



Mediterranean Marine Science

Vol 18, No 2 (2017)



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doi: 10.12681/mms.1980

To cite this article:

MOSBAHI, N., DAUVIN, J., & NEIFAR, L. (2017). Polychaete fauna from the intertidal zone of the Kneiss Islands (central Mediterranean Sea). *Mediterranean Marine Science*, *18*(2), 215–228. https://doi.org/10.12681/mms.1980

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 http://dx.doi.org/10.12681/mms.1980

Polychaete fauna from the intertidal zone of the Kneiss Islands (central Mediterranean Sea)

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Handling Editor: Argyro Zenetos

Received: 14 November 2016; Accepted: 20 March 2017; Published on line: 13 July 2017

Abstract

The spatial and temporal distribution, abundance and assemblage structure of polychaete communities in the Kneiss Islands (central Mediterranean Sea) was studied at 42 stations selected among seagrass *Zostera* (*Zosterella*) noltei Hornemann meadows and unvegetated habitats sampled from April 2014 to January 2015. The Kneiss Islands represent a site of international interest in terms of their ornithological diversity (Important Bird Area, Ramsar Site and SPAMI). A total of 18,026 individuals and 92 species of polychaetes belonging to 25 families are identified. Analysis of the trophic structure reveals that the majority of stations are strongly dominated by deposit feeders (51.2%), followed by carnivores (34.8%) and suspension feeders (14%). Polychaete diversity and abundance are higher on the vegetated stations. Four polychaete assemblages are identified using MDS analysis. The distribution of polychaete assemblages are influenced by edaphic factors, particularly sediment structure and organic matter content. Seasonal variations of the polychaete community patterns at 20 stations show a maximum abundance and diversity during spring and summer and a minimum during winter. Seasonal fluctuations follow the seasonal variations of the environmental factors such as temperature and salinity, and correspond also to the lifestyle of the dominant species.

Keywords: Polychaete assemblages, spatial-temporal variations, sediment structure, *Zostera noltei*, trophic structure, Mediterranean Sea.

Introduction

Polychaetes are one of the most important groups of benthic organisms in marine ecosystems, because of their high species richness, high density and biomass, as well as their high level of tolerance to adverse effects (pollution and natural disturbance); they also play a major role in ecosystem processes such as secondary production, provision of food resources, nutrient recycling and pollutant metabolism. Some species of polychaetes are ecosystem engineers (e.g. *Diopatra neapolitana*) or bioturbators (e.g. *Arenicola marina*). These species increase the biodiversity of the sediment and its structure (Carvalho *et al.*, 2005; Kedra *et al.*, 2014).

Polychaetes are considered to be the component of benthic communities most characteristic of soft-bottom sediments (Arvanitidis *et al.*, 2002). As such, polychaete species can act as appropriate indicators in both monitoring and conservation programmes (Del-Pilar- Ruso *et al.*, 2010; Mikac *et al.*, 2011), and have been frequently utilized as indicators of environmental conditions. The use of polychaetes in marine environmental assessment is potentially very powerful because: (1) they are the most

abundant macrobenthic group, readily available and easy to sample, but currently difficult to identify due to the numerous revisions (see Dauvin, 2005); (2) they include a great diversity of trophic guilds and reproductive strategies that could account for their success in many environments; (3) they respond to disturbances induced by different kinds of pollution reflecting quantifiable changes in the community structure, and, since they are effective in identifying major changes in benthic communities following disturbances, they have been used in several ecological indices. Indeed, the analysis of polychaete assemblage structure has been shown to be an efficient tool for assessing environmental health, and is commonly used as a biological criterion for water quality and also in monitoring studies (Musco et al., 2011; Dauvin et al., 2016). Moreover, polychaetes are classically considered as poor biogeographic indicators because their distribution tends to reflect ecological rather than geographic factors (Kupriyanova & Badyaev, 1998).

In the Mediterranean Sea, many polychaete inventories have been produced, especially in the Western Basin, including those due to the work of Fauvel (1940); Bellan (1964) and Castelli *et al.* (2008). In the eastern

Mediterranean, studies on polychaetes have been carried out, among others, by Kurt-Şahin & Çinar (2009), Çinar *et al.* (2012), Faulwetter *et al.* (2011), Dorgham *et al.* (2013, 2014), D'Alessandro *et al.* (2016) and Kurt-Sahin & Çinar (2016).

Following the pioneering research of McIntosh (1912) and Fauvel (1924 a, b), rather few studies have focused on the polychaete fauna of Tunisia (central Mediterranean), including the work of Westheide (1972) and Zghal & Ben Amor (1980). More recently, several ecological studies have been carried out along the northwestern and eastern Tunisian coast by Ayari et al. (2009) and Zaâbi et al. (2009, 2010 and 2012). Zaâbi et al. (2012) presents an inventory of polychaete species from the north-east coast of Tunisia, along with a historic review of the previous literature from Tunisian coasts. Altogether, 40 families, 146 genera, and 375 polychaete species are currently known from this area. This inventory accounts for 36.54 % of the polychaete species estimated for the whole Mediterranean, which is currently 1,172 species (Zenetos et al., 2010). The polychaete communities on the north coast of Tunisia are mainly structured by environmental conditions and types of sediment (Zaâbi et al., 2010).

Despite the work cited above, polychaete annelids from the south-eastern Tunisian coast (i.e. Gulf of Gabès) remain relatively poorly studied compared with those on the northern coast, and our knowledge is based on rather scarce and fragmented data (El Lakhrach *et al.*, 2012; Mosbahi *et al.*, 2015, 2016). In fact, the inventory, ecology and patterns of polychaete distribution remain largely unknown in this southern area.

