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The Atlantic-Mediterranean ecological connection: a study on decapod larval communities

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Abstract

Larval dispersal mechanisms, although significantly studied, are far from being completely resolved. Local studies are needed to clarify key interactions between individual life cycles and transport processes. The Atlantic-Mediterranean connection through the Strait of Gibraltar is a particularly important area to explore these processes, as a biodiversity hotspot for detecting species fluxes and/or invasions between several Large Marine Ecosystems. However, both the area dynamics and the mechanisms used by the larvae to cope with the system hydrological conditions are scantly explored. Summer data on decapod larvae and ocean water masses from an extended area of southern Portugal, Gulf of Cadiz, Strait of Gibraltar and Alboran Sea were analysed, and the larval assemblages and their potential retention/dispersal mechanisms were explored. Different larval assemblages were linked to the hydrological conditions of each basin. Shelf width differences and its influence in along/cross-shore transport were the main drivers of decapod distribution, acting as biological barriers. Larvae of mesopelagic species dominated the northern Alboran Sea inner-shelf, highly influenced by offshore currents. Here, the nearshore processes were limited to surface waters, while in the Gulf they extended more deeply and onto the outer shelf. Results on species ecological traits can be applied to similar oceanographical world coastal areas and could be used for further development of ecological modelling studies.

Keywords: Decapoda; connectivity; Gulf of Cadiz; Alboran Sea; Strait of Gibraltar.

Introduction

The high abundance, diversity and commercial value of decapod crustacean adults, but also their complex life cycles, contribute to the numerous studies on decapod larval dispersal and retention mechanisms (González-Gordillo & Rodríguez, 2003). This knowledge is fundamental for the evaluation of marine ecosystems, the sustainable use of exploited species, the definition of Marine Protected Areas and the implementation of coastal management plans (e.g. Corell *et al.,* 2012).

Larval stages, important components of marine meroplankton, are the main dispersal propagules linking the parental habitats to settlement grounds (e.g. Queiroga *et al.,* 2007), shaping the genetic connectivity and the resilience of populations (e.g. Cowen *et al.,* 2006). Factors, such as time and place of larval emission, larval duration and the position occupied in the water column define the dispersal distance (e.g. Landeira *et al.,* 2010; Morgan *et al.,* 2009; Pires *et al.,* 2013) and, partly, the recruitment to adult populations. By occupying shallow shelf areas, constrained by alongshore currents parallel to the coast, coastal decapods remain near their natal sites (e.g. dos Santos *et al.,* 2008; Landeira *et al.,* 2009). Topographically-induced eddies can also maintain larvae close to their origin, even at small scales (Alvarez *et al.,* 2015). Connectivity (henceforth “ecological” unless specified) between subpopulations determines the maintenance of populations and the colonization of new areas, and can only be fully understood by analysing the biophysical conditions that influence larval transport (Cowen *et al.,* 2007).

The southern Portuguese coast and the Gulf of Cadiz (north-eastern Atlantic) are highly productive areas with frequent summer wind-driven upwelling regimes, particularly near the Cape S. Vicente (Relvas *et al.,* 2007) that, forced by cyclonic cells and slope currents, extend eastward (Garcia-Lafuente *et al.,* 2006; Relvas *et al.,* 2007; Peliz *et al.,* 2009). These productive Atlantic waters are transported to the Mediterranean through the narrow and shallow (~300 m) Strait of Gibraltar (Echevarria *et al.,* 2002), carrying nutrients and biological productivity (Bruno *et al.,* 2013).

Atlantic waters enter the Mediterranean at surface, while the outflow of colder and more saline Mediterranean waters occurs at depth (García-Lafuente *et al.,* 2002). The Atlantic Jet, associated with the Gulf of Cadiz slope current, creates two anticyclonic gyres in the Alboran Sea basin (e.g. Lacombe 1971; Flexas *et al.,* 2006) (see Fig. S1 for the main circulation patterns in the area). Wind-driven upwelling, dependent on the Atlantic Jet angle and speed, occurs in the northern Alboran Sea coast, injecting nutrients into the system (Sarhan *et al.,* 2000; Macías *et al.,* 2007, Macías *et al.,* 2011). Retentive coastal features enhance productivity and can explain the northern Alboran Sea high surface chlorophyll *a* (chl *a*) values, which contrast with the weaker signals at basin level (e.g. Echevarria *et al.,* 2002; Peliz *et al.,* 2013; Pérez-Folgado *et al.,* 2003). The Almeria-Oran front (linked to the gyre circulation) is another key oceanographic feature with great impact on the Alboran Sea dynamics and a stronger biological barrier to dispersal than the Strait (e.g. Patarnello *et al.,* 2007), limiting the circulation between the eastern and western Mediterranean (Tintoré *et al.,* 1988). Indeed, different communities (e.g. zooplankton, sponges) were reported at both sides of this front (e.g. Youssara & Gaudy, 2001; Xavier & Soest, 2012). The Atlantic-Mediterranean connection is paramount as a pathway for the exchange of species and a potential geographic barrier separating different ecosystems (Skliris & Beckers, 2009; Coll *et al.,* 2010). However, few studies address the biological transport processes in the area (e.g. Bruno *et al.,* 2013, Catalán *et al.,* 2013). This is, partly, due to the lack of fundamental data on propagules amenable to be transported within Lagrangian transport models.

In this work, we tested the hypothesis that distribution patterns of decapod larval assemblages differ among potentially connected areas of the two basins during summer conditions, the seasonal peak of decapod larval abundance and diversity (e.g. Champalbert, 1996; González-Gordillo & Rodríguez, 2003). The study incorporates data from several cruises, conducted close in time at the Algarve, the Strait of Gibraltar and the Alboran Sea. The most relevant taxa, their abundances, and horizontal and vertical distribution were analysed for all areas in relation to potential factors that would explain the observed patterns. Multiple larval stages were considered to account for potential transport pathways.

Methods

Fieldwork and sample processing

Zooplankton samples were obtained for 59 sites in the northwestern Gulf of Cadiz (Algarve), during a survey between the Cape S. Vicente and the Guadiana estuary (Fig. 1a, b) during 2010 (early August). Bongo nets of 90 cm aperture (B090, 750 µm mesh) were used in all stations on double-oblique hauls to collect megalopae/decapodid stages. Hauls were conducted at two knots from surface to 10 m above bottom (200 m at deeper stations), integrating the entire water column. A Longhurst Hardy Plankton Recorder (LHPR, 280 µm mesh) was used at 16 stations to study the vertical distribution of decapod larvae. Oblique hauls from surface to near bottom (400 m at deeper stations), were performed at four knots, with the sample collection occurring during the descent (25 m depth intervals). Stations not sampled by the LHPR were sampled for early stages (zoeas) with Bongo nets of 60 cm diameter (BO60, 335 µm mesh). All nets were fitted with "General Oceanics" flowmeters. Vertical profiles of temperature (ºC), salinity and chl *a* (mg.m^{-3}) were conducted with a Seabird SBE 911p CTD fitted with a Chelsea Aqua Tracka III Fluorometer.

For the western Strait of Gibraltar, summer cruises were conducted in early May and August 2006, July 2009 and August 2011. Two sites were sampled in each of the 2006 cruises (two on the same location) and four in both the 2009 and 2011 cruises (Fig. 1a). Double-oblique zooplankton hauls were conducted at 2-2.5 knots using a 40 cm diameter Bongo net (200 µm mesh), equipped with "General Oceanics" flowmeters, to a maximum of 5 m depth above bottom (depth integrated).

For the Alboran Sea, mesozooplankton sampling was conducted at 28 sites off Malaga Bay during a late July 2008 summer cruise (Fig. 1a). A Hydro-Bios multinet (5 nets, 200 µm mesh) with a 50×50 cm aperture was used. Zooplankton was collected at 25 m depth intervals in oblique hauls from surface down to 100 m depth. Temperature (ºC), salinity and chl *a* (mg.L^{-1}) data were gathered with depth by a Seabird-25 CTD.

Plankton samples were preserved in 4%–5% borax-buffered formaldehyde. Biovolume was determined by the volume displacement method (Postel *et al.,* 2000). A Folsom splitter was used for samples with more than 400 decapod larvae. Decapod larvae were sorted, identified to species level, whenever possible, and their development stage analysed according to dos Santos & González-Gordillo (2004) and dos Santos & Lindley (2001).

Data analysis

The analyses had a two-way focus. For comparative purposes, presence-absence matrices were used to overcome the potential bias of using different nets. For within-cruise analyses, abundances were calculated considering the filtered water volume for each sampling site and used as individuals per 10 m^3 (Postel *et al.,* 2000). Biovolume values were transformed into biomass applying the Wiebe (1988) equations. The Alboran Sea multinet data were depth integrated to allow similar spatial distribution analyses with the Algarve BO60 data and some comparisons for presence/absence data. LHPR and multinet data were examined in 25 m depth intervals down to 100 m, the maximum depth of the Alboran Sea vertical data, to examine larval vertical distribution.

