

FIRST INVESTIGATION OF THE COMPOSITION AND SPATIAL DISTRIBUTION OF POLYCHAETE FEEDING GUILDS FROM ESSAOUIRA PROTECTED COASTAL AREA (ATLANTIC COAST OF MOROCCO)

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Abstract. Several researches have been conducted to explain patterns of the abundance, richness and taxonomic diversity of benthic polychaetes; however, such analyses have ignored the functional diversity of polychaete communities, especially feeding guilds in intertidal rocky shores. The present study was carried out to describe and analyse the polychaete feeding guilds on intertidal rocky shores and then examine the effects of environmental factors. Twelve intertidal rocky shores from the coastal protected area of Essaouira (Atlantic coast of Morocco) were sampled during the summer of 2016. A total of 42 polychaete species belonging to 29 genera and 16 families were identified among the 4517 specimens collected. The medium biomass per sampling site was found to be $37.61 \pm 15.80 \text{ g.m}^{-2}$. The polychaete species were classified into five feeding guilds, and nine feeding modes. The filter feeders were the dominant feeding guild (32%) followed by omnivores (23%), burrowers (20%), carnivorous (15%) and surface deposit-feeders (10%). The FDT (filter feeder, discretely motile, with tentacles) was the most abundant feeding mode, accounting for 24% of abundance (mainly represented by *Sabellaria alveolata*), followed by the ODJ feeding mode (omnivorous, discretely motile, with jaw apparatus) with 22%, and the SDT feeding mode (surface deposit feeder, discretely motile, with tentacles) with 18.9%. The highest trophic importance index and index of trophic diversity values were recorded in the southern region of Essaouira coastline. Based on the canonical correspondence analysis, composition and spatial distribution of polychaete feeding guilds were mainly related to the length of rocky shores and water temperature.

Keywords: rocky shores, intertidal, environmental factors, functional diversity, feeding modes, filter feeders, trophic importance index

Introduction

Polychaetes (Annelida) are one of the most important taxa in macrobenthic communities in coastal and marine environments, in terms of diversity and abundance (Fauchald and Jumars, 1979; Grassle and Maciolek, 1992; Hutchings, 1998). With more than 13,000 species described to date, polychaetes species are considered the most numerous among benthic taxa (Minelli, 1993; Jumars et al., 2015; Han et al., 2016).

Indeed, the polychaetes represent about one third of the total macrobenthic species in terms of richness and up to 80% of the total abundance (Fauchald and Jumars, 1979; Belan, 2004; Manokaran et al., 2013; Han et al., 2016). They are also crucial in marine food chains as important prey and predators for many organisms (Serrano Samaniego, 2012), and exhibit a high diversity of feeding modes, reproductive strategies and different levels of tolerance to the negative impacts induced by pollution and natural perturbations (Giangrande et al., 2005; MacDonald et al., 2010; Sivadas et al., 2010; Han et al., 2016).

According to Fauchald and Jumars (1979), feeding guild of any organism is defined as the set of relations among food particle size and composition, the mechanism involved in food intake, and the motility patterns associated with feeding. These authors classified feeding guilds of each polychaete family as herbivore, carnivore, filter feeders, surface deposit feeders, and sub-surface deposit-feeders. Later, Ruppert and Barnes (1994) suggested that omnivores also exist in the marine environment. According to Pinnet (2000), organisms of the same feeding guild would dominate a particular type of substrate. Indeed, the filter-feeders are the dominant feeding guild on hard substrate (Porrás et al., 1996; Damianidis and Chintiroglou, 2000), while deposit-feeders are the dominant feeding guild on soft substrates (Paiva, 1994; Muniz and Pires, 1999; Mattos et al., 2012). Deposit feeders usually inhabit low-energy, muddy substrates because such substrates tend to have a high content of organic matter (Muniz and Pires, 1999; Wang, 2004; Méndez, 2013). By contrast, filter-feeders would not find enough suspended food in muddy substrates, but could be abundant on gravel and coarse-sand bottoms, since currents provide a continuous supply of suspended organic detritus and plankton (Wang, 2004).

Several biotic or abiotic factors can affect the composition and distribution patterns of polychaete feeding guilds. These include total organic carbon (Denisenko et al., 2003; Taurusman, 2010; Han et al., 2016), food availability (Dauwe et al., 1998; Rosenberg, 2001), depth and salinity (Rosenberg, 2001; Han et al., 2016). Physical characteristics of substrates and hydrodynamic factors may also modify distributions (Arruda et al., 2003; Sanders, 1958). Thus, feeding guilds can be used as a tool to analyse polychaete assemblage patterns, due to their dependence on the environmental variables, and studies on feeding guilds can permit ecologists to understand the ecological function of each species and predict if an ecosystem was susceptible to invasion by certain species (Fauchald and Jumars, 1979).

In Morocco, polychaetes represent an important group in terms of abundance and diversity on the continental shelf. The first attempt to explain patterns of abundance, richness and diversity of benthic polychaetes goes back to the beginning of 20th century with Charrier (1921) who drew up the first list of polychaetes from the region of Tangier. Subsequently, many studies have been carried out on the polychaetes of Morocco, up to the recent description of *Boccardia polybranchia* as a new species along the rocky shores of Safi (Goumri et al., 2017). However, these analyses did not consider the overall functional structure of polychaete communities. Some studies examined polychaete feeding guilds in sandy beach environments, such as the investigations of macrofauna communities carried out on the Atlantic coast between Tangier and Tarfaya by Bayed (1991), in Bou Regreg estuary by Cherkaoui et al. (2003) and in Merja Zerga by Bazaïri et al. (2003) and Touhami et al. (2017). On the Mediterranean coast, the lagoon of Smir was also studied by Chaouti and Bayed (2011). However, analyses of polychaete feeding guilds on intertidal rocky shores are virtually absent. The aim of this

paper was to describe, for the first time, the composition and spatial distribution patterns of polychaete feeding guilds in the intertidal rocky shores of Essaouira (Atlantic coast of Morocco), and their dependence to various environmental variables.

Materials and methods

Study area

The study area is located along the Atlantic coast of Essaouira province, Morocco. It lies between longitudes $9^{\circ} 20'$ and $9^{\circ} 90'$ West and between latitudes $31^{\circ} 10'$ and $31^{\circ} 50'$ North (Fig. 1). This coastal zone is made up of sandy beaches, rocky shores and dunes (fixed and shifting) with elevations ranging from 0 to 43 m. The lithology is composed of quaternary conglomerate, colluvial, and alluvial deposits and Jurassic limestone (Molua Mwambo et al., 2007). The hydrographic network includes a few rivers. The main ones are oued Ksob, oued Tidzi and oued Aghbalou which are located in the south of Essaouira while oued Tahria is located in the north. The area climate is semi-arid with a long dry period that lasts from April to October. The aridity decreases from east to west. In the western narrow coastal fringe around the town of Essaouira, the influence of the cold currents that flow onshore from the Canaries Island, create a microclimate with a very homogeneous average temperature of about 16.7°C during the year (Bazairi et al., 2010). There is little difference between the average temperatures of the hottest and the coldest months. The coastal zone of Essaouira is endowed with ecological assets that have earned it a double protection status: Arganeraie Biosphere Reserve and site of biological and ecological interest (SIBE). The major economic activities in the Essaouira province include agriculture, fishing, mining, trade, industries, tourism, artisanal activities and handicraft industry.

