



Mediterranean Marine Science

Vol 22, No 3 (2021)

VOL 22, No 3 (2021)



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ANNALISA PATANIA, ERHAN MUTLU

doi: 10.12681/mms.26142

To cite this article:

PATANIA, A., & MUTLU, E. (2021). Spatiotemporal and ecological distribution of megabenthic crustaceans on the shelf-shelf break of Antalya Gulf, the eastern Mediterranean Sea. *Mediterranean Marine Science*, *22*(3), 446–465. https://doi.org/10.12681/mms.26142

Mediterranean Marine Science Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS The journal is available on line at http://www.medit-mar-sc.net DOI: http://dx.doi.org/10.12681/mms.26142

Spatiotemporal and ecological distribution of megabenthic crustaceans on the shelf-shelf break of Antalya Gulf, the eastern Mediterranean Sea

Annalisa PATANIA¹ and Erhan MUTLU²

Department of Earth and Marine Science, University of Palermo, Via Archirafi 18, 90123 Palermo, Italy
 Akdeniz University, Fisheries Faculty, Main Campus, Antalya, Turkey

Corresponding author: emutlu@akdeniz.edu.tr

Contributing Editor: Giorgio MANCINELLI

Received: 13 February August 2021; Accepted: 9 July 2021; Published online: 06 August 2021

Abstract

The spatiotemporal distribution and ecology of the suprabenthic and benthic mega-crustaceans were studied in the shelf-shelf break of Turkish waters of the eastern Mediterranean Sea (Antalya Gulf). Sampling was conducted seasonally in May 2014, August, October, and February 2015 using an otter trawl at depths of 10, 25, 75, 125 and 200 m along three transects. A total of 59 species were identified comprising 53 decapods (Eumalacostraca: Eucarida), 3 isopods (Eumalacostraca: Peracarida), and 3 stomatopods (Hoplocarida). Eighteen of the total identifiable species were invasive, and some of them significantly influenced the crustacean community structure. *Parapenaeus longirostris, Pagurus prideaux, Charybdis (Goniohellenus) longicollis* and *Medorippe lanata* were the most common species. *Parasquilla ferussaci* was reported for the first time in Turkish water of the Levantine Sea. Community structure showed seasonal patterns and differed along the depth gradient of habitat heterogeneity. The megabenthic crustacean assemblage was driven mainly by seafloor depth and was related to the fishing disturbance in the area (fishing/no-fishing zones). Environmental parameters were measured for each sample and tested in relationship to crustacean abundance by multivariate analysis CCA (canonical correspondence analysis). The results revealed significant differences in community structure related to substrate and the fine fraction of the bioseston.

Keywords: Benthos; crustacean; distribution; diversity; ecology; Levantine Sea.

Introduction

Information on the spatio-temporal distribution of marine communities has been widely used in marine science as important information for fisheries management stock assessments and as an indicator of the conservation status of vulnerable species (Koslow, 2009; Koukouras *et al.*, 2010; Papiol *et al.*, 2012). These are highly useful to study ontogenic migration and their response to environmental factors (Lea *et al.*, 2018). Coastal and shelf areas represent highly productive ecosystems due to primary production and nutrient inputs from river runoff. These areas serve as the source of organic matter exported to offshore marine food webs from shelf to basin (Bell *et al.*, 2016).

The spatiotemporal dynamics of megabenthic assemblages at different trophic levels have been broadly studied in the Mediterranean Sea (Coll *et al.*, 2010; Papiol *et al.*, 2012; Kallianiotis *et al.*, 2000). The Mediterranean marine ecosystem has undergone rapid changes over the last few decades, mainly due to anthropogenic factors, including climate change, pollution, over-exploitation

of marine resources, and the establishment of invasive species (Gambi, 2014). Data on invasive crustacean species from the Mediterranean Sea revealed a total of 153, the majority of which were decapods (78 species). Approximately 77% of all invasive Mediterranean decapod species had an Indo-Pacific/Indian/Red Sea origin while only 23% had an Atlantic origin (Zenetos *et al.*, 2010).

Megabenthic communities have long been considered as possible indicators for monitoring anthropogenic impacts, or natural long-term alterations in marine ecosystems. Such communities provide valuable information that cannot be obtained from other biological groups. Examples include bioaccumulation of toxic substances and changes in the flux of energy to the seafloor (Bilyard, 1987; Kroncke, 2003; Cartes *et al.*, 2009). Benthic crustaceans have been considered to be the most sensitive taxa to environmental changes, and may serve as useful biological indicators of the complex structure of the marine bottom habitat (Gesteira & Dauvin, 2000; Kramer *et al.*, 2013; Sanchez-Moyano & Garcia-Gomez, 1998). Furthermore, crustaceans are economically important to the seafood industry as well as being ecologically import-

ant scavengers in marine systems.

Decapod crustaceans are an important component of commercial catches in the Mediterranean where they dominate the crustacean megafauna. 384 species of Decapoda were reported from the Mediterranean Sea (Coll et al., 2010). Many studies have been carried out in the Mediterranean Sea to describe the spatio-temporal dynamics of Decapoda and megabenthic assemblages (Cartes et al., 2009; DeLaHoz et al., 2018; Koukouras et al., 1992; Koukouras et al., 2010; Maynou & Cartes, 2000). However, most of these studies have been conducted in the central and western Mediterranean, as well as in Greek waters (Katsanevakis et al., 2007; Kallianiotis et al., 2020). In contrast, studies on the distribution and ecology of crustacean assemblages in the Levantine Sea are generally lacking.

The Levantine Sea displays unique environmental features compared to the western Mediterranean. The Levantine basin is characterized by a negative freshwater balance, high evaporative rates, rapid surface water warming, low production of organic matter and ultra-oligotrophic conditions (Sisma-Ventura et al., 2017). Furthermore, the ecosystem of the eastern Mediterranean Sea has been affected by significant changes due to the biological invasion of invasive species transported from the Red Sea via the Suez Canal, since its opening in 1869 (Por, 1978). The enlargement of the Suez Canal in August 2015 has raised concerns over increasing propagule pressure allowing the continuous introduction of new invasive species, leading to associated degradation and loss of native populations and habitats (Galil, 2006, 2011; Koukouras et al., 2010; Zenetos et al., 2010). Many invasive benthic crustaceans are well established in the Levantine Sea, replacing native benthic crustacean species (Mutlu, 2015). Moreover, invasive species could greatly affect the crustacean fisheries of the Levantine Sea, with adverse economic consequences (Boudouresque & Verlaque, 2005).

To date, most existing studies have focused on deep sea megafauna and to a lesser extent on the species-environment relationships occurring at the transition between the shelf and the shelf break. The present study outlines the spatio (depth, habitats, fishing and non-fishing zone)-temporal (season) distribution and ecology (hydrography, physical, chemical, optic, sedimentary, planktonic) of the megabenthic crustacean along the shelf-shelf

break of the Turkish waters of the eastern Mediterranean Sea. As a consequence of the ecological importance of megabenthic crustaceans along the shelf-shelf break and the historical lack of comprehensive information on their distribution and ecology, the aim of this study was to provide baseline information on depth and seasonal distributions and biodiversity patterns (diversity, density; abundance/biomass and richness) of the megabenthic and suprabenthic crustacean assemblages. The present study focused on soft bottom areas of the Continental Shelf and upper Slope of the Antalya Gulf, between 10 m and 300 m in a region of the most ultra-oligotrophic waters of the Mediterranean Sea.

Materials and Methods

Study area and environmental parameters

The environmental parametes of the present study area were descibed in detail by de Meo et al. (2018) and Mutlu et al. (2021). The study area covered the widest portion of the shelf and the shelf break in the Gulf of Antalya (Fig. 1). A few rivers feed into the Gulf with low flow rates compared to other rivers feeding the north-easternmost area of the Turkish coast in the Mediterranean Sea. The bottoms were dominated by macrophytes, mainly Caulerpa prolifera (Forsskål) J.V.Lamouroux 1809, between Region 1 (R1) and Region 2 (R2) and then by Posidonia oceanica (Linnaeus) Delile, 1813 (Mutlu & Balaban, 2018) east of region R2 where the bottoms shallower than 30 m were rocky and vegetated. Commercial fishing is prohibited within 3 miles from the coastline all year, and the area from Region 3 (R3) to east of the Gulf of Antalya is closed for commercial fishing all year. Refer to Figure 1 for the areas that define these regions. Commercial fishing is subjected to seasonal restrictions and is legally closed between September and April.

Sampling and design

Mutlu *et al.* (2021) descibed the general material collection. In brief, samples were collected with an otter trawl on the shelf of the Antalya Gulf in May 2014, August, October, and February 2015. The wing mesh size

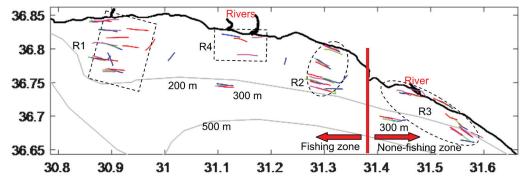


Fig. 1: Study area shown in the red frame of the insert and track lines of the trawls obtained in different seasons (blue; May 2014, green; August 2014; red; October 2014 and magenta; February 2015). Dashed lines denote border of the regions.

of the trawl was a diamond eye of 88 mm and the codend was meshed with a diamond eye of 44 mm. During the trawl surveys, the cod-end had a shroud with a diamond eye of 22 mm. The float line (headrope) of the trawl was 35 m long and the trawl had a lead line. The study area was split into four regions and seasonally sampled. R1 was a fishing zone with a non-vegetated soft bottom located close to the city of Antalya (36.51830° N, 30.50498° E) and the main discharge site of the city's wastewater treatment plant. R2 was also a fishing zone that is vegetated by P. oceanica meadows with a rocky bottom at depths less than 35 m (Mutlu & Balaban, 2018). R3 was a no-fishing zone characterized by less vegetation and a non-vegetated bottom with steep cliff slopes (Mutlu & Balaban, 2018) when compared with the other two regions (Fig. 1). Each region (R1-R3) was transected at the 10, 25, 75, 125 and 200 m isobaths. There were two transects along the 10 m isobath in R3; one located in front of the Manavgat River and the other one far from the river mouth to the east. Additionally, Region 4 (R4) was sampled in front of two rivers, but the samples encompassed only 15, 50 and 75 m isobaths.