The objectives of this study of the polychaete fauna from the mudflats of the Kneiss Islands in the Gulf of Gabès are: 1) to analyse the spatial and temporal patterns of polychaete assemblages, and 2) to identify the role of the main environmental factors in relation to the distribution of polychaete assemblages.

Materials and Methods

Study area

The Kneiss Islands are located in the north-western part of the Gulf of Gabès, between latitudes 34°10′-34°30′N and longitudes 10-10°30′E (south-eastern Tunisia), characterized by an extensive continental shelf (Fig. 1). This area displays the highest tidal range in the Mediterranean Sea; the tide is semi-diurnal, with a distinct spatial pattern in amplitude showing a maximum of 2.3 m at the margins and decreasing towards the middle of the gulf at spring tides (Sammari *et al.*, 2006). The intertidal zone around the Kneiss Islands extends over an area of 220 km². At low tide, the Kneiss Islands are surrounded by vast mud and sand flats covered by eel-

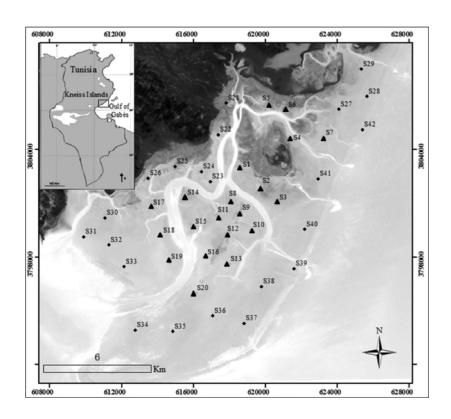


Fig. 1: Map of the study area showing location of stations sampled in April 2014 (♦) and seasonally (▲) from April 2014 to January 2015.

grass beds *Zostera* (*Zosterella*) *noltei* Hornemann (Bali & Gueddari, 2011). The Kneiss Islands represent a site of international interest in terms of their ornithological diversity, which was declared a national nature reserve in 1993, and then established as a "Specially Protected Area of Mediterranean Importance" (SPAMI) in 2001, an "Important Bird Area" (IBA) in 2003 and designated as a "RAMSAR site" since 2007.

Sampling and laboratory procedures

Four sampling expeditions were carried out at 42 stations (Fig.1; Table 1), with samples being collected

at low tide using a 15-cm-diameter corer, covering a surface area of about 0.0225 m². The depth of sampling was about 20 cm. Five replicates were collected at each station, representing a total sampled area of 0.112 m². A total of 42 stations were sampled in April 2014, and then, to identify the seasonal changes in polychaete diversity, 20 stations (numbered 1 to 20) were sampled four times (in April, July and October 2014, and in January 2015); all the 20 stations are covered by *Zostera* (*Zosterella*) *noltei* mudflats unperturbed by human activities. The station positions were accurately determined using a GPS (WGS84). Each sample was immediately sieved

Table 1. Main characteristics of the sampled stations: FS: fine sand; MS: medium sand; CS: coarse sand; M: mud; OM: organic matter content; P: present; A: absent.

Sites	Coordinates (WGS84)			Sediment features			Vegetation	
	Latitude N	Longitude E	Sand (%)	Mud (%)	Q50 (mm)	Sediment type	OM (%)	(Zostera noltei meadows)
S1	38.02851°	32.618667°	69.18	30.82	0.20	FS	16.1	P
S2	38.01975°	32.619772°	96.40	3.60	0.17	FS	17.3	P
S3	38.01022°	32.620687°	98.70	1.30	0.18	FS	15.8	P
S4	38.04376°	32.621468°	86.62	3.38	0.16	FS	18.1	P
S5	38.06586°	32.619753°	41.11	58.89	0.058	M	19.2	P
S6	38.06205°	32.621201°	27.80	72.20	0.053	M	21.2	P
S7	38.04642°	32.623278°	94.63	5.37	0.17	FS	14.8	P
S8	38.01251°	32.617905°	87.01	2.99	0.45	MS	12.8	P
S9	38.00451°	32.618629°	76.60	23.40	0.38	MS	11.2	P
S10	37.99498°	32.619239°	72.89	17.11	0.36	MS	8.8	P
S11	38.00336°	32.617257°	64.92	25.08	0.32	MS	10.2	P
S12	37.99270°	32.617791°	78.48	21.52	0.37	MS	9.8	P
S13	37.97593°	32.617981°	82.63	17.37	0.48	MS	12.6	P
S14	38.01289°	32.615581°	77.38	22.62	0.52	MS	10.3	P
S15	37.99689°	32.616019°	94.46	5.54	0.72	MS	11.6	P
S16	37.97974°	32.616705°	62.18	37.82	0.56	MS	7.5	P
S17	38.00756°	32.613675°	73.80	26.20	0.63	MS	12.3	P
S18	37.99193°	32.614247°	78.69	21.31	0.68	MS	7.8	P
S19	37.97707°	32.614666°	82.21	17.79	0.49	MS	6.4	P
S20	37.95954°	32.616114°	86.96	13.04	0.67	MS	5.8	P
S21	38.06586°	32.617829°	32.36	67.64	0.062	M	18.2	P
S22	38.04833°	32.617371°	28.79	71.21	0.048	M	22	P
S23	38.02204°	32.616952°	43.14	56.86	0.062	M	20.3	P
S24	38.02775°	32.616438°	37.57	62.43	0.050	M	16.8	P
S25	38.03042°	32.614971°	40.02	59.98	0.048	M	15.4	P
S26	38.02394°	32.613485°	21.91	78.09	0.040	M	16.2	P
S27	38.06243°	32.624097°	94.85	5.15	0.21	FS	14.8	P
S28	38.06967°	32.625640°	31.59	68.41	0.060	M	18.3	A
S29	38.08491°	32.625335°	42.16	57.84	0.056	M	20.2	P
S30	38.00184°	32.611084°	45.29	54.61	0.046	M	19.6	P
S31	37.99117°	32.609903°	36.08	63.92	0.052	M	16.5	A
S32	37.98660°	32.611313°	99.26	1.74	0.31	MS	14.6	A
S33	37.97441°	32.612151°	61.02	39.98	0.30	MS	6.9	A
S34	37.93897°	32.612761°	98.11	1.89	1.22	CS	2.2	A
S35	37.93821°	32.614857°	96.84	3.16	1.11	CS	2.5	A
S36	37.94697°	32.617086°	62.33	37.67	1.14	CS	7.3	P
S37	37.94278°	32.618814°	89.82	10.18	1.02	CS	2.1	A
S38	37.96336°	32.619791°	94.56	5.44	1.02	CS	2.4	P
S39	37.97326°	32.621601°	97.20	2.80	1.18	CS	3.2	A
S40	37.99536°	32.622192°	88.84	11.16	1.31	CS	2.7	A
S41	38.02356°	32.622954°	98. 86	1.14	0.14	FS	14.5	P
S42	38.05100°	32.625392°	78.19	21.81	1.72	CS	3.5	A

