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Unravelling the effects of exploitation on the size–structure of the intertidal topshell *Phorcus sauciatus* in harvested and non-harvested Atlantic regions

Ricardo Sousa [a,b,c], Joana Vasconcelos [c,d,e,*], Rodrigo Riera [e,f]

[a] *Observatório Oceânico da Madeira, Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação (OOM/ARDITI) – Edifício Madeira Tecnopolo, 9020-105 Funchal, Madeira, Portugal*
[b] *Direção de Serviços de Monitorização, Estudos e Investigação do Mar (DSEIMar) – Direção Regional do Mar, Avenida do Mar e das Comunidades Madeirenses n°23, 1° andar, 9000-054 Funchal, Madeira, Portugal*
[c] *MARE — Marine and Environmental Sciences Centre, Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação (ARDITI), Edifício Madeira Tecnopolo Piso 0, Caminho da Penteada, 9020-105 Funchal, Madeira, Portugal*
[d] *Secretaria Regional da Educação, Avenida Zarco, Edifício do Governo Regional, 9004-528 Funchal, Madeira, Portugal*
[e] *Departamento de Ecología, Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Casilla 297, Concepción, Chile*
[f] *Grupo en Biodiversidad y Conservación, IU-ECOAQUA, Universidad de Las Palmas de Gran Canaria, Marine Scientific and Technological Park, Crta.Taliarte s/n, 35214 Telde, Spain*

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ABSTRACT

Intertidal molluscs are keystone species often used as biological indicators of human-driven perturbations. The increasing levels of harvesting pressure on these intertidal grazers, due to the expansion of human population on coastal areas, is known to affect negatively the exploited populations by altering population size–structure and decreasing abundances. A comparative study on the effect of harvest on the size–structure of *Phorcus sauciatus* populations was conducted according to the exploitation level, harvested and non-harvested, throughout the intertidal zone of mainland Portugal, Azores, Madeira, and the Canaries. The comparative analysis of the size–structure of 10,480 individuals of *P. sauciatus* showed that the largest individuals were recorded in the Azores and the smallest in Madeira. In harvested populations, *P. sauciatus* showed to be under greater harvesting pressure in the archipelago of Madeira, where the lowest mean size was observed. In the Canaries the harvesting is regulated whilst in the mainland Portugal the regulation is scarce. The Azores showed no harvesting pressure. Marine Protected Areas showed individuals with the highest mean sizes supporting their effectiveness in preserving the size–structure of this species, regardless the ecoregion and thus, the harvesting pressure. The present results highlight the importance of harvesting regulation of *P. sauciatus* in Madeira, as well as the implementation of management measures aiming at the sustainable exploitation and conservation of this species.

1. Introduction

Intertidal grazers, i.e. limpets and topshells, among others, play an important role in intertidal rocky ecosystems and are commonly used as biological indicators of anthropogenic impacts (Sousa et al., 2018a). The increasing levels of harvesting pressure on these keystone species, due to the expansion of human population on coastal areas (Neumann et al., 2015), is known to negatively affect the exploited populations by altering population size–structure and decreasing abundances (Tuya et al., 2006; Riera et al., 2016). Size-selective harvesting has a major impact on intertidal species worldwide (Branch and Moreno, 1994; Castilla, 1999; Roy et al., 2003; Martins, 2009; Sousa et al., 2018a), affecting life history and ecology of these species (Fenberg and Roy, 2008). Non-targeted small-sized individuals may be indirectly affected by harvesting pressure, through shift on the reproductive output and growth rate, and also by affecting the ecosystem processes through trophic cascades (e.g. Roy et al., 2003). Moreover, the depletion and even collapse of populations of intertidal key species has pervasive implications in coastal ecosystems through bottom-up processes (Roy et al., 2003). Specifically, larger individuals keep their feeding space devoid of interspecific intruders, e.g. other limpets or topshells (Shanks, 2002). Hence, selective removal gives space to fast-growing competitors, i.e. macroalgae, cirripeds and mussels (Fenberg and Roy, 2008). This situation is even more accentuated in areas with low primary productivity

* Corresponding author at: Secretaria Regional da Educação, Avenida Zarco, Edifício do Governo Regional, 9004-528 Funchal, Madeira, Portugal.
E-mail address: joana.pr.vasconcelos@madeira.gov.pt (J. Vasconcelos).