The trawl was towed from the RV *Akdeniz Su* on the bottom of each station at a speed of 2.5 - 3.0 knots (1.3 - 1.5 m s⁻¹) for about 30 minutes. Coordinates from a differential GPS (D-GPS) were recorded at 1 Hz during each trawl to measure the swept distance. After each trawl, materials were sorted into litter, benthos and fishes. Abundant species were sub-sampled in a ratio of one-third or one-fourth of the total catch of the species. Crustacean species were preserved in 5% buffered formaldehyde for later identification and laboratory studies.

At each station, the following parameters were measured at the surface and bottom: temperature, salinity, dissolved oxygen, pH using a using multi-parameter probes (YSI, HiTech) and total suspended solids (material was dried in an oven at 60° C for 24 h, and then weighed before the weight of the dried membrane was subtracted from the total dry weight), and chlorphyll *a* (chl-*a*) using a method described by Lorenzen (1967). Secchi disk depth was recorded once at each station while photosynthetically active radiation (PAR) was measure through the water column from surface to bottom using a

LI-COR (LI-193SA Spherical Quantum Sensor, ampoule and LI-1400 data logger). A Nansen plankton net (70 cm diameter, 300 µm mesh) collected a vertically-integrated (bottom to surface) sample of zooplankton and seston. A 200 kHz split-beam echosounder (Biosonics) recorded the seabed scattering and these data informed a Visual Bottom Classifier (VBT) program (ver. 1.10.3.5, BioSonics). Bottom types were categorized with number corresponding to each bottom type for the statistical analyses (see Fig. 2). Detailed descriptions of the hydrographic sampling are provided in Meo *et al.* (2018) and Mutlu *et al.* (2021).

Laboratory studies

In the laboratory, individuals were identified to species and the numbers of individuals of each species were counted and then the total weight of each species was measured with an electronic scale with a precision of 0.0001 g. The WoRMS (World Register of Marine Species) database (http://www.marinespecies.org) was used for the taxonomic nomenclature of the species (Appendix 1).

Data standardization

Geographical coordinates from D-GPS were converted to the trawling distance. The swept width (wingspread) of the trawl was estimated as half the float line width (Pauly, 1980). The swept area of the trawl was therefore the product of the swept width and distance travelled. Biomass (B) and abundance (Ab) of crustacean species per trawl (i) were estimated by converting catches over the swept area of the trawl to values in km² area for each station using an equation of $B_i = A_i C / a_i q_i$, where A_i is 1 km², C is the catch per trawl in kg, a is the swept area of the trawl in km^2 and q is the trawl efficiency coefficient for fishing, 1 is used here for biomass estimate. The equation was also used to estimate abundance by replacing B_i with Ab, (number of individuals per trawl). These data were then used to derive the following characteristics: number of species, biomass, abundance, and three diver-

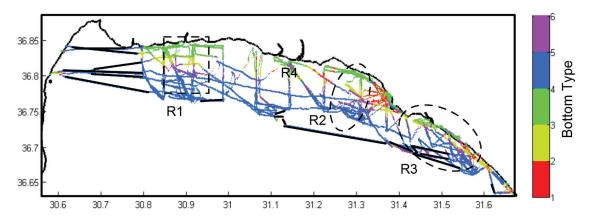


Fig. 2: The study area showing the different bottom types from the acoustical tracklines from all cruises: ■ mud; ■ fine sand mud ■ sand; ■ coarse muddy sand; ■ rock and rock covered by *Posidonia oceanica*; ■ lost and too deep to be characterized by the echosounder.

sity indices: Margalef's richness index, Pielou's evenness index and Shannon-Weiner diversity index.

Statistical analyses

Statistical analyses were applied to evaluate differences in the biomass and abundance of each species over time, space (depth, region) and sexes among the species and to evaluate responses to the environmental parameters. The normalized environmental parameters were subjected to a Principal Component Analyses (PCA) to relate spatio-temporal structure of crustacean assemblages in the sampling stations (PRIMER, vers.6+). A three-way ANOVA was run to test the differences in each diversity index, abundance and biomass among season, depth and transect (region) using a command "anovan" in Matlab (Matworks Inc.). Faunistic characteristics of the crustacean assemblage were represented by the number of species (S), abundance (N), biomass (B), Margalef's richness index (d), Pielou's evenness index (J') and Shannon-Weiner diversity index (H') as calculated using PRIMER. Non-metric multidimensional scaling (MDS) was applied to detect a biogeographical summary of crustacean assemblages based on Log₁₀(abundance+1). A SIMPER (Similarity percentage) analysis was performed to identify the percent contribution of the contributor species most responsible for the average Bray-Curtis dissimilarity between groups and average Bray-Curtis similarity within groups. The biodiversity of the four groups of stations was compared by means of rarefaction curves (Biodiversity Pro, ver. 2). This method has the advantage of being sample-size and density-independent, and is able to provide an indication of the biodiversity in terms of species richness across the different regions, seasons and depth strata. Soyer's index (Soyer, 1970) based on dominance (D%) and further frequency of occurrence (FO%) and numerical occurrence (NO%) was evaluated to determine the constancy of the species occurrence in the study area (Holden & Raitt, 1974). Abundances of the crustacean species were subjected to PERMANOVA and a Monte Carlo test to examine differences among sampling years, months and bottom depths using PRIMER. Canonical Correspondence Analyses (CCA) was applied to matrices of Log₁₀-transformed biomass and abundance and the corresponding matrix of environmental parameters to examine species-environment relationships using the CANOCO software (vers. 4.5) (teer Braak & Smilauer, 2002).

Results

Environmental parameters

Detailed results from the environmental parameters and laboratory analyses are presented in de Meo *et al.* (2018). Overall, the physical properties at the sea surface and near-bottom waters in the study area showed a regular pattern in space among seasons. The distribution pat-

tern of physical parameters in August and October were similar but different from those in May and February. The PC1 was organized along water temperature, dissolved oxygen and water density axes and this component explained 23.1% of the variance. However, salinity did not contribute to the linearization of PC1. The stations were discriminated mainly by salinity, particularly subsurface salinity, pH and chl-*a*, and minorly by the seston on the PC2 which explained 19.8% of the variance.

Based on the acoustic data, five main bottom classes were identified in the study area: mud, fine sandy mud, sand, coarse muddy sand and rocks covered by *P. oceanica* (Fig. 2). The bottom type changed along the bathymetric gradient. At shallow depths near the coast, a continuous strip of sand occurred, occasionally followed by coarse muddy sand strata. In the eastern area, the superficial sediment pattern became more complex, due to the irregular presence of a rocky substrate covered by vegetation (Mutlu & Balaban, 2018). Down to the greater depths a muddy bottom predominated interrupted by fine sandy mud. Stations deeper than 300 meters were not classified because they exceeded the effective range of the 200 kHz echosounder (Appendix 2, Fig. 2). In those deep stations, the bottom was likely muddy.

Species distribution

A total of 59 megacrustacean species were collected (Appendix 1). In addition, one European spiny lobster, Palinurus elephas (Fabricius, 1787), was found at the phyllosoma stage at one station in October. Decapods (Eumalacostraca: Eucarida) accounted for 53 species, isopods (Eumalacostraca: Peracarida) were represented by three species; and three species of stomatopods (Hoplocarida) were present. Invasive species constituted 18 of the 59 species present. Among decapod species, the Brachyura was the infraorder with the most species (23), followed by the suborder Dendrobranchiata (12), the infraorders Caridea (9) and Anomura (9). Parapenaeus longirostris, Pagurus prideaux, Charybdis (Goniohellenus) longicollis and Medorippe lanata were reported as common species for the entire sampling year according to the Soyer's index (25<D<50%) (Appendix 1). Pagurus prideaux was only common (D>50%) in October, Pisa armata was reported among common species in May and the invasive penaeid shrimp *Penaeus aztecus* in October.

Derilambrus angulifrons, Penaeus semisulcatus, and P. armata (FO: 4.5%) were frequently occurring species throughout the year. Homola barbata, Calappa granulata, Dardanus arrosor, Derilambrus angulifrons and Erugosquilla massavensis were additionally-contributing species in May, while Ixa monodi, Penaeus pulchricaudatus and Thalamita poissonii were frequently occurring species in August and F. aztecus was a frequent species in October.

The numerical occurrence of *P. longirostris* decreased from the warm water to cold water seasons (Appendix 1). *Charybdis (Goniohellenus) longicollis* had its highest abundance in October whereas *Pagurus prideaux* had its

highest numerical occurrence when the water was cold (October-February). Eight species had a maximum abundance of more than 1000 ind/km² and 4 of these were invasive species. The species with the highest maximum biomass were the pink shrimp *P. longirostris* (126.771 kg km²) followed by the invasive species *C. (G.) longicollis* 28.767 kg km², Appendix 1).

A total of 15 species occurred at stations deeper than 100 m. Seven species were ubiquitous at stations deeper than 75 m. Nine species were ubiquitous species in the shelf zone and two species occurred only on the shelf break (Appendix 1). Only one invasive species was found at depths deeper than 100 m. Nine invasive species were found between the shallowest depths out to 125 m and four invasive species were ubiquitous over the shelf zone with only two invasive species extending to the shelf break (Appendix 1).

Faunal characteristics

Species richness ranged from 36-39 in R1-R2 (fishing zones) to 44 species in R3 (no-fishing zone; Tables 1-3). R4 had only 14 species. The number of species decreased from R1 and R2 to R3. Accordingly, the regional average number of species ranged closely from 5.07 ± 0.59 in R1 through 5.13 ± 0.62 in R2 to 4.48 ± 0.61 in R3 whereas R4 had a number of 3.80 ± 1.35 . The number of species was not statistically different across months (seasons) at p < 0.05; however the calculated p value (0.0622) was close to significant, and the abundance (N) was significantly different (p = 0.0088) only among the depths (3-

way ANOVA, Table 2). The evenness indices (J') were significantly different among depths, among the region and for the depth x region interaction. The number varied between 21 species in August and 45 species in February to 47 species in October (Table 1). The number of species was not significantly different among the bottom depths at p<0.05 (3-way ANOVA, Table 2). The number of the species increased from 22 at 10 m to 34 species at 75 m, and then decreased to 29 species at 125 m, 23 species at 200 m and 13 species at 300 m (Table 1).