(1 mm mesh) and the retained fractions were preserved in 5 % formaldehyde saline solution. In the laboratory, after staining with Rose Bengal, polychaete fauna were sorted, identified under the stereomicroscope, and then counted. Sexual maturity was determined by microscopic inspection in order to find gametes.

Also, the topmost 3 cm of the sediment sample was sampled at each station and sediment fractions were analysed and characterized according to the methods of certain authors (Zaâbi *et al.*, 2009). The organic matter content of the sediment was estimated by the method of Do *et al.* (2011). Moreover, some parameters of the water column, such as, temperature, salinity and pH were measured in situ during each expedition using a thermometer (WTW LF 196), a salinometer (WTW LF 196), and a pH meter (WTW 3110).

Data analyses

Univariate analysis

The data allow us to calculate abundance (ind.m⁻²) and the most commonly used biodiversity indices for the polychaete fauna at each station, i.e. Shannon-Weaver's diversity index H' and Pielou's evenness (J').

Functional biodiversity was analysed taking into account the nature, origin, and food feeding mode of each species: carnivores (C), detritus feeders (Dt), surface-deposit feeders (sD), subsurface deposit feeders (ssD) and suspension feeders (SF). These trophic groups were considered according to the classification schemes available in the literature (Bazairi *et al.*, 2005; Afli *et al.*, 2008; Jumars *et al.*, 2014).

ANOVA (Analyses of variance) was used with a one-factor between-subjects design for statistical testing of the differences in the values of species richness, abundance (for single species or total abundance), diversity index and evenness between all the stations and seasonal samples. A *post hoc* Tukey test (p < 0.05) was used for *a posteriori* multiple comparisons. A Shapiro-Wilk normality test and a Bartlett's test for homogeneity of variances were performed prior to each ANOVA. Then, ANOVA was performed to assess the influence of vegetation cover and seasonal variations (spring, summer, autumn and winter) on patterns of polychaete diversity in the intertidal domain of the Kneiss Islands. These statistical procedures were carried out using the SPSS Statistics 20 software.

Multivariate analysis

Prior to carrying out ascending hierarchical clustering based on the Bray-Curtis similarity, principal component analysis was applied to the 'stations × sedimentary fractions' matrix to determine homogenous groups among the stations according to the type of sediment.

The original data consists of a 'stations × species' matrix, which was obtained after removing rare species (7 species are considered as rare, in cases where they occur at less than three stations). Polychaete abundances were firstly square-root transformed to minimize the influence of the most dominant taxa. A non-metric multidimensional scaling method (n-MDS) based on the Bray-Curtis similarity allows us to assess differences in polychaete assemblages between stations. A SIMilarity PERcentages (SIMPER) test was performed using PRIMER®-v6 to determine which species contribute most to within-group similarity.

Results

Environmental parameters

Cluster analysis of the 'grain size × 42 stations' matrix (April 2014) reveals four groups (A, B, C and D) that are distinguished according to the percentage of each sediment grain-size fraction. Group A comprises the fine-sand stations located around Bessila Islet, group B the medium-sand stations around Laboua Islet, group C the coarse-sand stations in the lower part of the intertidal zone without *Zostera* (*Zosterella*) noltei beds and group D the mud stations in the upper part of the intertidal zone (Fig. 2).

All the physical and chemical parameters were only determined in April 2014 for the whole set of 42 sampled stations. The surface water temperature ranges from 22.5 to 24.8°C (mean = $23.5 \pm SD 0.48$), the salinity from 38.9 to 40.2 (mean = $39.6 \pm SD 0.38$), and pH lies between 7.88 and 8.76 (mean = $8.4 \pm SD 0.20$). Temperature (ANOVA; F=23.1; p>0.05), salinity (ANOVA; F=14.98; p>0.05) and pH (ANOVA; F=4.6; p>0.05) show similar values at all 42 stations over the whole period of the study.

The organic matter content of the sediment ranges from 2.1 to 22%, showing significant differences between sediment types (ANOVA; F= 1.67; p < 0.05). The highest percentages are recorded in fine sediments (mud and fine sand), while the lowest values are found in coarse sands (Table 1).

The chemical-physical parameters show a seasonal variability with respect to the annual mean value in the water column, with higher temperatures in autumn and summer (31.6 \pm 0.8 and 29.4 \pm 1.6, respectively), but lower temperatures in winter and spring (12.8 \pm 0.6 and 22.8 \pm 0.6, respectively). The mean salinity is higher during autumn and summer (42 \pm 2.4 and 38.6 \pm 5.9, respectively), while the lowest values are recorded during winter and spring (35.1 \pm 1.7 and 36.6 \pm 0.3, respectively). The mean pH value remains stable and close to 8; (i.e. summer: 8.6 \pm 0.2; autumn: 8.4 \pm 0.8; spring: 8.3 \pm 0.9; winter: 8.4 \pm 0.1) (ANOVA; F= 0.75; p > 0.05) (Fig. 3).

