolerate bottom water oxygen concentrations below 0.2 mL L^{-1} (measured at the LTZ in this study). The decrease in food availability (i.e. macrofauna) (see above) at depths greater than 1200 m probably favours the survival of oplophorid shrimps before other taxa, as they have lower feeding intensity than other dominant groups such as pandalids (Cartes 1993*a*, 1993*c*). In the deep Mediterranean, *Acanthephyra eximia* replaced the pandalid *Plesionika martia* in the depth gradient, inhabiting less productive areas and showing a similar diet but lower feeding intensity. This seems parallel to a possible bathymetric substitution of the pandalid *H. affinis* (LB) by *A. brevicarinata* (in the OW assemblage).

Although the composition of the community of decapod crustaceans remained constant throughout the year, the mean individual weight of organisms varied, and higher densities of smaller decapod crustaceans were reported in June. Seasonal variations in the size structure of deep-sea megafauna communities have been reported previously (e.g. Moranta *et al.* 2008; Fanelli *et al.* 2013) as a consequence of the periodicity in reproduction and recruitment (Gage 1994; Ruhl *et al.* 2008) and of variations in the food inputs (Papiol *et al.* 2012).

Environmental drivers of deep benthopelagic assemblages

Concurring with what has been repeatedly argued in the past for hypoxic environments, our results suggest that both oxygen and food, specifically food derived from surface production, played some role in the distribution of decapod crustaceans below the OMZ core. Furthermore, temperature was also important. A large amount of variation was not explained by the models obtained in our study. This is attributable to the complex distribution of decapod crustaceans across the south-east Gulf of California and to the lack of more detailed information on food quality (e.g. prey availability, $\delta^{13}C$ of sediments, sedimentary pigments) rather than quantity, which has been identified as an important driver of megafauna distribution in OMZ areas (Murty *et al.* 2009; Quiroga *et al.* 2009; Sellanes *et al.* 2010; Hunter *et al.* 2011).

Bathymetric changes in community composition were mainly driven by oxygen and temperature. The shift from slow moving to swimming organisms seems, at least partially, related to the greater minimum oxygen thresholds observed in decapod crustaceans with increasing swimming capacity (Childress *et al.* 1990; Maynou and Cartes 1998). Swimming species were virtually absent from hypoxic environments and were mainly collected deeper, where DO may be sufficient to meet their metabolic demands. Besides, the aerobic capacity of most ectothermic animals is restricted within a range of temperatures that is species-specific (Frederich and Pörtner 2000; Pörtner 2001; Ekau *et al.* 2010), and therefore, specific combinations of both oxygen and temperature may restrict the distribution of the species to definite depth ranges. In this same sense, the LTZ and deeper assemblages were distributed in the two different water masses observed in the area: the North Pacific Intermediate Water and the Pacific Bottom Water, those being defined by temperature and salinity combinations which ultimately modulate bottom-water oxygen conditions.

The faunal patterns observed in the present study were not related to the availability of food in the sediments (i.e. organic carbon in sediments) but to surface production taking place before the samplings. This suggests some role of vertical input of fresh organic matter from the overlying surface water in the community dynamics of benthic and benthopelagic decapod crustaceans below this OMZ core. This concurs with what has been observed in other areas of the world. In the Mediterranean Sea, for instance, a time lag of 1–3 months has been observed between surface primary production and the community response of decapod crustaceans (Cartes *et al.* 2007, 2008; Papiol *et al.* 2012; Fanelli *et al.* 2013). The greater flux of organic matter together with the lower attenuation coefficients observed under OMZ areas (Levin 2003; Roullier *et al.* 2013) enhance the more direct deposition of particulate organic matter, favouring the relationships between surface production and decapod crustacean dynamics. The biomass below the OMZ core is likely sustained by the high surface productivity levels in the area (Álvarez-Borrego and Lara-Lara 1991), which lead to large inputs of labile organic matter to bathyal depths (Cowie *et al.* 1999; Devol and Hartnett 2001; Honjo *et al.* 2008). However, the biomasses of the different depth assemblages responded to surface production with different time lags (Fig. 9). Although the OMZ is supposed to act as a barrier for most pelagic organisms (Wishner *et al.* 1995), some temporal excursions into the OMZ core cannot be discarded (Morrison *et al.* 1999; Luo *et al.* 2000; Ashjian *et al.* 2002), and the quicker response by benthopelagic predators located at the LB and OW could be enhanced by their, or their prey's, active vertical transport. In this sense, although the role of food in regulating community composition was not captured in our results, it is likely that the taxonomic shift with depth was enhanced by bathymetric changes in the food sources available (Cartes and Carrassón 2004). The replacement of detritivores by predators on macrofauna seems to be associated with the proliferation of their potential prey in narrow bands under OMZ cores, which has been repeatedly reported (e.g. Wishner *et al.* 1990, 1995; Levin *et al.* 2009).