A total of 113920 individuals were recorded in the study area (Table 1) with an average abundance of 4833 ind km⁻². The abundance was significantly different among the bottom depths at p < 0.05 (Tables 1-3). The average abundance decreased two-fold from region R1 $(2105 \pm 571 \text{ ind km}^{-2})$ that had a bottom with *Posidonia* beds, to R2 (1262 \pm 607 ind km⁻²) - R3 (1140 \pm 582 ind km⁻²) where *Posidonia* beds existed only in waters shallower than 30 m. The riverine region (R4) with seagrass meadow bottoms had the lowest average abundance (323 \pm 1303 ind km⁻²) (Table 1). The highest abundance was estimated to be 2068 ± 636 ind km⁻² in October comprising mostly the decapods Dendrobranchiata, Anomura, Brachyura and Caridea, followed by May (1664 ± 621 ind km⁻²) and February (1156 \pm 668 ind km⁻²) while the lowest abundance was recorded in the warmest season, August (699 \pm 706 ind km⁻²), with an abundance almost three times lower than the highest one recorded (Fig. 3). The depth wise-abundance distribution was characterized along two different depth zones; 10-75 m with the increment ranging from 300 ± 668 ind km⁻² at 10 m to 1616 ± 647 ind km⁻² at 75 m, and 125-300 m where the

Table 1. Annual distributions of number of species (S), total and average abundance (N, ind km⁻²) and biomass (B, kg km⁻²), Margalef's richness index (d), evenness (J') and Shannon-Weiner (H') indices, on standardized data over km² area, across regions, months (M; May, A; August, O; October and F; February) and bottom depths.

		Total	Average						
Regions	S	N	В	d	J'	<i>H</i> '	N	В	d
R1	36	54751	318.11	3.21	0.33	1.17	2105	12.23	4.57
R2	39	29044	115.57	3.70	0.50	1.81	1262	5.02	5.32
R3	44	28506	175.30	4.19	0.56	2.13	1140	7.01	6.11
R4	14	1618	27.28	1.76	0.80	2.11	323	5.45	2.25
Months									
M	31	36625	202.16	2.85	0.40	1.39	1664	9.18	4.04
A	21	11889	61.65	2.13	0.39	1.18	699	3.62	3.05
O	47	43431	257.03	4.31	0.57	2.19	2068	12.23	6.03
F	45	21974.16	115.42	4.40	0.53	2.02	1156	6.07	6.24
Depths (m)									
10	22	4502	67.95	2.50	0.69	2.14	300	4.53	3.68
25	27	6793	56.13	2.95	0.70	2.31	485	4.01	4.20
75	34	25847	140.40	3.25	0.60	2.11	1615	8.77	4.47
125	29	12971	60.62	2.96	0.43	1.43	926	4.33	4.10
200	23	19845	78.32	2.22	0.43	1.36	1653	6.52	2.97
300	13	43959	232.84	1.12	0.15	0.38	5494	29.10	1.39

Table 2. Significance values, P estimated from the 3-way ANOVA of number of species (S), total abundance (N), biomass (B), Margalef's richness index (d), evenness (J') and Shannon-Weiner (H') indices among the regions, months (seasons) and bottom depths. Bold numbers show p<0.05 level.

Source	S	N	В	d	J'	<i>H</i> '
Region	0.9136	0.2887	0.6191	0.9391	0.0363	0.4969
Season	0.0622	0.1819	0.4059	0.0514	0.0814	0.0099
Depth	0.2210	0.0088	0.0966	0.1031	0.0030	0.0223
Region*Season	0.8284	0.4497	0.7151	0.6600	0.1638	0.5440
Region*Depth	0.7555	0.1652	0.5030	0.5540	0.0338	0.0756
Season*Depth	0.9603	0.1878	0.4632	0.7761	0.1205	0.4726
Region*Season*Depth	0.9237	0.2138	0.6596	0.8243	0.2838	0.3784

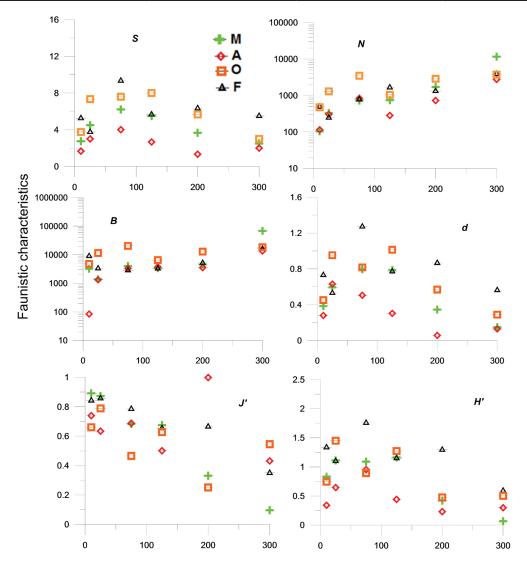


Fig. 3:. Seasonal distribution (M; May, A; August, O; October and F; February) of the average number of species (S), abundance (N, ind km⁻²), biomass (B, g km⁻²), species richness (d), evenness (J') and Shannon-Weiner (H') indices.

abundance ranged from 927 ± 691 ind km⁻² at 125 m to 5495 ± 915 ind km⁻² at 300 m (Table 1, Fig. 3). Of the decapods, Dendrobranchiata had the highest abundance, followed by Anomura which was the most abundant taxon. Brachyuran abundances were two times higher in R2 and R3 than in R1. Isopoda were virtually absent in R2. Annual abundances of Isopoda and Stomatopoda were 8

ind km⁻² and 25 ind km⁻², with their highest abundances in October-February, respectively.

A total of biomass of 636 kg was recorded in the study area (Table 1) with an overall mean of 7.43 kg km⁻². The biomass was not significantly different among the regions, seasons and bottom depths (Table 2, Fig. 3). The biomass along the depth gradient varied from 4.01 ± 4.16

Table 3. 3-way PERMANOVA on abundance of the crustacean species using Bray-Curtis similarity index. The bold numbers show P < 0.05 level (P(perm)) with permutated test and P(MC) with Monte Carlo test).

Source	df	SS	MS	F	p(perm)	p(MC)
Depth	5	71977	14395	5.512	0.001	0.001
Region	3	16008	5335.9	1.9833	0.003	0.023
Season	3	14872	4957.5	1.6	0.233	0.130
Depth x Region	11	29978	2725.3	1.3181	0.031	0.0 50
Depth x Season	15	37299	2486.6	0.80251	0.766	0.816
Region x Season	8	21079	2634.9	0.85038	0.661	0.699
Depth x Region x Season	24	49133	2047.2	0.66071	0.958	0.976
Residuals	6	18591	3098.5			
Total	75	281290				

kg km⁻² at 25 m to 6.52 ± 4.49 kg km⁻² at 200 m with an increment to 8.77 ± 3.89 kg km⁻² at 75 m. The maximum biomass recorded (29.11 \pm 5.50 kg km⁻²) occurred on the shelf break at 300 m.

Margalef's richness index (d) for the crustaceans was not significantly different among the regions, seasons, and bottom depths nor their interactions at p < 0.05(Table 2). The regional Margalef's richness index varied between 0.578 ± 0.084 in R3 (no-fishing zone) and 0.659 ± 0.087 in R2. The riverine shallow zone (R4) had the lowest richness (0.492 \pm 0.184). The richness index decreased gradually by seasons from February 0.784 ± 0.086 to August 0.312 ± 0.097 , followed by an increase in October similar to the values observed in February (Fig. 3). The lowest richness occurred in August (0.718 \pm 0.082), which was significantly lower than that in the rest of the seasons. The Margalef's richness index increased from 0.487 ± 0.101 at 10 m to a high of 0.837 ± 0.094 at 75 in the photic zone and then decreased to a low of 0.282 \pm 0.133 at 300 m in the aphotic zone (Fig. 3). The highest values were at 10 m, 200 m and 300 m (Table 1).

Pielou's evenness index was significantly different among the regions and bottom depths (3-way ANOVA, Table 2). The crustacean abundance was distributed more evenly in R3 (0.719 \pm 0.061, no-fishing zone) than R2 (0.575 ± 0.063) and R1 (0.601 ± 0.057) . The shallow riverine region, which was undisturbed by the fishery, had the highest index value (0.827 \pm 0.126. The evenness among the crustaceans decreased slightly from February (0.726 ± 0.065) to October (0.551 ± 0.063) (Fig. 3). Overall, the indices decreased from the coast to offshore from 10 m (0.804 ± 0.075) to 25 m (0.806 ± 0.075) to 75 m (0.635 ± 0.065) - 125 m (0.629 ± 0.072) and then decreased gradually from 200 m (0.474 \pm 0.082) to 300 m (0.392 ± 0.098) (Fig. 3). The crustacean abundances of the shallowest waters (10-25 m) had a significantly higher evenness than the deepest waters (200-300 m) (Table 1).

The Shannon-Weiner diversity indices were significantly different among the seasons, and the bottom depths, but not among the regions at P<0.05 (Table 1). The regions had a similar crustacean species diversity with the indices ranging from 0.837 ± 0.127 in R2 to

 0.933 ± 0.119 . The riverine region had the highest index (1.021 ± 0.273) . The greatest diversity in crustacean species was recorded in February (1.238 ± 0.127) , followed by a decreasing trend to August (0.496 ± 0.135) and by an increment in October (0.921 ± 0.121) (Fig. 3). The diversity of crustacean species increased gradually from $10 \text{ m} (0.845 \pm 0.145)$ to $75 \text{ m} (1.127 \pm 0.141)$, and then decreased from 75 m through $125 \text{ m} (1.037 \pm 0.151)$ to $300 \text{ m} (0.365 \pm 0.199)$. The deepest zone of the study area had the poorest diversity in crustacean species (Fig. 3).

