



# Habitat associations and seasonal abundance patterns of the sea cucumber *Holothuria arguinensis* at Ria Formosa coastal lagoon (South Portugal)

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**Abstract** Sea cucumbers have an important economic value and high demand. Despite that, there is a lack of knowledge about their biology, ecology and habitat distribution patterns, which is very important for sea cucumber stock management, establishment and sizing of no-take zones, restocking actions and selection of grow-out areas. This work aimed to determine the density, abundance and habitat associations of *Holothuria arguinensis* for a better understanding of its distribution along the coastal lagoon Ria Formosa and to select suitable areas for grow-out. In the duration of a year, monthly visual censuses were performed in two locations at Ria Formosa along the intertidal zone. The number and length of *H. arguinensis*' individuals found were registered, and the coverage of algae and seagrass was estimated. It was found that *H. arguinensis* was distributed along the lower intertidal zone, linked to *Zostera noltii* meadows on muddy and sandy bottoms. These areas showed the densest population and the largest sizes of *H. arguinensis*. However, during the warmer months, *H. arguinensis* seemed to migrate to deeper waters in the channels, to avoid exposition to high temperatures

and solar/UV irradiance during low tides. Areas located in the lower intertidal zone with *Z. noltii* meadows on sand-muddy bottoms should be selected for *H. arguinensis* grow-out sites.

**Keywords** Sea cucumber · Visual censuses · Density · Low intertidal · Seagrass

## Introduction

Sea cucumbers are a diverse group of marine invertebrates that play an important ecological role in benthic communities as deposit feeders for creating bioturbation, nutrient recycling and habitat structuring (Bruckner et al. 2003; Preston 1993; Uthicke and Karez 1999; Uthicke 2001a, b). Through their feeding activity, sea cucumbers process large volumes of benthic sediments, assimilating bacterial, fungal and detrital organic matter (Michio et al. 2003; Yokoyama 2013). Additionally, sea cucumbers have an important economic value since they are commercially exploited and provide an income to millions of fishers worldwide (Purcell et al. 2013), who extract 200 million animals each year (Purcell et al. 2016) and sell around 10,000 tons of dried sea cucumber (Purcell et al. 2013). The high market demand has driven uncontrolled over-exploitation of many sea cucumber stocks around the world (Conand 2004).

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In the 1980 s, the sea cucumber aquaculture started to be developed in China and Japan focused on *Apostichopus japonicus* (Chen 2004); however, nowadays another six species are cultured and important efforts have been done to other many species (Eriksson et al. 2012; Purcell et al. 2012a; Domínguez-Godino et al. 2015; Domínguez-Godino and González-Wangüemert 2017, 2018a, b, c). In spite of their ecological and economic importance, there is a lack of knowledge about the ecology, biology and behaviour of most sea cucumber species from the Mediterranean Sea and NE Atlantic (Anderson et al. 2011; Bruckner et al. 2003; Conand 1990, 2004; Graham and Battaglene 2004; Navarro et al. 2014; Purcell et al. 2012a, b; Uthicke 2001b).

Most of the deposit-feeder sea cucumbers show a distribution linked with the sediment features in natural habitats; however, their density and movement patterns have been described to be dependent mainly on sediment type, habitat, substrate type, food abundance, migrations, aggregation behaviour, light intensity, depth and salinity (Sewell 1990; Brava 2005; Uthicke and Karez 1999; Sloan and von Bodungen 1980; Li et al. 1994; Slater et al. 2009; Dong et al. 2011; Hamel et al. 2001; Mercier et al. 2000a; Navarro et al. 2013, 2014; Shiell and Knott 2008). Characterisation of sea cucumber habitats is necessary to understand the main variables linked directly and/or indirectly to their patchy distribution and their environmental preferences. In addition, the different life stages should be considered in these studies, since for some species there is a habitat segregation associated with the age of individuals (Mercier et al. 2000a; Morgan 2011; Yamana et al. 2006). Juveniles of some sea cucumber species, such *Holothuria scabra* and/or *Australostichopus mollis*, are generally related to complex structures where juveniles are hidden from predators and attach themselves to macroalgae, seagrass leaves, rocks and/or shells (Mercier et al. 2000a; Morgan 2011). When they reach a determined size, juveniles migrate to soft sediment substrate (Conand 1993; Mercier et al. 2000a). However, adults are usually linked to more exposed areas (Yamana et al. 2006). Despite the reduced number of studies on sea cucumbers' habitat preferences and movement patterns, this information is vital and very useful for sea cucumber stock management, establishment and sizing of no-take zones, restocking actions and selection

of nursery and grow-out areas (Purcell and Kirby 2006; Shiell and Knott 2008; Ceccarelli et al. 2018).

The temperate sea cucumber *Holothuria arguinensis* (Koehler and Vaney 1906) is distributed along the North-Eastern Atlantic, from the Berlengas Island (Portugal) to Morocco and Mauritania, including the Canary Islands (Thandar 1988; Costello 2001; Rodrigues 2012; Rodrigues et al. 2015). However, this species has recently colonised the Mediterranean Sea (El Mojón, SE Spain and Bay of Algiers, Algeria) (González-Wangüemert and Borrero-Pérez 2012; Mezali and Thandar 2014). *H. arguinensis* has achieved high economic value, being intensively and illegally harvested in South Portugal and South Spain (González-Wangüemert et al. 2018). In the Natural Park Ria Formosa coastal lagoon, the management program and legislation (Decreto-Lei n° 373//87, de 9 de Dezembro; Resolução do Conselho de Ministros n° 78/2009, de 2 de Setembro) recognise the capture of 2 kg/person/day of marine invertebrates (no cephalopods) on the permitted areas. Despite the regulation, illegal captures were registered by the Maritime Police along the lagoon. Additionally, the aquaculture techniques for *H. arguinensis* have begun to be developed in the last years and important improvements have been achieved (Domínguez-Godino et al. 2015; Domínguez-Godino and González-Wangüemert 2017, 2018a, b, c).

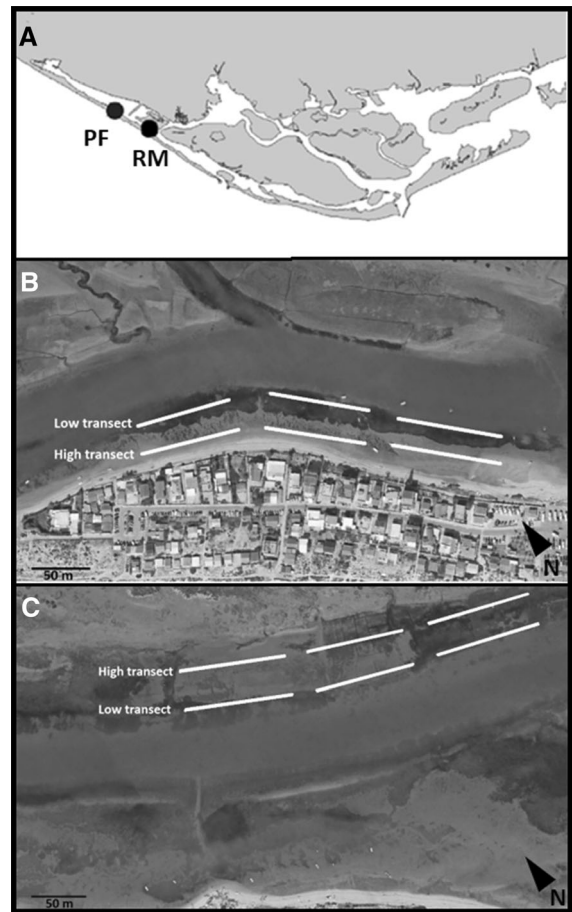
*Holothuria arguinensis* has been described to be associated with sand, muddy, seagrass meadows and macroalgae habitats from 0 to 50 m (González-Wangüemert and Borrero-Pérez 2012; González-Wangüemert et al. 2013; Navarro et al. 2014; Siegenthaler et al. 2015), where it shows different densities depending on habitats (González-Wangüemert et al. 2013; Navarro et al. 2014; Siegenthaler et al. 2015). In the Ria Formosa Natural Park (S Portugal), *H. arguinensis* is the most abundant sea cucumber species distributed across the intertidal areas, showing different patterns of distribution and densities (González-Wangüemert et al. 2013; Siegenthaler et al. 2015). *H. arguinensis* is found to be a sea cucumber species that actively moves through its habitats for 24 h (Siegenthaler et al. 2015). *H. arguinensis* has a seasonal reproduction period from June to October (Domínguez-Godino et al. 2015, Marquet et al. 2017). However, no study has been done until now to establish the drivers that explain its patchy distribution at Ria Formosa. The aim of this work was to study the