Seasonal variations in the distribution and structure of bathyal and abyssal megafauna communities have been related to changes in hydrographic conditions and food quantity and quality (e.g. Smith *et al.* 1994; Papiol *et al.* 2012; Fanelli *et al.* 2013). The latter are driven by seasonal patterns of surface production (Thunell 1998; Jeffreys *et al.* 2009*b*). In the Gulf of California, surface productivity is greatest from December to May following upwelling (Álvarez-Borrego 2010), which translates to larger amounts of food of biogenic origin during late autumn–spring at 500 m (Thunell 1998). In our study, greater surface production between February and April favoured aggregations of small decapods in June, probably through greater availability of small particulate food or small meio- and macrofaunal organisms that proliferate with the arrival of fresh organic matter (Galéron *et al.* 2001; Cartes *et al.* 2002; Riaux-Gobin *et al.* 2004). Similar seasonal feeding aggregations among decapod crustaceans have been observed in the Mediterranean Sea, in relationship with the availability of food and reproductive processes (Fanelli and Cartes 2004; Cartes *et al.* 2008).

It can be concluded from our study that the benthic and benthopelagic decapod crustacean community below the OMZ core in the south-east Gulf of California presents bathymetric patterns that concur with those observed previously in other areas subjected to oxygen minima (Murty *et al.* 2009; Quiroga *et al.* 2009). Also, seasonal changes take place, mainly in the size structure of the community. The combined effect of oxygen, temperature and food plays a major role as a driver of community structure and dynamics, as it occurs in non-oxygen-restricted areas (Cartes *et al.* 2013; Fanelli *et al.* 2013). This emphasises the potential susceptibility of bathyal megafauna communities to the global pattern of expansion of OMZs resulting from climate change, so the study of deep-water communities in these areas should be considered a priority.

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Appendix 1. Sampling locations and sampling details of benthic sledge hauls performed within the oceanographic cruises TALUD IV–VII and environmental parameters measured at the bottom level

*, samples without decapod crustaceans; $T_{20\ \mathrm{m\ AB}}$, temperature recorded 20 m above the bottom; $DO_{20\ \mathrm{m\ AB}}$, dissolved oxygen concentration in the water 20 m above the bottom; TOC, total organic carbon in sediments

