

Modelling the habitat preferences of the NE-Atlantic Sea cucumber *Holothuria forskali*: Demographics and abundance

P.M. Félix^{a,*}, F. Azevedo e Silva^a, T. Simões^a, A. Pombo^b, T.A. Marques^{c,d,e}, C. Rocha^{c,f}, J. Sousa^b, E. Venâncio^b, A.C. Brito^{a,g}

^a MARE - Marine and Environmental Sciences Centre / ARNET - Aquatic Research Network, Faculdade de Ciências, Universidade de Lisboa, Portugal

^b MARE - Marine and Environmental Sciences Centre / ARNET - Aquatic Research Network, ESTM, Polytechnic Institute of Leiria, Portugal

^c CEaul - Centro de Estatística e Aplicações, Faculdade de Ciências, Universidade de Lisboa, Portugal

^d Centre for Research into Ecological and Environmental Modelling, The Observatory, University of St Andrews, UK

^e Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Portugal

^f Departamento de Estatística e Investigação Operacional, Faculdade de Ciências, Universidade de Lisboa, Portugal

^g Departamento de Biologia Vegetal, Faculdade de Ciências, Universidade de Lisboa, Portugal

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ABSTRACT

Sea cucumbers' historical demand, together with the depletion of several traditional species in the market, has popularized new target species from new fishing grounds. *Holothuria forskali* is one of those emergent species in the trade market. However, there is no relevant information to allow sustainable stock management. Fundamental knowledge of the populations' structure and habitat preferences are key elements without which any measure is inconsequential. This work aims to fill that gap by modelling temporal and spatial patterns of abundance and demographic structure of this species in a NE-Atlantic area, as a function of environmental features.

For a period of 15 months, nine regular sampling campaigns collected data on density, individual length, individual conditions of occurrence (e.g. sheltered, on sand, on algae cover) and environmental parameters (water column, sediment, substrate cover and type), using random transects throughout a coastal rocky-reef, considering habitat heterogeneity and substrate types. To determine the species' habitat preferences Generalized Linear Models were used to model density and demographic structure of the species as a function of environmental conditions. The models revealed that the main drivers shaping the distribution of *H. forskali* are neither abiotic nor biotic parameters of the water column, but physical stressors, like current intensity and depth, and substrate type in a patchy distribution pattern. Estuarine conditions are generally avoided, although with a size-dependent opportunistic strategy. Larger individuals show temporal and spatial displacement patterns towards suitable reproductive conditions (pre-breeding aggregation) and favourable feeding grounds and smaller size-classes tend to aggregate in higher numbers in more stable environments.

Sustainable sources for market supply, like aquaculture, are still a long way from commercial production. So, these results are fundamental to support effective conservation measures for stock management of *H. forskali*.

1. Introduction

Sea cucumbers are globally occurring marine echinoderms, with a wide bathymetric distribution, that perform crucial ecological functions. Due to their feeding behaviour, deposit-feeding holothurians play a critical role in habitat structuring through bioturbation, recycling and redistributing nutrients (e.g. Floren et al., 2021; MacTavish et al., 2012). Unlike suspension feeders, deposit feeders sustain the physicochemical

processes of benthic habitats, by decomposing sediment organic matter and controlling populations of bacteria, fungi, and phytoplankton (e.g. Michio et al., 2003; Namukose et al., 2016; Uthicke, 1999).

The historical and increasing demand for sea cucumbers (Félix et al., 2024) has led to a depletion scenario (Purcell et al., 2013) that has been extending to new regions, as new fishing grounds, and new species are being targeted by the global trade market (e.g. González-Wangüemert et al., 2018; Hernández-Flores et al., 2018; Lök et al., 2022). Sea

* Corresponding author.

E-mail address: pmfelix@fc.ul.pt (P.M. Félix).

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Fig. 1. Study area at Arrábida's coast, in the southwest of Portugal ($38^{\circ}29'19''\text{N}$ $8^{\circ}57'03''\text{W}$), with sampling sites and respective code.

cucumbers are particularly susceptible to overfishing, due to their slow growth, density dependent reproduction and aggregation behaviour (Azevedo e Silva et al., 2021; Hamel and Mercier, 1996; Kinch et al., 2008). This set of factors will inevitably lead to loss of ecological functions in the affected areas, potentially creating cascading effects in those ecosystems.

Apart from developing sources of supply that do not depend solely on harvesting natural populations, like aquaculture, fisheries regulations are key for stock management and as a tool to prevent stock depletion. Positive outcomes have arisen in regions where new policies have been implemented (e.g. González-Wangüemert et al., 2015; Lök et al., 2022) and these should be a first-line approach to sea cucumber stock management. With the exception of *Apostichopus japonicus* and *Holothuria scabra*, the development of aquaculture remains a long way from commercial production. Hence, fisheries management must take the lead with the implementation of early measures, but informed and successful choices of fishing policies require baseline knowledge on biology, ecology, life-history traits or demographics of the species or population. However, such knowledge is scarce or inexistent for most of the species in the trade market. Focus has been on aquaculture development rather than on the study of natural populations for sea cucumber species. Nearly all commercial sea cucumbers are detritivorous species and share reproductive, ecological or feeding features (Purcell et al., 2016). However, several of these traits are not only species specific but often population specific. *Holothuria mammata*, for example, does not share the same habitat preferences and patterns of distribution between two NE-Atlantic populations from a mesotidal lagoon and a rocky-reef (Félix et al., 2021; Siegenthaler et al., 2017). Naturally, this has implications in decision making processes for stock management.

Sea cucumbers density dependence and frequent patchy distribution (Eckert, 2007; Félix et al., 2021) are traits that increase their capturability and vulnerability by generating fishing hotspots in high density areas. This is particularly true for coastal species, hand caught by divers, or on foot at low tides, unlike deep sea species harvested by trawlers or other unselective fishing methods. Easy access to high densities and selective capture weighed considerably in the initial economic interest of species like *Holothuria (Panningothuria) forskali* Delle Chiaje, 1823. This is an Atlanto-Mediterranean species with a distribution range extending from the British Isles to the Canary Islands and Morocco and along the northern Mediterranean coast (Koehler, 1925; Pérez-Ruzafa and López-Ibor, 1987). It is generally described as a rocky-reef and low depth species, but this characterization may vary throughout its

Table 1

Variables considered for empirical models assessing habitat preferences for *Holothuria forskali*.

Variable	Type	Unit	Relevance
Substrate	Binary	Sand/ Rock	Indicates sampling at sandy bottoms or rocky substrates. The former are transects set in open and more exposed areas, with less potential shelter
Depth	Continuous	m	Represents a response to physical environmental stressors, as site hydrodynamics decrease with depth Chosen as a proxy of environmental stress, as it represents distance to estuary mouth (Longitude increases with distance). Estuarine environments have more environmental variability than its adjacent coastal areas
Longitude	Continuous	decimal	Represents the hydrodynamism of each site, as an environmental stressor. Reflects the tolerance of sea cucumbers to hydrodynamic conditions when related to density or size class
Current	Continuous	m.s^{-1}	A granulometric feature of the sediment that may be related to feeding preferences. Of all sand fractions, the coarse sand was the one which best explained the granulometry of the sediment, by correlating with all others
Coarse Sand	Continuous	%	A granulometric feature of the sediment that may be related to feeding preferences. Silt represents the finer fraction ($< 63 \mu\text{m}$) of the sediment
Silt	Continuous	%	A measure of organic content availability that may be related to feeding preferences, although not providing information on nutritional quality
Total Organic Matter (TOM) in the sediment	Continuous	%	Represents the primary productivity of the site Chosen as an environmental stressor that can vary spatially according to hydrodynamism and different ecological processes, particularly relevant for benthic species as a result of stratification in brackish systems
Chlorophyll <i>a</i>	Continuous	$\mu\text{g.L}^{-1}$	Chosen as an environmental stressor that is higher in estuarine sites, as a result of run-off from the hydrographic basin
Dissolved Oxygen (ODO)	Continuous	mg.L^{-1}	Represents the variability of each site. Temperature variations can be a seasonal indicator or reflect the exposure of each site to currents
Turbidity	Continuous	FNU	Chosen as an environmental stressor that can influence physiological processes in invertebrates
Temperature	Continuous	$^{\circ}\text{C}$	
pH	Continuous	–	

distribution range (e.g. Ballesteros et al., 2021; Cherbonnier, 1958; Simunovic et al., 2000). It is also an emergent species, illegally harvested in Portugal for exportation. It was mentioned in national regulations at an early stage within the onset of sea cucumber exploitation in Europe (Regulamento de Apanha, Portaria 1228/2010 – no expressed fishing limits). Still, the knowledge on ecological traits for this species is almost inexistent (Ballesteros et al., 2021; Despalatović et al., 2003; Santos et al., 2016; Simunovic et al., 2000; Tuwo and Conand, 1992), and much of what is known was based on macroinvertebrate community