habitat association and spatial distribution pattern of *H. arguinensis* in Ria Formosa Natural Park (S. Portugal) along representative habitats. To achieve this objective, *H. arguinensis* abundance and sizes were recorded by visual censuses throughout 1 year in two sampling sites. Additionally, substratum coverage was registered, and sediment and faeces samples were collected to assess the habitat preference of this target species. This study will increase the ecological knowledge of *H. arguinensis* at Ria Formosa where a large and stable population can be found. Such information will be very useful for the selection of sea ranching and sea pens areas for the grow-out culture of this species in this lagoon where large areas are available. In addition, this ecological information will be also interesting for establishing further regulations of its fishery at Ria Formosa Natural Park and restocking programs since a many incidents of illegal harvesting have occurred in the last years (González-Wangüemert et al. 2018).

## Materials and methods

### Study area and sampling

The Ria Formosa Natural Park is a coastal lagoon sheltered by a sand barrier island system. It extends for about 55 km with a width of up to 6 km along the south coast of Portugal (Fig. 1) (Barbosa 2010). The lagoon has a surface of 170 ha, and it is connected to the ocean by 6 outlets (Pacheco et al. 2010; Pilkey et al. 1989). The Ria Formosa has a semi-diurnal tide with amplitudes ranging from 0.7 m for neap tides to 3.5 m for spring tides, favouring a water exchange of 50 to 75% each tide depending on the tide's amplitude (Águas 1986). The lagoon, which includes barrier islands, barrier platforms, back barrier lagoons and mainland, is composed of a highly branched system of creeks and channels. The intertidal area covers 1/3 of the total area, 14% of which is composed by permanent submersed subtidal channels (Newton and Mudge 2003; Ribeiro et al. 2008). The average depth is 3–4 m with a maximum depth up to 20 m in the channels (Malaquias and Sprung 2005; Sprung 2001). Water temperature ranges from 12 to 13 °C in winter to 27–28 °C in summer (Ribeiro et al. 2008) and the salinity from 35.5 to 36.9 psu (Ribeiro et al. 2008); however, during heavy rainfalls, salinity can drop to



**Fig. 1** a Map showing the location of each sampling site Praia de Faro (PF) and Ramalhete (RM). Map showing the location of the Low and High transects at Praia de Faro (b) and Ramalhete (c) sites

25 psu in some places (Pilkey et al. 1989). The main habitats composing the Ria Formosa lagoon are sand, mud and seagrass meadows, which show *Zostera noltii* in the intertidal areas, *Zostera marina* and *Cymodocea nodosa* in the subtidal areas, and *Spartina maritima* in the higher intertidal (Malaquias and Sprung 2005). During winter, thick mats of the macroalgae *Ulva* spp. and *Enteromorpha* spp. can be found (Sprung 2001).

Bi-monthly samplings were done at two sites at Ria Formosa, Praia de Faro (PF) and Ramalhete (RM) from August 2014 to August 2015 (Fig. 1) to cover the possible changes of habitat association and spatial distribution pattern of *H. arguinensis* along the year seasonality on Ria Formosa. The two sites were composed of the main subtidal habitats from Ria Formosa and where large densities of *H. arguinensis*

could be found. Visual censuses were conducted at each site during the lowest tide of the month at daytime (<http://www.hidrografico.pt/previsao-mares.php>). At each sampling site, two transects of  $100 \times 2$  m were established at the minimum level (Transect 1: Low; 2 m deep) and maximum level (Transect 2: High; 1 m deep) of low tide, with a distance of 20 m between them along the shore (González-Wangüemert et al. 2013). For each transect, three replicates were carried out; therefore,  $600 \text{ m}^2$  of the surface was sampled by transect and sampling site. Along each transect, the number of *H. arguinensis* individuals, their total relaxed length and position were recorded (metre on transect and right/left position). The weight of each individual was estimated using the following formula:  $\text{weight} = 9.016 \text{ length} = 3.6$  (González-Wangüemert et al. 2016). For the total area covered in each transect and site, the density and biomass of *H. arguinensis* were calculated. Since habitat substratum composition is an important factor for sea cucumber distribution and density, the habitat along the transects was characterised; every 5 m, the substratum coverage was estimated by the same sampler estimating the coverage percentage of sand, mud, rock, seagrass *Z. noltii* and/or algae on  $1 \text{ m}^2$  quadrant (González-Wangüemert et al. 2013). Sediment samples ( $n = 3$ ) close to the mouth and faeces samples close to the anus of the sea cucumbers ( $n = 3$ ) were collected at the beginning, middle and end of each replicate transect using a spun. The sediment and faeces samples were oven-dried at  $60 \text{ }^\circ\text{C}$  for 48 h, and the organic matter content was estimated by loss of ignition (LOI). Three sub-samples of 1 g were placed in a furnace for 5 h at  $525 \text{ }^\circ\text{C}$  and then re-weighed, the total organic matter (TOM) being the difference of weight. The absorption efficiency (AE) (Conover 1966) of organic matter was estimated for each sampled individual using its set of sediment and faeces samples, calculated as follows:

$$\text{Absorption efficiency}(\%) = 100 \times ((\text{TOM faeces} - \text{TOM sediment}) / (1 - \text{TOM sediment}) \times \text{TOM faeces}).$$

Since *H. arguinensis* has been described to be associated with seagrass meadows at Ria Formosa

(González-Wangüemert et al. 2013; Siegenthaler et al. 2015), two parameters related to this were considered. First, when the individuals were found in the seagrass meadows of *Z. noltii* (only seagrass species were found along the transect), a core sample was collected (8 cm of diameter) to estimate *Z. noltii* shoots density. After the sampling, the core samples were washed at the laboratory, to eliminate the mud and the *Z. noltii* shoots were counted. Secondly, the mean distance from each individual of *H. arguinensis* to a seagrass quadrat with minimum a 20% of coverage was estimated.

#### Statistical analysis

The statistical analyses were performed in R statistic software (Core Team 2013). Mean values of the obtained and estimated variables previously described were compared among transects and sites for the sampling period using one-way ANOVA, posterior assessment of normality using Shapiro–Wilk’s test (Shapiro and Wilk 1995) and homogeneity of variance with Bartlett test (Bartlett 1937). Tukey’s test (Tukey 1949) was used as post hoc analyses. If data do not accomplish normality and homogeneity, comparisons of mean values of variables were done using Kruskal–Wallis test (Kruskal and Wallis 1952) or Mann–Whitney–Wilcoxon test (Mann and Whitney 1947). Differences were considered significant if  $P < 0.05$ .