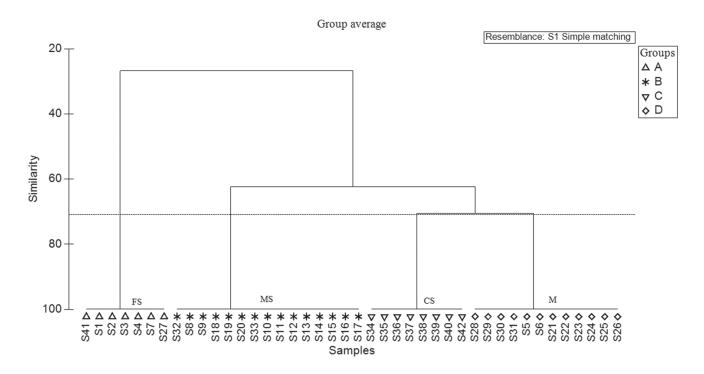
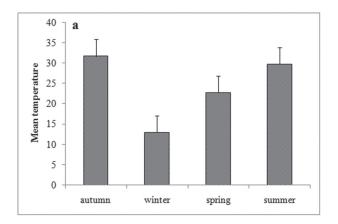
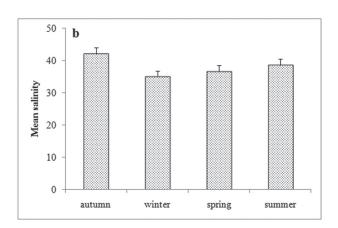


Fig. 2: Cluster dendrogram showing four distinct subgroups of stations (A, B, C, and D) according to the sediment grain size: M: mud; FS: fine sand; MS: medium sand; CS: coarse sand.





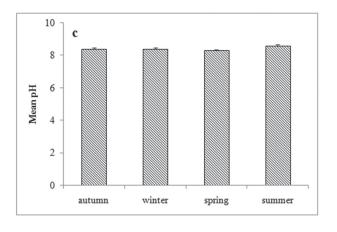


Fig. 3: Seasonal variations of main physico-chemical parameters in the Kneiss Islands: (a) Temperature (°C), (b) Salinity, (c) Hydrogen potential.

The Tukey test reveals that temperature and salinity differ significantly between the four seasons (p < 0.05).

Faunal parameters

Faunal analyses of samples taken from the intertidal zone of the Kneiss Islands yield a total of 92 polychaete species (18,026 individuals) belonging to 25 families, based on the taxonomic identification of polychaetes from the 42 stations: Nereididae, Glyceridae, Eunicidae, Maldanidae, Terebellidae and Serpulidae are the dominant families in number of species. The infauna represents 84% of the total number of polychaete species, while, by contrast, the epifauna accounts for only 15 species.

The faunistic parameters show a marked variability, with abundance ranging from 1,860 to 9,690 ind.m⁻² (with a mean abundance of 3,884 \pm 2,300 ind. m⁻²), specific richness from 10 to 32 taxa, Pielou's evenness from 0.62 to 0.94 and the Shannon index from 2.88 to 5.12 bits.ind. The vegetated stations display higher diversity indices compared with unvegetated samples.

Among the collected polychaetes, 42 species (46 %) are new records for the Gulf of Gabès (Appendix). In the intertidal zone of the Kneiss Islands, the 10 top dominant species sampled at the 42 stations are: *Perinereis cultrifera* (Grube, 1840), *Glycera tridactyla* Schmarda, 1861, *Platynereis dumerilii* (Audouin & Milne Edwards, 1834), *Eunice vittata* (Delle Chiaje, 1828), *Marphysa bellii* (Audouin & Milne Edwards, 1833), *Cirratulus cirratus* (O. F. Müller, 1776), *Euclymene oerstedii* (Claparède, 1863), *Amphitritides gracilis* (Grube, 1860), *Melinna palmata* Grube, 1870 and *Orbinia sertulata* (Savigny, 1822) (Table 2).

According to trophic level and feeding mode, 32 carnivorous species (i.e. 34.8%), 14 detrital feeders (i.e. 15.2%), 22 surface deposit feeders (i.e. 24%), 11 subsurface deposit feeders (i.e. 12%) and 13 suspension feeders (i.e. 14%) are identified. Overall, deposit feeders (Dt, sD and ssD) are the dominant group with 47 species (i.e. 51.2 % of the specific richness), followed by carnivores and suspension feeders (see Appendix).

In terms of relative frequency of species, carnivores and deposit feeders are the most common on vegetated stations. Note that the unvegetated stations show a relatively balanced distribution between carnivores, deposit feeders and suspension feeders.

Characteristics of the different polychaete assemblages

At 65 % similarity level, the non-metric multidimensional scaling (n-MDS) plot reveals a separation among the 42 stations, discriminating four groups of stations which correspond to different polychaete assemblages (Fig. 4).

Table 2. Ten dominant polychaete species in the intertidal zone of the Kneiss Islands sampled at 42 stations during spring 2014.

Dominant species	% of occurrence	Mean abundance (ind.m ⁻²)
Cirratulus cirratus Cirratulidae	84	664
Perinereis cultifera Nereididae	58	628
Euclymene oerstedii Maldanidae	64	612
<i>Platynereis dumerilii</i> Nereididae	48	480
<i>Glycera tridactyla</i> Glyceridae	52	442
Eunice vittata Eunicidae	54	384
<i>Marphysa belli</i> Eunicidae	38	340
Melinna palmata Ampharetidae	41	312
Amphitrides gracilis Terebellidae	39	294
<i>Orbinia cuvieri</i> Orbiniidae	33	220

Group A is clustered together at seven stations located to the north of islands, mainly made up of fine sand, and is characterized by numerical dominance and a major contribution (SIMPER test) of polychaete species such as *Orbinia sertulata* (Savigny, 1833), *Platynereis dumerilii* and *Nephtys hombergii* Savigny in Lamarck, 1818.