Survey	Station		Location				Date	Depth range (m)	$T_{20\ \mathrm{m\ AB}}$ (°C)	$DO_{20\ \mathrm{m\ AB}}$ (mL L^{-1})	TOC (%)
IV	4	*	21°59′00″	N	106°35′00″	W	23 Aug 00	1200–1290	3.60	0.84	3.67
IV	5	*	22°03′18″	N	106°41′18″	W	23 Aug 00	1340–1360	2.80	1.60	3.00
IV	13		23°17′30″	N	107°29′51″	W	24 Aug 00	860	2.80	0.34	5.21
IV	14		23°13′24″	N	107°41′48″	W	24 Aug 00	2220–2250	1.90	2.45	4.00
IV	18	*	24°15′12″	N	108°17′10″	W	25 Aug 00	908–944	2.80	0.43	3.00
IV	19		24°15′18″	N	108°24′06″	W	25 Aug 00	1196–1200	3.69	0.70	3.33
IV	20		24°27′24″	N	108°35′16″	W	25 Aug 00	1500–1540	2.99	1.26	3.50
IV	25		24°53′12″	N	108°59′24″	W	26 Aug 00	778–800	5.03	0.25	3.28
IV	26		24°56′24″	N	109°05′36″	W	26 Aug 00	1200–1274	3.72	0.76	3.67
IV	27		24°59′00″	N	109°12′06″	W	26 Aug 00	1605–1620	2.90	1.35	3.67
IV	28	*	24°52′30″	N	109°37′00″	W	28 Aug 00	2024–2040	2.00	2.10	4.36
IV	33		25°45′54″	N	109°48′06″	W	27 Aug 00	1060–1080	2.75	0.55	4.00
IV	34		25°40′42″	N	109°54′24″	W	27 Aug 00	1240	3.50	0.79	3.40
IV	35		25°53′59″	N	110°11′17″	W	27 Aug 00	2000–2100	2.50	1.68	3.67
V	5		22°00′57″	N	106°40′00″	W	13 Dec 00	1515–1620	3.00	1.15	5.09
V	6		22°00′00″	N	106°48′05″	W	13 Dec 00	1950–2010	2.20	1.88	4.56
V	11		23°14′00″	N	107°00′00″	W	17 Dec 00	850–870	6.00	0.07	5.78
V	12		23°18′00″	N	107°26′59″	W	14 Dec 00	1160–1170	4.00	0.54	5.39
V	14		23°16′20″	N	107°40′45″	W	14 Dec 00	2080–2140	2.00	1.98	4.83
V	18		24°15′12″	N	108°17′09″	W	15 Dec 00	940–990	5.50	0.15	6.83
V	19		24°16′24″	N	108°24′18″	W	15 Dec 00	1180–1200	4.00	0.38	5.55
V	20		24°14′44″	N	108°35′18″	W	15 Dec 00	1470–1525	3.00	1.20	4.82
V	25		24°51′46″	N	108°57′59″	W	16 Dec 00	800–860	5.00	0.13	5.01
V	26		24°56′18″	N	109°11′48″	W	16 Dec 00	1280–1310	4.00	0.53	5.36
V	32	*	25°46′01″	N	109°42′39″	W	17 Dec 00	850–900	5.00	0.10	3.90
VI	4		22°00′51″	N	106°34′42″	W	13 Mar 01	1190–1250	2.40	0.84	5.84
VI	5	*	22°00′42″	N	106°39′55″	W	13 Mar 01	1470–1530	-	1.74	4.95
VI	11	*	23°14′59″	N	106°59′00″	W	14 Mar 01	825–855	6.00	0.17	6.81
VI	12		23°18′36″	N	107°26′56″	W	14 Mar 01	1050–1160	4.10	0.50	5.24
VI	18		24°14′56″	N	108°16′17″	W	15 Mar 01	850–890	5.00	0.29	4.69
VI	19		24°16′24″	N	108°24′18″	W	15 Mar 01	1160–1200	3.70	0.73	5.22
VI	20		24°14′48″	N	108°35′11″	W	15 Mar 01	1250–1440	3.00	1.27	5.96
VI	25		24°51′41″	N	108°57′54″	W	16 Mar 01	830–850	5.60	0.22	5.51
VI	26		24°56′18″	N	109°06′42″	W	16 Mar 01	1190–1270	3.70	1.40	4.74
VI	27		25°01′12″	N	109°11′36″	W	16 Mar 01	1580–1600	2.80	1.44	5.42
VI	33	*	25°45′49″	N	109°48′40″	W	17 Mar 01	1120–1160	3.50	0.57	4.37
VI	34		25°43′50″	N	109°53′59″	W	17 Mar 01	1240–1270	3.50	0.86	4.06
VII	4		22°03′18″	N	106°34′42″	W	05 Jun 01	1200–1230	3.60	0.82	3.05
VII	5		22°00′24″	N	106°39′54″	W	05 Jun 01	1490–1520	2.80	1.81	4.04
VII	11	*	23°16′54″	N	106°59′48″	W	06 Jun 01	780–790	5.60	0.15	4.67
VII	12		23°18′18″	N	107°26′48″	W	06 Jun 01	1040–1120	3.90	0.18	5.17
VII	18		24°14′30″	N	108°16′24″	W	07 Jun 01	950–1010	5.20	0.15	3.65
VII	19		24°16′12″	N	108°23′42″	W	07 Jun 01	1160–1180	3.60	0.46	4.09
VII	20		24°14′48″	N	108°35′12″	W	07 Jun 01	1480–1520	2.90	0.79	4.02
VII	25		24°52′48″	N	108°58′00″	W	08 Jun 01	780–850	4.70	0.04	2.87
VII	26		24°25′24″	N	109°05′21″	W	08 Jun 01	1180–1220	3.60	0.35	3.75
VII	27		25°01′30″	N	109°12′00″	W	08 Jun 01	1580–1600	2.70	1.39	3.58
VII	13B		23°30′18″	N	107°44′00″	W	06 Jun 01	1400–1450	3.00	1.04	3.62
VII	32B		26°03′00″	N	109°55′24″	W	09 Jun 01	850–880	5.90	0.15	3.82
VII	33B		26°06′30″	N	110°06′42″	W	09 Jun 01	1260–1300	3.60	0.60	2.34
VII	34B		26°05′30″	N	110°10′30″	W	09 Jun 01	1500–1520	3.20	0.78	4.04