Linear correlation between the *H. arguinensis* variables (length, weight, density and biomass) and the environmental parameters (substratum coverage, number of shoots, TOM of sediment samples) and TOM of the faeces was tested using Spearman correlation, which was considered significant when  $R > 0.70$  ( $P < 0.05$ ). A redundancy analysis (RDA) was used to examine the relationships between *H. arguinensis*’ variables (length, density and biomass) and environmental parameters, which could play an

important role in the sea cucumber habitat association and spatial distribution pattern.

**Table 1** Summary of the length (cm), estimated weight (g), density (ind/Ha), biomass (kg/Ha) and absorption efficiency (AE, %) from *H. arguinensis* in each site

	Praia Faro High	Praia Faro Low	Ramalhete High	Ramalhete Low
<b>Length (cm)</b>				
<i>N</i>	8	77	19	250
Mean ± SD	20.25 ± 6.04 <sup>a</sup>	24.07 ± 5.62 <sup>b</sup>	20.08 ± 5.52 <sup>a</sup>	21.87 ± 4.84 <sup>b</sup>
Min	14	12	12	10
Max	30	41	31	35
<b>Weight (g)</b>				
<i>N</i>	8	77	19	250
Mean ± SD	178.97 ± 54.47 <sup>a</sup>	213.08 ± 51.23 <sup>b</sup>	177.43 ± 49.75 <sup>a</sup>	193.54 ± 43.59 <sup>b</sup>
Min	122.624	104.592	104.592	86.56
Max	266.88	366.056	275.896	311.96
<b>Density (ind/Ha)</b>				
Mean ± SD	19.05 ± 29.48 <sup>a</sup>	183.33 ± 194.51 <sup>b</sup>	45.24 ± 120.32 <sup>a</sup>	595.24 ± 412.58 <sup>c</sup>
<b>Biomass (kg/Ha)</b>				
Mean ± SD	3.41 ± 5.53 <sup>a</sup>	38.05 ± 42.7 <sup>b</sup>	8.027 ± 23.19 <sup>a</sup>	115.21 ± 79.15 <sup>b</sup>
<b>AE (%)</b>				
Mean ± SD	60.84 ± 15.82 <sup>ac</sup>	32.61 ± 30.77 <sup>3</sup>	25.99 ± 45.03 <sup>a</sup>	– 47.05 ± 124.07 <sup>ab</sup>

Different letters indicate significant differences (Nemenyi post hoc,  $P < 0.05$ )

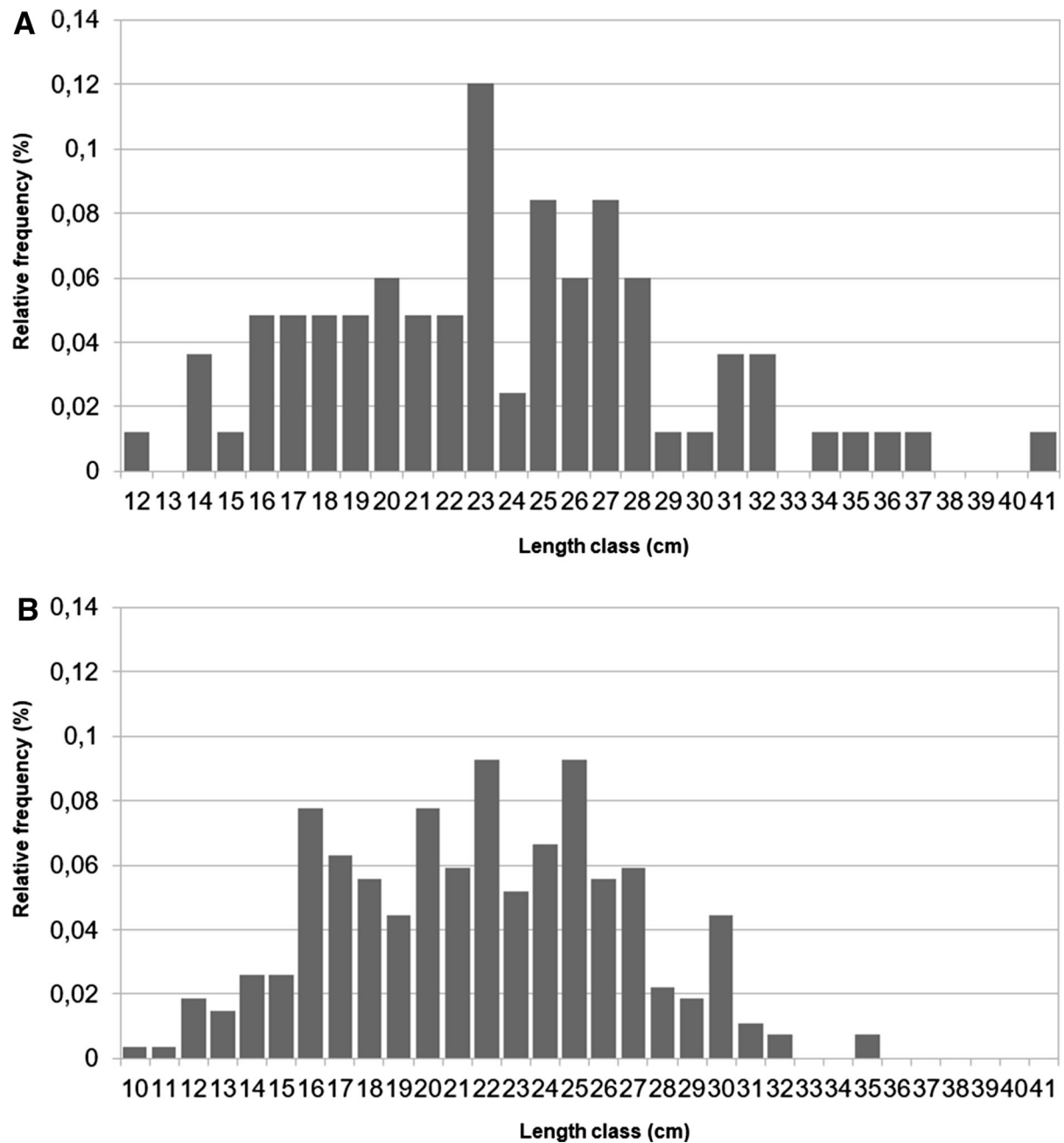
## Results

### *Holothuria arguinensis*' population variables

A total of 354 individuals of *H. arguinensis* were found and measured along the sampling period, corresponding to 85 individuals at Praia de Faro and 269 at Ramalhete sites (Table 1). The mean length and weight of *H. arguinensis* individuals at the two High transects were similar among them (Table 1, Kruskal–Wallis,  $P > 0.05$ ) and significantly smaller than the values obtained for the two Low transects (Table 1, Kruskal–Wallis,  $P < 0.05$ ). The individuals found at the Low transect at Praia de Faro were slightly larger and heavier ( $24.04 \pm 5.62$  cm and  $213.08 \pm 51.23$  g) than the ones registered at the Low transect at Ramalhete ( $21.87 \pm 4.84$  cm and  $193.54 \pm 43.59$  g); however, they were not significantly different (Table 1, Kruskal–Wallis,  $P > 0.05$ ). The smallest and lightest individual was found at Ramalhete Low transect with 14 cm length and 122.624 g weight, and the largest and heaviest individual at Praia de Faro Low transect with 41 cm length and 366.056 g weight. *H. arguinensis* individuals from Praia de Faro ranged in length from 12 to 41 cm, showing multimodal size–frequency distribution, with the highest frequency for the size class of 23 cm (Fig. 2a). At Ramalhete site, the individuals ranged in length from 10 to 35 cm, showing similar multimodal size–frequency

distribution; however, the highest frequencies were found for the size classes of 22 and 25 cm (Fig. 2b). The weight of individuals from Praia de Faro and Ramalhete sites showed a multimodal distribution with the most frequent weight between 221 and 240 g (Fig. 3).