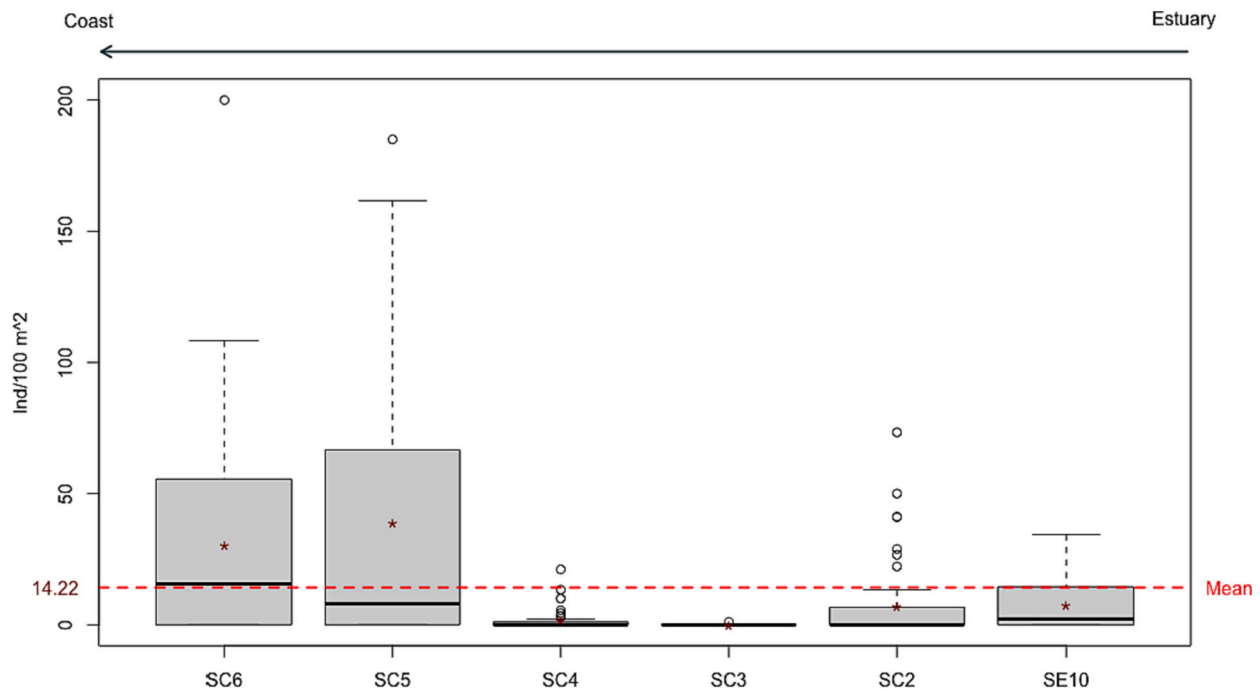


Fig. 2. Boxplot depicting density of *Holothuria forskali* by sampling site, arranged from left to right according to decreasing distance to estuary. The red dotted line represents the overall mean value (Ind·100 m⁻²). A red asterisk represents the mean of each sampling station. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

studies (Cherbonnier, 1958; Koehler, 1925; Pérez-Ruzafa and López-Ibor, 1987). Protection of natural populations of holoturidae via stock management is supported by little to no ecological background. This is particularly true for emergent species in the trade market, such as *H. forskali*. By modelling *H. forskali* body length and population density as a function of environmental characteristics, this study aims to reduce that knowledge gap, determining its habitat preferences, considering temporal and spatial patterns of abundance and demographic structure in a NE-Atlantic area, SW Portugal.

2. Methodology

2.1. Study area

The study was carried out at a NE-Atlantic coastal area, adjacent to the Sado Estuary, in the southwest of Portugal (Fig. 1), within the Arrábida Marine Park (38°26'50.4"N; 9°01'58.7"W), a marine protected area (MPA). The area is dominated by rocky substrate that gradually transitions into sandy sea floor. The subtidal area displays a complex diversity of macro- and microhabitats, supporting a high diversity of algae, invertebrates and fish benefiting from the existing hydro- and geomorphological conditions. The productivity of these coastal waters increases in the summer, as a consequence of upwelling events (Costa et al., 2013; Wooster et al., 1976). A previous study (Félix et al., 2021), was able to determine, through a large sampling area, range of habitat types (including the estuary) and bathymetry, the distribution area of commercially relevant sea cucumbers (*H. mammata*, *H. arguinensis* and *H. forskali*). This study area builds on that work, covering only sampling sites within the rocky-reef distribution area of *H. forskali*. The estuary areas composed solely of soft sediment and even patches of seagrass beds do not sustain sea cucumbers of any of the species. Site SE10, despite being estuarine and unlike what is characteristic of the estuary, is located at the estuary mouth and represented by a subtidal isolated rocky outcrop resembling coastal rocky reefs. Fisheries are banned in most areas of the MPA, with tight surveillance for illegal activities by marine authorities.

2.2. Sampling

The sampling sites (Fig. 1) were defined to represent the spatial heterogeneity of the area, with a range of hydromorphological characteristics (exposure to tidal currents), shelter frequency (available crevices in rock and in sand/rock transition areas), available substrates (sand and rock, and density of algae cover in each of the previous), distance to the estuary and species' densities.

A total of nine sampling campaigns were carried out between January 2018 and March 2019, at 1.5 months intervals. Visual census of 30 m × 3 m transects, parallel to the coastline, were carried out by scuba diving. Transects were sampled between 9:00 to 12:00 AM. After selecting a first random transect two adjacent parallel transects at a non-fixed distance on either side were sampled. Transects were never repeated during the study. Given all sampling sites had both rock and sand bottoms, three replicates were set for each substrate type in a total of six transects *per site* and *per sampling occasion*. *H. forskali* counts *per unit of area* were recorded.

The body length of individuals detected on the transect was measured *in situ* to the nearest mm using a flexible measuring tape. This way, handling of individuals was avoided, thus, preventing muscle contraction and, consequently, increase in variability and underestimation of length (Azevedo e Silva et al., 2021). Additional observations: (i) algal cover may play a role in shelter selection; (ii) rock transects can have sandy patches; (ii) sandy transects may have, although less often, small rock outcrops. Therefore, for each detected individual habitat characteristics were recorded in Boolean variables, e.g. sheltered or not, on sand or rock, or on algae cover or not.