Rarefaction curves revealed that regional richness in R3 (no-fishing zone) was greatest, followed by a similar richness in R1 and R2 (fishing zones) (Fig. 4A). The seasonal richness was the highest in the cold-water months (February, October). The month with the lowest richness occurred in the warmest season during August (Fig. 4B). The bottom depths containing the greatest richness were between 25 m and 125 m. Moderate richness was found at 200 m while the most depauperate depth was 300 m (Fig. 4C).

Species assemblages and ecological distributions

The result of 3-way PERMANOVA showed that abundance was significantly different among the depths and regions, as well as for their interaction terms (depth x region) (Table 3). The statistical significances were also supported by the results of the Monte Carlo test (Table 3).

The nMDS showed that there were three broad groups according to depth: the shallowest depth group (10 m- 25 m), an intermediate depth group (75 m- 125 m), and a deepest depth group (200 m- 300 m) (Fig. 5). No seasonal or regional groupings could be observed in the nMDS.

The SIMPER analysis revealed that the average percent similarity increased with depth, with an average similarity of 40.32% for the 200 m stations and 52.82% for the 300 m stations (Table 4). This implies that the dissimilarity of the shallow water stations was higher than the deeper water stations. The contributing species of each depth groups are listed in Table 4. Two commercial shrimps (*P. pulchricaudatus* and *Penaeus hathor*) and two crabs (*T. poissonii* and *Portunus segnis*) were

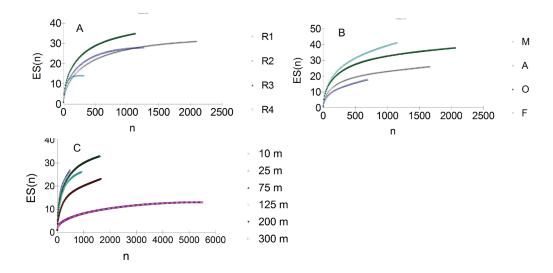


Fig. 4: Regional (A), seasonal; M; May, A; August, O; October and F; February (B) and bottom depth (C) rarefaction curves.ES(n) denotes expected number of species for n abundance.

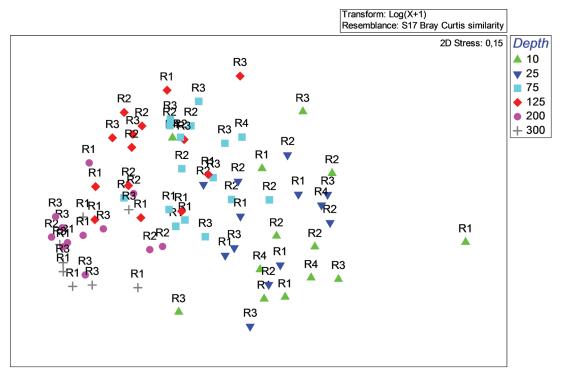


Fig. 5: Non-parametric multidimensional scaling plot performed on \log_{10} -transformed abundance of the crustacean species using Bray-Curtis similarity index. Labels indicate the regions of the hauls.

the contributing species at 10 m; the shrimp *P. pulchri-caudatus* and the crab *C. (G.) longicollis* at 25 m; *C. (G.) longicollis*, *P. prideaux* and *M. lanata* were the contributing species at 75 m; *P. prideaux* and *M. lanata* at 125 m; the commercial pink shrimp, *P. longirostris*, was the only contributing species at the deepest stations (200–300 m) (Table 4).

The highest average dissimilarity was found among the pairs of depth groups far apart from one another (10 m & 200 m 97.90%) whereas the pairs of consecutive depth groups had the lowest average dissimilarity (200 m & 300 m 58.28%; 75 m & 125 m 74.51%). The species *P. prideaux, C. (G.) longicollis, P. armata, D. angulifrons,*

M. lanata, P. pulchricaudatus, H. barbata, P. hathor and C. granulata were the discriminator species between depth groups of the shallowest group (10-25 m) and the intermediate group (75–125 m). Parapenaeus longirostris, P. prideaux, P. armata, D. angulifrons, H. barbata, Plesionika edwardsii and M. lanata were the discriminator species between depth groups of the intermediate group and the deepest group (200–300 m).

The Canonical Correspondence analysis (CCA) showed the correlation between crustacean distribution and environmental variables in the Gulf of Antalya. The first four CCA axes together explain 37.2% of the total variation in the data. The first CCA axis contributed with

Table 4. Similarity table and contributing species, * within each depth station, determined from an analysis of a similarity of percentages, SIMPER. (Avg. Sim.: Average similarity at each bottom depth, Avg. Abn: Average abundance, Avg. Sim; average similarity, Sim/SD; correction term; Con.%: percent contribution and Cum.%; percent cumulative contribution of the similarities, and SD; standard deviation of the similarity).

10 m, Avg sim: 11.94	Avg Abn	Av.Sim	Sim/SD	Con.%	Cum.%
Penaeus pulchricaudatus *	1.81	2.67	0.40	22.34	22.34
Penaeus hathor *	1.57	2.37	0.40	19.87	42.21
Thalamita poissonii *	1.59	2.23	0.32	18.72	60.93
Portunus segnis *	0.90	1.54	0.22	12.87	73.80
Pisa armata	0.63	0.73	0.16	6.12	79.92
Charybdis (G.) longicollis	0.81	0.58	0.17	4.88	84.79
25 m, Avg sim: 23.47					
Charybdis (G.) longicollis *	3.70	15.07	1.30	64.22	64.22
Penaeus pulchricaudatus *	1.87	2.77	0.41	11.80	76.02
Erugosquilla massavensis	1.38	1.59	0.33	6.78	82.79
Penaeus hathor	1.17	0.99	0.24	4.22	87.02
75 m, Avg sim: 27.01					
Pagurus prideaux *	4.03	9.62	0.87	35.63	35.63
Pisa armata *	2.24	3.28	0.52	12.14	47.77
Derilambrus angulifrons	1.65	2.75	0.45	10.18	57.95
Medorippe lanata *	1.90	2.45	0.52	9.07	67.02
Charybdis (G.) longicollis *	2.49	2.43	0.49	9.00	76.02
Homola barbata	1.66	1.60	0.44	5.94	81.96
125 m, Avg sim: 25.25					
Pagurus prideaux *	3.99	10.81	0.84	42.83	42.83
Medorippe lanata *	2.20	4.04	0.61	16.01	58.84
Derilambrus angulifrons	1.36	2.11	0.40	8.37	67.20
Calappa granulata	1.20	2.10	0.42	8.30	75.50
200 m, Avg sim: 40.32					
Parapenaeus longirostris *	6.15	35.57	1.80	88.23	88.23
Pagurus excavatus	1.14	1.14	0.29	2.82	91.05
300 m, Avg sim: 52.82					
Parapenaeus longirostris *	7.82	43.26	3.61	81.90	81.90
Plesionika edwardsii	3.42	8.05	0.65	15.23	97.13

14.4% to the species-environment relation, revealing that the crustacean distribution was positively correlated with the depth gradient, and negatively with fine fragments of bioseston (Appendix 2, Fig. 6). Furthermore, Secchi disk depth, subsurface water salinity and near-bottom chl-a concentration were also slightly correlated to the crustacean assemblage based on the first CCA axis (Appendix 2, Fig. 6).

Bottom type (Figs. 2, 7) showed a high negative correlation with the second CCA axis (Appendix 2, Fig. 6). The study area may be divided by the bottom type in two main regions: the shallower sand-dominated bottom (10-25 m) and the deeper mud-dominated bottoms (125-200 m) on the shelf of the Gulf of Antalya. Therefore, the bottom depth of 75 m was recognized as the intermediate water. Species-environment correlations were significant

on the first and second CCA axes, which were assessed by the Monte Carlo test (F = 3.483, p = 0.0020 for the PCA1 and F = 1.410, p = 0.0020 for all four CCA).

Depending on the bottom depth, the finest bioseston was negatively correlated with the crustacean assemblages across the bottom depth gradient; high concentration of the bioseston between 10 and 75 m depth and low at the greater depths (Figs. 6, 7A, B). The shallower waters were characterized by a high number of *P. pulchricaudatus* and *P. hathor*, the intermediate waters by *C.* (*G.*) longicollis and *P. armata*, and the deeper waters of the shelf by *P. prideaux* and *M. lanata*. The shelf break was characterized by the pink shrimp *P. longirostris* (Fig. 8).

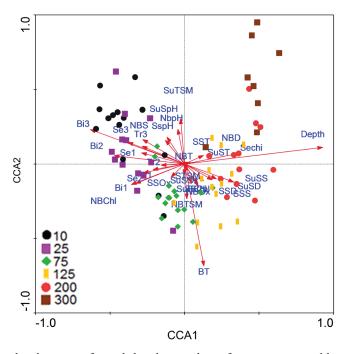


Fig. 6: Biplot of CCA performed on \log_{10} -transformed abundance values of crustacean assemblages and environmental parameters (arrows) for the stations classified by the bottom depths (colors) (see Appendix 2 for abbreviations).

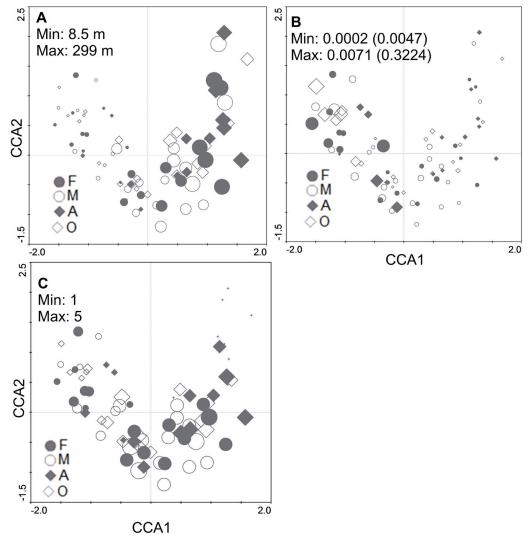


Fig. 7: Monthly (F; February, M; May; A; August and O; October) classified distributions of depth in meters (A), the finest bioseston in g m⁻³ (g m⁻²), Bi3 (B) and bottom types, BT (1-5; 1; rocky, 2; sandy, 3; fine sandy, 4; coarse muddy and 5; muddy bottom) (C) on the configuration of the CCA.