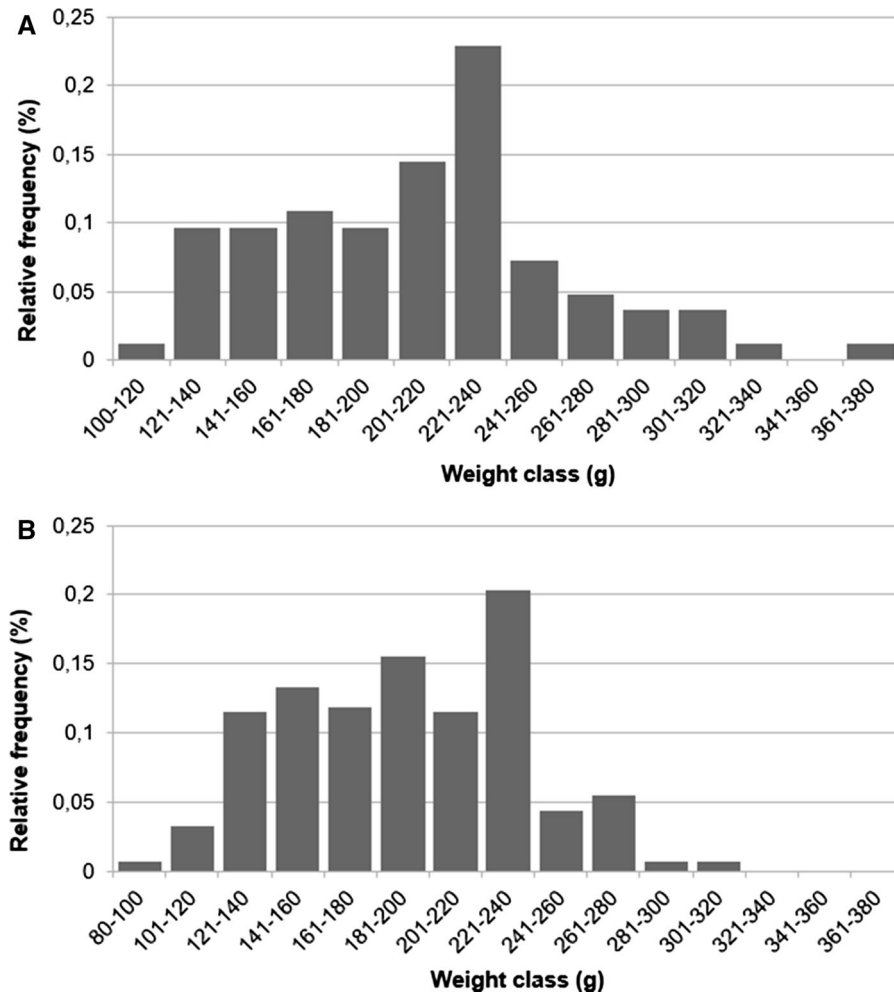
The density range was smaller at the two High transects compared to the Low transects: Praia de Faro from 0 to 50 ind/Ha and Ramalhete from 0 to 200 ind/Ha. Larger density was found at the two Low transects, which oscillated from 66 to 316 ind/Ha in Praia de Faro and from 316 to 933 ind/Ha in Ramalhete. The lowest mean density was obtained in the High transect at Praia de Faro with  $19.05 \pm 29.48$  ind/Ha (Table 1, Fig. 4a, Kruskal–Wallis,  $P > 0.05$ ). Significantly higher density was found at the Low transect at Ramalhete with a mean value of  $595.25 \pm 412.58$  ind/Ha (Table 1, Fig. 4a, Kruskal–Wallis,  $P < 0.05$ ). Significant lower mean biomasses were also found at both High transects in Praia de Faro and Ramalhete sites in comparison with the Low transects at both sites (Table 1, Fig. 4b, Kruskal–Wallis,  $P < 0.05$ ); however, significant differences were not found among High transects (Table 1, Fig. 4b, Kruskal–Wallis,  $P > 0.05$ ). The highest biomass was obtained at each Low transect with a total of  $38.05 \pm 42.7$  kg/Ha and  $115.21 \pm 79.15$  kg/Ha for Praia de Faro and Ramalhete, respectively; however, the differences found among them were not significant (Table 1, Fig. 4b, Kruskal–Wallis,  $P > 0.05$ ).



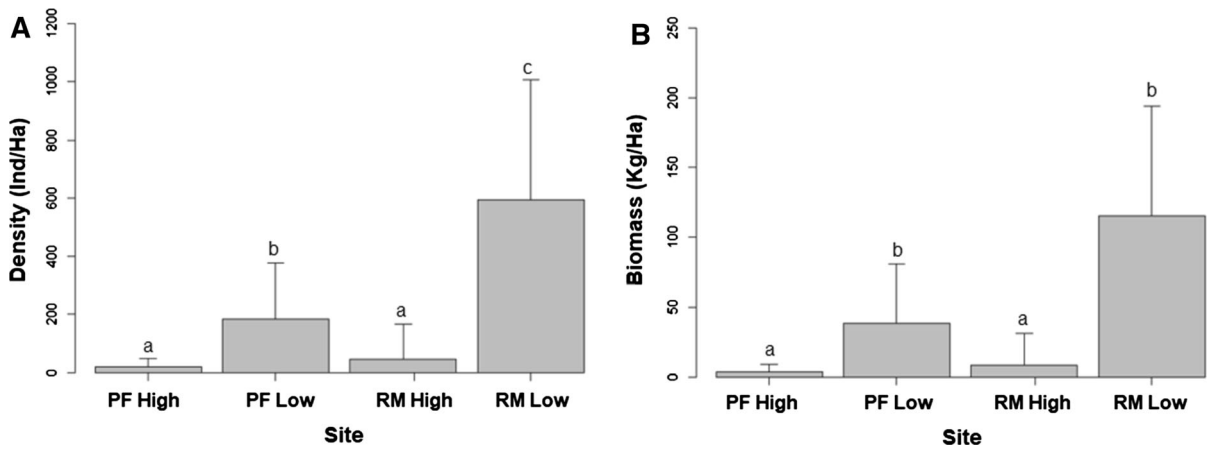
**Fig. 2** Frequency distribution of total length for *H. arguinensis* at **a** Praia de Faro and **b** Ramalhete sites

The highest mean absorption efficiency (AE) was obtained for *H. arguinensis* individuals found at the High transect at Praia de Faro (Table 1). The Low transect at Praia de Faro and the High transect at Ramalhete had similar values of AE, which were approximately half of the value obtained for the High transect at Praia de Faro, without showing significant

differences (Table 1, Kruskal–Wallis,  $P > 0.05$ ). A negative value of AE was obtained for the Low transect at Ramalhete which was significantly different from the AE value obtained for the High transect at Praia de Faro (Table 1, Kruskal–Wallis,  $P < 0.05$ ).