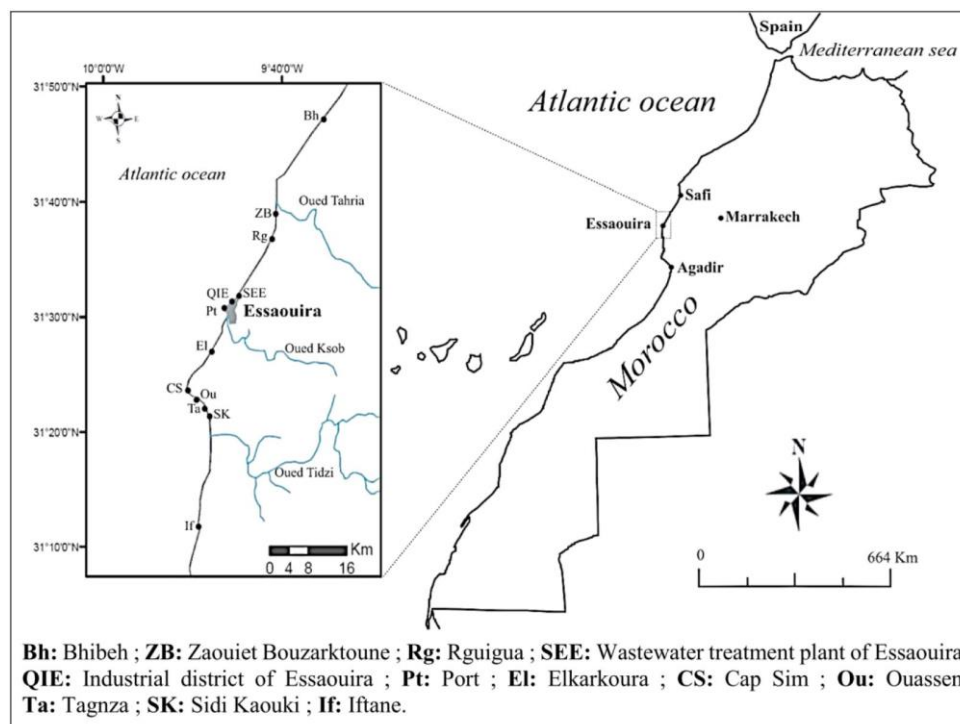


Figure 1. Geographical position of study area and sampling sites for benthic polychaetes along the coast of Essaouira ($9^{\circ} 20'$ and $9^{\circ} 90'$ W; $31^{\circ} 10'$ and $31^{\circ} 50'$ N), NW Morocco

Sampling and laboratory techniques

Twelve sampling sites were investigated in summer 2016 (Fig. 1; Table 1). The samples were collected using a quadrat method (Misra, 1968) with four quadrats (each 25 × 25 cm, surface area 0.0625 m²) in the intertidal zone of each site. Sampling was done by scraping the surface layer (sediments, algae) and digging 2 cm deep in the hard substratum using a hammer. The material was manually collected and then fixed in formaldehyde (8%). Water parameters such as pH, conductivity and temperature were recorded *in situ* using a multi-parameter (type VMR MU 6100 H, Germany), and the salinity was calculated from the conductivity and temperature of sea water (Aminot and K  rouel, 2004). At the same time, the length (m) of each rocky shore was measured from the low water to high water using a measuring tape. Rocks of 20 cm in length and 15 cm in width were collected for each sampling site using a hammer. All these samples were at least triplicated at each site to ensure the representativeness of the samples and measured parameters. In the laboratory, biological samples were rinsed in freshwater and preserved in 70% ethanol and the polychaetes were identified to species when possible with assistance of Dr. Patrick Gillet (Catholic University of the West, France) using various guides, e.g., Fauvel (1923, 1927) and Fauchald (1977), and then counted and weighed. The rock samples were cut and dozens of thin sections were prepared (Fig. 2), then grains size from these thin sections were measured using polarizing optical microscope (OLYMPUS BH 2), and the void percentage in each thin section was estimated using "Chart for estimating mineral grain percentage composition of rocks and sediments" (Compton, 1962).

Table 1. Numbers, names, abbreviation codes and GPS coordinates of the sampling sites

Site number	Site name	Abbreviation code	Latitude	Longitude
1	Bhibeh	Bh	31° 47' 55" N	9° 34' 59" W
2	Zaouiet Bouzarktoun	ZB	31° 38' 51" N	9° 40' 41" W
3	Rguigua	Rg	31° 36' 46" N	9° 41' 12" W
4	Wastewater treatment plant of Essaouira	SEE	31° 31' 53" N	9° 45' 02" W
5	Industrial district of Essaouira	QIE	31° 31' 21" N	9° 45' 38" W
6	Port	Pt	31° 30' 43" N	9° 46' 27" W
7	Elkarkoura	El	31° 26' 55" N	9° 48' 01" W
8	Cap Sim	CS	31° 24' 02" N	9° 50' 37" W
9	Ouassen	Ou	31° 23' 02" N	9° 49' 12" W
10	Tagnza	Ta	31° 22' 18" N	9° 48' 31" W
11	Sidi Kaouki	SK	31° 21' 24" N	9° 48' 08" W
12	Iftane	If	31° 11' 54" N	9° 49' 20" W

Polychaetes feeding guild assignments

In this study, we assigned feeding guilds to all polychaetes collected according to the definitions of Fauchald and Jumars (1979), MacDonald et al. (2010) and Jumars et al. (2015), which are based on the stomach content analysis of polychaetes and also direct observations of feeding behavior. Feeding guilds of polychaetes are divided into two modes (macrophagous and microphagous) and five or six sub-modes (herbivores, carnivores, filter feeders, surface deposit feeders, burrowers and omnivores), according

to their major feeding modes. The motility pattern was classified into motile, discretely motile and sessile, and the morphological structures used in feeding were classified into jawed, pumping, tentaculate or other structures, which are usually eversible sac-like pharynges (Fauchald and Jumars, 1979; MacDonald et al., 2010; Jumars et al., 2015). The feeding guilds annotations was performed as follows (*Table 2*): in the three letter codes, the letter in the first position indicates major mode, the second the motility pattern, and the last letter indicates the morphological structure used in feeding; in position 1: B, subsurface deposit feeder (burrower); C, carnivore; F, filter feeder; H, herbivore; O, Omnivore; S, surface deposit feeder; in position 2: D, discretely motile; M, motile; S, sessile; in position 3: J, jawed; T, tentaculate; X, other structures, usually eversible sac-like pharynges.