Group B clusters fifteen stations located in the southern sector of the islands (Fig. 1), composed solely of muddy sediment and showing the greatest organic matter enrichment. This assemblage is mostly represented by *Hediste diversicolor* (O.F. Müller, 1776), *Melinna palmata*, *Cirratulus cirratus*, *Sabella pavonina* Savigny, 1822 and *Mediomastus fragilis* Rasmussen, 1973.

Group C corresponds to the eight stations sampled in the lower intertidal zone farthest from the coast characterized by coarse sand, relatively poor in organic matter. This group is characterized by the dominance of *Scoletoma tetraura* (Schmarda, 1861), *Marphysa belli, Eunice vittata* and *Glycera tridactyla*.

Finally, Group D comprises the other 12 stations composed of medium sand located closest to the coast, more strongly represented by *Perinereis cultrifera* (Grube, 1840), *Euclymene oerstedii*, *Heteromastus filiformis* (Claparède, 1864) and *Amphitritides gracilis*.

The non-metric multidimensional scaling shows that the distribution of polychaete assemblages is strongly correlated with edaphic factors such as sediment type and organic matter content.

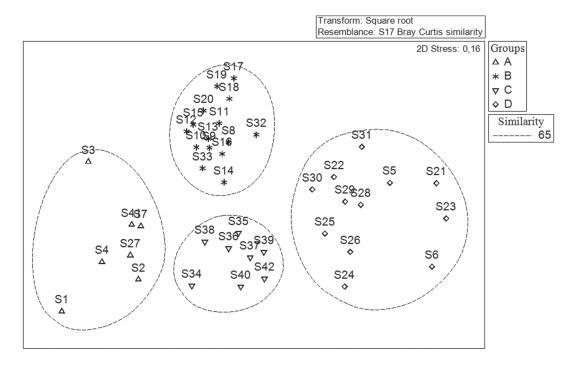


Fig. 4: Non-metric multidimensional scaling (n-MDS) of stations based on Bray-Curtis similarity matrix after square root-transformation of abundance data. Four groups of stations are identified by Cluster Analysis at a 65% similarity level.

Seasonal variation of both ecological and diversity indices of polychaete communities

An analysis of the temporal variations in the ecological and diversity indices (Fig. 5) reveals that species richness reaches a value of 28 in winter (mean: 9; max: 13 at S12; min: 6 at S1 and S3), 46 in spring (mean: 21.5; max: 32 at S6; min: 14 at S12), 56 in summer (mean: 24; max: 34 at S18; min: 11 at S20) and 50 during the autumn (mean: 12; max: 20 at S10; min: 8 at S16). The number of species varies significantly between seasons (ANOVA; F=19.56; p<0.05).

The abundance of polychaetes also shows a significant seasonal variation (ANOVA; F=23.5; p<0.05), with maximum values in summer (13,866 ind.m⁻²) and spring (i.e. 12,950 ind.m⁻²), whereas the lowest abundances are recorded in winter (i.e. 1,016 ind.m⁻²).

As regards diversity indices, Shannon's index expressed in bits.ind varies from 3.6 (at S7) to 4.8 (at S11 and S16) during spring, from 3.2 (at S 17) to 3.9 (at S13) in summer, from 2.8 (at S12) to 3.4 (at S8) in autumn, and from 2.1 (at S15) to 3.1 (at S13 and S19) in winter. The highest values of Pielou's index are recorded during spring (0.98 at S14) and summer (0.96 at S12), while the lowest values is found in winter (0.64 at S1 and S3).

The trophic groups show considerable seasonal fluctuations (carnivores: F = 11.3; p < 0.05; suspension feeders: F = 8.64; p < 0.05; subsurface deposit feeders: F = 12.24; p < 0.05; surface deposit feeders: F = 13.46; p < 0.05; detritus feeders: F = 16.24; p < 0.05). All year

round, it is noteworthy that carnivores and surface deposit feeders are the most abundant trophic groups (Fig. 6).

Polychaete spatial distribution according to sediment types

The four polychaete assemblages identified by n-MDS appear similar for all four groups of sediment separated by the cluster analysis, indicating that the distribution of polychaete communities in the intertidal soft bottom of the Kneiss Islands is predominantly related to edaphic factors, particularly by sediment characteristics and organic matter content.

Discussion

The present study describes the patterns of biodiversity and distribution of polychaete assemblages on the tidal flats of the Kneiss Islands, i.e. inventory of species, abundance, spatial and temporal distribution of polychaete assemblages according to the main environmental variables. The Kneiss Islands represent a site of international interest in Mediterranean Sea in terms of their ornithological diversity (Important Bird Area, SPAMI and Ramsar Site) (Mosbahi *et al.*, 2015). From this study, we identify a total of 92 polychaete species belonging to 25 families unequally distributed between the sampling stations, including the Nereididae, Glyceridae, Eunicidae, Maldanidae, Terebellidae and Serpulidae, which are the