**Fig. 3** Frequency distribution of estimated weight for *H. arguinensis* at **a** Praia de Faro and **b** Ramalhete sites



**Fig. 4** **a** Mean density (ind/Ha) and **b** mean biomass (kg/Ha) for *H. arguinensis* in the High and Low transects at Praia de Faro (PF) and Ramalhete (RM) sites. Values are given as mean  $\pm$  SD. Different letters indicate significant differences (Nemenyi post hoc,  $P < 0.05$ )

### *Holothuria arguinensis*' seasonality patterns density, weight and biomass

*Holothuria arguinensis* showed different patterns of density, mean weight and total biomass along the seasons for the different transects. The High transect at Praia de Faro showed the highest densities, mean weight and biomasses at autumn and winter, the density and biomass being higher in autumn than in winter (Table 2, Fig. 5a–c). During summer in the High transect at Praia de Faro, no sea cucumbers were found and low density was registered during spring with small and light individuals; therefore, low biomass was also recorded to be significantly different compared to the values obtained for the winter (Table 2, Fig. 5a–c; Kruskal–Wallis,  $P < 0.05$ ). At the Low transect at Praia de Faro, the highest density and biomass were found for autumn and winter, with the lowest values found during the summer season (Table 2, Fig. 5b, d, f); however, heavier individuals were found in spring and summer than for autumn and winter (Table 2, Fig. 5f). For the case of the High transect at Ramalhete, the largest density, weight and biomass were registered in winter (Table 2, Fig. 6a–c), with significantly heavier sea cucumbers than the ones found in summer (Kruskal–Wallis,  $P < 0.05$ ). Along this transect, no sea cucumbers were found during spring (Table 2, Fig. 6a). The Low transect at Ramalhete showed high density and biomass along the

different seasons, summer being the season with the largest density and biomass (Table 2, Fig. 6d, e). At this transect, the lowest density of sea cucumbers was found in spring, with the lightest individuals registered during winter (Table 2, Fig. 6d–f).

### Habitat description

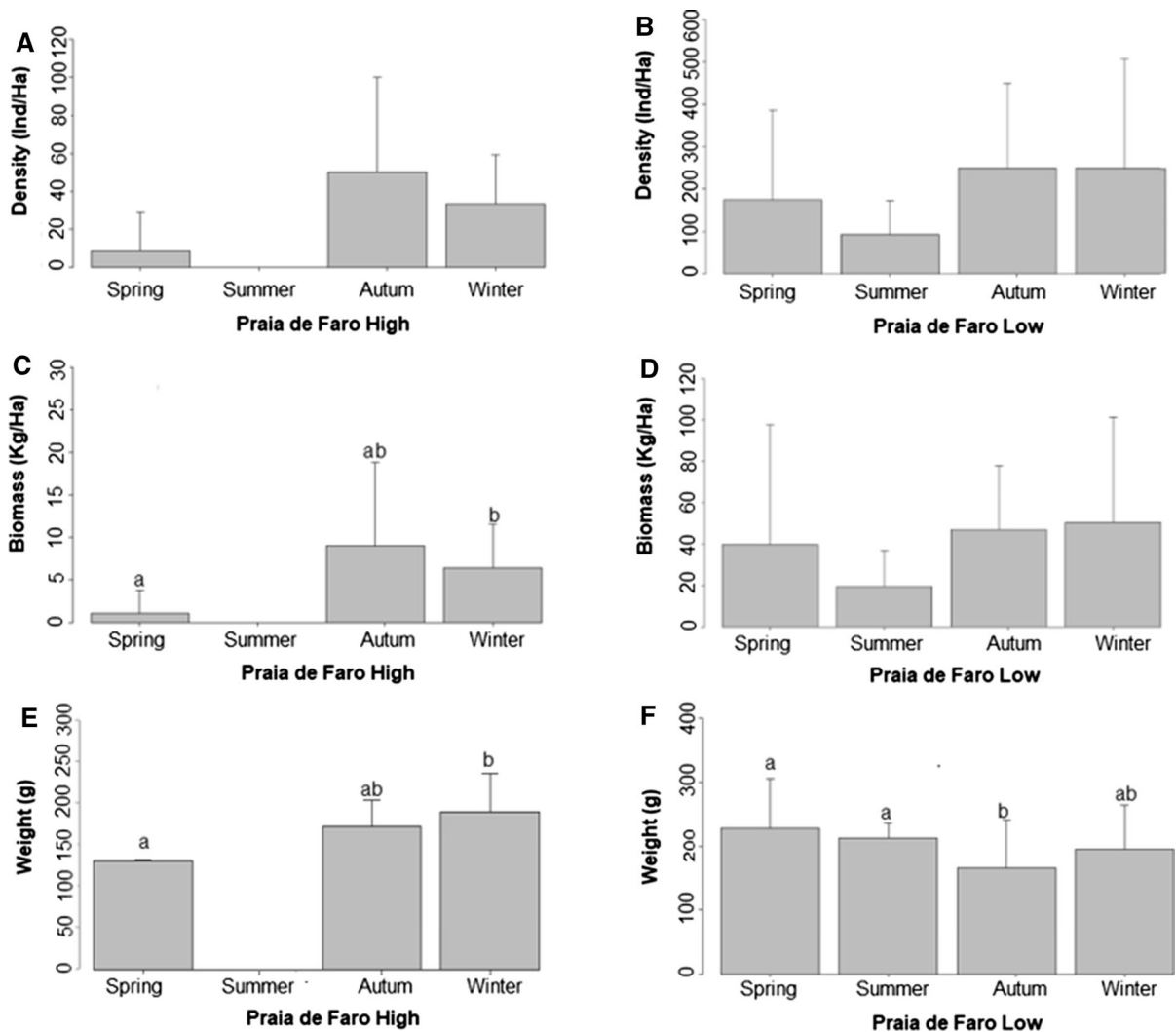
Three different major habitats were identified in our sampling sites. The High transect at Praia de Faro was characterised by a coverage of 89.63% of sand: a percentage significantly higher than the sand coverage registered in the others transects (Table 3, Kruskal–Wallis,  $P < 0.05$ ). Additionally, along this transect was found a 10.37% of *Ulva* spp. covering the sand. The Lower transect at Praia de Faro was significantly dominated by a dense seagrass meadow of *Zostera noltii* accounting to a 93.09% coverage (Table 3, Kruskal–Wallis,  $P < 0.05$ ). The seagrass was crossed by several sandy and muddy channels covering 2.89% and 2.9% of the transect, respectively. The two transects at Ramalhete were characterised by a heterogeneous habitat composed of medium level of *Z. noltii* coverage (48.64% and 44.02% for the High and Low transect, respectively; no significant differences were found among them; Table 3, Kruskal–Wallis,  $P > 0.05$ ), sand (22.51% for the High and 39.24% for the Low transect; showing significant differences; Table 3, Kruskal–Wallis,  $P < 0.05$ ) and

**Table 2** Mean density (ind/Ha), mean estimated weight (g) and mean biomass (kg/Ha) for *H. arguinensis* in each site and transect during the different seasons