To characterize decapod larval assemblages, multivariate analyses were performed on the lowest taxonomic level identified in Table S1, using both abundance (log

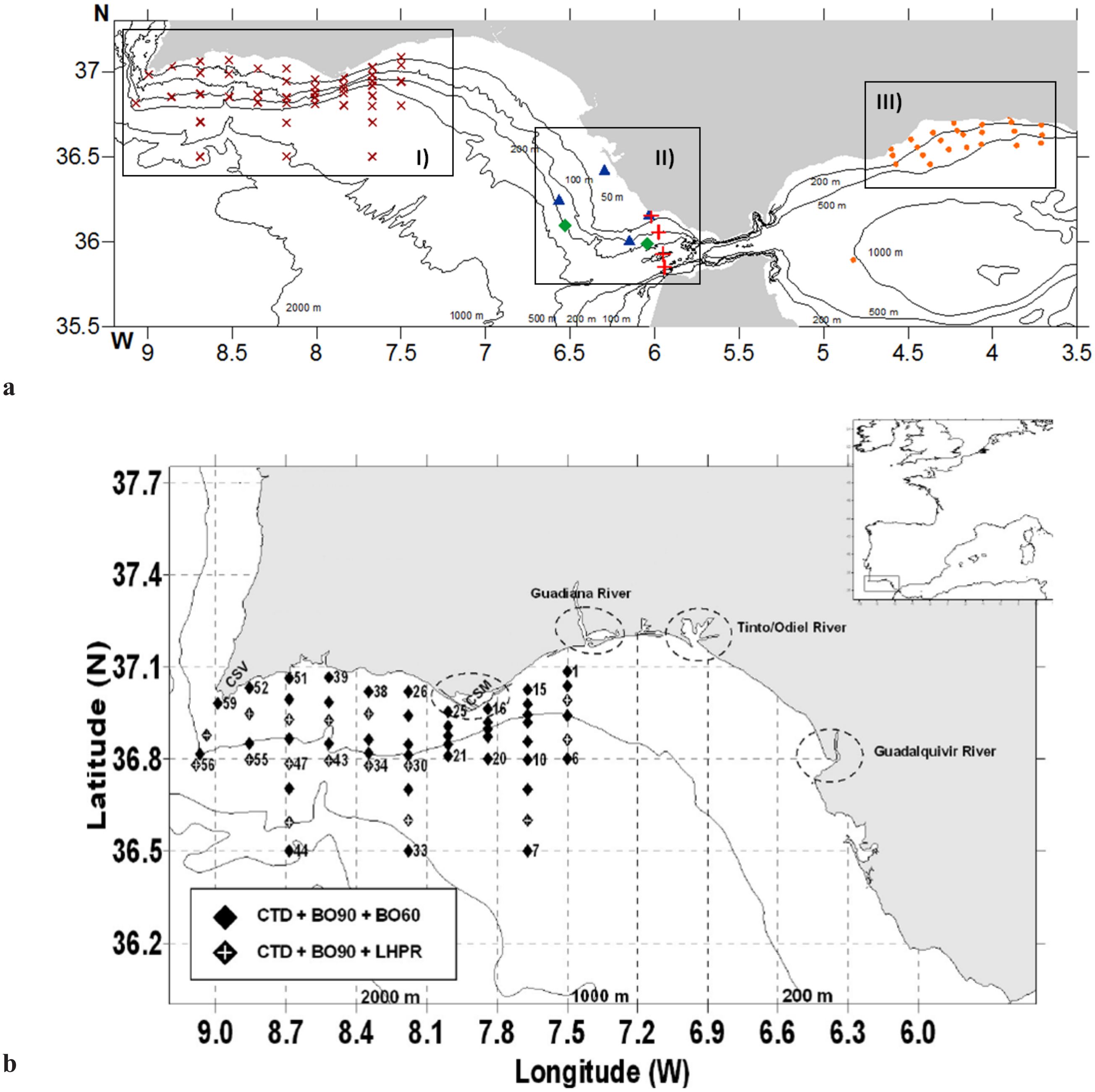

Fig. 1: Sampling locations and main coastal features. a) Gulf of Cadiz and Alboran Sea regions showing the sites covered in the sampling cruises: I) MedEx (x mark - Aug 2010); II) STOCA (triangle - August 2011, cross - July 2009) and GOLFO (diamond - May and August 2006); III) SESAME (filled circle - July 2008). b) Southwestern coast of Portugal detail (Algarve region; area I in Fig. 1a) showing the nets used in each sampling station (BO90: Bongo 90 cm; BO60: Bongo 60 cm - black diamond; LHPR: Longhurst Hardy Plankton Recorder - black diamond with white cross) and the main coastal features (CSV: Cape S. Vicente; CSM: Cape Sta. Maria) and river mouths.

[x+1] transformed) and presence/absence data. The first and last larval stages were extracted from the above dataset and analysed separately to assess potential distribution differences with impact on settlement. Permanova (Permutational multivariate analysis of variance) analyses were used to examine the origin of nearshore megalopae: outer shelf or innershelf areas. Rare taxa were not included in the analysis (less than 5% of total abundance) (Clarke & Warwick, 2001; Clarke & Gorley, 2006; Somerfield & Clarke, 2013). For inter-area comparisons, Algarve and Gibraltar offshore stations were also excluded. In community analyses, taxa were combined a priori according to: the number of stages in the larval cycle (not cycle duration) (C; C1 – short, C2 – medium, C3 – long, C4 – very long), adult habitats (H; H1 – intertidal, H2 – coastal, H3 – endobenthic, H4 – oceanic epibenthic, H5 – epipelagic, H6 – mesopelagic, H7 – cosmopolite), taxonomic group (T; T1 – shrimps, T2 – caridean shrimps, T3 – hermit crabs, T4 – ghost shrimps, T5 – slipper lobsters, T6 – squat lobsters, T7 - crabs), larval cycle vs. adult habitats (C×H), larval cycle vs. taxonomic group (C×T), taxonomic group vs. adult habitats (T×H) and larval cycle vs. adult habitats vs. taxonomic group (C×H×T). Non-parametric ANOVA Kruskal-Wallis (K-W) and correlation (Pearson) analyses were used to test the effect of the distance from coast and site depth. To explore within-area oceanographic relationships between the environmental conditions of the samples (temperature, salinity and chl *a*) and global properties (diversity and distinctness), a Principal Component Analysis (PCA) was performed on transformed (log[x+1] and 10^x-1) and normalised data, including the effects of the distance from coast and site depth. BIO-ENV analyses (Clarke & Ainsworth, 1993) were used to ascertain the correlation between individual environmental factors and biological communities (presence/absence data).

Non-metric multidimensional scaling (NMDS) analyses were conducted on the Bray-Curtis similarity matrices and applied to explore the structural similarity among samples for each location (Algarve, Gibraltar and Alboran Sea). Clustering (UPGMA) tests were combined with the NMDS to study the mutual consistency of the analyses. The effect of each factor (station depth, distance to coast) was examined through Permanova analyses and, when significant, pair-wise tests were used to identify differences in their interaction. The dissimilarity percentage routine (SIMPER, Warwick *et al.,* 1990) was used to identify the species that explain the differences and similarities between samples of a given location. Biodiversity measures - Shannon diversity index (H') and taxonomic distinctness (delta*) - were calculated, and their relationship with depth and distance from coast examined in PCA analyses.

Results

Oceanographic conditions during the surveys

Upwelling-favourable winds occurred before and during the Algarve survey, with a wind relaxation to easterlies right before the cruise started (see Pires *et al.,* 2013 for details on the physical data). Northerlies enhanced the upwelling at Cape S. Vicente and the jet recirculation into the northwestern Gulf of Cadiz. Upwelled waters at Cape S. Vicente had a distinct cold signature, detectable in the first 50 m, extending to the east (Fig. S2a). Salinity values above 36 were found horizontally and vertically in the Algarve coast (Fig. S2b), except near the Guadiana River plume that registered low values down to 10 m depth (Fig. S2b) and at 300 m due to the intrusion of upwelling waters close to the Cape S. Vicente (Fig. S2b). Chl *a* values were higher near the Cape S. Vicente down to 10 m depth (Fig. S2c), extending to the east at 25 and 50 m depth (Fig. S2c). No significant correlations were found between the sampling site depth or distance from the coast and the environmental factors (Fig. 2a and Table S2a). However, the nearshore sites (< 10 km) were characterized by low temperatures and salinity (Fig. 2a).

Predominant easterly winds changed to westerlies (upwelling favourable) just before the Alboran Sea survey and were maintained throughout it (see Macías *et al.,* 2011 for details on the physical data). A coastal upwelling of cooler waters was evident at the end of the survey. Surface temperature values were around 25ºC in the nearshore Alboran Sea sites, decreasing with depth and distance from coast (Fig. S3a). Surface salinity values were around 36, significantly increasing with depth as the more saline Mediterranean outflow waters were sampled (Fig. S3b). High chl *a* values were registered at 50 m depth and nearshore (Fig. S3c). No significant relationship was found between sampling site depth, distance from coast and environmental factors (Fig. 2b, Table S2b).

Zooplankton biomass and decapod larvae spatial abundance

Average zooplankton biomass values of 25.2 ± 30 mg C.m^{-3}., 36.9 ± 33.1 mg C.m^{-3} and 38.5 ± 22.4 mg C.m^{-3} were registered for Algarve, Gibraltar and Alboran Sea, respectively. Nearshore sites were the most productive (Fig. S4a - c) (K-W H=15.1, $p < 0.01$). In the Algarve, this was more evident near Cape S. Vicente and in areas under the influence of the Guadiana plume (Fig. S4a). In Gibraltar, the high nearshore values (Fig. S4b) were non-significant in the statistical analyses. In the Alboran Sea, some deeper sites also showed high biomass values (Fig. S4c). Shannon diversity (H') and taxonomic distinctness (delta*) indices were highly correlated in the PCA analyses and, thus, only the former was represented (Fig. 2). The innershelf sites of Algarve and Alboran Sea (< 10 km) were the most diverse (Fig. 2, Table S2).