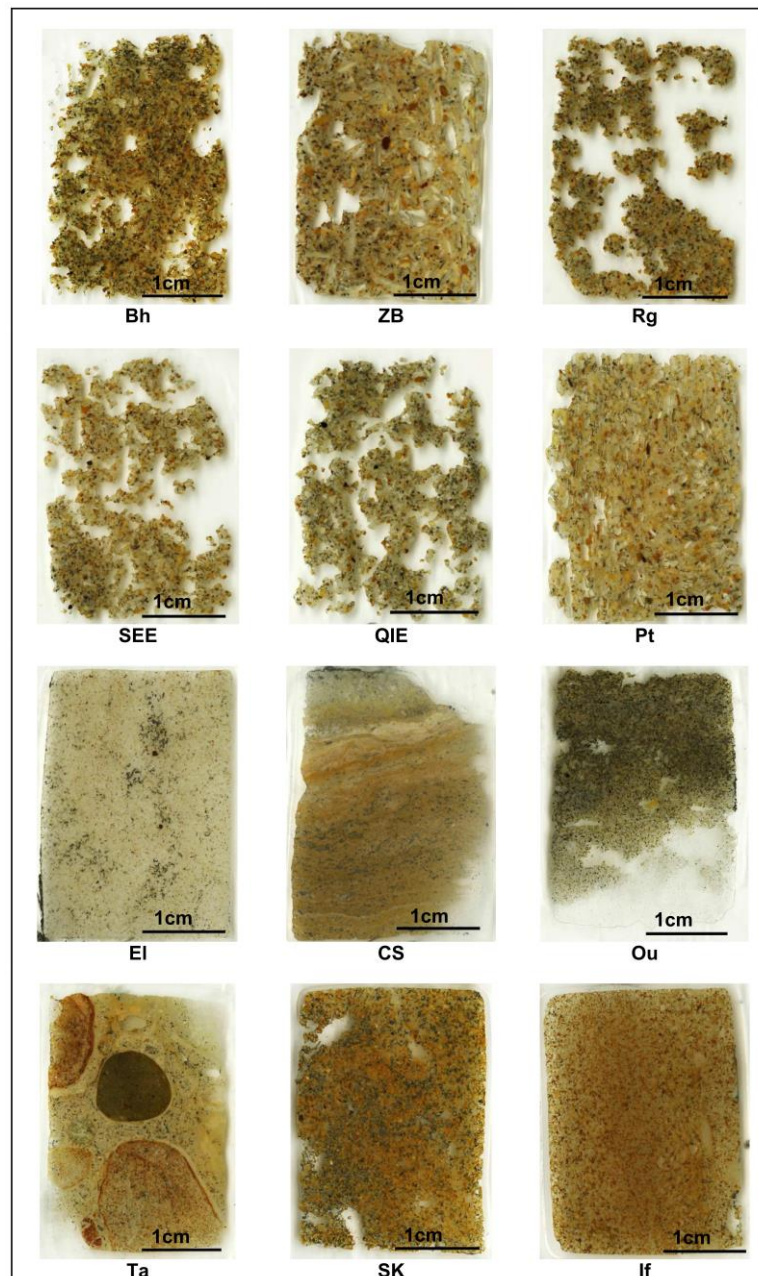


Figure 2. Photos of thin sections showing grain size of sampled rocks in the study area

Table 2. Feeding guilds annotations of polychaetes after Fauchald and Jumars (1979), MacDonald et al. (2010) and Jumars et al. (2015)

	Motile	Discretely motile	Sessile
Macrophagous modes			
Herbivores			
Unarmed pharynx	HMX		
Jawed pharynx	HMJ	HDJ	
Carnivores			
Unarmed pharynx	CMX		
Jawed pharynx	CMJ	CDJ	
Microphagous modes			
Filter feeders			
Tentaculate		FDT	FST
pumping		FDP	FSP
Surface deposit feeders			
Unarmed pharynx	SMX	SDX	
Jawed pharynx	SMJ	SDJ	
Tentaculate	SMT	SDT	SST
Burrowers			
Unarmed pharynx	BMX	BDX	BSX
Jawed pharynx	BMJ		
Tentaculate	BMT		

Statistical analysis

The trophic importance of each group was evaluated according to the trophic importance index (TI) proposed by Paiva (1994) and modified by Muniz and Pires (1999), using the following equation (Eq. 1):

$$TI = \sum_{i=1}^s \ln ni (+0.1) \quad (\text{Eq.1})$$

where s is the number of species of a trophic group in the sample, \ln is the natural logarithm, n_i is the number of individuals of the i th species in the sample, and 0.1 is a constant.

The index of trophic diversity (1-ITD) was calculated as follows (Eq. 2):

$$ITD = \sum \theta^2 \quad (\text{Eq.2})$$

where θ is the contribution of the density of each trophic group to the total polychaete density. The 1-ITD ranged from 0.90 (the highest trophic diversity) to 0.0 (the lowest diversity; i.e. one trophic guild accounts for 100% of the polychaete density: Heip et al., 1985). The taxonomic similarity between sampling sites was elucidated by a cluster analysis (Bray-Curtis similarity, Complete Link) based on the values of trophic

importance index (TI). This analysis was carried out using the BioDiversity Pro statistical program (Version 2.0).

One-way ANOVA (analysis of variance) and Tukey's test were used to evaluate statistically significant differences of environmental variables means and Trophic Index means between the sampling sites. CCA (canonical correspondence analysis) was performed to explore the distribution of the polychaete feeding guilds in relation to the rocky shores and environmental factors. One-way ANOVA, Tukey's test and CCA analysis were conducted using the PAST software package (Hammer et al., 2001), Statistical Version 3.15 for Windows software.

Results

Environmental variables

The environmental characterization of the study area was presented in *Table 3*. The longest and shortest rocky beach measured were of 271.67 ± 12.58 m (CS) and 88.33 ± 7.64 m (Pt), respectively. The void percentage in the rock ranged from $1.00 \pm 0.04\%$ (El) to $43.00 \pm 5.77\%$ (QIE). The mean grain sizes varied from 0.19 ± 0.10 mm to 6.83 ± 6.27 mm on the (CS) and (Ta) rocky shores, respectively. The seawater temperature showed fluctuations between the sampling sites with a minimum value recorded at Pt (17.50 ± 0.50 °C) and a maximum value at SEE (21.00 ± 0.15 °C). The pH value showed a similar trend, ranging from 8.00 ± 0.01 (Ou) to 8.51 ± 0.01 (If). The values of conductivity were typical of seawater, (~ 50 ms.cm⁻¹, Rodier et al., 2009). The salinity was relatively high compared to the average oceanic salinity (35‰) and ranged from 36.26 ± 0.24 ‰ (SEE) to 39.81 ± 0.08 ‰ (Pt). The differences in mean values of these environmental variables were found to be significant at all sites ($p < 0.05$) except for conductivity.