For each site and survey environmental parameters were measured with a calibrated multiparametric sonde YSI-EXO2: water temperature, pH, salinity, dissolved oxygen (ODO), dissolved solids, turbidity, chlorophyll *a*, and depth. Current was measured with a Doppler Current Sensor 4100. Also recorded was substrate biological cover type: seagrass, macroalgae, or none; and the dominant type of rock surface for each replicate: plain or presenting crevices and seams. Grab samples were collected at each site for determination of sediment grain size and

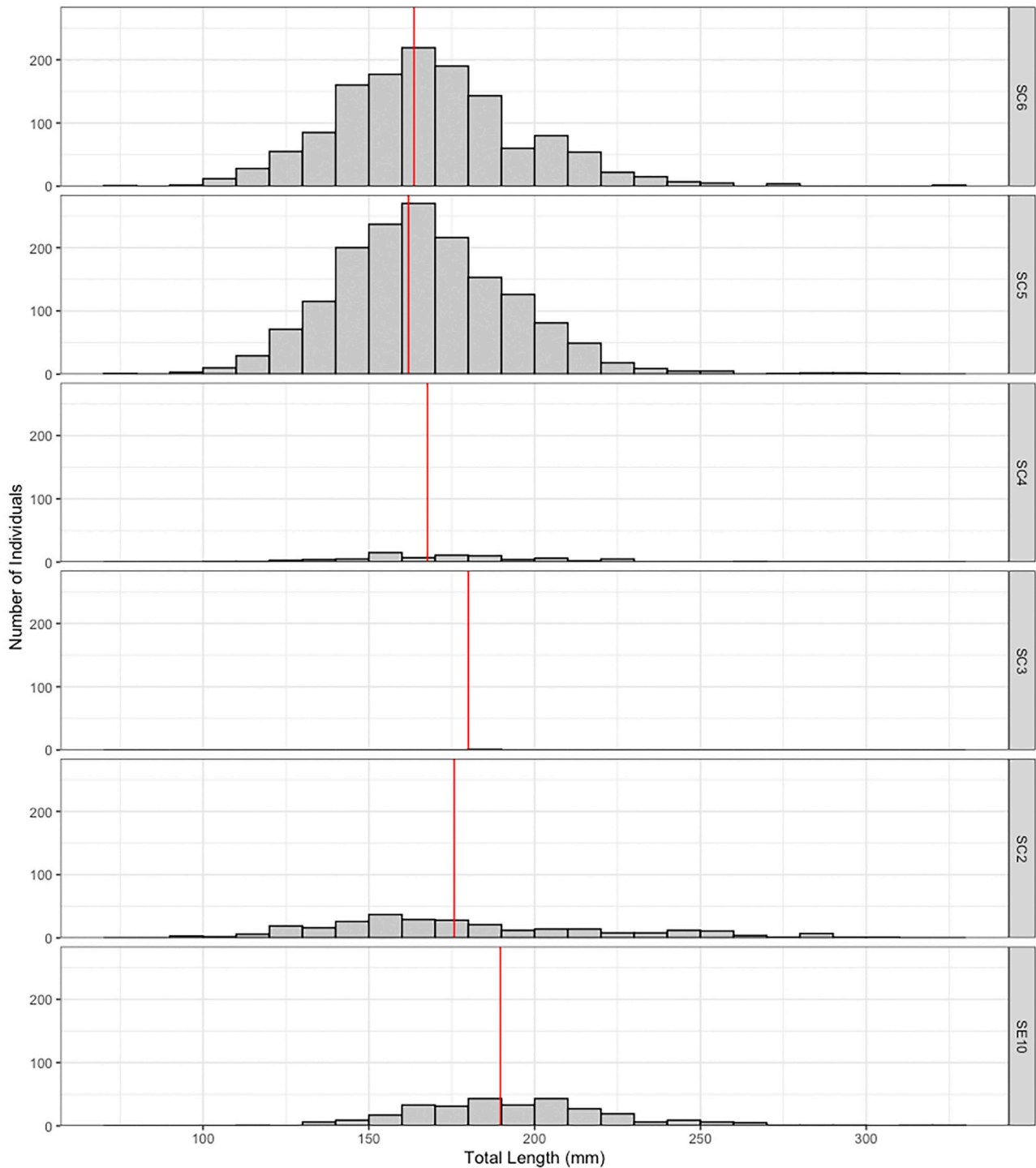


Fig. 3. Size-class distribution of *Holothuria forskali* by sampling site, arranged according to increasing distance to estuary (bottom to top). Vertical lines represent the site mean.

total organic matter (TOM) of sediments. The latter was obtained by loss on ignition (480 °C) and the former determined using 63 µm to 2 mm sieves to separate, respectively, the silt, sand and gravel fractions. Each fraction was then dried and weighed, sediments assorted according to their percentages (Blott and Pye, 2001) and classified with Shepard diagrams (Shepard, 1954).

2.3. Data analysis

The data analysis was conducted in two stages: (1) identification of

spatial and temporal differences in *H. forskali* distribution and (2) use of empirical models to model population density and body length as a function of environmental factors. Statistical analyses were implemented in R software (R Core Team, 2020) and a significance level of 0.05 was considered.

Spatial and temporal differences on animal density and body length were assessed with a Kruskal–Wallis test, when the assumptions of the parametric correspondent ANOVA were not met. For multiple comparisons the Hochberg method with adjusted *p*-value was used (Hochberg, 1988).