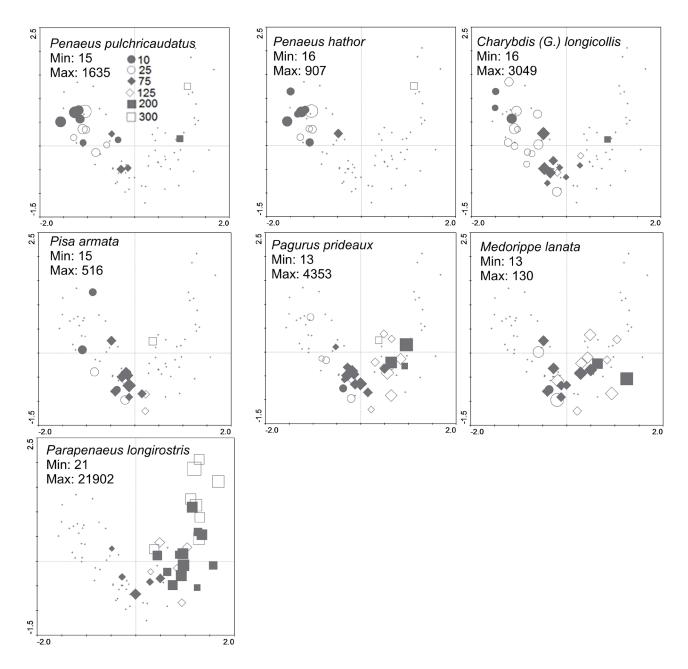


Fig. 8: Abundance (ind km⁻²) distribution of contributing species for each depth at the sampling stations classified by the depths on the CCA plot. Symbol size is proportional to log₁₀-transformed abundance of each species. + denotes zero value.

Discussion

Species distribution

The decapod species were composed of 12 prawns (Dendrobranchiata), 9 shrimps (Caridea: Pleocyemata), 23 crabs (Brachyura: Pleocyemata), and 9 anomurans (Anomura: Pleocyemata). Regional numbers of species varied between 36-39 species in R1-R2 (fishing zone) and 44 species in R3 (no-fishing zone). The shallower bottoms (up to 30 m) in region R2-R3 were characterized by meadows of *P. oceanica* (Mutlu & Balaban, 2018; Olguner & Mutlu, 2020). However, the decapods did not respond with a specific assemblage and aggregation to the meadow beds (Sánchez-Jerez *et al.*, 2000). Some studies (de Juan *et al.*, 2007; Mangano *et al.*, 2013) have revealed

that trawled areas had a higher abundance of burrowing epifaunal scavengers and motile burrowing infauna, were more resilient to the effects of fishing, and those could benefit from the carrion supply and from the increase in organic matter (de Juan *et al.*, 2007; Mangano *et al.*, 2013). Therefore, fishing activities could be one of the factors influencing the decapod assemblage between the regions, and during the year.

The number of species found in the present study was similar to that reported for other regions of the Mediterranean Sea with a few exceptions (Table 5).

The total number of species during each season changed with higher numbers of species in October (n=47) and February (n=45) and lower numbers of species in May (n=31) and August (n=21). Similarly, in Mersin Bay, which neighbors the present study area, the

Table 5. Number of megabenthic crustacean species in different areas of the Mediterranean Sea.

Number of Species	Zone	Study area	Citation*
34 decapods	bathyal zone	Study area	1
58 decapods	entire shelf of Turkey	Aegean Sea	2
79 decapods	Greek shelf-shelf break	Aegean Sea	3
109 decapods, 4 stomatopods	Shelf	Rhodes Island	4
12 stomatopods	Mediterranean Sea	eastern Mediterranean	5,6,7
52 crustaceans; 43 decapods	Shelf-shelf break	off Maltese Island	8
37 decapods	shelf-shelf break	central Mediterranean Sea	9
80 decapods	shelf-middle slope	off Catalan coasts, western Mediterranean	10
36 crustaceans	80 m-160 m depth	Biscay Bay, NE Atlantic	11

^{*1,} Deval et al., 2017; 2, Ateş and Katagan, 2008; 3, Koukouras et al., 1992; 4, Corsini-Foka & Pancucci-Papadopoulou, 2012; 5, Colmenero et al., 2009; 6, Froglia, 2010; 7, Zenetos et al., 2009; 8, Terribile et al., 2016; 9, Colloca et al., 2003; 10, Abello et al., 1988; 11, Le Loc'h et al., 2008.

number of crustacean species was highest during the cold seasons (60 species in February and 53 species in November; Mutlu & Ergev, 2013).

The depth distribution of the number of species was characterized with an increase from 10 m (n=22) to 75 m (n=34), and then a decrease to 125 m (n=29) to 300 m (n=13). The pink shrimp *P. longirostris* was a common species at depths of 100-500 m off Cretan waters (Kallianiotis et al., 2000) which was a similar depth range (75-300 m) as in the present study. *Plesionika heterocarpus* (max abundance at 194 m) was found in the same depth range as P. longirostris (max abundance at 299 m), according to a study in the central Mediterranean Sea of some canyons with bottom depths deeper than 150 m (Pierdomenico et al., 2019). Beyond 40 m depth, the hydrodynamic processes become less effective and the bottom sediments are generally undisturbed. In areas deeper than 40 m, the presence of bio-detrital deposits induced a source of variability in the sediment composition down to 100 m, similar to findings by Karakassis & Eleftheriou (1998) on the Cretan shelf. Sixty megafaunal species were found on the upper slope of the island of Crete (Smith et al., 2000). Smith et al. (2000) determined that the number of different species was similar between the no-trawling area and the pre-trawl samples, which were both characterized by anequal dominance in the numbers of echinoderm, mollusk, and crustacean species. Molluscs were the dominant taxon and the crustaceans were the smallest taxon after the trawling season, which explains the differences in species composition between fishing zone and non-fishing zone found in the present study.

A study conducted in a depth range of 200-900 m in the Antalya Gulf, revealed that the upper slope (shallower than 500 m; 200 and 300 m) was characterized by *P. longirostris* and *P. heterocarpus* (Deval *et al.*, 2017). Other previous studies in the Mediterranean Sea showed that *P. longirostris* had eurybathic distribution and was one of the contributor species to the demersal assemblage, and had an increasing contribution from the middle shelf (50-100 m) and slope edge (100-200 m) (Colloca *et al.*, 2003; D'Onghia *et al.*, 2003; Massutí & Reñones, 2005;

Terribile et al., 2016). In the upper slope Plesionika spp. was identified as one of the contributor species as already found in the studies conducted in the central Mediterranean Sea, Ionian Sea and Balearic Sea (Maynou & Cartes, 2000; Colloca et al., 2003; D'Onghia et al., 2003; Terribile et al., 2016). The discriminator species were P. edwardsii, P. longirostris, P. heterocarpus and P. prideaux within the shelf-slope transition whereas Cartes et al. (1994) found P. heterocarpus as a characteristic species from bottoms of 146 m to 296 m deep in the Catalan Sea.

Number of megabenthic species was low in shallow water stations (10-25 m) in R3 where the drifting dead leaves of P. oceanica substantially covered the bottom in August and October, and in R2 (10 m) where drifting algae was rather high in August. Martin et al. (2005) concluded that the algae acted as a nesting and protective area for 23 decapods and several mobile crabs whereas the drifting Posidonia leaves did not attract the mobile fauna, presumably because they are more compact than the drifting algae. The invasive stomatopod Parasquilla ferussaci was previously recorded in the Aegean Sea (Özcan et al., 2008). In the present study, it was recorded for the first time in Turkish waters of the Levantine Sea. The presence of the invasive knight rock-shrimp Sicyonia lancifer was previously recorded for the Mediterranean Sea from the authors (Patania & Mutlu, 2016) and was also recorded in Iskenderun Bay, Turkey and on the Israeli coast (Gönülal et al., 2016).

Faunistic characteristics

Seasonal density variations in Mediterranean communities were characterized by increases in weight and density of individuals in spring and summer, followed by an abrupt decrease in winter (de Juan *et al.*, 2007). The westernmost Mediterranean Sea has been found to be much richer and higher in terms of number of species, biomass and abundance of non-crustacean megabenthos (DeLaHoz *et al.*, 2018) compared with the easternmost Mediterranean Sea (Garuti, 2015) as was observed in the

current study for the crustaceans (Table 5). In shallower waters, seasonal faunistic variation was likely a consequence of crustacean reproduction, recruitment and migration over time, and particle settlement of sediments due to low currents in summer (Díaz et al., 1990; de Juan et al., 2007; DeLaHoz et al., 2018).

Colloca et al. (2003) reported that the depth in the Mediterranean Sea reduced food availability from the shelf to the slope. This has been suggested as an explanation for the decline in abundance of teleosts and cephalopods andthe increased abundance of crustacean decapods. Parapenaeus longirostris was the most abundant species during the sampling year, followed by P. prideaux and C. (G.) longicollis. After the fishing season, P. longirostris and Solenocera membranacea showed the greatest reductions in abundance, presumably due to trawling activities, in contrast with the results for the anomuran species, Alpheus glaber off the island of Crete (Smith et al., 2000). Similar observations in the abundances of P. heterocarpus and P. edwardsi have been reported in a study conducted off Barcelona Coast (Company & Sarda, 2000).

Deval *et al.* (2017) estimated an average decapod biomass of 38.5 ± 59.3 kg km⁻² at 200 m and 56.7 ± 56.5 kg km⁻² at 300 m, slightly higher than the numbers found in the present study. The distribution of crustacean biomass in the central Mediterranean Sea showed the same depth trend (Colloca *et al.*, 2003). Food reduction at the seafloor affected the epibenthic and demersal assemblage (Pérès, 1985; Sanders & Hessler, 1969) by increasing the biomass of the crustacean decapods in contrast to those of the teleosts and cephalopods (Colloca *et al.*, 2003).