Table 3. Environmental characterization of the study area, based on variables measured at the 12 rocky shores of Essaouira coastline (mean value \pm standard deviation, $N = 3$)

Site	Length (m)	Void percentage in the rock (%)	Grain size (mm)	Water temp. (°C)	pH	Conductivity (ms.cm ⁻¹)	Salinity (‰)
Bh	$160.33 \pm 7.09^{D*}$	20.00 ± 3.92^B	0.47 ± 0.29^B	18.70 ± 0.60^C	8.20 ± 0.07^{CD}	50.90 ± 0.90^A	38.65 ± 0.21^{BC}
ZB	150.00 ± 7.07^{DE}	9.00 ± 1.41^C	0.67 ± 0.53^B	20.90 ± 0.14^A	8.28 ± 0.01^{BC}	50.80 ± 0.24^A	36.59 ± 0.11^{FG}
Rg	164.33 ± 5.13^{CD}	42.00 ± 10.61^A	0.28 ± 0.17^B	19.10 ± 0.08^{BC}	8.18 ± 0.03^{CD}	50.90 ± 0.13^A	38.28 ± 0.05^{CD}
SEE	109.33 ± 9.02^{FG}	38.00 ± 3.56^A	0.38 ± 0.20^B	21.00 ± 0.15^A	8.15 ± 0.13^{CD}	50.50 ± 0.44^A	36.26 ± 0.24^G
QIE	131.67 ± 10.41^{EF}	43.00 ± 5.77^A	0.60 ± 0.24^B	18.38 ± 0.17^{CD}	8.08 ± 0.13^{CD}	50.90 ± 0.52^A	38.95 ± 0.29^{BC}
Pt	88.33 ± 7.64^G	7.00 ± 0.41^C	0.68 ± 0.25^B	17.50 ± 0.50^D	8.04 ± 0.14^D	50.90 ± 0.56^A	39.81 ± 0.08^A
El	188.33 ± 10.41^C	1.00 ± 0.04^C	0.23 ± 0.07^B	20.00 ± 0.87^{AB}	8.10 ± 0.01^{CD}	50.60 ± 0.26^A	37.22 ± 0.65^{EF}
CS	271.67 ± 12.58^A	1.50 ± 0.41^C	0.19 ± 0.10^B	20.70 ± 0.30^A	8.43 ± 0.03^{AB}	50.80 ± 0.13^A	36.76 ± 0.21^{FG}
Ou	163.33 ± 5.77^{CD}	10.00 ± 3.65^C	0.33 ± 0.11^B	19.00 ± 0.03^{BC}	8.00 ± 0.01^D	50.00 ± 0.01^A	37.61 ± 0.03^{DE}
Ta	230.00 ± 15.00^B	1.00 ± 0.12^C	6.83 ± 6.27^A	18.00 ± 0.50^{CD}	8.10 ± 0.03^{CD}	51.00 ± 0.08^A	39.41 ± 0.42^{AB}
SK	172.67 ± 7.51^{CD}	7.00 ± 1.15^C	0.67 ± 0.16^B	18.20 ± 0.27^{CD}	8.19 ± 0.05^{CD}	51.00 ± 0.62^A	39.22 ± 0.37^{AB}
If	170.00 ± 10.00^{CD}	3.00 ± 0.41^C	0.52 ± 0.10^B	18.50 ± 0.10^{CD}	8.51 ± 0.01^A	50.90 ± 0.09^A	38.84 ± 0.05^{BC}

*The different upper-case letters in the same row show the differences between sites ($p < 0.05$)

Taxonomic and feeding guild composition

In this study, 42 polychaete species belonging to 29 genera and 16 families were identified among the 4517 specimens collected (see *Appendix*). The mean biomass

(expressed as g wet weight per m², with 0.001 g accuracy) was found to be 37.61 ± 15.80 g.m⁻². The abundance of polychaetes varied from 388 individuals per m² (ind.m⁻²) at Elkarkoura site to 3388 ind.m⁻² at Iftane site. The number of species ranged between 13 and 27 with the highest number (27 species) observed at Iftane site which is 51 km from any source of urban pollution of Essaouira city, and the lowest species number (13 species) at the site SEE. The latter site is within the effluent outflow of the wastewater treatment plant of Essaouira. Families such as Sabellaridae (24% of the individuals), Nereididae (23%), Orbiniidae (9%), Lumbrinereidae (9%) and Terebellidae (8%) were found to be dominant in terms of abundance. *Sabellaria alveolata* ranked as the top species in abundance (24%), followed by *Perinereis cultrifera* (12%), *Platynereis dumerilii* (8%), *Terbella lapidaria* (8%), *Scoletoma impatiens* (8%) and *Scolaricia typica* (8%).

The polychaete assemblage found in the study area comprised five different feeding types, namely; surface deposit feeders, carnivores, filter feeders, subsurface deposit feeders, omnivores, and nine feeding modes: BDX (burrower, discretely motile, other structures), CMX (carnivore, motile, other structures), SDT (surface deposit feeder, discretely motile, with tentacles), CMJ (carnivore, motile, with jaw apparatus), BMJ (burrower, motile, with jaw apparatus), ODJ (omnivore, discretely motile, with jaw apparatus), BMX (burrower, motile, other structures), FDT (filter feeder, discretely motile, with tentacles) and FST (filter feeder, sessile, with tentacles) (Table 4).

Table 4. List of polychaete taxa recorded throughout the sampling sites and relevant feeding guilds. In the three letter codes, the letter in the first position indicates major mode, the second the motility pattern, and the last letter indicates the morphological structure used in feeding; in position 1: B, subsurface deposit feeder (burrower); C, carnivore; F, filter feeder; H, herbivore; O, Omnivore; S, surface deposit feeder; in position 2: D, discretely motile; M, motile; S, sessile; in position 3: J, jawed; T, tentaculate; X, other structures, usually eversible sac-like pharynges

Species	Feeding guilds	Feeding modes	Species	Feeding guilds	Feeding modes
Capitellidae sp	B	BDX	Orbiniidae sp	B	BMX
<i>Bhawania goodei</i>	C	CMX	<i>Eulalia viridis</i>	C	CMX
Cirratulidae sp	S	SDT	<i>Mysta picta</i>	C	CMX
<i>Cirriformia tentaculata</i>	S	SDT	<i>Pyhllodoce maculta</i>	C	CMX
<i>Lysidice ninetta</i>	C	CMJ	<i>Lepidonotus clava</i>	C	CMJ
<i>Marphysa sp</i>	C	CMJ	Polynoidae sp	C	CMJ
<i>Nematonereis unicornis</i>	C	CMJ	<i>Sabellaria alveolata</i>	F	FDT
<i>Scoletoma funchalensis</i>	B	BMJ	<i>Dasychone lucullana</i>	F	FST
<i>Scoletoma impatiens</i>	B	BMJ	<i>Jasmineira elegans</i>	F	FST
<i>Lumbrinereis sp</i>	B	BMJ	<i>Spirobranchus triqueter</i>	F	FST
<i>Johnstonia clymenoides</i>	B	BDX	<i>Spirorbis sp</i>	F	FST
<i>Petaloproctus terricola</i>	B	BDX	<i>Serpula vermicularis</i>	F	FST
Maldanidae sp	B	BDX	Serpulidae sp	F	FST
<i>Perinereis cultrifera</i>	O	ODJ	<i>Nerinides cantabra</i>	S	SDT
<i>Perinereis marionii</i>	O	ODJ	<i>Polydora ciliata</i>	S	SDT
<i>Platynereis dumerilii</i>	O	ODJ	<i>Aonides oxycephala</i>	S	SDT
<i>Nereis irrorata</i>	O	ODJ	<i>Syllis armillaris</i>	C	CMJ
<i>Nereis sp</i>	O	ODJ	Syllidae sp 1	C	CMJ
Nereididae sp	O	ODJ	Syllidae sp 2	C	CMJ
<i>Scolaricia typica</i>	B	BMX	<i>Terbella lapidaria</i>	S	SDT
<i>Nainereis laevigata</i>	B	BMX	Terebellidae sp	S	SDT