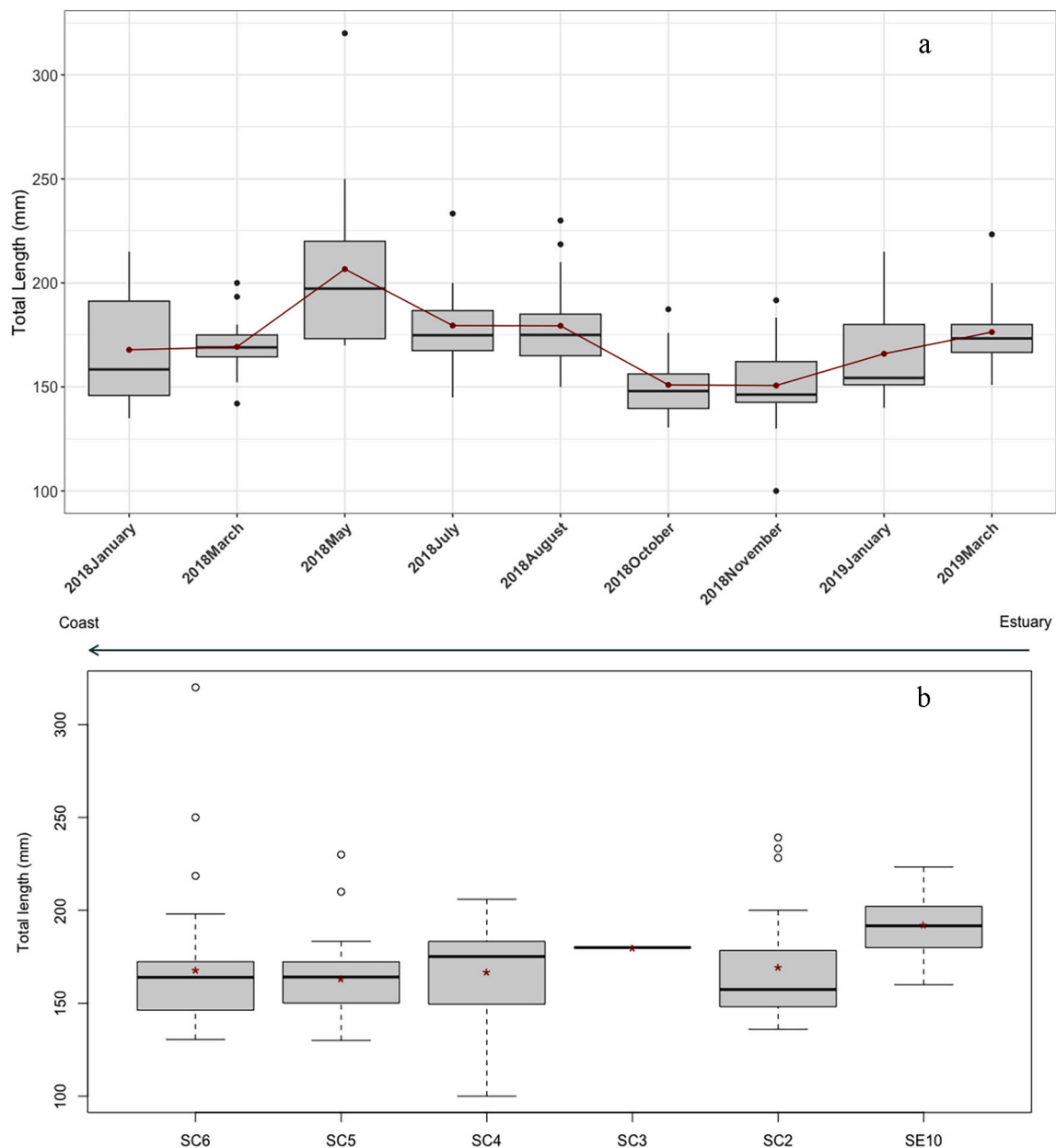


Fig. 4. Boxplots depicting (a) temporal (all sites) and (b) spatial (all months) size distribution for *Holothuria forskali* at Arrábida, Setúbal, during the 15-month sampling period and in all sampling sites arranged according to decreasing distance to estuary (left to right). Red dots connected by a line (a) and asterisks (b) represent the evolution of the mean. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The habitat preferences of *H. forskali* were assessed via Generalized Linear Models (GLM). To facilitate ecological interpretation (Morrissey and Ruxton, 2018) predictor collinearity was assessed before model fitting. A stepwise trait selection based on variance inflation factors (VIF) was implemented via function *vifstep* in the R package *usdm* (Naimi et al., 2014). A VIF threshold was set to 8, and checked with correlation plots, keeping the easiest to interpret variables from highly correlated subsets of predictors. This resulted in discarding the variables dissolved solids, fine and medium sand fractions, and gravel. Selected predictors are described in Table 1. Additionally, two other variables were discarded. Salinity in the coastal area is more conservative than in estuarine environments. Since sampling logistics did not allow a standardised sampling regarding the tide, the single site in the estuarine environment (SE10) could result in confounding results due to salinity variations based on tidal regimes. Since salinity variations in estuaries are tidal dependent and sea cucumbers are low mobility animals, this parameter

would be a poor predictor for the distribution patterns. Thus, other variables were chosen to represent proximity to the estuary (e.g., longitude, turbidity, and ODO). Shelter, the presence or absence of crevices or seams where sea cucumbers can find shelter in, was also removed to prevent the model convergence issues caused by its high correlation to site current, since sites with high current were, simultaneously sites without shelter.

The GLM were implemented for two response variables measured at the transect level: (1) animal density and (2) mean body length, with Tweedie and Gamma distributions, respectively, both with log-link functions (Shono, 2008; Tweedie, 1984), as density required a zero-inflated model and mean size was positively skewed. A more detailed description on the models used and the analytical procedures that supported the interpretation of the results are presented in Félix et al. (2021). For both variables, after fitting the full models, model selection was made through an evaluation of all possible combinations of

Table 2

Fixed-effect GLM averaged model results with a Tweedie distribution (averaged $R^2 = 65\%$, as the average of all models weighted by their model weights), explaining density distribution patterns of *Holothuria forskali* at Arrabida, Setúbal.

Parameter	β	Std. Error	z-value	p-value
Intercept	-150.7378	26.9495	5.572	< 2e-16 ***
Depth	-0.3129	0.27251	1.144	0.2527
Substrate(Sand)	-3.4233	0.20952	16.276	< 2e-16 ***
Longitude	-17.5594	3.09170	5.658	< 2e-16 ***
Current	-0.4644	0.11550	4.006	6.19e-05 ***
Sediment organic matter (% TOM)	-0.0224	0.04476	0.499	0.6175
pH	-0.0920	0.22078	0.416	0.6774
Chla	0.0141	0.04047	0.349	0.7274
Dissolved oxygen (ODO)	0.0199	0.07397	0.269	0.7879
Depth:Current	0.0492	0.01923	2.547	0.0109 *

p-values significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Table 3

Model importance values extracted from the GLM averaged model, considering the five top models with a $\Delta AIC < 2$.

Predictor	Sum of weights	Variable in N of 5 models
Depth	1.00	5
Substrate(Sand)	1.00	5
Longitude	1.00	5
Current	1.00	5
Depth:Current	1.00	5
Sediment organic matter (%TOM)	0.27	1
pH	0.22	1
Chla	0.17	1
Dissolved oxygen (ODO)	0.13	1

variables via the *dredge* function from the *MuMIn* R package (Bartón, 2020) and ΔAIC , which represents the difference in the Akaike Information Criterion between two models. If $\Delta AIC < 2$ for more than one model, model-averaged coefficients (full and conditional averaging) were considered. Since model averaging makes model parameters p -value interpretation harder, interpretation was complemented with model averaged predictors' weight (Grueber et al., 2011). The full model-averaged approach sets coefficients to zero when the respective covariate is not included in a given model when averaging, whereas the conditional coefficients ignore the predictors whenever they are not included in a model, only considering them in the models where they are represented. Thus, full model-averaged coefficients are more conservative (Burnham and Anderson, 2002). Significant interactions were assessed considering the signs of the coefficients for the interaction and for individual terms, to assess the type, and surface plots for interpretation (Feld et al., 2016). For relevant time varying predictors, a causality test, based on the cross-correlation function, was used to determine relationships between two time series: the response variable and the relevant predictor variable, across the sampling period. The results were plotted with all tested time-lags with autocorrelation function (ACF).

3. Results

3.1. Space-time distribution patterns

In total, 3574 individuals, ranging from 70 to 330 mm were counted in a total sampled area of 29,160 m², resulting in a mean density across sampling occasions and sites of 14.22 Ind/100 m², with densities per replicate ranging from 0 to 200 Ind/100 m² (or 20,000 Ind/ha –reached its maximum at SC6). Only the two furthest sites from the estuary never had replicates with zero individuals (Fig. 2). There were significant

differences between sites (KW, p -value < 2.2e-16) and a general decreasing trend towards the estuary ($R^2 = 0.1$, $F_{1,142} = 14.14$, $p = 0.0002$). There were, however, no temporal differences for density (p -value = 0.8761).

Size-classes presented a unimodal distribution at all sites (Fig. 3) and total length showed significant temporal (KW: $p = 6.684e-08$) and spatial (KW: $p = 1.388e-06$) differences (Fig. 4). The former revealed differences between spring and the autumn months (KW, Hochberg, adjusted $p < 0.01$) and the latter only between SE10 and every other site (KW, Hochberg, adjusted $p < 0.01$), except SC3. Despite the negative correlation between density and mean total length ($p = 0.03$), the Spearman coefficient correlation was low at 0.17, depicting a high variability in densities, particularly, between 140 and 180 mm in length.

On average only 3.4% of individuals were found on sandy substrate (transect-wise). Even so, 12% of those individuals were found settled on rock outcrops within sandy transects. During the entire sampling period, only 2.8% of individuals were found on algae cover and no animals were found in exposed areas, without shelter. Of all specimens, 20% were found to be sheltered in crevices at the time of sampling (daytime) and these individuals were overall smaller in size than those not sheltered (ANOVA: $p = 0.0013$). When comparing sizes between substrates of settlement, individuals occurring on rock were also smaller than those on sand (ANOVA: $p = 1.84e-06$).

3.2. Density distribution models

The GLM used to explain the density of *H. forskali* rendered five top models based on the $\Delta AIC < 2$ criterion, after testing all models with all combinations between the predictive variables. Full and conditional model averages included the same set of predictors, therefore only the full averaged results, more conservative, are presented (Table 2). The averaged model includes substrate, distance to estuary (longitude) and current as the most relevant predictors to explain the density of *H. forskali*. The model also depicts a significant interaction between depth and current. Although the individual term depth shows no significance in the (final) average model, it was represented in all five models (Table 3) and the interaction will, thus, be assessed. TOM, pH, Chla and ODO were only included in one of the five models, and none of these terms were statistically significant predictors in the averaged model. Hence, these variables can be deemed poorer predictors for this sea cucumber density distribution pattern, particularly Chla and ODO that have a low sum of weights. These results were corroborated by the assessment of the confidence intervals of the predictor's coefficients (Fig. 5).

Nonetheless, of the less important predictors, TOM and Chla provided more precise estimate of effect sizes (narrower confidence intervals). On the other hand, although with a higher importance than Chla (sum of weights), zero is well within the wide confidence interval for the effect of pH, suggesting pH to be less relevant to explain animal density. Overall, the key predictors explaining density were substrate, distance to estuary (longitude) and current (lower densities on sand, closer to the estuary and at more hydrodynamic areas, respectively) and, to a lesser extent, TOM and Chla, with lower densities at sites with a higher organic content (values between 0.3 and 8.5%) and higher densities at more productive sites. Of the predictors, TOM and Chla, only the latter showed a (temporal) relationship with density (cross-correlation), with higher average values in the summer months, which is followed by an average increase in density (Fig. 6a). This is corroborated by a significant positive correlation at lag = -1.5 (months) showed by the cross-correlation function (Fig. 6b).