The no-fishing zone was depauperate in species compared to the fishing zone during the present study. This could be due to a comparatively higher proportion of surface infauna and suspension feeders in the no-fishing zone, compared to epifaunal scavengers and motile burrowers in the fishing zone (de Juan et al. 2007). Abello et al. (1988) revealed a discontinuity in the decapod assemblages and faunistic indices between the shelf and the upper slope. This feature was attributed to seasonal variation in environmental parameters such as water temperature at the upper slope, and to the changes in sediment structure that were a function of the steepness of the bottom (Wenner & Read, 1982). The species richness was highest in the coldest season and then decreased gradually to minimal value in the warmest season, followed by an abrupt increment in October. Regional richness showed that the region R3 (no-fishing zone) was the richest zone, followed by a similar richness in R1 and R2 (fishing zone). Abdul Jaleel et al. (2015) and Liu et al. (2020) observed the same results for the macrobenthic epifauna due to the effects of intensive trawling and seasonal environmental gradients, regardless of seasonal fishing pressure. Similar to the species richness, the seasonal richness was the highest in February, while August was the poorest month for richness. Unlike the species richness, the most diverse bottoms were between 25 m and 125 m which could possibly indicate a boundary between photic and disphotic zones or a transition from a sandy to a muddy bottom (Abello *et al.*, 1988). The poorest richness was found at 300 m. Ramalho *et al.* (2018) found similar trends, highlighting the combined effects of intensive trawling and seasonal environmental gradients on the macrobenthic epifauna.

Unlike the species richness and the rarefaction curves, the diversity indices had a similar range between the fishing and no-fishing zones. Liu *et al.* (2020) studied the effects of the trawl fishery on the microbenthic epifaunal assemblages before, during and after fishery seasons. All faunistic parameters, particularly with respect to the macro epibenthic crustaceans, with the exclusion of the evenness index, were significantly higher during, and after, the fishing season compared to the pre-fishing season.

Overall, the crustacean richness, evenness and diversity showed a seasonal cycle from February (winter) through May and August (warmest seasons) to October. This could be due primarily to the existence of disturbances (fishing, pollution and seasonal environmental variation) in the study area. Leopardas *et al.* (2016) underlined the combined effects of intensive trawling and seasonal environmental gradients on the macrobenthic epifauna. The low diversity of the decapod communities was attributed to the hydrographic heterogeneity and to commercial exploitation (Abello *et al.*, 1988). Furthermore, increasing environmental stability with depth allowed for a more mature and varied decapod assemblage (Abello *et al.*, 1988).

Species assemblages and ecological distribution

The distribution of megabenthic crustacean assemblages in the Antalya Gulf can be explained by different environmental factors. The main ecological factors structuring the community were the depth gradient, the depth-related bottom types and the presence of fine fragments of bioseston. Rex (1981) briefly explained that the causes of the depth gradient of the megafauna were associated with nutrient input and trophic relationships, biological interactions and species-area relationships. Megafauna and macrofauna depended on the food availability (annual organic carbon flux) in the Mediterranean Sea (Gambi et al., 2017) and this was valid also for macrofauna in oligotrophic ecosystem (Karakassis & Eleftheriou, 1997). The depth extensions increased linearly with increasing organic carbon flux to the sediments down to 4500 m in the eastern (oligotrophic) and nonlinearly down to 1500 m for the megafauna, and 3000 m for macrofauna in the western (eutrophic) Mediterranean Sea (Gambi et al., 2017). These communities of low trophic consumers were related to depth-dependent environmental parameters, mainly photosynthetic activity in the shallow waters, light availability down to the disphotic region in the intermediate waters, and at greater depths hydrostatic pressure inducing physiological changes (Gage & Tyler, 1992; Cartes et al., 2009; López-Fernández et al., 2013) along with sedimentary parameters (Mutlu & Ergev, 2008). Total organic carbon in the sediment increased with increasing seafloor depth in the northern Levantine Sea, (Mutlu & Ergev, 2008, 2013; Mutlu, 2015). The mega-demersal assemblages including fish were segregated first by the seafloor depths and these contributed mostly to the megabenthic fauna in the central Mediterranean Sea (Colloca *et al.*, 2003). Terribile *et al.* (2016) determined two cluster groups based on the megabenthic species within continental shelf of Malta: circalittoral and shelf edge.

The status of fishing or no-fishing zones played an important role in explaining the species and assemblage distributions. Deval et al. (2017), in Antalya Gulf area, discriminated decapod assemblages at 200 m clearly from those at 300 m on the continental slope area with Margalef's richness index increasing from 1.694 to 1.942, respectively. This was rather higher than was observed in the present study. Some decapod species (M. lanata, Polycheles typhlops, Liocarcinus depurator) were influenced by trawling activities and had lower abundances (Mangano et al., 2013) compared to the no-fishing zone, whereas surface infauna and suspension feeders had higher abundances. Epifaunal scavengers and motile burrowers had higher abundances on trawled bottoms (de Juan et al., 2007). Depth was the main factor structuring the spatial distribution of the demersal fauna for the shelf and slope off Rome (Italy) but was more pronounced for the Continental Shelf (Colloca et al., 2003), off Malta (Dimech et al., 2008; Terribile et al., 2016). The decapod assemblages were different between the Continental Shelf and shelf break/upper slope off the Catalan coast (Abello et al., 1988). In the Mediterranean Sea, the Levantine Intermediate Water (LIW) is usually found below 250 m, which leads to changes in salinity (Serravall & Cristofalo, 1999) and in the decapod community (Castellón & Abelló, 1983). The eastern Mediterranean Sea has attracted the attention of many scientists who have categorized this area as ultra-oligotrophic (Ignatiades et al., 1998). In our study area, the shelf break was more oligotrophic than the shelf in terms of surface and near-bottom water chl-a, seston, bioseston and total suspended mater. Therefore, the distinctive deep-sea fauna was in oligotrophic conditions and are adapted to be stenohaline, stenothermal and stenophotic (Ghidalia & Burgois, 1961; Maynou & Cartes, 2000). The present results clearly indicated that within one of the most oligotrophic environments of the Mediterranean Sea, at least in terms of chl-a and productivity (Moutin & Rainbault, 2001), biodiversity indices remain within acceptable ranges.

Benthic communities are affected by the depth of the seasonal thermocline along the shelf break of the NE Atlantic deep waters (Howell, 2010). Hydrological differences between shelf and slope may also influence demersal fauna as suggested by Colloca *et al.* (2003) who recorded very distinctive crustacean fauna between the shelf-and shelf break. In the Mediterranean Sea, the seasonal water temperature changes were more pronounced on the shelf than on the slope (Colloca *et al.*, 2003). In addition, the bottom type divided the study area into two regions separated by the 75 m isobath: the shallowest sand-dominated bottom (10-25 m) and the deepest

mud-dominated bottoms (125-300 m). Regardless of bottom depth, the number of species changed depending on the sediment structure (sandy, sandy muddy and muddy bottoms) in the Turkish shelf of the Aegean Sea (Ateş & Katagan, 2008). Colloca *et al.* (2003) found a similar fauna distribution pattern in the central Mediterranean Sea, where Peres & Picard (1964) observed that the demersal fauna assemblage exhibited a strong relationship with depth-related sedimentary texture from sandy detritic bottom to muddy detritic bottoms.

Conclusions

In an oligotrophic area (the Gulf of Antalya), we assert that crustacean diversity is still at an acceptable level, with 53 decapod species compared to the other euphotic areas of the western Mediterranean. Almost all invasive species were found at shallower depths where the physical and environmental conditions were likely ideal for their settlement. The presence of these invasives likely contributes additional pressure to this ecosystem. More research should be regularly conducted in Antalya Bay to monitoring the status of marine species invasions in the Levantine Basin. Crustacean community variability was driven primarily by depth and depth-related bottom types, and secondarily by the presence to fine fragments of bioseston. Based on faunistic indices and ecological parameters, two main groups of crustacean assemblages were identified in the Gulf of Antalya separated by a depth of 75 m. Furthermore, the inshore region (10-75 m depth) could be subdivided between the shallowest waters (10-25 m) containing a high species diversity characterized by muddy-sand communities and communities associated with P. oceanica meadows, and intermediate waters (75 m), where the crustacean assemblages composition was characterized by a sand community with the highest number of species with C. (G.) longicollis and P. armata as common species. The offshore region (125-300 m depth) could be subdivided into intermediate waters of 125m depth, characterized with sand crustacean community, and the deepest oligotrophic waters (200 -300 m) of the shelf-shelf break, characterized by muddy sediment structure with few numbers of species and low number of invasive species. The shelf break (300 m) was typified with the commercial *P. longirostris*.

Acknowledgements

The data in the presented work was derived from experimental trawl surveys within a framework of the project number: 2014.01.0111.001 coordinated by Erhan Mutlu and supported by the Scientific Research Project Coordination Unit of Akdeniz University. The present study was part of the MSc thesis of Annalisa Patania, co-supervised by Erhan Mutlu. The authors would like to thank Ahmet Şahin, Claudia Miglietta, Ilaria de Meo, Cansu Balaban (Olguner) and M. Tunca Olguner for their help on board. The authors thank Mark Benfield (Lou-

isiana State University) for providing English grammar revision and comments, and Georgia Tickle for editing English of the first draft of the manuscript. We are indebted to thank all anonymous referees for very kind of their helps to revise the manuscript significantly.

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Appendix 1. Native and non-native crustacean species with their annual and seasonal dominance, D (%), frequency of occurrence, FO (%) and numerical occurrence, NO (%) in the sampling months and year, and ranges of abundance, A (minimum-maximum, ind/km²), biomass, B (minimum-maximum, kg/km²) and bottom depth, D (minimum-maximum, depth where the maximum abundance ocurred) of the species, and their status, Sts (MS: Native species of Mediterranean Sea; AS: Alien species).