On the intertidal rocky shores of Essaouira, the filter feeders were the dominant feeding guild (32%) followed by omnivores (23%), burrowers (20%), carnivores (15%) and surface deposit-feeders (10%) (Fig. 3A). The FDT was the most abundant feeding mode, accounting for 24% of abundance (mainly represented by *Sabellaria alveolata*), followed by the ODJ feeding mode with 22%, and the SDT feeding mode with 18.9% (Fig. 3B), it seems that these 3 groups were present in almost similar proportions. Most feeding modes occurred at all studied sites (12 sampling sites), except for SDT feeding mode absent from the EL site, and the BMX feeding mode absent from the SEE and EL sampling sites.

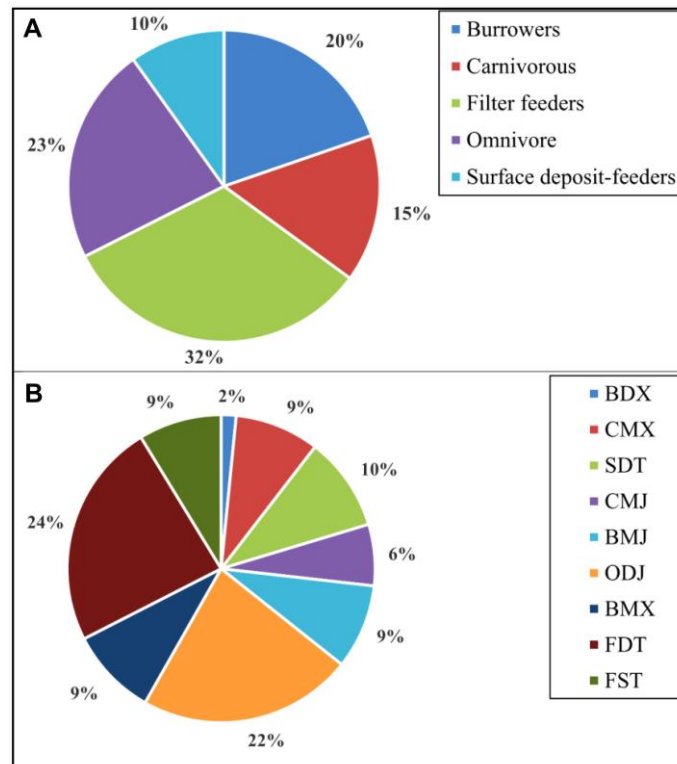


Figure 3. Relative abundance (%) of the feeding guilds (A) and feeding Modes (B) of polychaetes sampled in the study area. BDX (burrower, discretely motile, other structures); CMX (carnivore, motile, other structures); SDT (surface deposit feeder, discretely motile, with tentacles); CMJ (carnivore, motile, with jaw apparatus); BMJ (burrower, motile, with jaw apparatus); ODJ (omnivore, discretely motile, with jaw apparatus); BMX (burrower, motile, other structures); FDT (filter feeder, discretely motile, with tentacles); FST (filter feeder, sessile, with tentacles)

Feeding guild characterization

The spatial distribution of feeding guilds at different sampling sites of Essaouira intertidal rocky shores is presented in Figure 4. The results of a one way ANOVA shows a highly significant difference ($F = 2.46$; $df = 11$; $N = 5$; $Pp < 0.05$) of Trophic Index mean between the investigated sites. The burrowers were very common in the studied area, and the most abundant species were *Scoletoma impatiens* and *Scolaricia typica*. The highest TI of this feeding guild was recorded at CS, SK and QIE sampling sites, with $TI = 33.97$, $TI = 32.91$ and $TI = 32.62$ respectively. The lowest TI was

recorded at ZB (TI = 12.23) and EL sites (TI = 15.58). Carnivores were very abundant in the study area, and the main species of this group were *Bhawania goodei* and *Eulalia viridis*. Their Trophic index was highest at If (TI = 42.45) and lowest at CS (TI = 12.80). Filter feeders were abundant in the whole study area, and represented mainly by *Sabellaria alveolata*. The highest TI of this group was recorded in the southern region of Essaouira, with TI = 34.54, TI = 32.91 and TI = 31.86 at Ta, SK and If, respectively. The lowest TI was recorded north of Essaouira at SEE (TI = 8.86) and ZB sites (TI = 12.80). Omnivores were also common in the study area, but not very abundant as compared to filter feeders. Their main representative species were *Perinereis cultrifera* and *Platynereis dumerilii*. The highest TI of this group was recorded in Essaouira city with TI = 22.40 at Pt. The lowest TI was recorded south of Essaouira at Ou (TI = 7.92). Finally, the surface deposit-feeders, represented mainly by *Terebella lapidaria*, were not very common in the study area because of their absence in the El sampling site. The highest TI of surface deposit-feeders was recorded at the southernmost site at If (TI = 26.57), and the lowest TI was recorded north of Essaouira at ZB (TI = 4.14).

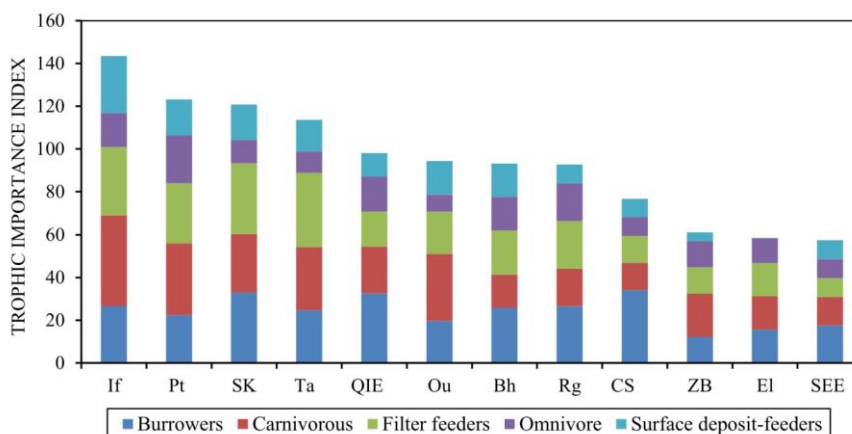


Figure 4. Trophic importance index values for sampling sites of Essaouira rocky shores

The index of trophic diversity (1-ITD) values were highest south of Essaouira (Ou, If, Ta, CS, El and SK sampling sites) and lowest in the urban area of Essaouira at QIE (Fig. 5).