Decapod larval abundances were on average of 14.3 ± 25.1, 36.4 ± 51.7 and 7.7 ± 18.7 ind.m^{-3} for Algarve, Gibraltar and Alboran Sea, respectively. Zoeal stages were mainly concentrated in nearshore sites, decreasing in abundance towards deeper sites (Figs. S5a, c, e) (depth tests were significant for Algarve; K-W H=16, $p < 0.01$). Higher similarity of decapod larval abundance was evident between the Algarve and Gibraltar samples, as well as a separation from the Alboran Sea (67.78% and 60.24% average dissimilarity from Algarve and Gibraltar, respectively) (Fig. 3). Distance from coast and depth, when individually considered, explained the NMDS groups in the Algarve area (permanova $p < 0.01$ in both cases). Considering the within-basin variability, sampling site depth contributed to most of the observed differences in the Alboran Sea (permanova $p = 0.02$).

Total abundances of first (ZI) and last (megalopae/decapodids) larval stages significantly decreased towards offshore in the Algarve (K-W H value from 11.6 to 18.2,

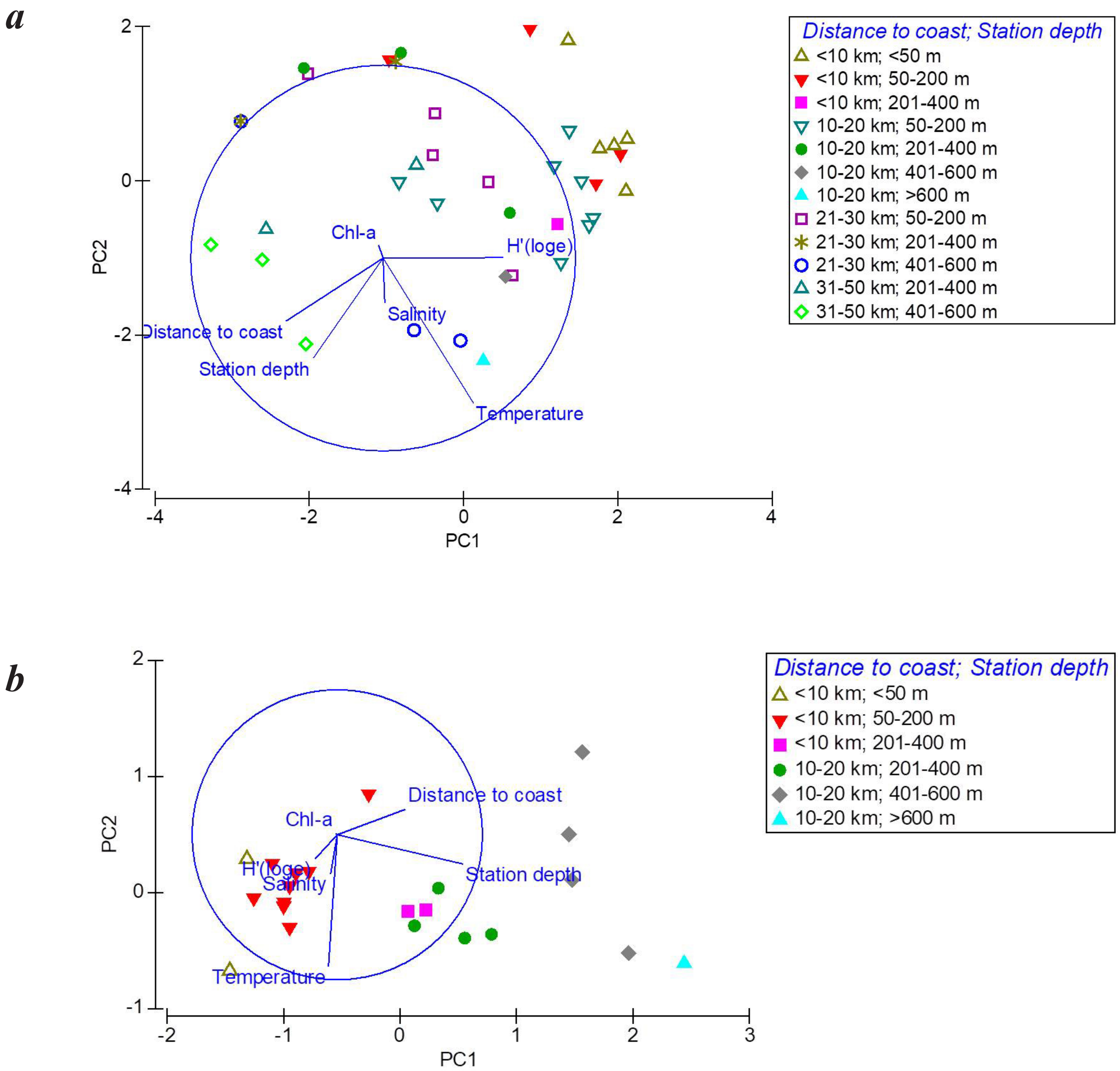

Fig. 2: Principal Component Analysis results presenting the main components that explain sample variability for the measured environmental factors, biomass and biodiversity indices (H'($\log_e$) - Shannon diversity) in each studied area: a) Algarve, b) Alboran Sea.

$p < 0.01$ in all cases) (Figs. S5a, b). For the Alboran Sea samples (Figs. S5e, f), this relationship was only significant for ZI larvae (K-W H = 11.6, $p < 0.01$), which registered low abundances (Fig. S5e). No relationship between these factors was observed in Gibraltar, with almost all sites registering high abundances (Figs. S5c, d). Permanova results for presence/absence comparisons between the three sampled areas, showed different ZI and megalopae assemblages occurring inshore (< 10 km) and offshore ($p < 0.01$ for all cases) (see also results below). High abundances were related with low salinities for the last larval stages in Algarve and with high salinities for both ZI and last stage larvae in the Alboran Sea ($r \geq 0.4$, $p \leq 0.04$ in all cases). High abundances of ZI and last stages were also related with high diversity in the Algarve and Alboran Sea sites ($r \geq 0.5$, $p < 0.01$ in all cases), and with high chl *a* in the Alboran Sea ($r \geq 0.5$, $p \leq 0.02$ in all cases).

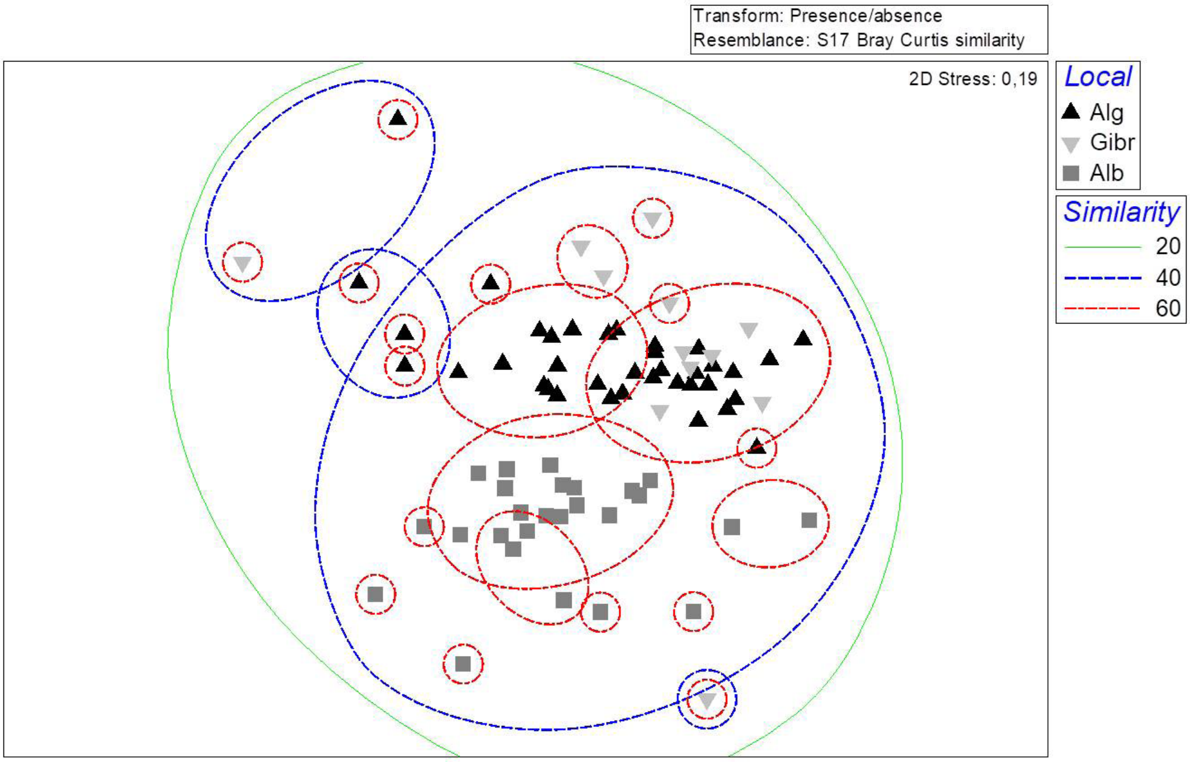

Fig. 3: Non-metric multidimensional scaling (NMDS) based on the Bray-Curtis similarity index between sampling sites of each location (Alg - Algarve, Gibr - Gibraltar, Alb – Alboran Sea) considering presence/absence data. The respective cluster similarity contours (bubbles) at 20%, 40% and 60% similarity are also presented.