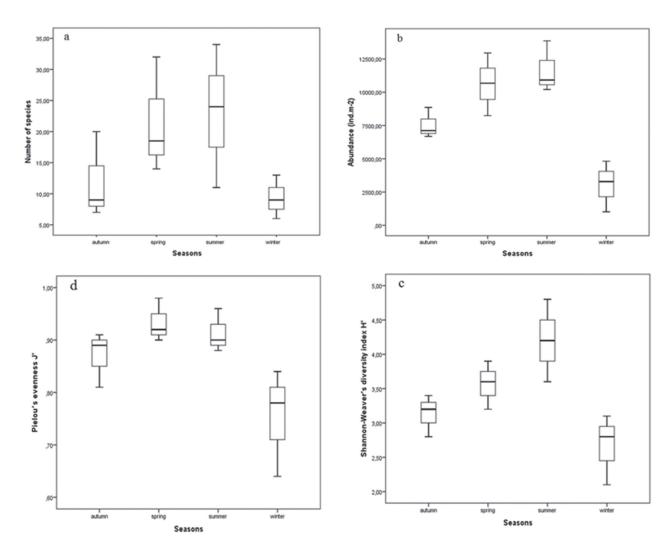


Fig. 5: Box plots of seasonal variability of the principal polychaete parameters in the Kneiss Islands during spring 2014: (a) number of species, (b) abundance, (c) Shannon-Weaver diversity index, and (d) Pielou's evenness.

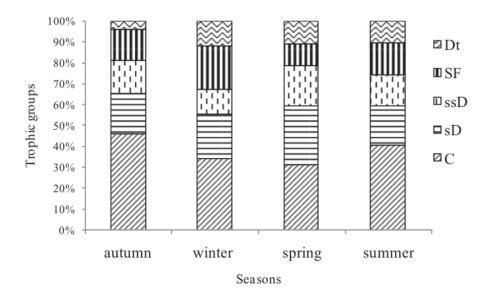


Fig. 6: Seasonal variation in abundance of trophic groups of polychaete communities in the Kneiss Islands.

dominant families in terms of abundance and number of species.

The present study lists 42 new species belonging to 20 families, representing new additions to the polychaete fauna of the Gulf of Gabès which were unreported by Ayari *et al.* (2009) and Zaâbi *et al.* (2012). This is related to the fact that most previous studies have covered the north coast of Tunisia rather than the southern sector concerned here.

The faunal analyses show that the area is diverse and hosts many species. The polychaete species composition in this area is similar to that previously reported from other sites such as the Gulf of Tunis (Ayari & Afli, 2009), the north-eastern coast of Tunisia (Zaâbi & Afli, 2006; Ayari et al., 2009; Zaâbi et al., 2009, 2010, 2012) and in other Mediterranean soft-bottom communities (Dorgham et al., 2014). The species richness observed here is relatively high, considerably exceeding values previously mentioned elsewhere (Dorgham et al., 2014; Gambi et al., 2016) and could be due to the major sampling effort concerning 42 stations over two years.

Several ecological studies have demonstrated that seagrass bed communities are usually characterized by a larger number of species and higher abundances than adjacent unvegetated sites (Bowden et al., 2001; Barnes & Barnes, 2012). This pattern has been mainly attributed to the "structural complexity" of the seagrass cover, often expressed in terms of plant density and/or standing crop, reflecting the plant "architecture" or configuration. Shoot density, being related to leaf surface area and biomass, strongly affects the composition and abundance of the fauna associated with seagrasses, since plants provide additional microhabitats, increasing the availability of substrates and food resources, as well as shelter from physical stress factors and predation (Fredriksen et al., 2005). Seagrass shoots also form a kind of "structure of retention" that may increase larval settlement and/or reduce larval emigration to other sites (Eckman, 1987).

The observed community structure of polychaetes comprising four assemblages is due to a complex environmental gradient that includes both abiotic (hydrodynamics, sediment characteristics) and biotic factors (e.g., shoot density and other seagrass features), with polychaete abundance and diversity being higher on the vegetated stations. MDS ordination is also able to discriminate four distinct polychaete assemblages on the tidal flats of the Kneiss Islands. These assemblages are characterized by spatial and temporal changes in the population, and their distribution pattern seems to be entirely governed by the sediment type. As a result, sediment grain-size plays a significant role in controlling the distribution of the benthic communities. The distribution of polychaete assemblages in the Kneiss Islands is related to sediment grain size and organic matter content, so it follows a closely similar pattern to the sediment types. These results are in agreement with the studies of Dorgham et al.

(2014) and Cosentino & Giacobbe (2006) on the coast of Alexandria, Egypt (eastern Mediterranean) and in the Strait of Messina, Italy (central Mediterranean), respectively. Indeed, some species colonize very fine-grained substrates, which represent the main constituent for tube building in agglomerated sand, and which are favourable for the settlement of tubicolous polychaetes such as *Melinna palmata* Grube, 1870. Other organisms prefer sand or coarse sediment with high porosities (Desroy & Retière, 2001). Thus, sediment texture is a major factor affecting the distribution of communities, and represents a key parameter that should not be ignored in the study of benthic fauna (Dauvin *et al.*, 2004).

Furthermore, numerous ecological studies suggest that polychaete distribution varies alongshore as well as according to water depth both on soft and hard bottoms, with increasing variability at shallower depth and changes in sediment texture and meadow cover contributing to assemblage heterogeneity (e.g. Mikac & Musco, 2010). As most of the environmental parameters are closely related to each other, it is difficult to separate the effect of any given parameter on the spatial distribution of polychaete communities (Carvalho et al., 2005). Nevertheless, it is generally observed that, although some taxa are associated with a given sediment-type habitat, their distribution is rarely restricted to that habitat alone. According to Gerino et al. (2007), the behaviours of these polychaete species would be related to their lifestyle mainly depending on predation, tube building and hunting activity.

Otherwise, the trophic structure of polychaetes in the Kneiss Islands appears to be developed around a small number of species, namely the carnivores *G. tridactyla*, *E. vittata*, *Scoletoma tetraura*, *P. dumerilii*, the detritus feeders *P. cultrifera* and *O. sertulata*, the subsurface deposit feeders *Heteromastus filiformis*, and *E. oerstedii*, the surface deposit feeders *C. cirratus*, *M. palmata* and *A. gracilis*, and the suspension feeder *Sabella pavonina*. Quantitatively, the dominance of the above species is probably linked to the availability in nutrient particles or habitat type. These observations are in agreement with those of Antoniadou & Chintiroglou (2006) and Bazairi *et al.* (2005), who noted the dominance of carnivores and deposit feeders in the northern Aegean Sea and Merja Zerga lagoon (Morocco), respectively.