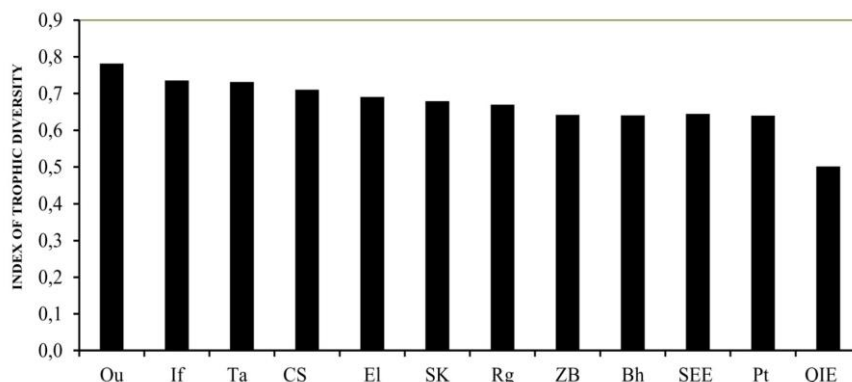


Figure 5. Index of trophic diversity values for the sampling sites of Essaouira rocky shores

The results of the cluster analysis based on the values of trophic importance index (TI) are illustrated in *Figure 6*.

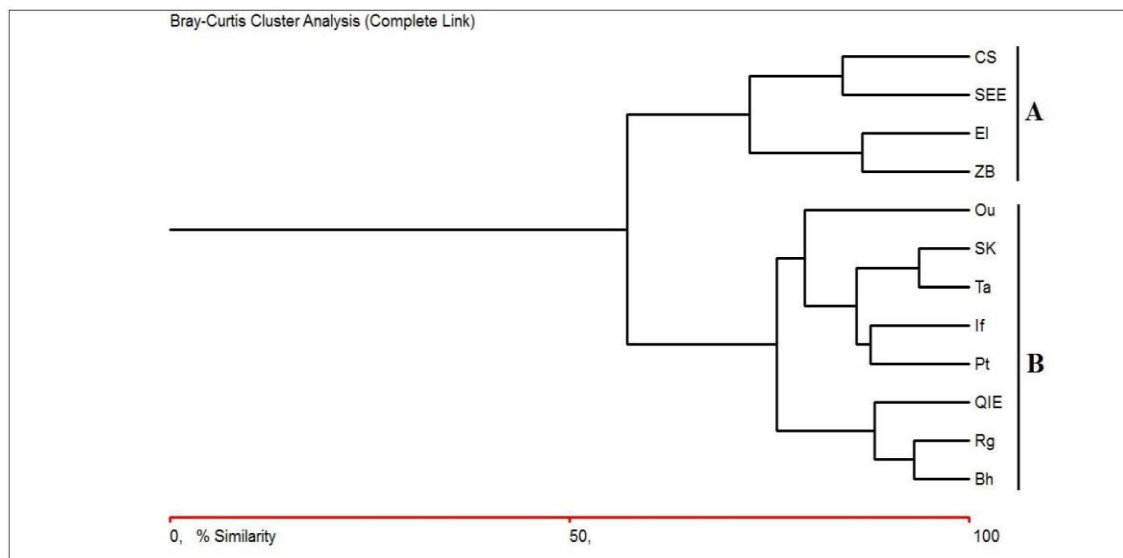


Figure 6. Distinct groups of sites established by cluster analysis for the 12 sampling sites considered on Essaouira coastline

According to these analyses, there are two distinct assemblages (A and B) with a level of dissimilarity less than 50% even though both groups included five feeding guilds and nine feeding modes:

- Group A consists of four rocky sites (ZB, El, SEE, and CS) and the dominant feeding guilds, burrower and filter feeder groups, comprised 26.89% and 26.77% of all individuals respectively, while ODJ was the most abundant feeding mode (23.84%). This assemblage was characterized by a medium Trophic Importance index ($TI = 63.47 \pm 8.96$) and moderately high Index of trophic diversity ($1-ITD = 0.67 \pm 0.034$) (*Table 4*).
- Group B includes eight rocky sites (Ou, SK, Ta, If, Pt, QIE, Rg and Bh). The dominant feeding guild was filter feeder with 35.84% of all, while FDT was the most abundant feeding mode (26.48%). This assemblage was characterized by a high Trophic Importance index ($TI = 109.93 \pm 18.47$) and moderately high Index of trophic diversity ($1-ITD = 0.67 \pm 0.085$) (*Table 5*).

Table 5. Feeding guild assemblage characteristics in the Essaouira coastline

Parameters	Group A	Group B
Site number	4	8
Total feeding guilds	5	5
Total feeding modes	9	9
Mean (TI)	63.47 ± 8.96	109.93 ± 18.47
Mean (1-ITD)	0.67 ± 0.034	0.67 ± 0.085
Dominant feeding guild	Burrower and Filter feeder	Filter feeder
Dominant feeding mode	ODJ	FDT

Relationships between feeding guild composition of polychaetes and abiotic factors

The canonical correspondence analysis (CCA) indicated that abiotic factors contributed significantly to explaining the variation in polychaete feeding guilds among the rocky shores studied. The first and second axes accounted for 39.7 and 29.9% of the variance observed in the feeding guild data, respectively. On the CCA plot (Fig. 7), communities at Bh, ZB, Pt, El, SK and If are moderately associated with salinity. By contrast, communities at Ta and Ou (but not Rg) positively related to the length of the rocky shores, higher grain-size and higher water temperature but negatively with salinity.

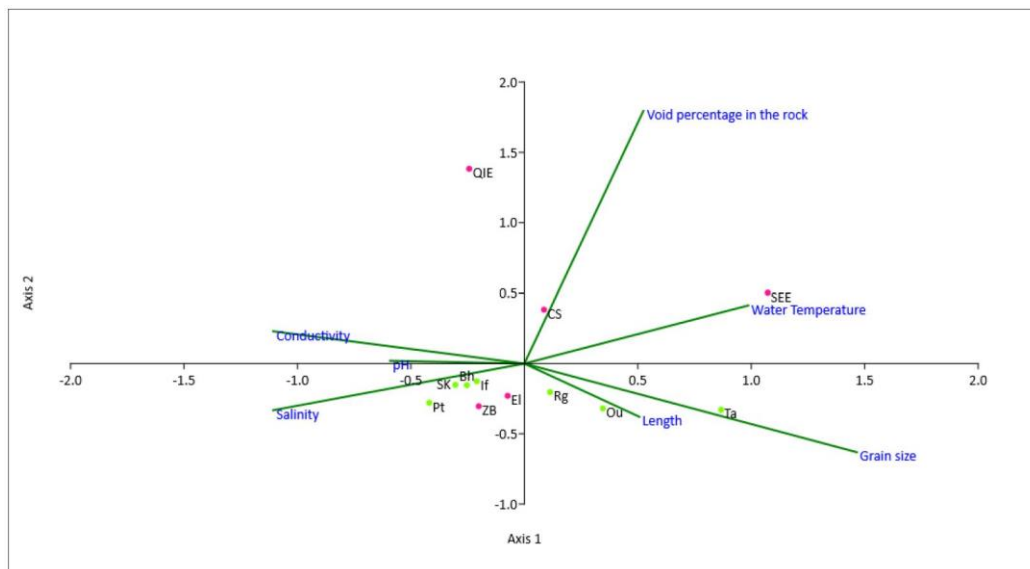


Figure 7. Canonical correspondence analysis (CCA) ordination of the polychaete feeding guild scores and environmental parameters in the study area (Axis 1: 39.7%; Axis 2: 29.9%)