Appendix 2. List of species (in terms of mean density by depth range, individuals ha^{-1}) collected by benthic sledge during cruises TALUD IV–VII between August 2000 and June 2001

LTZ, lower transition zone (800–1000 m); LB, lower oxygen minimum zone boundary (1000–1200 m); OW, oxic waters (>1200 m). Feeding strategies: P, predator; D, detritivore; S, scavenger; Unk., unknown

	LTZ				LB				OW				Feeding strategy
	Aug	Dec	Mar	Jun	Aug	Dec	Mar	Jun	Aug	Dec	Mar	Jun	
Suborder Dendrobranchiata													
Superfamily Penaeoidea													
Family Benthesicymidae													
Benthesicymus tanneri Faxon, 1893	1.31				1.54	9.85	3.94	0.88	0.38	4.21	1.33	0.79	P^{A}
Family Sicyoniidae													
Sicyonia disedwardsi (Burkenroad, 1934)				0.42									P^{B}
Family Solenoceridae													
Solenocera mutator Burkenroad, 1938				6.35									P^{A,C}
Suborder Pleocyemata													
Infraorder Stenopodidea													
Family Stenopodidae													
Odontozona foresti Hendrickx, 2002											0.35		Unk.
Infraorder Caridea													
Superfamily Oplophoroidea													
Family Acanthephyridae													
Acanthephyra brevicarinata Hanamura, 1984					6.56	2.46	2.63	2.63	3.77	3.15	1.58	1.25	P^{A,D}
Superfamily Nematocarcinoidea													
Family Nematocarcinidae													
Nematocarcinus faxoni Burukovsky, 2001	6.56				2.63			55.14	2.63	1.58	26.78	8.39	P^{E,F}
Superfamily Alpheoidea													
Family Thoridae													
Lebbeus scrippsi Wicksten & Méndez, 1982					18.38			21.88	0.75		0.72	0.38	P^{A,G}
Superfamily Pandaloidea													
Family Pandalidae													
Heterocarpus affinis Faxon, 1893	1.31	28.99	36.76		7.88	17.89	6.56	5.25			2.90		P/D^{H,I}
Pandalopsis ampla Bate, 1888					5.25	6.24	1.31	4.38			4.92		P/D^{J}
Plesionika trispinus Squires & Barragán, 1976				2.95							0.35		P^{K,L}
Superfamily Crangonoidea													
Family Crangonidae													
Parapontophilus occidentalis Faxon, 1893												0.75	P^{C,M}
Sclerocrangon atrox Faxon, 1893	1.31				2.63		1.31	2.63			1.76		P^{G}
Family Glyphocrangonidae													
Glyphocrangon sicaria Faxon, 1893									0.38				P^{N}
Glyphocrangon spinulosa Faxon, 1893					5.25	22.16	2.63	2.92	1.55	4.73	16.16	1.55	P^{N}
Glyphocrangon taludensis Hendrickx, 2010				0.88					0.38			1.55	P^{N}
Infraorder Astacidea													
Superfamily Nephropoidea													
Family Nephropidae													
Nephropsis occidentalis Faxon, 1893					7.88	22.16	1.31	6.13	0.38	1.54	8.93		P^{A}
Infraorder Axiidea													
Family Callianassidae													
Callianopsis goniophthalma (Rathbun, 1902)			1.31										D^{O}