Composition and distribution of decapod larvae assemblages

From the 176 total decapod taxa found (~87000 larvae), 98 were identified to the species level, 45 to the genus and the remaining to the sub-family or family (Table S1). The main pool of Gibraltar larvae was captured in 2009 and 2011 (~19000 larvae against ~1500 in 2006).

High biodiversity (K-W H = 7.2, p = 0.03) and taxonomic distinctness (K-W H = 22.7, p < 0.01) were found in Gibraltar and in the Alboran Sea (Fig. 4). The Shannon biodiversity index was negatively correlated with the distance to coast in the first 10 km of Algarve and Alboran Sea shelves (K-W H between 12.8 and 17.1, p < 0.01 in all cases). The taxonomic distinctness was also negatively related with the distance to coast in Algarve (K-W H = 8.8, p = 0.03).

Gebiidea larvae comprised more than 50% of the total average abundance of decapod zoeal stages in the Atlantic samples, followed by the Anomura larvae (~20% in both areas) (Table S1). Gebiidea was also the most abundant infraorder in the Alboran Sea (~30%), with the Axiidea and Dendrobranchiata larvae being also highly important (~20% and 15%, respectively).

Caridean shrimps, crabs, hermit crabs and ghost shrimps were common, but differently shelf-distributed in each area. Ghost shrimps were highly abundant in the nearshore Alboran Sea region, contrasting with a more offshore occurrence in the Atlantic sites (Table 1). *Upogebia* spp. and *Callianassa truncata* were the most abundant of this group in the Atlantic and the Alboran Sea sites, respectively (Table 2). Mesopelagic shrimps with a high number of larval stages, mainly *Gennadas elegans*, were highly relevant in the nearshore Alboran Sea analyses (Table 2; K-W H = 4.5, p = 0.05) and the main responsible for the differences between sites related to the adult habitat preferences (Table 3). Caridean shrimps, mainly oceanic epibenthic in Algarve, occupied nearshore regions; *Processa* spp. was the most abundant taxa (Tables 1-3). However, in the Alboran Sea most caridean larvae were cosmopolite, mainly *Alpheus glaber* (Tables 1, 2). The Algarve sites, between 10 and 50 km from the coast, registered important abundances of intertidal taxa (Table 1). *Pachygrapsus* spp. was the most represented in this case (Table 3).

ZI abundance followed the above results (Table S1). Gebiidea and Anomura dominated the Atlantic areas, while Gebiidea and Axiidea dominated the northern Alboran Sea. Dendrobranchiata larvae were less than 1% of total Atlantic decapods and 5% in the Alboran Sea. Intertidal/coastal crabs with long/medium larval cycles and endobenthic ghost shrimps (*Pachygrapsus* spp., *Goneplax rhomboides* and *Upogebia deltaura*) were highly abundant in the first 30 km of the Algarve shelf, while

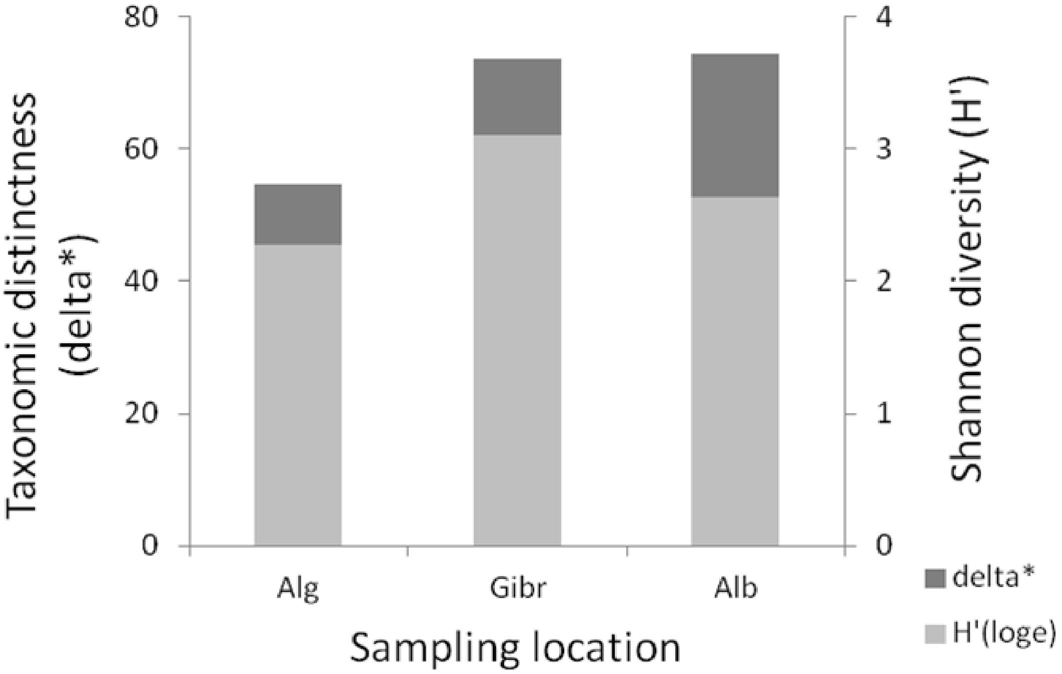

Fig. 4: Biodiversity measures by sampling location (Alg - Algarve, Gibr - Gibraltar, Alb – Alboran Sea) for abundance data: Shannon biodiversity [$H'(\log_e)$] and taxonomic distinctness (delta*) indices.

Table 1. SIMPER results summary (Contrib% - contribution percentage) for the most abundant taxa contributing to the similarities between samples within each sampling area across all distance to coast groups. Taxa were grouped (average abundance) according to the combination of factors: number of stages in the larval cycle (C2 - medium, C3 - long), adult habitats (H1 - intertidal, H3 - endobenthic, H4 - oceanic epibenthic, H7 - Cosmopolite) and taxonomic group (T1 - Shrimps, T2 - Caridean shrimps, T3 - Hermit crabs, T4 - Ghost shrimps, T7 - Crabs).

	Algarve		**Gibraltar**		**Alboran Sea**	
	Taxa	Contrib%	Taxa	Contrib%	Taxa	Contrib%
Group < 10 km	(Average similarity: 35.92%)		(Average similarity: 22.40%)		(Average similarity: 31.37%)	
	C3 x T2 x H4	18.79	C3 x T2 x H4	23.1	C3 x T2 x H4	15.16
	C2 x T7 x H7	14.36	C2 x T3 x H1	11.76	C3 x T2 x H7	14.14
	C3 x T7 x H1	11.27	C2 x T7 x H7	11.18	C2 x T7 x H7	11.6
	C2 x T3 x H7	11.03	-	-	C2 x T3 x H7	10.65
Group 10-20 km	(Average similarity: 26.34%)		(Average similarity: 8.55%)		(Average similarity: 34.92%)	
	C3 x T7 x H1	17.81	C3 x T1 x H4	100	C3 x T2 x H7	20.26
	C3 x T1 x H4	16.1	-	-	C2 x T4 X H3	13.17
	C3 x T2 x H4	14.66	-	-	C2 x T3 x H1	11.63
	-	-	-	-	C2 x T7 x H7	9.87
Group 21-30 km	(Average similarity: 18.90%)		(Average similarity: 3.03%)		-	-
	C3 x T7 x H1	32.5	C3 x T1 x H4	100	-	-
	C3 x T1 x H4	18.26	-	-	-	-
Group 31-50 km	(Average similarity: 58.47%)		(Average similarity: 6.20%)		-	-
	C3 x T7 x H1	27.37	C3 x T2 x H4	42.99	-	-
	C2 x T7 x H7	22.17	C2 x T7 x H7	20.1	-	-

Table 2. SIMPER results summary (Contrib% - contribution percentage) presenting the most abundant taxa contributing to the similarities between samples within each sampling area across all groups of distance to coast and sampling site depth.

Taxa	Contrib%
Group Algarve (Average similarity: 50.47%)	
Upogebia pusilla	9.65
Liocarcinus spp.	8.95
Processa spp.	7.83
Diogenes pugilator	7.55
Upogebia deltaura	6.32
Alpheus glaber	4.78
Athanas nitescens	4.07
Eualus cranchii	3.67
Group Gibraltar (Average similarity: 33.24%)	
Pagurus spp.	7.87
Alpheus glaber	6.98
Liocarcinus spp.	6.42
Lysmata spp.	5.99
Processa spp.	5.48
Upogebia deltaura	5.45
Eualus occultus	4.96
Galathea dispersa	4.63
Diogenes pugilator	3.7
Group Alboran (Average similarity: 41.69%)	
Gennadas elegans	22.86
Callianassa truncata	8.86
Eusergestes arcticus	8.08
Alpheus glaber	7.38
Goneplax rhomboides	6.79

mainly cosmopolite hermit crabs (*Pagurus* spp.) occurred in the same shelf region of Gibraltar (Table S3). The Alboran Sea shelf was characterized by the occurrence of endobenthic ghost shrimps (*Callianassa truncata*) in the first 10 km, and mesopelagic shrimps with long cycles (*Gennadas elegans*) between 10 and 20 km (Table S3).

In Gibraltar and in the Alboran Sea, megalopae/decapodid stages were mainly Anomura and Brachyura (45% and 25% of total average abundance, respectively) (Table S1), and Gebiidea and Anomura (30% each) in the Algarve. Cosmopolite crabs with medium larval cycles occurred throughout the entire shelf of all areas (Table S3). The first 20 km of the Algarve shelf, and a large part of the Gibraltar samples, were characterised by the presence of intertidal hermit crabs (Table S3). In the Alboran Sea area, meso- and epipelagic shrimps with long cycles were also abundant between 10-20 km from coast (*Eusergestes arcticus* and *Sergestes* spp.) (Table S3).