The significant interaction between depth and current showed an antagonistic effect, with a positive coefficient contrasting with the negative coefficients of its individual variables, i.e., depth cancelled the negative effect of current on density. The interaction plot (Fig. 7), detailing the effect, shows that between the depth values of 8 and 10 m, there was little variation in density, as opposed to lower depth values

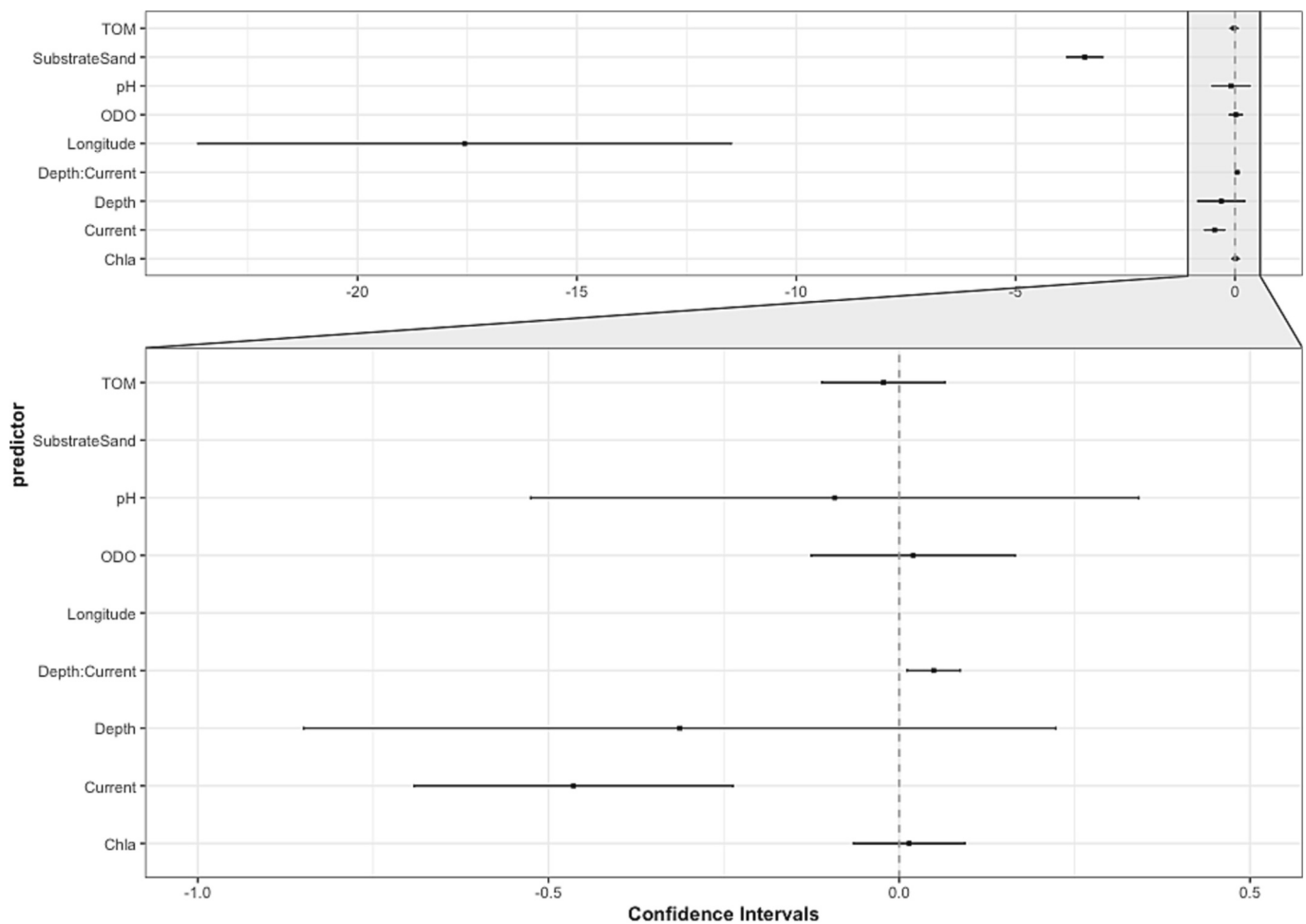


Fig. 5. Confidence intervals for the predictor coefficients of the model – Fixed-effect GLM averaged model with a tweedie distribution – explaining the density distribution patterns of *Holothuria forskali* at Arrábida, Setúbal.

where the current had an effect on density, which decreased as current increased. In other words, the intensity of current only had a negative influence on density at low depths, because at greater depths the hydrological characteristics of the site had less impact on density, as at the two deepest sites it even increased (dots in the plot).

3.3. Size distribution models

Five top models were selected, based on the $\Delta AIC < 2$ criterion, to explain the size distribution of *H. forskali*. Same as for the density outputs, only the full average is presented (Table 4) given equivalent interpretation of the conditional average model. The most significant variables in model were Chla (larger individuals at sites with higher productivity); substrate (larger individuals on sand); longitude (larger individuals closer to the estuary); TOM (larger individuals at sites with a higher percentage of organic matter in sediment: between the 0.3 and 8.5% full sampling range); and temperature (larger individuals at lower temperatures). From those predictors deemed less relevant in the model, all are represented in only one of the five top models and, of those, turbidity and depth have a higher sum of weights (Table 5), which is corroborated by the confidence intervals (Fig. 8).

Whenever there is an increase in Chla, the average length also increases, like for density. So, the larger individuals are found in the spring and summer (Fig. 9a). Temperature also displays a temporal pattern (KW: p -value $< 2.2 \times 10^{-16}$) but it is the onset of temperature rise that matches the average increase in size (Fig. 9a). Unlike the previous environmental variables, TOM and turbidity showed a spatial pattern

(KW: p -value = 4.876×10^{-14} ; and KW, Hochberg, adjusted $p < 0.001$, respectively). However, for turbidity only SE10 showed significant higher values than all other sites, representing the estuary mouth. The largest mean and median individuals were found precisely at SE10 (Fig. 4b). Despite the larger dispersion in TOM values found at SC4, SE10 also had the highest median TOM values (Fig. 9b).

4. Discussion

Holothuria forskali wild populations are understudied. Apart from three studies on the reproductive biology (Ballesteros et al., 2021; Santos et al., 2016; Tuwo and Conand, 1992), extant data is based on generalist epibenthic or macroinvertebrates surveys (Cherbonnier, 1958; Koehler, 1925; Pérez-Ruzafa and López-Ibor, 1987; Simunovic et al., 2000). With no previous dedicated efforts targeting the species, this study is the first of its kind, focussing on ecological traits for this species.

The assessment of distribution patterns in two different substrata, revealed rock to be the preferential habitat, particularly for smaller size-classes. This may be related to feeding selectivity. Unlike the other species in the area that feed on sand, this *H. forskali* population ingests primarily benthic algal (and associated) items (Azevedo e Silva et al., 2021). For sea cucumbers, habitat segregation between sympatric species appears to be more common in areas of heterogeneous substrates and associated biota (Rupp et al., 2023) than in more homogeneous areas (Husain and Lamangantjo, 2023). So, habitat type can modulate the co-occurrence patterns of sea cucumbers. The largest *H. forskali*, with