Site	Transect	Season	Density (ind/Ha)	Weight (g)	Biomass (kg/Ha)
Praia Faro	High	Spring	8.33 ± 20.41	131.64 ± 0.01 <sup>a</sup>	1.09 ± 2.69 <sup>a</sup>
		Summer	0	0	0
		Autumn	50 ± 50	179.72 ± 76.68 <sup>ab</sup>	8.99 ± 9.82 <sup>ab</sup>
		Winter	33.33 ± 25.82	190.24 ± 45.67 <sup>b</sup>	6.34 ± 5.22 <sup>b</sup>
Praia Faro	Low	Spring	175 ± 211.54	239.15 ± 61.64 <sup>a</sup>	39.86 ± 57.9
		Summer	91.66 ± 80.1	212.78 ± 22.8 <sup>a</sup>	19.51 ± 17.45
		Autumn	250 ± 200	187.54 ± 45.1 <sup>1b</sup>	46.88 ± 30.91
		Winter	250 ± 256.9	208.43 ± 47.93 <sup>ab</sup>	50.37 ± 51.07
Ramalhete	High	Spring	0	0	0
		Summer	25 ± 28.63	139.15 ± 28.63 <sup>a</sup>	3.48 ± 5.51
		Autumn	50 ± 50	140.66 ± 36.06 <sup>ab</sup>	7.03 ± 8.08
		Winter	108.33 ± 217.75	194.75 ± 48.27 <sup>b</sup>	21.09 ± 42.27
Ramalhete	Low	Spring	508.33 ± 171.51	193.49 ± 41.78 <sup>a</sup>	98.36 ± 38.85
		Summer	683.33 ± 136.63	203.55 ± 47.58 <sup>ac</sup>	139.09 ± 41.19
		Autumn	533.33 ± 448.14	220.67 ± 32.69 <sup>b</sup>	117.69 ± 107.59
		Winter	625 ± 728.53	171.07 ± 33.37 <sup>c</sup>	106.92 ± 126.92

Different letters indicate significant differences among season within transect in each site (Nemenyi post hoc,  $P < 0.05$ )



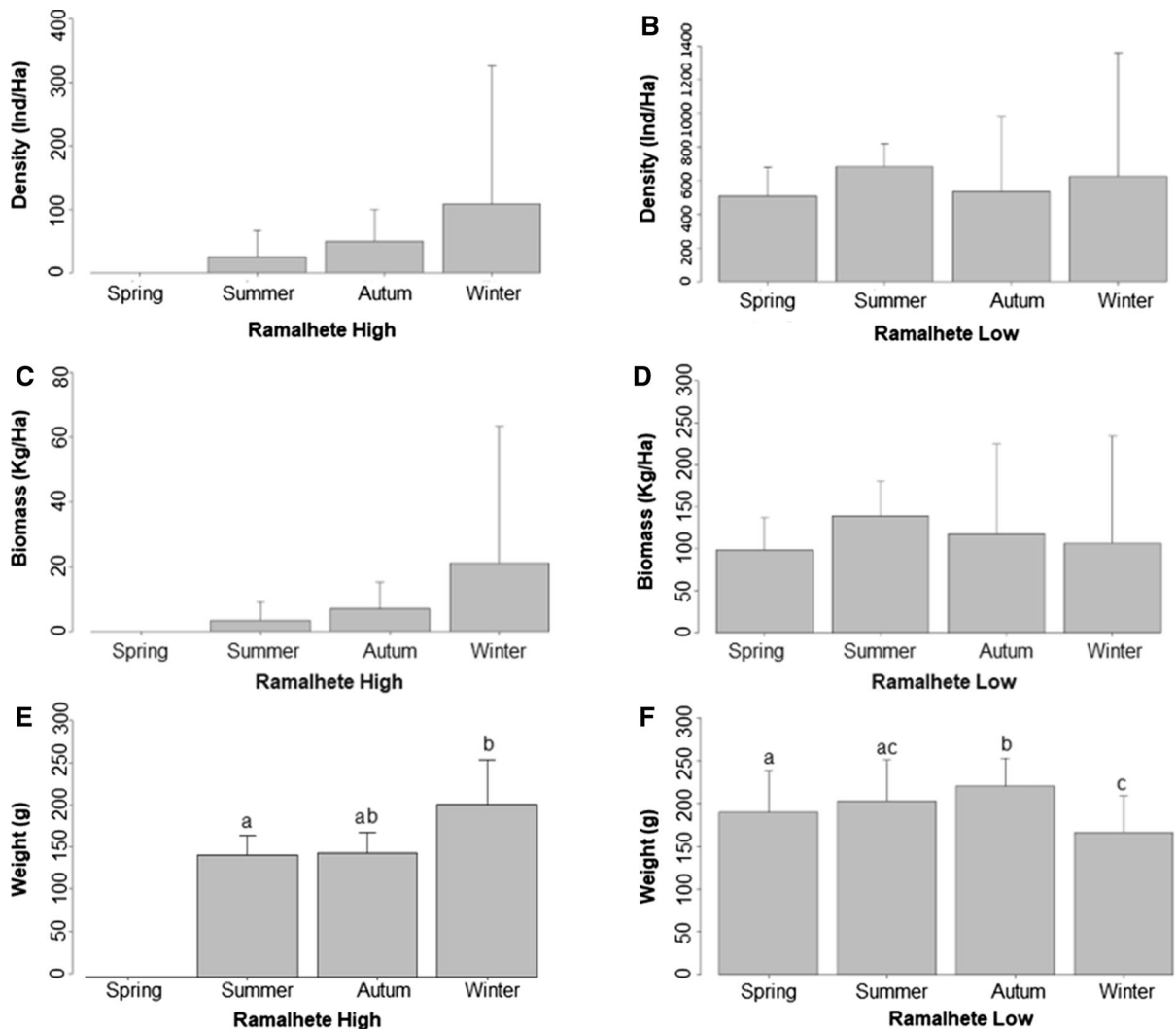


**Fig. 5** Mean density (ind/Ha), mean biomass (kg/Ha) and mean estimated weight (g) for *H. arguinensis* in the High transect (**a**, **c**, **e**, respectively), and in the Low transect (**b**, **d**, **f**, respectively),

at Praia de Faro (PF) site in the different seasons. Values are given as mean  $\pm$  SD. Different letters indicate significant differences (Nemenyi post hoc,  $P < 0.05$ )

mud (16.15% for the High and 9.36% for the Low transect, showing significant differences among them; Table 3, Kruskal–Wallis,  $P < 0.05$ ). Along these two transects at Ramalhete site, a similar mean coverage of *Ulva* spp. was registered ( $\sim 5\%$ ), with a 7.24% and 1.58% of *Enteromorpha* spp. for the High and Low transects, respectively. The Ramalhete site recorded the lowest and highest estimation of *Z. noltii*'s shoots for the High and Low transects, respectively; however, no significant differences were obtained (Table 2, Kruskal–Wallis,  $P > 0.05$ ). No significant differences were registered between transects among sampling sites (Kruskal–Wallis,  $P > 0.05$ ). The Praia de Faro

site showed the highest and lowest percentage of total organic matter (TOM): 6.72% for the Low transect and 1.18% for the High transect. The two transects at Ramalhete showed medium values, the records for the Low transect being slightly higher (3.31% TOM) than the ones obtained for the High transect (2.38% TOM). More significant differences of the percentage of TOM were found among the High transects in comparison with the Low transects (Kruskal–Wallis,  $P < 0.05$  (Table 3). Similar significant differences were found in the percentage of TOM in *H. arguinensis*' faeces (Table 3) (Kruskal–Wallis,  $P < 0.05$ ). No significant lineal correlation was found between *H. arguinensis*'



**Fig. 6** Mean density (ind/Ha), mean biomass (kg/Ha) and mean estimated weight (g) for *H. arguinensis* in the High transect (a, c, e, respectively), and in the Low transect (b, d, f, respectively),

at Ramalhete (RM) site in the different seasons. Values are given as mean  $\pm$  SD. Different letters indicate significant differences (Nemenyi post hoc,  $P < 0.05$ )

variables (length, weight, density and biomass) and the environmental parameters (substratum coverage, number of shoots, TOM of sediment samples) and TOM of faeces (Spearman correlation:  $R > 0.70$ ,  $P > 0.05$ ). The transect at Ramalhete could be defined as a complex mosaic habitat, where seagrass meadows with different shoot density and coverage were mixed with sandy and muddy patches; Praia de Faro, however, was found to be a homogeneous muddy substratum of dense seagrass meadow (Table 3).