Vertical distribution

Vertical data revealed a higher productivity in Algarve with respect to the Alboran Sea (K-W H = 68.29, df = 1, $p < 0.01$), but without significant differences related to depth in Algarve (Fig. S6). Conversely, the first 25 m of the Alboran Sea water column registered the highest biomass values in that area (Fig. S6), separated statistically from the deeper layers (K-W H = 54.6, $p < 0.01$). In Algarve, higher depths corresponded to low temperatures and low salinities (BIO-ENV correlation of 0.294 for temperature x depth x distance to coast and of 0.292 for temperature x salinity x depth x distance to coast). In the Alboran Sea, low temperatures and high salinities were not significantly correlated with depth in the statistic results.

The abundance of zoeal and ZI stages decreased with depth in the Algarve and Alboran Sea (K-W H = 9.1 and 40.8, respectively; $p \leq 0.03$ and df = 3 in all cases). The same relationship was found for last larval stages in the Alboran Sea (K-W H = 23.98, $p < 0.01$, df = 3), mainly distributed at surface waters (0-25 m). The biodiversity decrease with depth was only significant for the Alboran Sea (K-W H = 40.3, $p < 0.01$).

The C×H×T combined analysis showed that taxa with long larval cycles dominated the Algarve water column - intertidal crabs in the first 50 m depth (*Pachygrapsus* spp., 16.74-19.36% within-similarity), epipelagic shrimps between 50-75 m depth (*Solenocera membranacea*, 16.75% similarity) and mesopelagic shrimps between 75-100 m (*Sergia robusta*, 12.19% similarity) (Table S4).

Mesopelagic shrimps with long cycles (*Gennadas elegans*) were also important below 50 m in the Alboran Sea shelf (within-depth similarity of 23.23% in the first 25 m to 65.54% between 75-100 m) (Table S4). Taxa occurring in the first 50 m depth were distributed at 10-20 km from the coast, while below this depth, taxa were mainly distributed at more than 20 km from coast (Fig. S7). The first 25 m of the Alboran Sea water column were clearly different in the analysis, showing the concentration of most of the taxa and a high abundance of Dendrobranchiata shrimps (Figs. S6, S7 and Table S4). In the Algarve shelf, shrimp larvae (Dendrobranchiata) were increasingly more abundant with depth (non-significant), with the first 75 m being dominated by ghost shrimp larvae (Fig. S7). The Algarve abundance of coastal crabs with medium size cycles, cosmopolite caridean shrimps and intertidal crabs with long larval cycles was correlated with depth, decreasing towards deeper layers (K-W H = 10.5-13.9, $p \leq 0.01$ in all cases). The main taxa also decreased with depth in the Alboran Sea (Fig. S7).

Discussion

Productivity and abundance

Important environmental and oceanographic differences between the Algarve/Gulf of Cadiz and the Alboran

Table 3. Summary of SIMPER percentages (Contrib% - contribution percentage) presenting the most abundant taxa contributing to the similarities between samples according to each combination of factors (number of stages in the larval cycle, habitat and taxonomic group) and sampling area (Alg - Algarve, Gibr - Gibraltar, Alb – Alboran Sea) (e.g. in the Algarve area, 83.70% of all intertidal hermit crab larvae with medium cycles were *Diogenes pugilator*).

Habitat	Larval cycle	Taxonomic group	Most important taxa		Contr%	
				Alg	Gibr	Alb
Intertidal	Medium	Hermit crabs	*Diogenes pugilator*	83.70	99.18	68.84
		Crabs	*Eriphia verrucosa*	100	-	-
			Carcinus aestuarii	-	-	100
	Long	Caridean shrimps	*Lysmata* spp.	39.77	78.62	29.22
			Processa edulis edulis	23.07	20.32	70.51
		Crabs	*Pachygrapsus* spp.	100	100	100
Coastal	Short	Crabs	*Pisidia longicornis*	95.93	73.88	48.87
	Medium	Caridean shrimps	*Philocheras bispinosus bipinosus*	75.15	-	99.06
			Philocheras bispinosus neglectus	21	51.31	-
		Hermit crabs	*Dardanus arrosor*	-	100	100
		Squat lobsters	*Galathea dispersa*	69.73	83.90	-
			Galathea spp.	-	-	100
		Crabs	*Goneplax rhomboides*	43.13	26.53	68.27
			Xantho spp.	37.54	41.40	15.78
	Long	Shrimps	*Melicertus kerathurus*	100	100	-
		Caridean shrimps	*Athanas nitescens*	20.28	11.68	12.79
			Eualus occultus	5.69	26.02	16.11
			Processa nouveli nouveli	16.14	9.52	39.28
	Very long	Slipper lobsters	*Scyllarus* spp.	100	100	-
Endobenthic	Medium	Ghost shrimps	*Upogebia pusilla*	72.53	47.69	15.13
			Upogebia deltaura	26.01	51.31	-
			Callianassa truncata	-	-	75.40
Oceanic epibenthic	Medium	Caridean shrimps	*Philocheras* spp.	99.98	65.69	100
		Crabs	*Ebalia tumefacta*	59.09	41.81	26.87
			Calappa granulata	35.14	41.81	70.47
	Long	Shrimps	*Solenocera membranacea*	96.49	74.65	98.92
		Caridean shrimps	*Processa* spp.	100	100	100
Epipelagic	Long	Shrimps	*Deosergestes corniculum*	60.09	-	100
Mesopelagic	Long	Shrimps	*Gennadas elegans*	72.26	-	63.42
Cosmopolite	Medium	Caridean shrimps	*Aegaeon* spp.	59.64	100	100
		Hermit crabs	*Pagurus* spp.	72.78	81.26	45.14
			Anapagurus spp.	27.22	18.74	54.86
		Crabs	*Liocarcinus* spp.	84.99	81.23	80.41
	Long	Caridean shrimps	*Alpheus glaber*	91.83	96.28	93.23

Sea basins, forced by the Strait of Gibraltar, have ecological impacts on the zooplankton communities. The nearshore region of both basins appears in the present study as highly productive and biologically/taxonomically diverse. The similar biomass and chl *a* values, spatially and vertically, in the Algarve area suggest high water mixing, probably related to the relatively wide shelf and the complex hydrodynamics, including upwelling areas. Shelves at the northern Alboran Sea and to west of Cape Sta. Maria are narrow (~5 and 25 km, respectively), while the

Gulf of Cadiz shelf is wider (~40 km) (Reul *et al.,* 2006). Moreover, higher oceanic exposition is expected between the Cape S. Vicente and the Guadiana River than in the north-eastern Gulf of Cadiz shelf (Prieto *et al.,* 2009).

Diminished freshwater inputs between Cape S. Vicente and Cape Sta. Maria, as well as in the Alboran Sea, contrast with the large fluvial discharge at the Gulf of Cadiz (Ruiz et al., 2006; Prieto et al., 2009; Vargas-Yañez et al., 2009). Lower salinity values enhance productivity, providing good conditions for the development of plankton. In fact, areas near river plumes and under upwelling influence are considered the most productive ones in the Gulf of Cadiz (Echevarria et al., 2009). In the north-eastern part of the Gulf, the fluvial input and seasonal water temperature variability are the main factors influencing the productivity (Prieto et al., 2009). Despite the different sampling methods, similar zooplankton biomass values to those reported here were found by Greze et al., (1985) for the western Strait of Gibraltar (30 mg.m-3), and several authors also reported high chl a values (e.g. Echevarria et al., 2009; Macías et al., 2009). Thus, the oceanographic and shelf features of the Gulf of Cadiz, responsible for a nearshore retention zone (e.g. Pires et al., 2013), contribute to the high productivity of this important fishery area (Reul *et al*., 2006).

The high Gibraltar zooplankton biomass and decapod abundance may reflect a larval accumulation due to the complex oceanography that drives the confluence of different nearshore currents entering the Mediterranean (Greze *et al.,* 1985). Here, the currents recirculating towards the northwestern Gulf of Cadiz coast without entering the Mediterranean may also play an important role (García-Merchán *et al.,* 2012).

The characteristic anticyclonic gyre circulation in the Alboran Sea creates a nearshore barrier, allowing the Atlantic jet to spread along the northern Alboran Sea coast (Sánchez-Arcilla & Simpson 2002; Echevarria *et al.,* 2009). This results in one of the most biologically diverse, productive and nutrient-rich Mediterranean areas, along the southern Spanish coast (Greze *et al.,* 1985; Sarhan *et al.,* 2000; Skliris & Beckers, 2009), as the biomass values presently reported suggest. Despite the different sampling methods, the biomass values match the ones reported in Camiñas (1981, 1983) for neritic waters of the Alboran Sea (Champalbert, 1996). Retention processes induced by Atlantic waters and the constricted oceanographic circulation, limiting the productivity to a nearshore area, result in more oligotrophic conditions at south of the gyres (Vargas-Yañez *et al.,* 2009).