It is noteworthy that the dominance of subsurface deposit feeders in soft-bottom sediments appears related to their burrowing lifestyle and the availability of large quantities of nutrients. This is in agreement with the observations of several authors (Carvalho *et al.*, 2005; Moreira *et al.*, 2006; Lourido *et al.*, 2008), who report that subsurface deposit feeders are predominantly found in sandy and muddy sediments. According to these authors, the distribution and abundance of these burrowing species is controlled by nutrients in the water column. Several studies show a positive correlation between carnivorous polychaetes and coarse sediments (Carrasco *et*

al., 1998), which is the case in the Kneiss Islands. Furthermore, the distribution of the carnivorous polychaetes is particularly closely related to the density of their potential prey. The role of predation is to control the community and prevent the monopolization of resources (food and space) by some populations (Parsons et al., 1995; Afli & Glémarec, 2000).

The polychaete communities show significant seasonal variations in abundance and species diversity, with a general increase during spring and summer and a decline during winter. These changes are correlated with seasonal changes in the environmental factors, which are normally regular and cyclic, thus allowing the different populations to realize their biological cycle (Glémarec, 1993). A significant difference regarding the abundance of the polychaete trophic groups is their response to different seasonal conditions. The seasonal variations in the community structure of polychaetes are caused by recruitment, which is also responsible for the high abundance and increase in the number of species observed during spring and summer, reflecting seasonal variations in food abundance. Recruitment is known to be highly variable in space and time, and is mainly influenced by several factors during the seasonal cycle such as food availability, water temperature, predation (carnivores) and the hydrodynamic regime (Reiss & Kroncke, 2005). The majority of the polychaetes collected in spring and summer are adults; since the microscopic inspection of random specimens indicates the presence of eggs, this period would be particularly favourable for the proliferation of certain populations (Prevedelli et al., 2007).

In conclusion, it would be very interesting to carry out studies on the trophic role of polychaete communities as prey for aquatic birds at low tide and fish at high tide in the Kneiss Islands. Likewise, this study shows the important biodiversity of polychaetes fauna in the central Mediterranean Sea and this aspect deserves increased attention for the conservation of marine areas in such rare intertidal zones.

Acknowledgements

The authors thank the fishers of the Kneiss Islands for their help during the sampling, the laboratory staff of GeoResources Materials, Environment and Global Changes (FSS) for their assistance during sediment analysis and Michael Carpenter for the English revision. They also thank the anonymous reviewers for their useful suggestions and their constructive comments.

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Appendix: Checklist of polychaetes collected in the Kneiss Islands: Inf: Infauna, Ep: Epifauna; Dt: detritus feeders; C: carnivores; SD: surface deposit feeders; SSD: subsurface deposit feeders; SF: suspension feeders; (*) new species reported for the first time in the Gulf of Gabès.

Species collected	Family	Habitat type	Trophic group
Amage gallasii Marion, 1876*	Ampharetidae	Inf	sD
Amphicteis gunneri (M. Sars, 1835)	Ampharetidae	Inf	sD
Melinna palmata Grube, 1870	Ampharetidae	Inf	sD
Anobothrus gracilis (Malmgren, 1866)*	Ampharetidae	Inf	sD
Laetmonice hystrix (Savigny in Lamarck, 1818)	Aphroditidae	Inf	С
Pontogenia chrysocoma (Baird, 1865)	Aphroditidae	Inf	С
Absarenicola claparedi Levinsen, 1883	Arenicolidae	Inf	sD
Arenicola marina (Linnaeus, 1758)*	Arenicolidae	Inf	sD
Notomastus latericeus Sars, 1851	Capitellidae	Inf	ssD
Capitella capitata (Fabricius, 1780)*	Capitellidae	Inf	ssD
Heteromastus filiformis (Claparède, 1864)*	Capitellidae	Inf	ssD
Mediomastus fragilis Rasmussen, 1973*	Capitellidae	Inf	ssD
Cirratulus cirratus (O. F. Müller, 1776)*	Cirratulidae	Inf	sD
Protocirrineris chrysoderma Claparède, 1868	Cirratulidae	Inf	sD
Cirriformia tentaculata (Montagu, 1808)	Cirratulidae	Inf	sD
Marphysa sanguinea (Montagu, 1813)*	Eunicidae	Inf	C
Marphysa bellii (Audouin & Milne Edwards, 1833)*	Eunicidae	Inf	C
Marphysa fallax Marion & Bobretzky, 1875	Eunicidae	Inf	C
Eunice vittata (Delle Chiaje, 1828)*	Eunicidae	Inf	C
Eunice aphroditois (Pallas, 1788)*	Eunicidae	Inf	C
Eunice schizobranchia Claparède, 1870	Eunicidae	Inf	C
Lysidice unicornis (Grube, 1840)*	Eunicidae	Inf	C
Euphrosine foliosa Audouin & Milne Edwards, 1833	Euphrosinidae	Ep	C
Glycera tridactyla Schmarda, 1861	Glyceridae	Inf	C
Glycera fallax Quatrefages, 1850	Glyceridae	Inf	C
Glycera unicornis Lamarck, 1818	Glyceridae	Inf	C
Glycera alba (O.F. Müller, 1776)	Glyceridae	Inf	C
Glycera tesselata Grube, 1840*	Glyceridae	Inf	C
Pariospilus affinis Viguier, 1911*	Iospilidae	Inf	C
Scoletoma tetraura (Schmarda, 1861)	Lumbrineridae	Inf	C
Scoletoma impatiens (Claparède, 1868)	Lumbrineridae	Inf	C
Hilbigneris gracilis (Ehlers, 1868)	Lumbrineridae	Inf	C
Lumbrineriopsis paradoxa (Saint-Joseph, 1888)*	Lumbrineridae	Inf	C
Euclymene oerstedii (Claparède, 1863)	Maldanidae	Inf	ssD
Euclymene lombricoides (Quatrefages, 1866)*	Maldanidae	Inf	ssD
Euclymene tomoricoides (Quatierages, 1800) Euclymene palermitana (Grube, 1840)	Maldanidae	Inf	ssD
Euclymene patermitana (Giuoe, 1840) Euclymene santanderensis (Rioja, 1917)	Maldanidae	Inf	ssD
Nicomache (Loxochona) trispinata Arwidsson, 1906*	Maldanidae	Inf	ssD
<i>Vicomacne (Loxocnona) trispinata</i> Arwidsson, 1906 Leiochone leiopygos Grube, 1860	Maldanidae		
		Inf	ssD
Nephtys hombergii Savigny in Lamarck, 1818	Nephtyidae	Inf	C
Nephtys caeca (Fabricius, 1780)*	Nephtyidae	Inf	C Dt
Perinereis cultrifera (Grube,1984)	Nereididae	Inf	Dt Dt
Perinereis macropus (Claparède, 1870)	Nereididae	Inf	Dt
Platynereis dumerilii (Audouin & Milne Edwards, 1834)	Nereididae	Inf	Dt