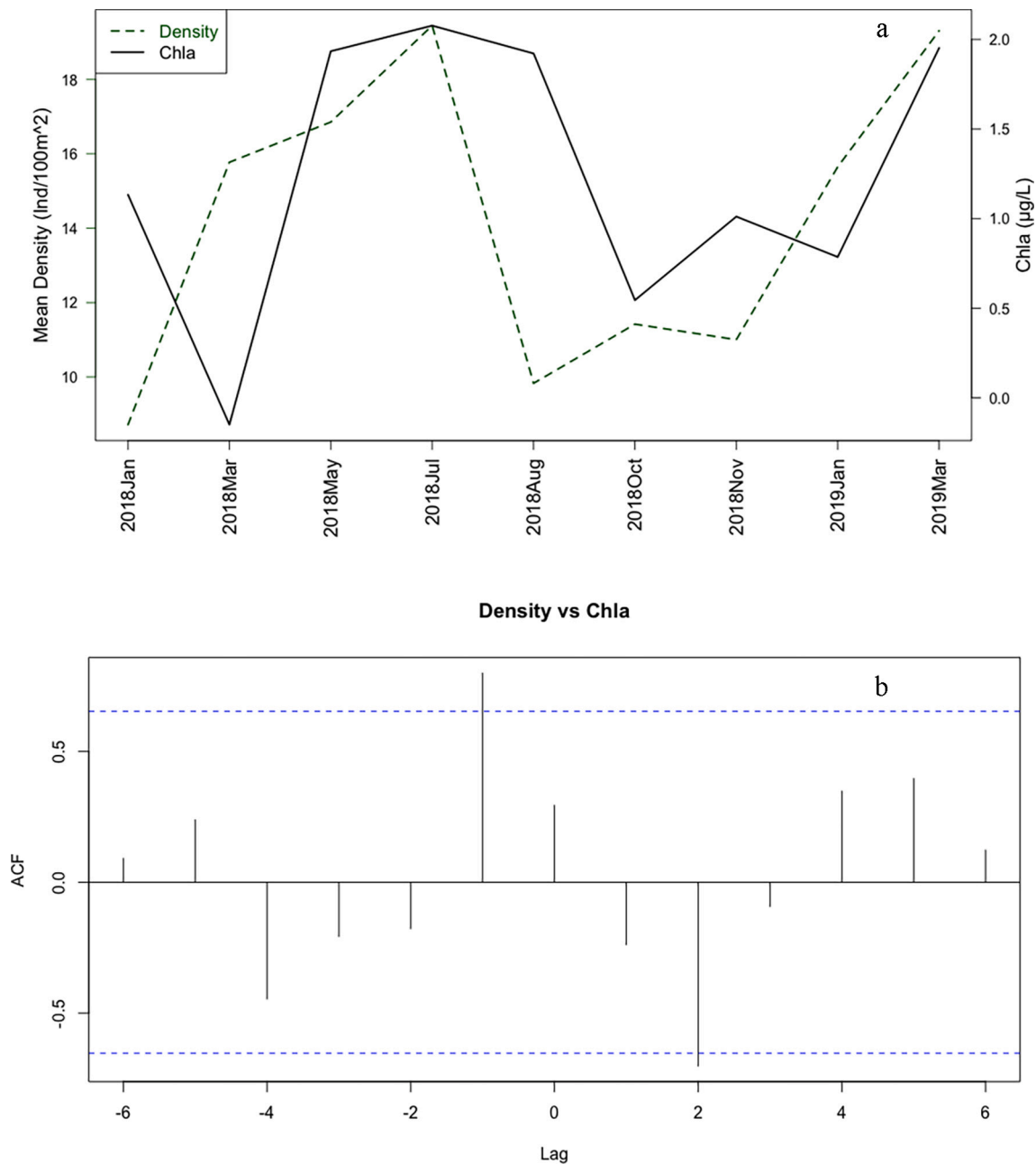


Fig. 6. Average periodic values (each 1.5 months) for Chla and mean density of *Holothuria forskali*, at Arrábida, Setúbal, during the 15-month sampling period (a) and the ACF plot depicting correlations (vertical lines) and significance threshold (horizontal dotted lines) (b).

total lengths up to 450 mm and 480 mm, have been found at higher latitudes, at Ria de Vigo (42°14') and in the Glénan Archipelago (47°43'), respectively (Ballesteros et al., 2021; Tuwo and Conand, 1992). This suggests that Bergmann's rule – individuals of larger size are found in colder environments – may also be observed in holothurians. This size pattern is also found for other sea cucumber species, with higher latitudes showing larger individuals, as for the two other sympatric species, *H. arguensis* and *H. mammata* (Azevedo e Silva et al., 2023; Félix et al., 2021). On the other hand, the densities found for *H. forskali* in the study area reveal the highest densities, compared to sympatric species (Azevedo e Silva et al., 2023; Félix et al., 2021) to other species from temperate and sub-tropical regions (e.g. Domínguez-Godino and González-Wangüemert, 2020; Mustapha and Hattour, 2017; Navarro et al., 2013; Siegenthaler et al., 2017), and even to tropical species (e.g. Al-Rashdi et al., 2007; Arya et al., 2022; Husain and Lamangantjo, 2023). Despite being commercially relevant (González-

Wangüemert et al., 2018), this particular population shows no sign of exploitation, as it reveals an unimodal size-class distribution. It also reveals a typical patchy distribution, a common trait in most sea cucumbers (Azevedo e Silva et al., 2023; Dissanayake and Stefansson, 2010; Domínguez-Godino and González-Wangüemert, 2020; Džeroski and Drumm, 2003; Eckert, 2007; Félix et al., 2021; Mendes et al., 2006; Shears and Babcock, 2007), with areas of high and low, or zero, abundance in near proximity. However, density is more often higher for smaller size-classes that aggregate in large groups in more stable environments (away from the estuary). Smaller sizes also showed a preference for rocky substrate and display a more cryptic behaviour, either in crevices or algal cover, which may suggest a survival strategy, since the risk of predation and the number of potential sea cucumber predators is higher at a juvenile stage (Francour, 1997) and decreases with size (Ceccarelli et al., 2018; Purcell, 2010; Shiell and Knott, 2008).