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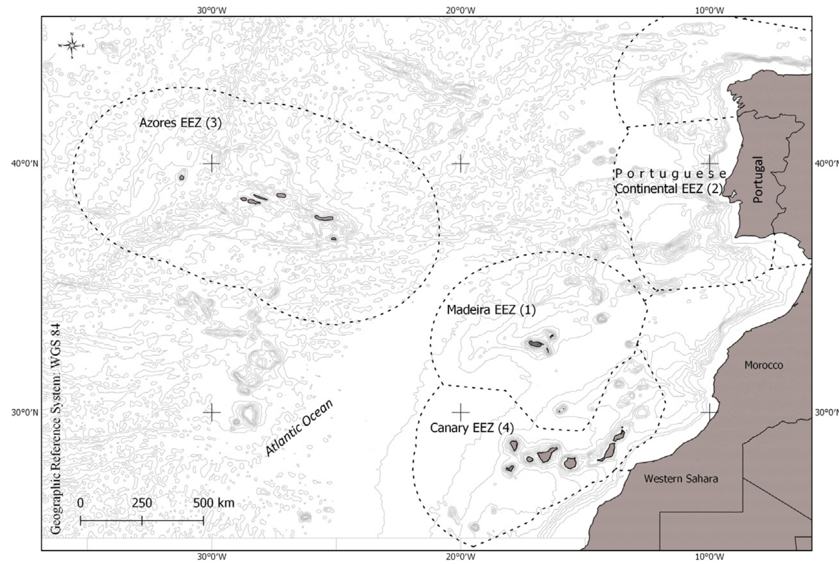

Fig. 1. Map showing the sampling areas of *Phorcus sauciatus*. (1) Madeira, (2) mainland Portugal, (3) Azores and (4) Canaries.

and highly isolated, with low pool sources from adjacent places, e.g. oceanic islands.

The Macaronesian ecoregion is often referred to the set of four archipelagos in the North Atlantic Ocean, off the coast of the continents of Europe and Africa including the Canaries, Madeira, Selvagens, Azores and Cape Verde Islands. However, Freitas et al. (2019) found no evidences to support the current concept of Macaronesia as a biogeographic unit and suggests the redefinition of the Lusitanian biogeographic province, including four regions: (i) the Webbnesia comprising the archipelagos of Canaries, Madeira and Selvagens; (ii) the Azores; (iii) the South European Atlantic Shelf; (iv) and the Saharan Upwelling.

The oceanic archipelagos of Azores, Madeira, Selvagens and the Canaries, are characterized by high harvesting pressure on intertidal ecosystems (Núñez et al., 2003; Martins et al., 2010), as demonstrated by the sharp decrease of exploited molluscs populations in Azores (Martins, 2009), Madeira (Sousa et al., 2018a) and the Canaries (Ramírez et al., 2009). However, the harvesting pressure of *Phorcus sauciatus* (Koch, 1845) shows variations according to proximity to human settlements and accessibility to the coast throughout the archipelago of Madeira (Sousa et al., 2019a,b). Madeira has an old tradition of harvesting sea snails, namely the species *P. sauciatus* (Sousa et al., 2018a), while the consumption of this species is not widespread in the Canaries varying among islands, being more intense in western islands, e.g. Tenerife (Moro and Herrera, 2000; Tuya et al., 2006; Ramírez et al., 2009).

The topshell *P. sauciatus* is widely distributed in the Northeastern Atlantic, including the archipelagos of Azores, Madeira, and the Canaries with its northern boundary in the Iberian Peninsula and its southern limit in the African mainland, with small genetic differentiation among them, suggesting either recent or continuing dispersal among these areas (Donald et al., 2012; Rubal et al., 2014; Ávila et al., 2015). We herein focus on the effects of harvesting pressure on the size–structure of *P. sauciatus* populations according to the exploitation level, harvested and non-harvested, throughout the intertidal zone of mainland Portugal, Azores, Madeira, and the Canaries.

2. Material and methods

The study was conducted on samples randomly harvested from the upper to the lower intertidal zones of the rocky shores of mainland Portugal and from the archipelagos of Azores, Madeira, and the Canaries, NE Atlantic (Fig. 1), during low tide and without selecting size. Each harvesting set was performed for a standardized period of 15 min, by the same experienced harvesters.

A total of 32 coastal settlements (locations) throughout the rocky shores were sampled between January 2017 and May 2018, including nine from mainland Portugal (4 in harvested and 5 in non-harvested zones), 1 in a non-harvested zone from the Azores, 17 from Madeira (13 in harvested and 4 in non-harvested zones), and 5 from the Canaries (2 in harvested and 3 in non-harvested zones). The natural reserves also known as no-take zone, where harvesting is not allowed, were considered as non-harvested zones. The locations were as similar as possible to each other and were selected considering the coastal settlements with analogous conditions (e.g. type of substrate, slope of the coast, rugosity, hydrodynamics) (Table 1).

All individuals were measured (total shell length, TL, mm) using a Vernier calliper to the nearest 0.01 mm.