Ondo Cracios/Months		Mox			1		٥	Ootobou		1407	Lohanour]		Dose		3
Orac-Species/Months				1	2	Ş		ionor			uar y		<			Naliges		SIS
ı	ם 	<u> </u>		a	S S		_ _	FO			S S		S S	S	A	B	D	
Decapoda																		
Aegaeon cataphractus (Olivi, 1792)	13.6	3.1	0.3	5.9	2.4).1 2	23.8	3.8	0 5.	3 0	0 6	1 12	12.7 2.	6 0.	5 13-216	0.013-0.233	57-194,94	MS
Aegaeon lacazei (Gourret, 1887)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0 5.	3 0	0 6	7	3 0.	3 0.	153-153	0.147-0.147	290-290,290	MS
Alpheus migrans Lewinsohn & Holthuis, 1978	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0 5.	3 0	0 6	1 1.	3 0.	3 0.) 25-25	0.001 - 0.001	128-128,128	AS
Alpheus rapacida de Man, 1908	0.0	0.0	0.0	0.0	0.0	7 0.0	8.4	0 8.0	0 0	0 0	0 0	0 1.	1.3 0.	3 0.) 16-16	0.079-0.079	25.7-25.7,25.7	AS
Anapagurus chiroacanthus (Lilljeborg, 1856)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0 5.	3 0	9 0.1		1.3 0.	3 0.) 25-25	0.008-0.008	128-128,128	MS
Anapagurus petiti Dechancé & Forest, 196)	0.0	0.0	0.0	0.0	0.0	7 0.0	4.8	0.8 0.	2 5.3	3 0	9 0.1	1 2.5	5 0.	5 0.	1 32-81	0.009-0.130	127-130.6,130.6	MS
Calappa granulata (Linnaeus, 1758)	18.2	1.1	0.2	11.8	4.8	3.1	9.0	3.1 0.	2 10	10.5 1	1.8 0.	6 15	15.2 3.1	1 0.	3 12-90	0.196-15.044	87-290,290	MS
Charybdis (Charybdis) hellerii (A. Milne-Edwards, 1867)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0 10	10.5 1	0.8.1	0.4 2.5	5 0.	5 0.1	1 25-71	0.138-0.978	11.2-77,77	AS
Charybdis (Goniohellenus) longicollis Leene, 1938	36.4	8.2	3.6	11.8	4.8	1.2	42.9	6.9	13.8 36	36.8 6	6.3 3	3.3 32.9	8.9 6.8	8 7.2	2 16-3049	0.089-28.767	11.5-188,84.2	AS
Chlorotocus crassicornis (A. Costa, 1871)	4.5	1.0	0.2	0.0	0.0	9.0	9.5	1.5 0.	3 5.3		0.9	0.1 5.1	1 1.0	0 0.	2 16-87	0.013-0.063	137-299,165.8	MS
Dardanus arrosor (Herbst, 1796)	18.2	4.1	9.4	0.0	0.0	7 0.0	4.8	0.8 0.1		10.5	1.8 0	0.2 8.9	9 1.8	8 0.2	2 11-82	0.033-0.285	76.5-194,77	MS
Dardanus calidus (Risso, 1827 in [Risso, 1826-1827])	0.0	0.0	0.0	5.9	2.4	2.	8.4		0.0 0.0		0.0	0.0 2.5	5 0.5	5 0.0	18-21	0.109-0.215	31.6-265.1,265.1	MS
Derilambrus angulifrons (Latreille, 1825)	18.2	4.1	0.3	23.5	9.5	1.0 2	23.8		0.3 21.1		3.6	0.9 21.5	5. 4.5	5 0.	5 13-68	0.005-0.422	12-286.4,76.5	MS
Dromia personata (Linnaeus, 1758)	9.1	2.0	0.1	0.0	0.0	9.0	9.5	1.5 0.		10.5	1.8 0	2 7.6	6 1.6	5 0.3	3 13-197	0.078-0.380	22.7-128.8,94	MS
Goneplax rhomboides (Linnaeus, 1758)	4.5	1.0	0.0	0.0	0.0	0.0	9.5	1.5 0.2	2 0.0		0.0	0 3.8	8 0.	8 0.1	17-64	0.013-0.058	25-84.2,84.2	MS
Gonioinfradens paucidentatus (A. Milne-Edwards, 1861)	0.0	0.0	0.0	0.0	0.0	7 0.0	8.4	0.8 0.0	0.0		0.0	0 1.	1.3 0.3	3 0.0	16-16	0.105-0.105	25.7-25.7,25.7	AS
Homola barbata (Fabricius, 1793)	27.3 (6.1	6.0	0.0	0.0	9.0	9.5	1.5 0.1	1 21.1		3.6	1.1	15.2 3.1	1 0.	5 11-154	0.005-0.302	73.7-154.9,77	MS
Inachus dorsettensis (Pennant, 1777)	22.7	5.1	0.3	0.0	0.0	0.0	0.0	0.0 0.0		15.8 2	2.7 0	3 10.1	.1 2.	1 0.	2 13-43	0.005-0.074	76.5-189,77.2	MS
Ixa monodi Holthuis & Gottlieb, 1956	0.0	0.0	0.0	11.8	4.8	.3 2	8.1	0.8 0.0	0 5.3		0.9 0.1	1 5.	1 1.0	0 0.1	13-26	0.009-0.089	21.5-78.3,78.3	AS
Latreillia elegans P. Roux, 1830 [in P. Roux, 1828-1830]	4.5	1.0	0.0	0.0	0.0	0.0	0.0	0.0 0.0		10.5 1	1.8 0.4	4 3.8	8 0.8	8 0.1	12-51	0.002-0.006	115-189,189	MS
Liocarcinus depurator (Linnaeus, 1758)	0.0	0.0	0.0	17.6	7.1	1.7	.5	.5 0.1		10.5	1.8 0.	1 8.9	9 1.8	8 0.2	2 13-157	0.019-0.401	11-189.4,189.4	MS
Lysmata seticaudata (Risso, 1816)	0.0	0.0	0.0	0.0	0.0	7 0.0	8.4	0.8 0.1	1 0.0		0.0	0 1.	3 0.	3 0.0	53-53	0.017-0.017	82.3-82.3,82.3	MS
Macropodia longirostris (Fabricius, 1775)	9.1	2.0	0.7	0.0	0.0	0.0	0.0	0.0 0.0		10.5	0.8.1	2 5.	1 1.0	0 0.3	3 11-218	0.003-0.062	23-127,23	MS
Macropodia tenuirostris (Leach, 1814 [in Leach, 1813-1815])	4.5	1.0	0.1	5.9	2.4	2.0	8.8	0.8 0.	0.0 10	10.5 1	1.8 0.	2 6.3	3 1.3	3 0.1	17-43	0.003-0.015	10.7-77.2,77.2	MS
Neomaja goltziana (d'Oliveira, 1889)	9.1	2.0	0.1	0.0	0.0	0.0	0.0	0.0 0.0	0 5.3		0.9	1 3.8	8 0.8	8 0.0	13-22	0.148-0.292	77-128.8,77	MS
Maja sp.	0.0	0.0	0.0	5.9	2.4	7.7	4.8	0.8 0.0	0.0		0.0 0.0	0 2.5	5 0.5	5 0.0	20-20	0.044-0.048	74-77.7,74	MS
Maja squinado (Herbst, 1788)	0.0	0.0	0.0	5.9	2.4 ().2	19.0	3.1 0.	3 5.3		0.9	2 7.6	6 1.6	6 0.2	20-53	0.324-5.366	22.7-188,82.3	MS
Medorippe lanata (Linnaeus, 1767)	36.4	8.2	1.5	17.6	7.1	1.2 2	23.8	3.8 0.6	6 26.3	.3	5 1.	3 26.6	6 5.5	5 1.1	13-130	0.044-1.961	13.5-194,77.2	MS
Metapenaeopsis aegyptia Galil & Golani, 1990	4.5	1.0	0.0	0.0	0.0	0.0	14.3	2.3 7.	5 10	10.5	1.8 0.	5 7.6	6 1.	6 2.9) 16-3049	0.021-9.048	8.5-84.2,84.2	AS
Metapenaeopsis mogiensis consobrina (Nobili, 1904)	0.0	0.0	0.0	0.0	0.0	7 0.0	4.8	0.0 8.0	0 5.3	3 0	9 0.1	1 2.5	5 0.	5 0.0) 11-16	0.024-0.026	11-25.7,25.7	AS
Metapenaeus monoceros (Fabricius, 1798)	4.5	1.0	0.0	0.0	0.0	7 0.0	4.8	0.0 8.0	0 5.3	3 0	0 6	1 3.8	8 0.	8 0.0	13-15	0.067-0.336	11-57,23	AS
Pagurus prideaux Leach, 1815 [in Leach, 1815-1875]	40.9	9.5	11.9	23.5	9.5	5.0 6	1.9	0.0 23	23.0 21	.1 3	.6 23.	· ·	38.0 7.	9 18.7	7 13-4353	0.025-7.020	13.5-265.1,130	MS
																	•	