Discussion

The present study provides the first characterization of the composition and spatial distribution patterns of polychaete feeding guilds along the rocky shores of Essaouira on the Atlantic coast of Morocco, and their relationship with environmental variables such as temperature, pH, conductivity, salinity, length and void percentage in the rock, and grain size of the rock. In this study, polychaete feeding communities at 12 sites were classified into five feeding guilds (Surface deposit feeders, Carnivores, Filter feeders, Subsurface deposit feeders and Omnivores), and nine feeding modes (BDX, CMX, SDT, CMJ, BMJ, ODJ, BMX, FDT and FST). We have included the omnivore feeding guild in this work since it is difficult to assign some Nereids in a particular feeding guild. Fauchald and Jumars (1979) classified several Nereid species as both carnivores and herbivores. Later, Gaston (1987) characterized them as surface deposit-feeders, Bianchi and Morri (1985) featured them once again as herbivores, and Jumars et al. (2015) specified that Nereids are clearly omnivorous, although digestive physiology suggests more likely specialization. According to Lindsay and Woodin (1995), Hentschel and Larson (2005), there are some species that can change their feeding mode depending on the availability of resources. As there are no consensus in the literature, we preferred classifying the Nereids of Essaouira intertidal rocky shores as omnivores.

The filter feeders were the dominant feeding guild (32%) followed by omnivores (23%), burrowers (20%), carnivores (15%) and surface deposit-feeders (10%), and the FDT (filter feeder, discretely motile, with tentacles) was the most abundant feeding mode, followed by the ODJ feeding mode (omnivores, discretely motile, with jaw apparatus) and the SDT feeding mode (surface deposit feeder, discretely motile, with tentacles) accounting for 24%, 22% and 18.9% of abundance, respectively. Denny (1988) suggested that the wave action is one of the main factors influencing the establishment and development of intertidal and shallow subtidal benthic communities. This factor represents a constant stress source that forces populations to acquire specific adaptations that allow them to survive in a stressful environment. One of these adaptative aspects is the suspension-feeding mode, which allows organisms to feed on material brought in by water movements (Okamura, 1990; Mann and Lazier, 1991). Thus, it is not surprising that in our case this feeding guild was dominant and present in all study areas, and is probably further enhanced by the influx of nutrient-rich cold waters brought to the surface by upwelling. This phenomenon usually occurs from June to October (Belvèze, 1983; Gentile, 1997; Simone, 2000; Bazairi et al., 2010; Benazzouz, 2014). The main representative species of this guild was *Sabellaria alveolata*, contributing 73.2% to total filter feeder abundance. Similarly, other studies have shown a large number of polychaete feeding guilds in marine environments (Table 6). According to these studies, the filter-feeders were the dominant feeding guild on hard substrate while the deposit-feeders were the dominant trophic group on soft substrates.

Table 6. Polychaete feeding guilds from different marine ecosystems and climate areas

Number of trophic group (number of guilds)	Number of species (number of family)	Dominant trophic guild	Substrate	Ecosystem	Geographical area	Reference
5 (9)	42 (16)	Filter-feeders	Hard	Intertidal	Essaouira (Atlantic coast of Morocco)	Present study
4 (9)	48 (16)	Filter-feeders	Hard	Mussel bank	Thessaloniki Bay (Greece)	Damianidis and Chintiroglou (2000)
4 (4)	22 (3)	Filter-feeder	Hard	Reef	Valencia Gulf Coast (Spain)	Porras et al. (1996)
5 (16)	160 (44)	Filter-feeders	Muddy to coarse sand	Subtidal	Campeche Bank (southern Gulf of Mexico)	Castanedo et al. (2012)
5 (n.a.)	75 (29)	Surface deposit-feeders	Medium sand to fine silt	Continental shelf	Southeast coast of India	Manokaran et al. (2013)
5 (10)	24 (21)	Deposit-feeders	Fine to coarse sand	Sandy beach	Sepetiba Bay (south-eastern Brazil)	Mattos et al. (2012)
3 (n.a.)	28 (13)	Surface deposit-feeders	Soft bottom	Deep-sea	Malta Escarpment (Western Ionian Sea)	Langeneck et al. (2017)
5 (n.a.)	92 (25)	Deposit-feeders	Sand and mud	Intertidal	Gulf of Gabès (Tunisia)	Mosbahi et al. (2017)
4 (13)	83 (12)	Deposit-feeders and carnivores		Subtidal	Hong Kong (China)	Cheung et al. (2008)
3 (n.a.)	15 (10)	Deposit-feeders	Fine to coarse sand	Mangrove	Quebra Pote, Maranhão (Brazil)	Cutrim et al. (2018)
5 (12)	80 (37)	Burrowers	Fine sand to coarse silt	Coastal bay	Sishili Bay, the northern Yellow Sea (China)	Han et al. (2016)

n.a.: not applicable

Paiva (1994) indicated that the density approach is more coherent to evaluate the importance of each feeding guild, especially when working with polychaete worms, since it indirectly estimates the biomass and production as these communities are composed of species with analogous life cycles. However, recruitment events and patchy distribution, not necessarily linked to increased food supply, can lead to an overevaluation of the feeding guild. Consequently, the use of the species richness gives more reliable results. During this study, we applied “Trophic group Importance index” (TI) proposed by Paiva (1994) which reduces the importance of density by applying log- transformation of abundances thus preserving the species richness factor. TI index was proved to be practical and very informative. Highest values of TI were recorded on the southern region of Essaouira where the beaches are sheltered and relatively far from human activities.

To accurately define the spatial organization of polychaete feeding guilds of Essaouira’s rocky shores, we used the cluster method which allows a discrimination between the sampling sites. Spatial differences in the structure of polychaete feeding guilds clearly discriminated between two groups: the first was group A (sites ZB, El, SEE, and CS) that characterized by the dominance of burrower and filter feeder feeding guilds, and ODJ feeding mode. The second one was group B which includes eight rocky sites (Ou, SK, Ta, If, Pt, QIE, Rg and Bh), with the dominance of filter feeder feeding guild and FDT feeding mode.