(*Continued*)

Appendix 2. (Continued)

	LTZ				LB				OW				Feeding strategy
	Aug	Dec	Mar	Jun	Aug	Dec	Mar	Jun	Aug	Dec	Mar	Jun	
Family Axiidae													
Calocarides sp.			15.76										D[C,P]
Infraorder Polychelida													
Family Polychelidae													
Stereomastis pacifica (Faxon, 1893)					1.54	2.46		0.88			1.23	0.54	P/S[A,Q]
Infraorder Anomura													
Superfamily Galatheoidea													
Family Munidopsidae													
Galacantha diomedeae Faxon, 1893					2.63		1.31		0.75	0.53	13.35	1.13	D/S[R,S]
Munidopsis depressa Faxon, 1893	416.21	162.88	24.95	85.38	5.25			0.88	55.89			0.26	D/S[R,S]
Munidopsis hystrix Faxon, 1893	9.20	13.13	2.63	0.44					0.38				D/S[R,S]
Munidopsis nitida (A. Milne-Edwards, 1880)					13.13							0.26	D/S[R,S]
Munidopsis palmatus Khodkina, 1973					2.63				0.38		0.72		D/S[R,S]
Munidopsis quadrata Faxon, 1893							1.31		0.38		1.76	1.37	D/S[R,S]
Superfamily Lithodoidea													
Family Lithodidae													
Neolithodes diomedeae (Benedict, 1895)												0.38	D/S[R]
Superfamily Paguroidea													
Family Parapaguridae													
Parapagurus foraminosus Lemaitre, 1999										4.73		7.13	P/D[A,C]
Infraorder Brachyura													
Superfamily Cancroidea													
Family Atelecyclidae													
Trichopeltarion corallinum (Faxon, 1893)						2.46					0.35		Unk.

[A] Lin *et al.* (2014).
[B] Kennedy *et al.* (1977).
[C] Cartes *et al.* (2007).
[D] Cartes (1993*a*).
[E] Cartes (1993*b*).
[F] Allen *et al.* (2000).
[G] Birkely and Gulliksen (2003).
[H] Andrade and Baez (1980).
[I] Rajasree and Kurup (2011).
[J] Savenkoff *et al.* (2006).
[K] Cartes (1993*c*).
[L] Fanelli and Cartes (2004).
[M] Papiol *et al.* (2013).
[N] Reid *et al.* (2012).
[O] Cadien (1992).
[P] Pinn *et al.* (1998).
[Q] Cartes and Abelló (1992).
[R] Escobar-Briones *et al.* (2002).
[S] Hoyoux *et al.* (2012).