(continued)

Species collected	Family	Habitat type	Trophic group
Nereis rava Ehlers, 1864	Nereididae	Inf	Dt
Nereis zonata Malmgren, 1867	Nereididae	Inf	Dt
Neanthes acuminata (Ehlers, 1868)	Nereididae	Inf	Dt
Neanthes nubila (Savigny, 1822)	Nereididae	Inf	Dt
Alitta succinea (Leuckart, 1847)	Nereididae	Inf	Dt
Nereis pelagica Linnaeus, 1758	Nereididae	Inf	Dt
Drilonereis filum (Claparède, 1868)	Oenonidae	Inf	C
Arabella iricolor (Montagu, 1804)	Oenonidae	Ер	C
Diopatra neapolitana Delle Chiaje, 1841	Onuphidae	Inf	C
Ophelia bicornis Savigny, 1818*	Opheliidae	Inf	ssD
Orbinia sertulata (Savigny, 1833)*	Orbiniidae	Inf	Dt
Orbinia latreillii (Audouin & Milne Edwards, 1833)*	Orbiniidae	Inf	Dt
Scoloplos (Scoloplos) armiger (Müller, 1776)	Orbiniidae	Inf	Dt
Phylo foetida (Claparède, 1869)	Orbiniidae	Inf	Dt
Mysta picta (Quatrefages, 1866)	Phyllodocidae	Ер	\mathbf{C}
Harmothoe extenuata (Grube, 1840)*	Polynoidae	Ep	C
Sabellaria alveolata (Linnaeus, 1767)	Sabellariidae	Inf	SF
Sabella pavonina Savigny, 1822	Sabellidae	Inf	SF
Stylomma palmatum (Quatrefages, 1866)*	Sabellidae	Inf	SF
Branchiomma bombyx (Dalyell, 1853)*	Sabellidae	Inf	SF
Amphiglena mediterranea (Leydig, 1851)*	Sabellidae	Inf	SF
Chone duneri Malmgren, 1867*	Sabellidae	Inf	SF
Desdemona ornata Banse, 1957*	Sabellidae	Inf	SF
Serpula vermicularis Linnaeus, 1767	Serpulidae	Ер	SF
Vermiliopsis infundibulum (Philippi, 1844)	Serpulidae	Ер	SF
Hydroides dianthus (Verrill, 1873)	Serpulidae	Ер	SF
Hydroides elegans (Haswell, 1883)	Serpulidae	Еp	SF
Ficopomatus enigmaticus (Fauvel, 1923)	Serpulidae	Ер	SF
Pileolaria militaris Claparède, 1870	Serpulidae	Еp	SF
Pelogenia arenosa (Delle Chiaje, 1830)	Sigalionidae	Еp	С
Sigalion mathildae Audouin & Milne Edwards, 1830	Sigalionidae	Inf	С
Dipolydora armata (Langerhans, 1880)*	Spionidae	Inf	sD
Polydora ciliata (Johnston, 1838)	Spionidae	Inf	sD
Pseudopolydora antennata (Claparède, 1869)*	Spionidae	Inf	sD
Spio decoratus (Müller, 1776)*	Spionidae	Inf	sD
Pygospio elegans Claparède, 1863	Spionidae	Inf	sD
Malacoceros fuliginosa (Claparède, 1870)	Spionidae	Inf	sD
Scolelepis (Scolelepis) squamata (O.F. Muller, 1806)*	Spionidae	Inf	sD
Syllis gracilis Grube, 1840	Syllidae	Ер	С
Syllis variegata Grube, 1860*	Syllidae	Еp	С
Salvatoria clavata (Claparède, 1863)*	Syllidae	Еp	sD
Syllis (Typosyllis) punctulata Haswell, 1920*	Syllidae	Еp	С
Amphitrite rubra (Risso, 1826)	Terebellidae	Inf	sD
Amphitritides gracilis (Grube, 1860)*	Terebellidae	Inf	sD
Terebella lapidaria Linnaeus, 1767	Terebellidae	Inf	sD
Eupolymnia nebulosa (Montagu, 1819)*	Terebellidae	Inf	sD
Lanice conchilega (Pallas, 1766)	Terebellidae	Inf	sD