Several authors have observed strong relationships between polychaete feeding guilds and environmental factors, among which granulometry of sediments seems to be the most important (Maurer and Leathem, 1981; Carrasco and Carbajal, 1998; Muniz and Pires, 1999; Pagliosa, 2005; Mattos et al., 2012). Muniz and Pires (1999) and Méndez (2013) concluded that organic matter level in sediments could also strongly influence the feeding guilds of polychaetes, while Carrasco and Carbajal (1998) found no relationship with this variable, but a strong influence of depth. According to Paiva (1994), depth contributes to the sediment stabilization and consequently increases the feeding guild variety. Salinity, dissolved oxygen and temperature were also found to be important factors in determining trophic structure (Maurer and Leathem, 1981; Castanedo et al., 2012). In this study, the CCA results indicate that the length of rocky shores and water temperature are the most influential factors on the composition and spatial distribution of polychaete feeding guilds. Indeed, the rocky shores of Essaouira are long and rich in microhabitats, providing habitats for a large range of species which favours the increase of feeding guild diversity in this area. However, water temperature acts negatively on the diversity and abundance of feeding guilds via its negative influence on species richness and abundance of polychaetes.

Conclusion

This study on the composition and spatial distribution of polychaete feeding guilds of Essaouira intertidal rocky shores led to the identification of five feeding guilds (Surface deposit feeders, Carnivores, Filter feeders, Subsurface deposit feeders and Omnivores), and nine feeding modes (BDX, CMX, SDT, CMJ, BMJ, ODJ, BMX, FDT and FST). Compared to other marine ecosystems and geographical areas, we can conclude that the rocky shore of Essaouira is relatively rich in polychaete feeding guilds. The abiotic factors such as length of rocky shores and water temperature are the major factors affecting the composition and spatial distribution of polychaete feeding guilds in this

area. The data from this study can be used as a baseline reference for future scientific research programs, and may be a useful tool for authorities in charge of protection and management of this protected coastal area. Nevertheless, a detailed study during different seasons is required, in order to better understand the biotic and abiotic factors determining the structure and organisation of feeding guilds, determine the possible anthropogenic influences on this ecosystem, as well as to predict if this protected coastal area can be invaded by some invasive species.

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APPENDIX

Total abundance of polychaete species identified in Essaouira intertidal rocky shores. Data presented has not been standardised to 1 m²

Species	Bh	ZB	Rg	SEE	QIE	Pt	El	CS	Ou	Ta	SK	If
Capitellidae sp	0	0	2	0	0	0	0	0	0	0	0	1
<i>Bhawania goodei</i> Webster, 1884	1	4	1	4	7	15	0	1	29	113	14	13
Cirratulidae sp	0	0	0	0	0	1	0	0	0	3	2	0
<i>Cirriformia tentaculata</i> (Montagu, 1808)	0	0	0	0	1	2	0	0	6	2	7	7
<i>Lysidice ninetta</i> (Audouin & Milne-Edwards, 1833)	0	2	1	0	0	1	2	0	27	17	4	5
<i>Marphysa</i> sp	0	0	0	0	0	0	0	0	1	0	0	0
<i>Nematoneis unicornis</i> (Grube, 1840)	0	0	0	0	0	1	0	0	0	0	0	0
<i>Scoletoma funchalensis</i> (Kinberg, 1865)	3	0	1	7	5	0	2	4	5	1	2	7
<i>Scoletoma impatiens</i> (Claparède, 1868)	38	7	12	80	58	16	7	19	13	16	29	69
<i>Lumbrinereis</i> sp	0	0	0	0	0	1	0	0	0	0	0	0
<i>Johnstonia clymenoides</i> Quatrefages, 1866	2	9	1	6	3	4	7	1	11	3	1	0
<i>Petaloproctus terricola</i> Quatrefages, 1866	0	0	0	0	1	0	0	1	10	0	0	0
Maldanidae sp	0	0	1	1	0	0	2	3	0	1	0	0
<i>Perinereis cultrifera</i> (Grube, 1840)	22	13	46	12	20	49	16	69	50	43	49	168
<i>Perinereis marionii</i> (Audouin & Milne-Edwards 1833)	11	2	16	0	26	30	0	0	0	0	0	1
<i>Platynereis dumerilii</i> (Audouin & Milne-Edwards 1834)	9	57	13	0	33	25	48	3	10	5	49	115
<i>Nereis irrorata</i> (Malmgren, 1867)	0	0	0	0	0	0	2	0	0	0	0	0
<i>Nereis</i> sp	0	0	0	3	0	0	0	0	0	0	0	0
Nereididae sp	0	0	2	0	0	1	0	0	0	0	0	0
<i>Scolaricia typica</i> Eisig, 1914	0	1	0	0	226	28	0	21	0	0	50	29
<i>Nainereis laevigata</i> (Grube, 1855)	4	0	1	0	8	0	0	8	0	0	2	29

Orbiniidae sp	2	0	0	0	0	0	0	2	5	1	1	0
<i>Eulalia viridis</i> (Linnaeus, 1767)	16	2	13	7	16	31	2	9	3	31	25	39
<i>Mysta picta</i> (Quatrefages, 1866)	0	0	0	0	0	0	0	0	0	0	0	1
<i>Pyhllodoce maculta</i> (Linnaeus, 1767)	0	0	0	0	0	0	0	0	0	0	0	4
<i>Lepidonotus clava</i> (Montagu, 1808)	0	2	0	0	0	0	0	0	0	0	23	0
Polynoidae sp	0	0	1	3	2	19	1	1	12	21	36	58
<i>Sabellaria alveolata</i> (Linnaeus, 1767)	172	29	81	3	11	264	3	10	22	44	237	199
<i>Dasychone lucullana</i> (Delle Chiaje, 1828)	1	0	3	0	0	0	1	1	5	7	9	15
<i>Jasmineira elegans</i> Saint-Joseph, 1894	7	3	18	4	1	13	2	11	13	40	38	31
<i>Spirobranchus triqueter</i> Linnaeus, 1758	3	7	43	0	3	7	1	0	11	18	25	18
<i>Spirorbis</i> sp	0	0	5	0	0	4	0	0	3	3	0	2
<i>Serpula vermicularis</i> Linnaeus, 1767	0	0	0	0	0	0	0	0	0	4	1	0
Serpulidae sp	0	0	0	0	0	3	0	0	0	5	3	2
<i>Nerinides cantabra</i> Rioja, 1919	1	0	0	0	0	0	0	0	0	0	0	0
<i>Polydora ciliata</i> (Johnston, 1838)	0	0	0	0	0	0	0	0	1	0	0	1
<i>Aonides oxycephala</i> (Sars, 1862)	0	0	0	0	0	0	0	0	18	0	0	2
<i>Syllis armillaris</i> Müller, 1776	0	0	0	0	0	0	0	0	4	1	0	2
Syllidae sp1	4	0	0	0	7	3	1	0	4	4	0	0
Syllidae sp2	0	1	0	0	0	0	0	0	4	0	0	16
<i>Terebella lapidaria</i> Linnaeus, 1767	34	2	42	74	16	18	0	15	10	137	20	6
Terebellidae sp	1	0	4	4	0	0	0	3	0	0	0	7