In the western Alboran Sea, a direct association between chl *a* concentration and zooplankton abundances was previously found (Vives *et al.,* 1975; Youssara & Gaudy, 2001). Moreover, the narrow Alboran Sea shelf and the constricted inshore oceanographic circulation lessen the cross-shore movements, due to the interplay of both nearshore and slope processes (García-Merchán *et al.,* 2012). The nearshore communities of the Alboran Sea are, therefore, spatially and vertically constricted when compared with the Atlantic sites, given the offshore influence in the innershelf. The occurrence of different water masses - resident Atlantic water (Mediterranean) interacting with new Atlantic water - also affects the coastal circulation, enhancing the biological diversity in the area. Thus, results suggest that the zooplankton is most affected by nearshore events and coast proximity in the distinct Alboran Sea surface strata (first 25 m depth). The water column stratification and the frequency of its occurrence are especially important in layers exposed to slope processes (García-Merchán *et al.,* 2012), considering that it can impact zooplankton distribution.

Upwelling events were favoured by westerly winds during the survey and are enhanced by the southward displacement of the Atlantic Jet. These conditions are common and increase the Alboran Sea basin productivity, and the summer nutrient redistribution (Pérez-Folgado *et al.,* 2003; Vargas-Yañez & Sabatés, 2007). Nutrient input from deeper layers contributed to the high abundance/high salinity correspondence found. In the northern Alboran Sea shelf, organisms are probably better adapted to higher temperatures, comparatively with Algarve, where deeper waters support higher zooplankton biomass. In fact, local oceanographic features are much more limiting to the distribution of species than temperature (Gaudy *et al.,* 2000). Moreover, in summer conditions, easterlies in the Alboran Sea can disrupt the westerlies dominance, increasing plankton abundance nearshore (Vargas-Yañez *et al.,* 2009) and reducing the Atlantic water entrance in the Alboran Sea (Echevarria *et al.,* 2009, Skliris & Beckers 2009). Therefore, easterly winds registered before the survey may have partly induced the high nearshore abundances observed.

ZI larvae are often associated with the adult habitats (e.g. Landeira *et al.,* 2009). Thus, the high nearshore and surface abundances found reflect the coastal taxa occurring in each area and the points close to their larval emission (e.g. Pires *et al.,* 2013). The same scenario was observed for last larval stages that need to settle in proper areas, meaning maintenance or return to coastal areas for intertidal/coastal larvae. The low ZI abundance in the Alboran Sea is probably merely reflecting the different sampling or larval emission periods. The different sampling methods employed can, indeed, overestimate the Alboran Sea productivity when comparing abundance values. Works as Stehle *et al.,* (2007) and Skjoldal *et al.,* (2013) should be considered in what concerns net efficiency and the bias it can introduce in our observations. However, following these works, we concluded that comparable mesh sizes, as it was the case, may provide similar zooplankton estimations even when employing different net types.

Spatial and vertical variability of decapod communities

Similar taxa were collected in both basins. However, the different hydrological conditions of each area produced different communities, probably as a combination of local physical conditions and taxa adaptations to optimize survival (e.g. Patarnello *et al.,* 2007).

Previous studies report the large Gulf of Cadiz shelf and the entrapment of alongshore currents by the gyres as generators of a retention zone parallel to coast, wider in the north-eastern shelf (e.g. dos Santos & Peliz 2005; Pires *et al.,* 2013). For cosmopolite taxa with medium size larval cycle, the large Gulf of Cadiz shelf suggests a lower dispersal risk (but see Catalán *et al*., 2006), and a higher probability of returning and recruiting to the adult habitats. This is especially true considering the high influence of offshore currents in the Alboran Sea shelf and the common summer upwelling regime. The same idea arises if we consider the important abundance of intertidal taxa with long cycles in the Algarve shelf, shelf-developing larvae that return later to the adult habitats as megalopae (e.g. Flores *et al.,* 2002). In this case, the observed upwelling regime may have contributed to the offshore dispersal. Coastal taxa (important in the Atlantic sites) need to ensure a retention close to the adult habitats, strongly limiting the dispersal range they can withstand. These factors explain the low taxonomic distinctness found farther from the coast.

Despite the different methods employed, the diversity registered in the Alboran Sea was higher than in other Mediterranean areas (Brucet *et al.,* 2006; Badosa *et al.,* 2007), confirming the complex oceanography in the area and its high productivity. The observation of the high faunistic richness of the Alboran Sea is not new, as Giron (1963) had already pointed the shelf characteristics and the Atlantic influence as potential drivers of this diversity. The specific conditions of this basin and the Atlantic-Mediterranean physical separation, throughout geological time, may have contributed to the accumulation of differences between taxa (e.g. Patarnello *et al.,* 2007). The Alboran Sea basin acts as a transition zone, separating truly Atlantic and Mediterranean species, and supporting a mixture of species from both basins (Abelló *et al.,* 2002), which results in highly diverse communities. The same may occur in the Strait of Gibraltar that functions as a pathway between both areas.

As in other Mediterranean Spanish waters (Fusté, 1987; Torres *et al.,* 2014), mesopelagic shrimps with long life cycles constitute an important part of the Alboran Sea innershelf decapod communities. The high influence of deep-water currents on nutrient redistribution in the basin and the retentive mesoscale structures, trapping long-lived early stages, can explain this pattern (González-Gordillo & Rodríguez, 2003). Dendrobranchiata larvae were registered as highly abundant in the Balearic Sea (Torres *et al.,* 2014) and other Mediterranean locations (Franqueville, 1971), and *Gennadas elegans* were closely associated with highly energetic areas (Torres *et al.,* 2014). Pelagic species are generally distributed according to the hydrodynamic patterns of a certain area increasing in abundance towards offshore waters (e.g. Landeira *et al.,* 2009). Narrow and shallow continental shelves, together with pronounced slopes, usually promote nearshore larval retention, given the local acceleration of the alongshore currents and the reduced cross-shore transport (e.g. Sánchez-Arcilla & Simpson, 2002). In the northern Alboran Sea, larvae are influenced by a similar current confinement limited by the slope gyres (e.g. Catalán *et al.,* 2013). The alongshore spread of the Atlantic Jet exposes the planktonic communities of the Alboran Sea to high oceanographic variability (Echevarria *et al.,* 2009; Vargas-Yañez *et al.,* 2009) that, together with the offshore influence, would result in a mixture of coastal and pelagic taxa (e.g. Sabatés, 1990). The easterly winds influencing the Alboran Sea shelf before the survey, enhancing a coastal counter-current to the north of the Western Atlantic Gyre, would also promote some nearshore retention of the species. The enhanced importance of Algarve's Dendrobranchiata shrimps below 75 m depth, illustrates the contrasting characteristics relatively to the northern Alboran Sea, with the influence of deep-water currents mainly manifested in the outer shelf.

The low occurrence of *Callianassa* species (Axiidea) in Algarve may be related with their preference for higher intertidal levels than *Upogebia* spp. (Gebiidea) (Thompson & Pritchard, 1969; Pérez, 1995). In agreement, their abundance was relatively large in the coastal areas of the north Alboran Sea. Also for Caridean shrimps, the importance of shelf availability on the settlement of Atlantic larvae was evident in the contrasting abundance of epibenthic (Atlantic sites) and cosmopolite (Alboran Sea) larvae, whose dispersal may be less impacted by the strong ocean dynamics. In both Gebiidea/Axiidea and Caridea cases, the lack of knowledge about the possible different rhythms of larval emission or slightly delayed spawning times can bias our observations. The same applies to the potential effect of interannual abundance variability, which could be large and depends both on physical and/or biological variations that regulate emission patterns (Paula, 1993).

The first and last larval stages, being mostly coastal benthic taxa in both basins, reproduce and settle nearshore. The importance of intertidal crabs in Algarve was evident in the ZI abundance, shelf-developing larvae that return as megalopae benefiting from a long larval cycle. However, whether this pattern was the result of a megalopae return or a selective survival nearshore could not be proved. As observed in other Iberian areas (e.g. dos Santos *et al.,* 2008; Torres *et al.,* 2014), crabs were a dominant group and megalopae of cosmopolite crabs were highly captured. The relatively wide shelf may account for the high capture of these megalopae in Algarve, implying available settlement grounds. Also, the high abundance of mesopelagic taxa beyond the 10 km nearshore area of the Alboran Sea, confirms the offshore influence in larval communities. Pelagic taxa conduct wide-range vertical migrations, and the larvae tend to occupy shallower waters than the adults (Pérez, 1995). In contrast, the first 10 km of the Alboran Sea shelf manifest once more the importance of nearshore processes, according to the dominant taxa found (endobenthic ghost shrimps).

Similarities (e.g. Madin, 1991; Champalbert, 1996; Xavier & Soest, 2012; Zaafa *et al.,* 2014) and differences (e.g. Triantafyllidis *et al.,* 2005) have been reported between Atlantic and Mediterranean communities for zooplankton and decapods. Gibraltar surface waters are, indeed, considered a favourable highway for the crossing of Atlantic species (e.g. Greze *et al.*, 1985). Furthermore, taxa composition resemblances between Torres *et al.,* (2014) work for the Balearic Islands and our own data suggest that the Atlantic influence may extend even further (e.g. García-Merchán *et al.,* 2012). The present results open the possibility of a two-way taxa connectivity between the Gulf of Cadiz and Alboran Sea basins, especially considering that species registered only in the Mediterranean as adults, are also present in the Gulf of Cadiz in the present study (e.g. *Processa* species). Thus, the study agrees with the hypothesis of Bouchet & Taviani (1992), who proposed the Strait as a weaker biological barrier compared to the hydrological/hydrodynamic conditions that organisms encounter in each basin. However, the inherent seasonal variability of decapod larvae release, related with food availability and local ocean conditions, can result in distinct peaks of emission for each area. Thus, larvae of the same species could have been captured at different stages of dispersal. The interannual abundance variability of species would also impact the patterns found. We therefore acknowledge the need of future inter-comparisons that consider those sources of variability. Understanding species movements in a system like the Atlantic-Mediterranean is of paramount importance for the management of over-exploited populations and to understand how future changes in the hydrographic features can affect the biological communities (Fogarty & Botsford, 2007; Cowen *et al.,* 2007). Given the large sampling area covered and the volume of data presented, the present work sets the stage for future studies that should incorporate the interannual and seasonal variability within this complex system.