The models reveal that the habitat preference of *H. forskali* depends

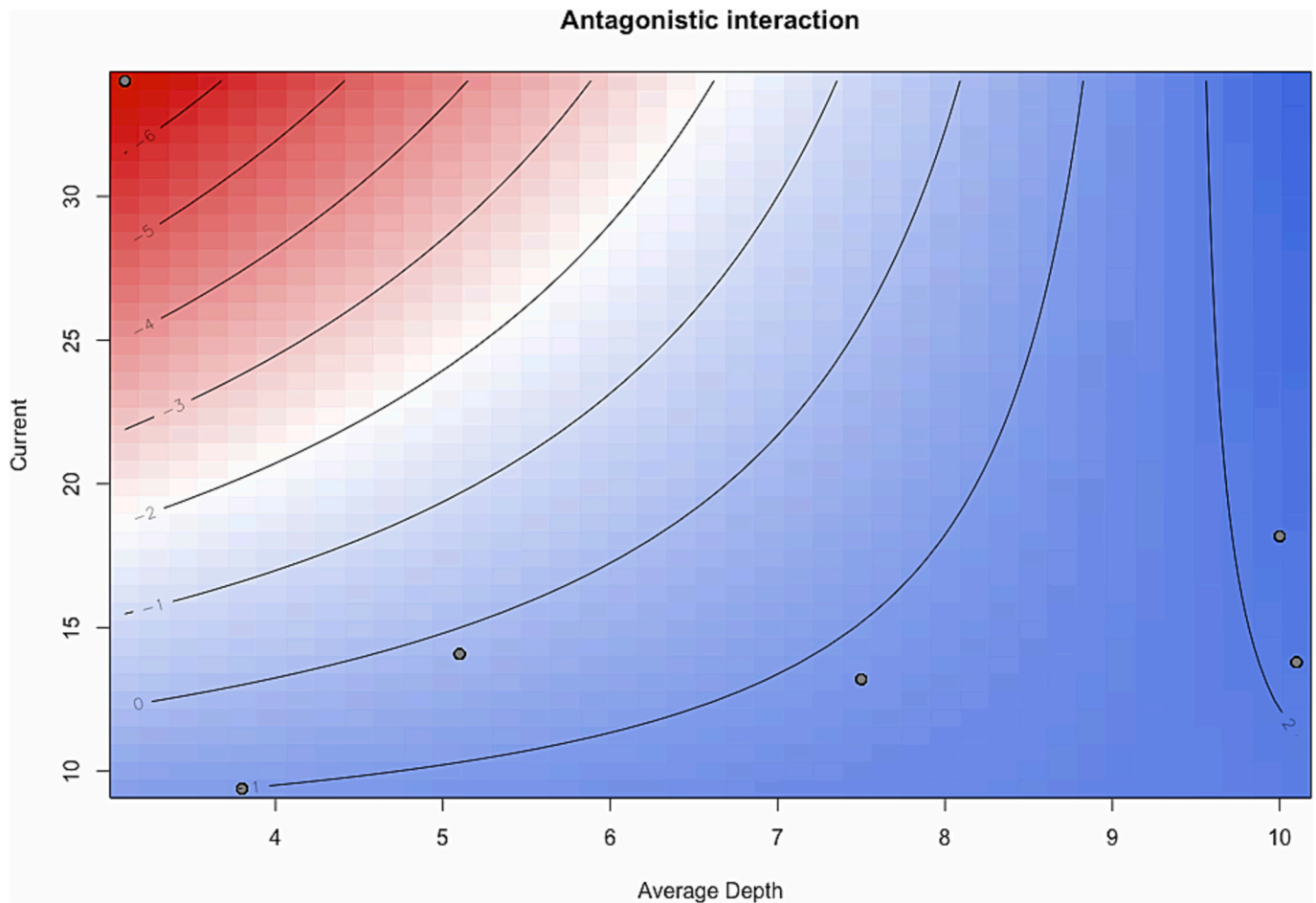


Fig. 7. Surface plot depicting the interaction behaviour between current and depth in the density model, explaining distribution patterns of *Holothuria forskali* at Arrábida, Setúbal. Grey dots represent the sites in the covariate space.

Table 4

Fixed-effect GLM averaged model results with a Gamma distribution (averaged $R^2 = 34\%$, as the average of all models weighted by their model weights), explaining size distribution patterns of *Holothuria forskali* at Arrabida, Setúbal.

Parameter	β	Std. Error	z-value	p-value
Intercept	14.0651	2.1869	6.379	< 2e-16 ***
Chla	0.0696	0.0113	6.085	< 2e-16 ***
Substrate(Sand)	0.1112	0.0293	3.758	0.000171 ***
Longitude	0.9801	0.2404	4.044	5.26e-05 ***
Temperature	-0.0146	0.0059	2.481	0.013094 *
Sediment organic matter (% TOM)	0.0304	0.0090	3.352	0.000803 ***
Turbidity	0.0203	0.0151	1.336	0.181400
Depth	-0.0058	0.0047	1.223	0.221301
pH	-0.0381	0.0588	0.642	0.521073
Coarse sand (%)	-0.0003	0.0004	0.570	0.568617

p-values significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

primarily on environmental stability, rather than abiotic and biotic parameters of the water column. Low hydrodynamic conditions and the presence of rocky substrate are preferential features that may offer shelter and habitat complexity, while estuarine influence is avoided. Similar preferences have also been observed for other sea cucumber species (Azevedo e Silva et al., 2023; Domínguez-Godino and González-Wangüemert, 2020; Félix et al., 2021; Mendes et al., 2006; Morgan, 2011; Sloan and von Bodungen, 1980; Sonnenholzner, 2003). This is further supported by the use of bathymetry. *H. forskali* can occupy

Table 5

Model importance values extracted from the GLM averaged model, considering the five top models with a $\Delta AIC < 2$.

Predictor	Sum of weights	Variable in N of 5 models
Chla	1.00	5
Substrate(Sand)	1.00	5
Longitude	1.00	5
Temperature	1.00	5
Sediment organic matter (%TOM)	1.00	5
Turbidity	0.25	1
Depth	0.22	1
pH	0.12	1
Coarse sand (%)	0.11	1

deeper zones in areas where the hydrodynamical conditions are more unfavourable, thus, objectively increasing its vertical distribution range. Nonetheless, when comparing sympatric species, this behaviour in areas with stronger currents and the importance of depth does not show the same relevance in explaining density as it does for *H. mammata* and *H. arguinensis* (Azevedo e Silva et al., 2023; Félix et al., 2021), suggesting *H. forskali* is more resilient to this physical stressor. However, unlike for those sympatric species, density increases when productivity (Chla) rises. This behaviour precedes the known spring to summer reproductive season of the species for the Portuguese west coast. Notwithstanding, in this region the species can have a second reproductive peak in the winter (Santos et al., 2016). This phenomenon and time-frames have also been observed for this particular study area (unpublished data from national project Newcumber - seacucumber.eu/en/proyecto/). The increase in

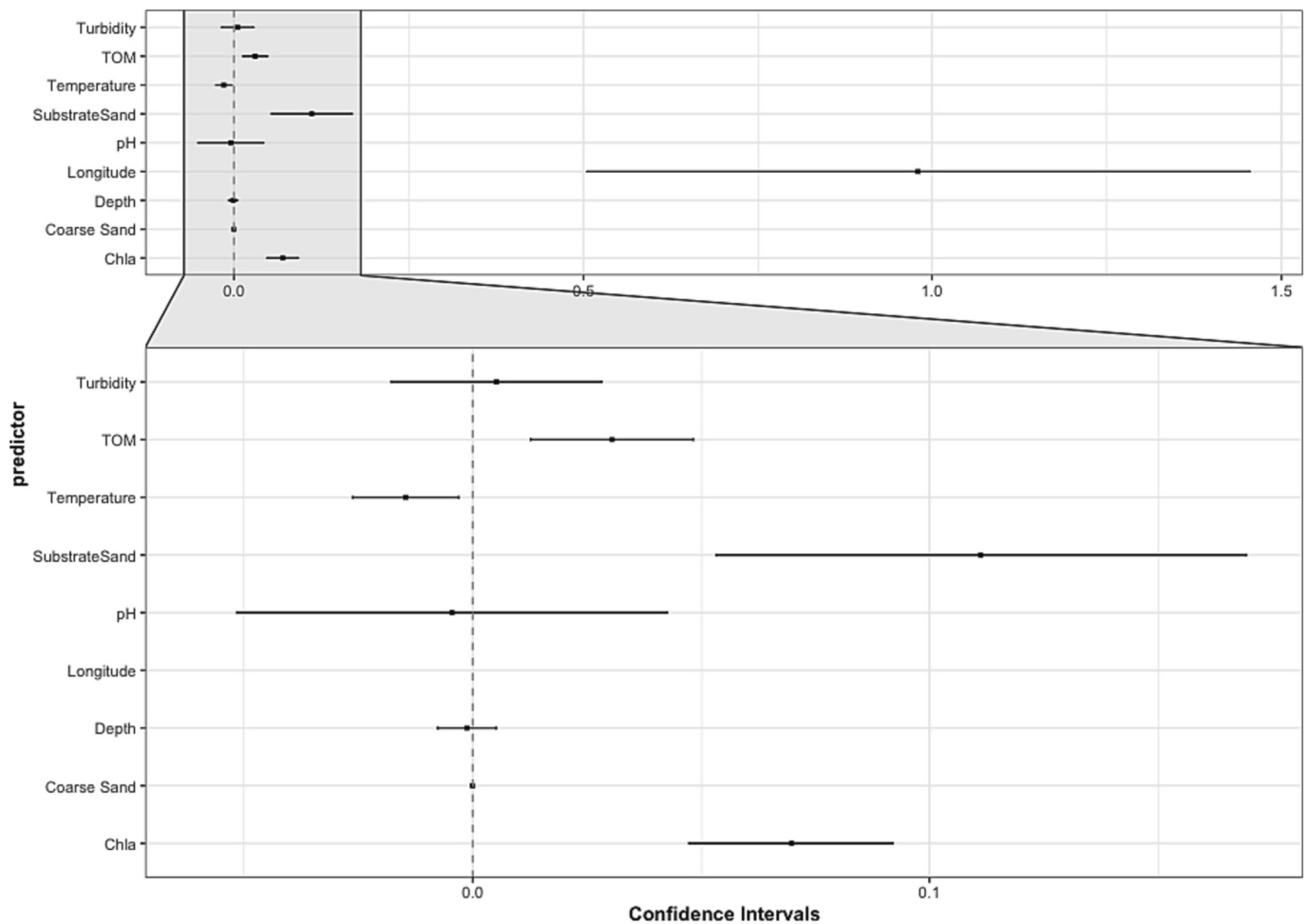


Fig. 8. Confidence intervals for the predictor coefficients of the model – Fixed-effect GLM averaged model with a Gamma distribution – explaining the size distribution patterns of *Holothuria forskali* at Arrábida, Setúbal.