#### Redundancy analysis (RDA)

The first two components explained 99.99% of the total variance. The first component has a strong positive correlation with density, while the second component has a negative correlation with the biomass, weight and length (Fig. 7). The environmental factors that are significantly important to the variability explained by the two components are the number of shoots (Nshoots), the percentage of coverage (Seagrass) and the percentage of TOM in the sediment (pOMsed), which were significantly and positively correlated with the first component



## Discussion

*Holothuria arguinensis* showed different distribution patterns across the study area with densities ranging from 0 to 933 ind/Ha depending on the transects with a mean value of  $212 \pm 328$  ind/Ha. The maximum density recorded in this study was higher than the described one for this species at Ria Formosa previously, using visual censuses (140–480 ind/Ha, González-Wangüemert et al. 2013); however, slightly lower mean density was obtained in our sampling ( $267 \pm 152$  ind/Ha, González-Wangüemert et al. 2013). In addition, our mean density was also smaller than the capture–recapture estimated density for this area (563 ind/Ha, Siegenthaler et al. 2015). The density of this species at the Canary Islands on seagrass meadows and macroalgal bed was also higher than in our sampling, with 250 ind/Ha and 460 ind/Ha, respectively (Navarro et al. 2014). Therefore, *H. arguinensis* shows different mean densities across habitats, location and time, what might also be influenced by the different sampling methods used in the different studies.

*Holothuria arguinensis* in our study showed a clear preference for the lower part of the intertidal zone, since significant lower density, length, weight and biomass were found at the two High transects. The area covered by the High transects, due to their position at the upper part of the intertidal, had longer emersion times along the year in comparison with the Low transects (Praia de Faro High transect 261.1 h and Low transect 10.93 h), which could be considered the main factor explaining the low presence of sea cucumbers at these transects. This is reinforced by the seasonal change of density and biomass registered in both High transects, showing the lowest density/biomass during the spring and summer periods. During the summer, the mean air temperature at Ria Formosa is 22–23 °C; however, the mean number of days with air temperature higher than 25 °C is 79 days (<http://portaldoclima.pt>). In addition, during these months, the highest global radiation is attained with a mean value of 250 W/m<sup>2</sup> (<http://portaldoclima.pt>), together with the highest level of UV radiation. Therefore, the upper part of the intertidal became an unsuitable habitat for sea cucumbers during summer due to the long periods of desiccation under high temperatures and UV irradiance, which can produce skin ulceration and some diseases (González-

Wangüemert et al. 2013, Cánovas et al. 2019). This fact can be also accentuated in the case of the High transect at Praia de Faro by the non-existence of seagrass meadow that could provide some covering protection to *H. arguinensis* against sun irradiance, which has been already described for this species at Ria Formosa (González-Wangüemert et al. 2013; Siegenthaler et al. 2015). Tidal level has already been described as a factor influencing sea cucumbers' density, as is the case of *Holothuria grisea* in the Brazilian coast, where higher densities were found in the subtidal zone (Tommasi 1969, Mendes et al. 2006). *H. grisea* showed a reduction in densities during summer, which could be driven by the high summer temperatures. In addition, high aggregations of *H. grisea* were found in tidal pools as emersion response during the low tide periods (Mendes et al. 2006). Studies focused on *Holothuria theeli* also suggested that its habitat preferences and occupation might be linked to the tidal level (Sonnenholzner 2003). Additionally, *H. arguinensis* has been described to have day/night movement pattern, showing displacement directed to the low part of the intertidal during the day and to the high part of the intertidal during the night: movements that were independent of habitat and mainly driven by avoidance of sunlight (Siegenthaler et al. 2015).

*Holothuria arguinensis*' length, weight, density and/or biomass were not linearly correlated with any of the environmental parameters assessed. However, some of them, such as the number of seagrass shoots, seagrass coverage, the distance to a seagrass coverage of 20% and the percentage of organic matter in the sediment, were significantly related to the variability of *H. arguinensis*' density, length and biomass according to the RDA analysis. *H. arguinensis*' density seems to be influenced by the shoot's density and the organic matter content in the sediment, and their length and biomass by the seagrass density and the distance to seagrass meadows. Ramalhete site showed higher density of smaller and lighter *H. arguinensis* individuals, and this sampling site is characterised by sand-muddy bottom, medium coverage of seagrass meadows with large shoots of *Z. noltii* and low organic matter content. In contrast, Praia de Faro showed lower densities of larger and heavier individuals; this site showed muddy bottom rich in organic matter and highly covered with thin *Z. noltii* shoots. In addition, *H. arguinensis* significantly

prefers the low intertidal of our study area, although differences in the studied parameters on *H. arguinensis* among the two Low transects from the different sampling places were found. The Low transect at Ramalhete site has significantly less dense seagrass meadow than Praia de Faro, showing slightly smaller and lighter sea cucumbers than the Low transect at Praia de Faro. These differences could be due to the habitat features linked to both transects. The transect at Ramalhete could be defined as complex mosaic habitat, where seagrass meadows with different shoot density and coverage were mixed with sandy and muddy areas. This complex and heterogeneous habitat could provide many diverse food sources for sea cucumbers, in contrast to a more homogeneous muddy substratum and dense seagrass meadow found at Praia de Faro. Therefore, it is likely that *H. arguinensis* prefers a more complex habitat which has different microhabitats across small areas, which is able to support importantly larger population density with smaller and lighter individuals. Diversity of microphytobenthos (MPB: microalgae, cyanobacteria and other photosynthetic bacteria) and their spatial–temporal biomass variability are partially controlled by tidal exposure and sediment features (Brotas et al. 1995). The sediment type is the parameter that explains most of the diversity (Paterson and Hagerthey 2001; Perkins et al. 2003), determining the presence of certain MPB groups: muddy sediments are dominated by diatoms and sandy sediments by more diverse groups, such as cyanobacteria and euglenids (Underwood and Barnett 2006). So, probably differences in MPB could be also found at the different sampling sites and influence the individual distribution. *H. arguinensis* can process large volumes of sand, showing a mean feeding rate of  $27.88 \pm 3.63$  g ind<sup>-1</sup> d<sup>-1</sup> for individuals with a mean weight of  $272.89 \pm 32.04$  g (Domínguez-Godino and González-Wangüemert 2018b). However, it could be expected that in muddy bottoms with dense seagrass meadow, this feeding rate could be smaller due to sediment size and compaction. This together with the poorest food source (lower diversity of MPB) of this habitat might influence the lower density and larger sizes of *H. arguinensis* at the Low transect in Praia de Faro. In spite of this hypothesis on habitat preference, it is important to highlight that *H. arguinensis* at Praia de Faro could have also suffered heavier illegal harvesting pressure than Ramalhete site, what could