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References

Abelló, P., Carbonell, A., Torres, P., 2002. Biogeography of epibenthic crustaceans on the shelf and upper slope off the Iberian Peninsula Mediterranean coasts: implications for the establishment of natural management areas. *Scientia Marina*, 66 (S2), 183-198.

Alvarez, I., Catalán, I.A., Jordi, A., Alemany, F., Basterretxea, G., 2015. Interaction between spawning habitat and coastally steered circulation regulate larval fish retention in a large shallow temperate bay. *Estuarine Coastal and Shelf Science*, 167 (B), 377-389.

Badosa, A., Boix, D., Brucet, S., López-Flores, R., Gascón, S. *et al.,* 2007. Zooplankton taxonomic and size diversity in Mediterranean coastal lagoons (NE Iberian Peninsula): Influence of hydrology, nutrient composition, food resource availability and predation. *Estuarine Coastal and Shelf Science*, 71, 335-346.

Bouchet, P., Taviani, M., 1992. The Mediterranean deep-sea fauna: pseudopopulations of Atlantic species? *Deep-Sea Research*, 39 (2), 169-184.

Brucet, S., Boix, D., López-Flores, R., Badosa, A., Quintana, X.D., 2006. Size and species diversity of zooplankton communities in fluctuating Mediterranean salt marshes. *Estuarine Coastal and Shelf Science*, 67, 424-432.

Bruno, M., Chioua, J., Romero, J., Vázquez, A., Macías, D. *et al.,* 2013. The importance of sub-mesoscale processes for the exchange of properties through the Strait of Gibraltar. *Progress in Oceanography*, 116, 66-79.

Camiñas, J.A., 1981. Distribution spatiale et temporelle de la biomasse zooplanctonique superficielle dans le secteur nord occidental de la mer d’Alboran. *Rapport Commission International Mer Méditerranee*, 27 (7), 125-127.

Camiñas, J.A., 1983. Datos preliminares sobre la biomasa zooplanctónica en el sector Suroccidental del mar de Alborán. *Boletin Instituto Espanol de Oceanografia*, 1, 1-18.

Catalán, I.A., Rubín, J.P., Navarro, G., Prieto, L., 2006. Larval fish distribution in two different hydrographic situations in the Gulf of Cádiz. *Deep Sea Research* II, 53, 1377-1390.

Catalán, I.A., Macías, D., Solé, J., Ospina-Álvarez, A., Ruíz, J., 2013. Stay off the motorway: Resolving the pre-recruitment life history dynamics of the European anchovy in the SW Mediterranean through a spatially-explicit individual-based model (SEIBM). *Progress in Oceanography*, 111, 140-153.

Champalbert, G., 1996. Characteristics of zooplankton standing stock and communities in the Western Mediterranean Sea: relations to hydrology. *Scientia Marina*, 60 (S2), 97-113.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, 92, 205-219.

Clarke, K.R., Gorley, R.N., 2006. *PRIMER v6 - User manual/Tutorial*. PRIMER-E Ltd, Plymouth, 190 pp.

Clarke, K.R., Warwick, R.M., 2001. *Change in marine communities: An approach to statistical analysis and interpolation*, 2nd edition. PRIMER-E, Plymouth, 176 pp.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Lasram, F.B.R. *et al.,* 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE*, 5(8), e11842.

Corell, H., Moksnes, P., Engqvist, A., Döös, K., Jonsson, P.R., 2012. Depth distribution of larvae critically affects their dispersal and the efficiency of marine protected areas. *Marine Ecology Progress Series*, 467, 29-46.

Cowen, R.K., Paris, C.B., Srinivasan, A., 2006. Scaling of connectivity in marine populations. *Science*, 311 (5760), 522-527.

Cowen, R.K., Gawarkiewicz, G., Pineda, J., Thorrold, S.R., Werner, F.E., 2007. Population connectivity in marine systems - An overview. *Oceanography*, 20 (3), 14-21.

Dos Santos, A., Lindley, J.A., 2001. Crustacea, Decapoda: Larvae, II. Dendrobranchiata (Aristeidae, Benthesicymidae, Penaeidae, Solenoceridae, Sicyonidae, Sergestidae and Luciferidae). *ICES Identification Leaflets for Plankton*, 186, 1-9.

Dos Santos, A., González-Gordillo, J.I., 2004. Illustrated keys for the identification of the Pleocyemata (Crustacea: Decapoda) zoeal stages, from the coastal region of southwestern Europe. *Journal of the Marine Biological Association of the United Kingdom*, 84, 205-227.

Dos Santos, A., Peliz, Á., 2005. The occurrence of Norway lobster (*Nephrops norvegicus*) larvae off the Portuguese coast. *Journal of the Marine Biological Association of the United Kingdom*, 85, 937-941.

Dos Santos, A., Santos, A.M.P., Conway, D.V.P., Bartilotti, C., Lourenço, P. *et al.,* 2008. Diel vertical migration of decapod larvae in the Portuguese coastal upwelling ecosystem: implications for offshore transport. *Marine Ecology Progress Series*, 359, 171-183.

Echevarria, F., Lafuente, J.G., Bruno, M., Gorsky, G., Goutx, M. *et al*., 2002. Physical-biological coupling in the Strait of Gibraltar. *Deep-sea Research* II, 49, 4115-4130.

Echevarria, F., Zabala, L., Corzo, A., Navarro, G., Prieto, L. *et al*., 2009. Spatial distribution of autotrophic picoplankton in relation to physical forcings: the Gulf of Cádiz, Strait of Gibraltar and Alborán Sea case study. *Journal of Plankton Research*, 31 (11), 1339-351.

Flexas, M.M., Gomis, D., Ruíz, S., Pascual, A., León, P., 2006. *In situ* and satellite observations of the eastward migration of the western Alboran Sea Gyre. *Progress in Oceanography*, 70, 486-509.

Flores, A.A.V., Cruz, J., Paula, J., 2002. Temporal and spatial patterns of settlement of brachyuran crab megalopae at a rocky coast in Central Portugal. *Marine Ecology Progress Series*, 229, 207-220.

Fogarty, M.J., Botsford, L.W., 2007. Connectivity and spatial management of marine fisheries. *Oceanography*, 20 (3), 112-123.

Franqueville, C., 1971. Macroplancton profond (invertébrés) de la Méditerranée nord-occidentale. *Tethys*, 3, 11-56.

Fusté, X., 1987. Distribución de larvas de Crustáceos Decápodos de la costa de Cataluña. *Investigacion Pesquera*, 51 (Supl. 1), 277-284.

García-Lafuente, J., Delgado, J., Vargas, J.M., Vargas, M., Plaza, F. *et al*., 2002. Low-frequency variability of the exchanged flows through the Strait of Gibraltar during CANIGO. *Deep-sea Research* II, 49 (19), 4051-4067.

Garcia-Lafuente, J., Delgado, J., Criado-Aldeanueva, F., Bruno, M., del Río, J. *et al.,* 2006. Water mass circulation on the continental shelf of the Gulf of Cádiz. *Deep-sea Research* II, 53, 1182-1197.

García-Merchán, V.H., Robainas-Barcia, A., Abelló, P., Macpherson, E., Palero, F. *et al.,* 2012. Phylogeographic patterns of decapod crustaceans at the Atlantic-Mediterranean transition. *Molecular Phylogenetics and Evolution*, 62, 664-672.

Gaudy, R., Cervetto, G., Pagano, M., 2000. Comparison of the metabolism of *Acartia clausi* and *A. tonsa*: influence of temperature and salinity. *Journal of Experimental Marine Biology and Ecology*, 247, 51-65.

Giron, F., 1963. Copépodes de la mer d'Alboran (Campagne du "Président-Théodore-Tissier", Juin 1957). *Revue des Travaux de l'Institut des Pêches Maritimes*, 27 (4), 355-402.

González-Gordillo, J.I., Rodríguez, A., 2003. Comparative seasonal and spatial distribution of decapod larvae assemblages in three coastal zones off the south-western Iberian Peninsula. *Acta Oecologica*, 24, S219-S233.

Greze, V.N., Kovalev, A.V., Baldina, E.P., Bileva, O.K., 1985. Zooplankton transfer through the Gibraltar Strait and peculiarities of its taxonomic composition and distribution in adjacent areas. *Investigacion Pesquera*, 49 (1), 3-13.

Lacombe, H., 1971. Le Dètroit de Gibraltar; Oceanographique Physique. Mèmorie explicatif de la carte gèotechnique de Tanger au 1/250000. *Notes et Mémoires du service Geòlogique du Maroc*, 222, 111-146.

Landeira, J.M., Lozano-Soldevilla, F., Hernández-León, S., Barton, E.D., 2009. Horizontal distribution of invertebrate larvae around the oceanic island of Gran Canaria: the effect of mesoscale variability. *Scientia Marina*, 73 (4), 761-771.