Chla in the summer is a common phenomenon in this area, due to seasonal upwelling cycles (Wooster et al., 1976). This productivity boost may act as a cue promoting an aggregation behaviour, common during pre-breeding season of sea cucumbers to improve reproductive success (Leite-Castro et al., 2016; Mercier and Hamel, 2009). There is a strong suggestion that primary productivity increase may favour larval feeding and development during the pelagic stage. Furthermore, Chla, and temperature that also starts to rise in the spring, are also correlated to demographic change. This temporal aggregation behaviour is more related to larger size-classes, i.e. adult individuals. So, the productivity increase may be a trigger for broodstock aggregation. One other sympatric species in the study area exhibits the same aggregation behaviour and relationship with primary productivity, *H. mammata* (Félix et al., 2021). However, these behavioural patterns and dependence on specific environmental cues can have deleterious effects on these species and add up to their depletion susceptibility under intense fishing pressure. The aggregation favours the harvesting of concentrated individuals and, consequently, the reduction of spawning biomass. It further hints for potential impacts of climate change on environmental factors that trigger life-cycle related behaviours, particularly if there is a narrow tolerance range to these environmental cues (Asch and Erisman, 2018).

Size distribution patterns are also explained by other environmental factors. Larger individuals are typically found at the estuary mouth (SE10). Although resembling the rocky-reef characteristics of the coastal area, this particular site is more directly influenced by the estuary, showing an increase in turbidity, sediment organic matter and stronger influence of the tidal currents due to the geomorphological bottleneck at

the estuary mouth, constricting water flow. Nevertheless, it also benefits from the estuary productivity (Santos et al., 2022). The higher occurrence of larger individuals in this area suggests an opportunistic use of space, like that of smaller size sheltered individuals, contrasting with larger size-classes found in more exposed areas (sand transects) without shelter nearby. Smaller individuals, more susceptible to predation and physical stressors, tend to benefit from the protection of geomorphology and biological complexity of the rocky substrate, whilst larger individuals can venture further into open areas, if those areas offer enhanced feeding and reproductive conditions (favourable currents for gamete dispersal (Pedrotti and Fenaux, 1992)). This behaviour appears to be common to other deposit-feeding sea cucumbers in the study area (Azevedo e Silva et al., 2023; Félix et al., 2021), indicating it may be a common trait in sea cucumbers. All these features suggest a displacement ability of larger individuals towards more favourable conditions at a lower risk of predation or due to a higher resilience, both privileged by size.

5. Conclusion

This study provided groundbreaking habitat preference information for *H. forskali* at a rocky-reef. It described the species ability to deal with physical environmental stressors, with size-dependent strategies based on opportunistic displacement patterns. While preferring hard substrates with available shelter, low tidal influence and less environmental variability, larger individuals rely on environmental cues to aggregate for the onset of reproduction and show a size related ability to deal with

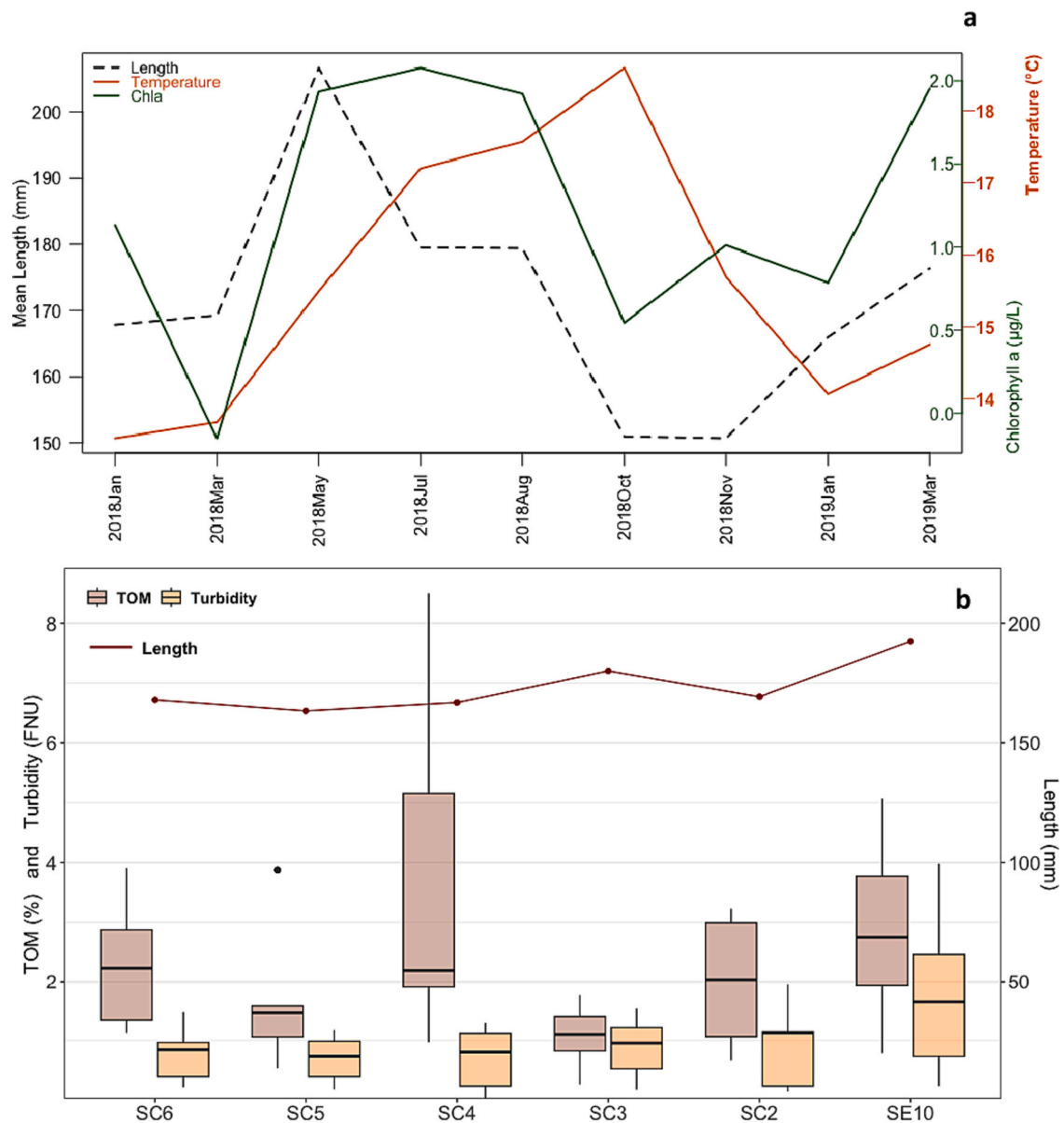


Fig. 9. Average periodic values for Temperature (°C), Chla ($\mu\text{g}\cdot\text{L}^{-1}$) and mean length of *Holothuria forskali* (a) and the spatial mean variation of total organic matter in the sediment (TOM), turbidity in the water and length data for *Holothuria forskali* at Arrábida, Setúbal, during the 15-month sampling period and in all sampling sites arranged according to decreasing distance to estuary (left to right).

physical stressors and use favourable feeding grounds.

These distribution patterns are key elements for stock management. The aggregation behaviour and designated hotspots are particularly sensitive areas for increasing capturability – high yield and low fishing effort – which can lead to a fast reduction in spawning biomass and potentially place the population outside safe biological limits. This work represents minimum baseline knowledge required for effective decision-making processes on stock management for *H. forskali*.

CRediT authorship contribution statement

P.M. Félix: Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **F. Azevedo e Silva:** Writing – review & editing, Methodology, Investigation. **T. Simões:** Writing – review & editing, Methodology, Investigation. **A. Pombo:** Writing – review & editing, Funding acquisition, Conceptualization. **T.A. Marques:** Writing - review & editing,

Methodology, Formal analysis. **C. Rocha:** Writing – review & editing, Methodology, Formal analysis. **J. Sousa:** Writing – review & editing, Methodology. **E. Venâncio:** Writing – review & editing, Methodology. **A.C. Brito:** Writing – review & editing, Project administration, Investigation, Funding acquisition.

Data availability

Data will be made available on request.

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