explain the obtained results. At Ria Formosa, since 2014, there have been an important incidence of illegal sea cucumber fishing mainly focused on *H. arguinensis*, whose density has reduced in areas such as Ramalhete Channel, Culatra Island and Armona Island, with a decrease in the largest sizes (González-Wangüemert et al. 2018). The same two transects at Praia de Faro were sampled from November 2012 to February 2013 using the same methodology (González-Wangüemert et al. 2013); however, higher densities were found more during that period (150 ind/Ha and 480 ind/Ha for the High and Low transects, respectively), than the obtained ones during our study (19 ind/Ha and 193 ind/Ha for the High and Low transects, respectively). In fact, the registered densities in the sampling of 2012–2013 at Praia de Faro are comparable with the ones obtained at the Ramalhete site in the Low transect during our study (595 ind/Ha). Similar important *H. arguinensis*' abundance reduction has been found along Ria Formosa in other locations due to illegal harvesting, such as in Armona Island where densities reduced from 118 ind/Ha in 2014 to 30 ind/Ha in 2016 (González-Wangüemert et al. 2018). In addition, *H. arguinensis*' size distribution changed from a mean size class between 26–30 and 21–25 cm in this location (González-Wangüemert et al. 2018). The sampling site at Praia de Faro is an accessible area of the Ria Formosa, which is the main beach of Faro city, residential area and fishermen urban area (Zacarias et al. 2011; Almeida et al. 2011). Along the lagoon, many species with commercial interest are harvested during low tides (e.g. cockles, ensis, clam, spiny dye-murex) by shellfish catchers; therefore, *H. arguinensis* could have been harvested illegally during the time period between the two samplings (González-Wangüemert et al. 2018; Pires 2016a, b). The Ramalhete site is located in the north of the main channel of Praia de Faro. Being less accessible from mainland, a ship was required to reach this area. Additionally, in the adjacent areas of the transects in Ramalhete, some clam and oyster farms are present, which are frequented by the farmers and not by fishermen harvesting other commercial species that could also restrict the incidence of illegal fishing.

*Holothuria arguinensis* showed two different patterns of density distribution in the Low transects along the year. At Praia de Faro, the same pattern of density' decrease during the warmer months was observed in

the High and Low transects; therefore, the individuals might move to deeper areas of the channel during this season. Although the data were not statistically significant, it is interesting to note that the Low transect at Ramalhete showed the opposite pattern, summer being the period with the highest density. As other sea cucumbers (e.g. *Holothuria tubulosa*, *Parastichopus californicus*), *H. arguinensis* has density-dependent reproduction and aggregation behaviour during reproductive season (Brava 2005; Bruckner et al. 2003; Cousteau and Dugan 1963; McEuen 1988), which is on summer months (Domínguez-Godino et al. 2015; Marquet et al. 2017). Therefore, it could be possible that Ramalhete site is an aggregation area of breeders during the period of summer, which explains the high density registered on Low Transects during summer.

*Holothuria arguinensis* showed different absorption efficiency along the different transects. Sea cucumbers can modulate their absorption efficiency as compensatory response to sediment quality and quantity (Roberts et al. 2003; Yuan et al. 2006; Zamora and Jeffs 2011). *H. arguinensis* showed the highest absorption efficiency at the High transect of Praia de Faro, which was characterised by sandy bottom with the lowest content of organic matter. However, in the Low transect at Praia de Faro and High transect at Ramalhete, similarly low values of absorption efficiency were obtained: in these places, the transects showed lower coverage of sand and high content of organic matter, due probably to the high coverage of mud and seagrass. Therefore, *H. arguinensis* needs to be more efficient in obtaining nutrients in poorer substratum such as sandy areas which are less efficient in rich muddy and seagrass meadows areas. It is important to highlight that the absorption efficiency obtained for the Low transect at Ramalhete was negative, meaning that most of the faeces collected had higher total organic content than the sediment samples. This result is typically associated with selective feeder sea cucumbers, which select organic-rich sediment from the surrounding areas. However, *H. arguinensis* has been categorised as non-selective feeder (Navarro et al. 2014), which is also supported by our results of absorption efficiency obtained from the other three transects. The negative values of absorption efficiency might be explained by the continuous feeding and movement of *H. arguinensis* along this heterogeneous transect (in terms of

coverage and organic matter content). In this way, the sediment collected underneath the sea cucumbers could not correspond to the faeces features (TOM), because the individual displaces along a very heterogeneous habitat during the time period from ingestion to defecation. This fact was observed during the collection of the mentioned samples, e.g. the individual was on sandy bottom; however, the faeces was composed of muddy sediment. Therefore, possible mismatching of sediment and faeces samples can be recorded due to sea cucumber displacement along its habitat. This should be considered when the absorption efficiency is applied on field surveys since they might induce some bias.

Sea cucumbers are unevenly distributed due to several factors such as food availability, bottom sediment features, substrate type, depth, tidal regime, predator avoidance. (Sloan and Von Bodungen 1980; Young and Chia 1982; Hammond 1983; Massin and Doumen 1986; Bulteel et al. 1992; Uthicke and Karez 1999; Mercier et al. 2000a, b; Uthicke et al. 2004; Abdl Razek et al. 2006; Eckert 2007; Entrambasaguas et al. 2008; Shiell and Knott 2010). Additionally, their habitat preferences have been described to be species-specific and within the same species with differences across life stages (Conand 1990; Mercier et al. 2000b; Purcell 2004; Shiel 2004; James 2005; Yamana et al. 2006; Conand 2008; Purcell et al. 2009). Therefore, the above mentioned parameters could have a certain influence on *H. arguinensis* distribution, density and size. Specially for our target species, the tidal regime together with the depth, which determine the number of emersions' hours for different areas of the lagoon, could be the most important factors. In addition, the bottom sediment features and substrate type which determine the food availability for *H. arguinensis* seem to also be decisive.

The results obtained in this study have important applications for *H. arguinensis*' aquaculture, target species in Europe whose biotechnology for its culture was being developed in the last years (Domínguez-Godino et al. 2015; Domínguez-Godino and González-Wangüemert 2017). However, there is a need for a better understanding of natural habitat selection of juveniles and adults to apply this information on grow-out selection sites. Sea cucumber could be cultured on sea pens and sea ranching in natural areas (Han et al. 2016). The Ria Formosa has an important potential to develop these culture systems, such as using them for

other commercial species, such cockles, clam and oysters along it (Newton et al. 2003). According to the obtained results, grow-out areas for large juveniles and adults of *H. arguinensis* should be allocated in medium and dense seagrass meadows at the lower intertidal areas along the Ria Formosa.

## Conclusions

*Holothuria arguinensis* showed different distribution patterns across the study areas, recording lower densities than the previously ones found for this species at Ria Formosa (S Portugal) and/or the Canary Islands (Spain). *H. arguinensis* was significantly more abundant in the lower areas of the intertidal, which could likely be driven by the tidal level at the lagoon Ria Formosa. Additionally, more dense populations with smaller and lighter individuals were found in sandy-muddy with medium coverage of *Z. noltii* seagrass meadows, due likely to the increase in food sources by the habitat complexity. However, the differences among sites could also have been driven by the illegal sea cucumber fishing affecting the Ria Formosa. These areas where large populations of *H. arguinensis* could be found should be protected and regulated as non-taking zones to ensure stable population which favour the persistence of the target species and production of offspring. Finally, *H. arguinensis* showed a modulation of absorption efficiency according to the associated substratum type. However, the presented methodology for field surveys might induce some bias which must be considered in ecology research on sea cucumbers. In addition, these results have an application for *H. arguinensis*' aquaculture in terms of selection of grow-out areas for large juveniles and adults; which should be allocated in the lower intertidal on sandy-muddy bottoms with medium dense *Z. noltii* seagrass meadows.

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