Appendix 1 Continued

Paguristes eremita (Linnacus, 1767) Per FO NO D FO Pagurus elatus Fabricius, 1775 4.5 1.0 0.1 0.0 0.0 Pagurus excavatus (Herbst, 1791) 13.6 3.1 2.2 0.0 0.0 Pagurus excavatus (Herbst, 1791) 13.6 3.1 2.2 0.0 0.0 Pagurus sp. 0.0 0.0 0.0 0.0 0.0 0.0 0.0 Pagurus sp. 1.0 1.0 0.0	ON	D I	FO N	ON				1	2		,	-	
1846) 1916 1917 1918 1918 1918 1918 1918 1918 1919					9	0N C	<u> </u>	Š	2	V	B	2	
0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	4.8	0.8 0	0.0 0.0	0.0	0.0	2.5	0.5	0.0	21-27	0.006-0.014	21.9-77,77	MS
13.6 3.1 2.2 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	0.0	0.0	0.0 5.3	3 0.9	9 0.1	1.3	0.3	0.0	19-19	0.049-0.049	298.6- 298.6,298.6	MS
9.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	4.8	0.8 0	0.0 21.	1 3.6	8.0 9	10.1	2.1	6.0	17-742	0.028-1.158	78.3-195,87	MS
31.8 7.1 66.2 41.2 16.7 9.1 2.0 0.3 5.9 2.4 4.5 1.0 0.1 0.0 0.0 0.0 0.0 11.8 4.8 4.5 1.0 0.1 5.9 2.4 4.5 1.0 0.1 5.9 2.4 0.0 0.0 0.0 11.8 4.8 13.8 3.1 0.5 5.9 2.4 9.1 2.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0	0.0	8.4	0.8 1	1.0 0.0	0.0	0.0	1.3	0.3	0.4	436-436	0.607-0.607	165.8- 165.8,165.8	
9.1 2.0 0.3 5.9 2.4 4.5 1.0 0.1 0.0 0.0 0.0 0.0 11.8 4.8 4.5 1.0 0.1 5.9 2.4 4.5 1.0 0.1 5.9 2.4 0.0 0.0 0.0 0.0 0.0 31.8 7.1 0.8 5.9 2.4 31.8 7.1 0.8 5.9 2.4 9.1 2.0 6.7 0.0 0.0 0.0 0.0 0.0 0.0 0.0 9.1 2.0 6.7 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	8.69	42.9	6.9 32	32.1 36.8	8 6.3	3 44.7	7 38.0	7.9	49.4	21- 21902	0.158- 126.771	73.7-299,299	MS
4.5 1.0 0.1 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	1 0.1	38.1 (6.2 1	1.5 10.5	5 1.8	8 0.2	16.5	3.4	0.7	16-235	0.138-6.840	10.5-130.6,57	AS
0.0 0.0 11.8 4.8 4.5 1.0 0.1 5.9 2.4 0.0 0.0 0.0 0.0 0.0 31.8 7.1 0.5 5.9 2.4 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.1 2.0 0.1 0.0 0.0 0.0 0.0 0.0	0.0	19.0	3.1 2	2.4 36.8	_	3 2.0	15.2	3.1	1.3	16-907	0.050-10.085	8.5-298.6,25.7	AS
4.5 1.0 0.1 5.9 2.4 0.0 0.0 0.0 0.0 0.0 31.8 7.1 0.8 5.9 2.4 1.0 1.4 5.9 2.4 2.1 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	3 0.3	19.0	3.1 0	0.6 26.3	-			•	9.0	15-1635	$\overline{}$	8.5-298.6,25.7	AS
13.6 3.1 0.5 5.9 2.4 0.0 0.0 0.0 0.0 0.0 31.8 7.1 0.8 5.9 2.4 1 Middendorf, 4.5 1.0 1.4 5.9 2.4 9.1 2.0 6.7 0.0 0.0 0.0 0.0 0.0 0.0 9.1 2.0 0.1 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	1 0.3	14.3	2.3 0	.7 0.0	0.0	0.0	6.3	1.3	0.3	13-236	0.134-3.884	21.5-84.2,84.2	MS
0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 31.8 7.1 0.8 5.9 2.4 4.5 1.0 1.4 5.9 2.4 9.1 2.0 6.7 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0	1 0.7	23.8	3.8 4	4.2 42.1	1 7.2	2 4.9	21.5	5.4.5	2.8	16-227	0.004-9.035	11-94,11.2	AS
von Middendorf, 4.5 1.0 6.8 5.9 2.4 () 9.1 2.0 6.7 0.0 0.0 0.0 0.0 0.0 0.0 0.0 9.1 2.0 0.1 0.0 9.1 2.0 0.1 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	0.0	0.0	0.0 5.3	3 0.9	9 0.1	1.3	0.3	0.0	17-17	0.002-0.002	189-189,189	MS
von Middendorf, 4.5 1.0 1.4 5.9 2.4 1) 9.1 2.0 6.7 0.0 0.0 0.0 0.0 0.0 0.0 0.0 9.1 2.0 0.1 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0	0.2	23.8	3.8 0	0.9 21.1	1 3.6	5 3.0	21.5	4.5	1.2	15-516	0.016-0.736	10.7-265.1,76.5	MS
() 9.1 2.0 6.7 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0	4 2.8	9.5	1.5 3	3.2 10.5	5 1.8	8 0.8	7.6	1.6	2.1	13-1390	0.025-5.392	137-299,258.3	MS
0.0 0.0 0.0 0.0 0.0 9.1 2.0 0.1 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	4.8	0.8	0.3 15.8	8 2.7	7 4.1	7.6	1.6	3.1	17-2453	0.008-1.673	84.2-299,194	MS
9.1 2.0 0.1 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	4.8	0.8	0.1 5.3	3 0.9	9 0.3	2.5	0.5	0.1	33-73	0.379-0.813	10.5-11,11	MS
0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	4.8	0.8	0.2 5.3	3 0.9	9 0.1	5.1	1.0	0.1	18-66	3.378-12.642	10.5-11.7,10.5	AS
0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	4.8	0.8 0	0.2 0.0	0.0	0.0	1.3	0.3	0.1	89-89	0.051-0.051	137-137,137	MS
0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	4.8	0.8 0	0.0 5.3	3 0.9	9 0.1	2.5	0.5	0.0	21-28	0.055-0.068	46-84.2,46	AS
0.0 0.0 0.0 11.8 4.8	0.0	9.5	1.5 0	0.2 5.3	3 0.9	9 0.2	3.8	0.8	0.1	40-52	0.028-0.106	137-188,165.8	MS
	3 4.1	9.5	1.5 2	2.6 15.8	8 2.7	7 0.9	8.9	1.8	1.6	16-1111	0.012-1.429	10.7-31.6,11.5	AS
Trachysalambria curvirostris (Stimpson, 1860) 0.0 0.0 0.0 5.9 2.4	1 0.1	9.5	1.5	0.5 0.0	0.0	0.0	3.8	0.8	0.2	16-218	0.016-0.279	12.3-141.1,25.7	AS
Isopoda													
Ceratothoa oestroides (Risso, 1816) 0.0 0.0 0.0 0.0 0.0 0.0	0.0	4.8	0.8 0	0.2 0.0	0.0	0.0	1.3	0.3	0.1	<i>L</i> 9- <i>L</i> 9	0.024-0.024	21.9-21.9,21.9	MS
Nerocila bivittata (Risso, 1816) 0.0 0.0 0.0 0.0 0.0 0.0	0.0	0.0	0.0	0.0 5.3	3 0.9	9 0.3	1.3	0.3	0.1	61-61	0.078-0.078	195-195,195	MS
Rocinela dumerilii (Lucas, 1849) 4.5 1.0 0.0 0.0 0.0	0.0	0.0	0.0	0.0 5.3	3 0.9	9 0.1	2.5	0.5	0.0	12-26	0.019-0.036	78.3-115,78.3	MS
Stomatopoda													
Erugosquilla massavensis (Kossmann, 1880) 18.2 4.1 0.4 0.0 0.0	0.0	14.3	2.3 0	0.4 10.5	5 1.8	8 0.7	11.4	1 2.4	0.4	20-93	0.121-1.121	8.5-117.7,25.7	AS
Parasquilla ferussaci (Roux, 1828) 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	4.8	0.8 0	0.0 0.0	0.0	0.0 0	1.3	0.3	0.0	17-17	0.054-0.054	165.8- 165.8,165.8	MS
Squilla mantis (Linnaeus, 1758) 0.0 0.0 0.0 0.0 0.0 0.0 0.0	0.0	9.5	1.5 0	0.1 0.0	0.0	0.0	2.5	0.5	0.0	11-17	0.401-0.841	130.6- 165.8,165.8	MS

Appendix 2. Summary of statistical measures of environmental parameters of CCA correlation (prefix of variables; SS: sea surface, Su: Sub-surface and NB: Near-bottom water).

Variables	Abbr.	PCA1	PCA2		
Bottom depth (m)	Depth	0.8818	0.2286		
Total Suspended Matter (mg l-1)	STSM	0.0232	-0.0388		
	SuTSM	-0.0049	0.2722		
	NBTSM	0.0146	-0.2156		
Secchi disk depth (m)	Secchi	0.3587	0.0506		
Oxygen (mg l ⁻¹)	SSOx	-0.0907	-0.0751		
	SuSOx	-0.0010	-0.0645		
	NBOx	0.0886	-0.1381		
Temperature (°C)	SST	0.0345	0.0070		
	SuST	0.0218	0.0077		
	NBT	-0.0061	0.0113		
Salinity (PSU)	SSS	0.2102	-0.1009		
	SuSS	0.3210	-0.1247		
	NBS	-0.2685	0.1600		
pH	SSpH	-0.1261	0.1531		
	SuSpH	-0.0438	0.2175		
	NbpH	-0.1155	0.1717		
Density, σ,	SSD	0.1268	-0.1075		
·	SuSD	0.1826	-0.1050		
	NBD	0.1277	0.0480		
Chl- <i>a</i> (mg l ⁻¹)	SSChl	0.0853	-0.1243		
	SuSChl	0.0482	-0.1224		
	NBChl	-0.3473	-0.1159		
Seston - 1 mm (g m ⁻³)	Se1	-0.2854	0.0818		
Seston $-0.5 \text{ mm (g m}^{-3})$	Se2	-0.2742	-0.0425		
Seston $-0.063 \text{ mm (g m}^{-3})$	Se3	-0.3725	0.1500		
Bioseston - 1 mm (g m ⁻³)	Bi1	-0.3225	-0.1069		
Bioseston – 0.5 mm (g m ⁻³)	Bi2	-0.4610	0.0704		
Bioseston -0.063 mm (g m ⁻³)	Bi3	-0.6203	0.2401		
Tripton $-1 \text{ mm } (\text{g m}^{-3})$	Tr1	-0.2092	-0.0255		
Tripton $-0.5 \text{ mm } (\text{g m}^{-3})$	Tr2	-0.1595	0.0000		
Tripton -0.063 mm (g m ⁻³)	Tr3	-0.2798	0.1212		
Bottom types	BT	0.1034	-0.6290		
Eigen values		0.677	0.459	0.330	0.282
Species-environment correlations		0.977	0.910	0.908	0.865
Cumulative percentage variance					
of species data		7.5	12.6	16.2	19.4
of species-environment relation		14.4	24.2	31.2	37.2