Landeira, J.M., Lozano-Soldevilla, F., Hernández-León, S., Barton, E.D., 2010. Spatial variability of planktonic invertebrate larvae in the Canary Islands area. *Journal of the Marine Biological Association of the United Kingdom*, 90, 1217-1225.

Macías, D., Martin, A.P., García-Lafuente, J., García, C.M., Yool, A. *et al.,* 2007. Analysis of mixing and biogeochemical effects induced by tides on the Atlantic-Mediterranean flow in the Strait of Gibraltar through a physical-biological coupled model. *Progress in Oceanography*, 74, 252-272.

Macías, D., Navarro, G., Bartual, A., Echevarría, F., Huertas, I.E., 2009. Primary production in the Strait of Gibraltar: carbon fixation rates in relations to hydrodynamic and phytoplankton dynamics. *Estuarine Coastal and Shelf Science*, 83, 197-210.

Macías, D., Catalán, I.A., Solé, J., Morales-Nin, B., Ruiz, J., 2011. Atmospheric-induced variability of hydrological and biogeochemical signatures in the NW Alboran Sea. Consequences for the spawning and nursery habitats of European anchovy. *Deep-Sea Research* I, 58, 1175-1188.

Madin, L.P., 1991. *Distribution and taxonomy of zooplankton in the Alboran Sea and Adjacent Western Mediterranean, A literature survey and field guide*. Woods Hole Oceanographic Institution Technical Report, 26, 1-147.

Morgan, S.G., Fisher, J.L., Mace, A.J., Akins, L., Slaughter, A.M. *et al.,* 2009. Cross shelf distributions and recruitment of crab postlarvae in a region of strong upwelling. *Marine Ecology Progress Series*, 380, 173-185.

Patarnello, T., Volckaert, F.A.M.J., Castilho, R., 2007. Pillars of Hercules: is the Atlantic-Mediterranean transition a phylogeographical break? *Molecular Ecology*, 16, 4426-4444.

Paula, J., 1993. *Ecologia da fase larvar e recrutamento de crustáceos decápodes no estuário do Rio Mira*. PhD Thesis, University of Lisbon, Lisbon, 282 pp.

Peliz, Á., Teles-Machado, A., Marchesiello, P., Dubert, J., Lafuente, J.G., 2009. Filament generation off the Strait of Gibraltar in response to Gap winds. *Dynamics of Atmospheres and Oceans*, 46, 36-45.

Peliz, Á., Boutov, D., Cardoso, R.M., Delgado, J., Soares, P.M.M., 2013. The Gulf of Cadiz-Alboran sea sub-basin: Model setup, exchange and seasonal variability. *Ocean Modelling*, 61, 49 – 67.

Pérez, J.A.G., 1995. *Catálogo de los Crustáceos Decápodos de las Islas Canarias. Gambas, langostas, cangrejos*. Publicaciones Turquesa, Santa Cruz de Tenerife, 282 pp.

Pérez-Folgado, M., Sierro, F.J., Flores, J.A., Cacho, I., Grimalt, J.O. *et al.,* 2003. Western Mediterranean planktonic foraminifera events and millenial climatic variability during the last 70 kyr. *Marine Micropaleontology*, 48, 49-70.

Pires, R.F.T., Pan, M., Santos, A.M.P., Peliz, Á., Boutov, D. *et al*., 2013. Modelling the variation in larval dispersal of estuarine and coastal ghost shrimp: *Upogebia* congeners in the Gulf of

Cadiz. *Marine Ecology Progress Series*, 492, 153-168.

Postel, L., Fock, H., Hagen, W., 2000. Biomass and abundance. p. 83-192. In: *ICES zooplankton methodology manual*. Harris, R.P., Wiebe, P.H., Lenz, J., Skjoldal, H.R., Huntley, M. (Eds). Academic Press, London.

Prieto, L., Navarro, G., Rodríguez-Gálvez, S., Huertas, I.E., Naranjo, J.M. *et al.,* 2009. Oceanographic and meteorological forcing of the pelagic ecossystem on the Gulf of Cadiz shelf (SW Iberian Peninsula). *Continental Shelf Research*, 29, 2122-2137.

Queiroga, H., Cruz, T., dos Santos, A., Dubert, J., González--Gordillo, J.I. *et al.,* 2007. Oceanographic and behavioural processes affecting invertebrate larval dispersal and supply in the western Iberia upwelling ecosystem. *Progress in Oceanography*, 74, 174-191.

Relvas, P., Barton, E.D., Dubert, J., Oliveira, P.B., Peliz, Á. *et al*., 2007. Physical oceanography of the western iberia ecosystem: Latest views and challenges. *Progress in Oceanography*, 74 (2-3), 149-173.

Reul, A., Muñoz, M., Criado-Aldeanueva, F., Rodríguez, V., 2006. Spatial distribution of phytoplankton < 13 μm in the Gulf of Cadiz in relation to water masses and circulation pattern under westerly and easterly wind regimes. *Deep-Sea Research* II, 53, 1294-1313.

Ruiz, J., Garcia-Isarch, E., Huertas, I.E., Prieto, L., Juárez, A. *et al.,* 2006. Meteorological and oceanographic factors influencing *Engraulis encrasicolus* early life stages and catches in the Gulf of Cadiz. *Deep-Sea Research* II, 53, 1363-1376.

Sabatés, A., 1990. Distribution pattern of larval fish populations in the Northwestern Mediterranean. *Marine Ecology Progress Series*, 59, 75-82.

Sánchez-Arcilla, A., Simpson, J.H., 2002. The narrow shelf concept: couplings and fluxes. *Continental Shelf Research*, 22, 153-172.

Sarhan, T., García-Lafuente, J., Vargas, M., Vargas, J.M., Plaza, F., 2000. Upwelling mechanisms in the northwestern Alboran Sea. *Journal of Marine Systems*, 23, 317-331.

Skjoldal, H.R., Wiebe, P.H., Postel, L., Knutsen, T., Kaartverdt, S. *et al.,* 2013. Intercomparison of zooplankton (net) sampling systems: Results from the ICES/GLOBEC sea-going workshop. *Progress in Oceanography*, 108, 1-42.

Skliris, N., Beckers, J., 2009. Modelling the Gibraltar Strait/Western Alboran Sea ecohydrodynamics. *Ocean Dynamics*, 59, 489-508.

Somerfield, P.J., Clarke, K.R., 2013. Inverse analysis in non-parametric multivariate analyses: distinguishing of groups of associated species which covary coherently across samples. Journal of *Experimental Marine Biology Ecology*, 449, 261-273.

Stehle, M., dos Santos, A., Queiroga, H., 2007. Comparison of zooplankton sampling performance of Longhurst–Hardy Plankton Recorder and Bongo nets. *Journal of Plankton Research*, 29 (2), 169-177.

Thompson, R.K., Pritchard, A.W., 1969. Respiratory adaptations of two burrowing crustaceans, *Callianassa californiensis* and *Upogebia pugettensis* (Decapoda, Thalassinidea). *Biological Bulletin*, 136, 274-287.

Tintoré, J., La Violette, P.E., Blade, I., Cruzado, A., 1988. A study of an intense density front in the Eastern Alboran Sea: The Almeria-Oran Front. *Journal of Physical Oceanography*, 18, 1384-1397.

Torres, A.P., dos Santos, A., Balbín, R., Alemany, F., Massutí, E. *et al.,* 2014. Decapod crustacean larval communities in the Balearic Sea (Western Mediterranean): Seasonal composition, horizontal and vertical distribution patterns. *Journal of Marine Systems*, 138, 112-126.

Triantafyllidis, A., Apostolidis, A.P., Katsares, V., Kelly, E., Mercer, J. *et al.,* 2005. Mitochondrial DNA variation in the European lobster (*Homarus gammarus*) throughout the range. *Marine Biology*, 146, 223-235.

Vargas-Yañez, M., Sabatés, A., 2007. Mesoscale high-frequency variability in the Alboran Sea and its influence on fish larvae distributions. *Journal of Marine Systems*, 68, 421-438.

Vargas-Yañez, M., Moya, F., García-Martínez, M., Rey, J., González, M. *et al.,* 2009. Relationships between *Octopus vulgaris* landings and environmental factors in the northern Alboran Sea (Southwestern Mediterranean). *Fisheries Research*, 99, 159-167.

Vives, F., Santamaria, G., Trepat, I., 1975. The zooplankton of the marine area of the Strait of Gibraltar (Spanish-Moroccan Bay and Alboran Sea) in June and July 1972. *Resultados Expediciones Cientificas del Bugue Oceanografico "Cornide de Saavedra"*, 4, 1-100.

Warwick, R.M., Clarke, K.R., Suharsono, 1990. A statistical analysis of coral community responses to the 1982–83 El Niño in the Thousand Islands, Indonesia. *Coral Reefs*, 8, 171-179.

Wiebe, P.H., 1988. Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction. *Fisheries Bulletin*, 86, 833-835.

Xavier, J.R., van Soest, R.W.M., 2012. Diversity patterns and zoogeography of the Northeast Atlantic and Mediterranean shallow-water sponge fauna. *Hydrobiologia*, 687, 107-125.

Youssara, F., Gaudy, R., 2001. Variations of zooplankton in the frontal area of the Alboran Sea (Mediterranean sea) in winter 1997. *Oceanologica Acta*, 24 (4), 361-376.

Zaafa, A., Ettahiri, O., Berraho, A., Elkhiati, N., Somoue, L. *et al*., 2014. A comparative study of marine zooplankton communities in the Tangier and M'Diq (Gibraltar Strait) regions. *Hydroécologie Appliquée*, 18, 67-80.