Data were analysed for deviations to the parametric assumptions of analysis of variance (ANOVA). Normality of the distribution of the data was verified through the Kolmogorov–Smirnov 2-sample test, and homogeneity of variance was determined using Levene's statistics. Analysis of variance was performed considering the Brown-Forsythe F test, when the variance of the data was not homogeneous. All statistical analyses were performed using SPSS v.24.0 (IBM Corp, 2016). For all tests, statistical significance was accepted when $p < 0.001$.

2.1. Comparative analysis of harvesting pressure among regions

A comparative study was conducted considering the size–frequency of *P. sauciatus* according to the exploitation level, harvested and non-harvested, throughout the intertidal zone of mainland Portugal, Azores, Madeira, and the Canaries. No geographic differences among regions were considered due to differences in sampling effort. Thus, the comparison of the effect of harvesting pressure on *P. sauciatus* size–structure on the four studied regions was carried out using an analysis of variance, considering both levels of exploitation (harvested *vs.* non-harvested) regardless the geographic location.

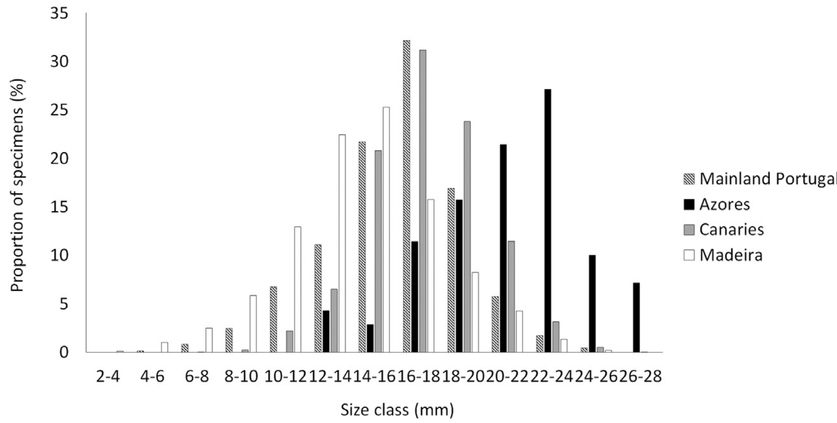

Fig. 2. Size–frequency distributions of *Phorcus sauciatus*, collected between January 2017 and May 2018 from mainland Portugal, Azores, Madeira, and the Canaries.

Table 1
Location of the sample areas by region and exploitation status.

Region	Island/country	Locality	Geographic coordinates	Exploitation status
Canaries archipelago	La Palma	Caleta Del Ancon	28°27′12″N–17°50′55″W	Non harvested
	Hierro	La Restinga	27°38′18″N–17°59′06″W	Non harvested
	Fuerteventura	Los Lapios	28°33′07″N–13°49′37″W	Non harvested
	Gran Canaria	La Estrella	28°00′48″N–15°22′50″W	Harvested
	Tenerife	Los Silos	28°22′40″N–17°48′39″W	Harvested
Madeira archipelago	Selvagens	Selvagem	30°08′38″N–15°51′33″W	Non harvested
	Desertas	Restinga	32°30′45″N–16°30′36″W	Non harvested
	Porto Santo	Ilhéu Cal	33°01′15″N–16°22′52″W	Non harvested
	Madeira	Rocha do Navio	32°48′36″N–16°51′56″W	Non harvested
	Madeira	São Jorge	32°49′50″N–16°56′33″W	Harvested
	Madeira	São Vicente	32°49′33″N–17°00′37″W	Harvested
	Madeira	Seixal	32°49′06″N–17°06′55″W	Harvested
	Madeira	Porto Moniz	32°52′02″N–17°10′33″W	Harvested
	Madeira	Calheta	32°42′54″N–17°09′58″W	Harvested
	Madeira	Paúl do Mar	32°45′09″N–17°13′30″W	Harvested
	Madeira	Jardim do Mar	32°44′22″N–17°12′45″W	Harvested
	Madeira	Ponta do Sol	32°40′42″N–17°05′20″W	Harvested
	Madeira	Ribeira Brava	32°40′19″N–17°04′06″W	Harvested
	Madeira	Funchal	32°38′34″N–16°57′38″W	Harvested
	Madeira	Reis Magos	32°38′39″N–16°49′40″W	Harvested
	Madeira	Santa Cruz	32°41′17″N–16°46′59″W	Harvested
	Madeira	Caniçal	32°44′08″N–16°44′30″W	Harvested
Mainland Portugal	Portugal	Olhos de Água	37°05′20″N–8°11′35″W	Harvested
	Portugal	Arrifana	37°17′20″N–8°51′52″W	Non harvested
	Portugal	Monte Clérigo	37°20′25″N–8°51′19″W	Non harvested
	Portugal	Rogil	37°22′00″N–8°50′11″W	Non harvested
	Portugal	Vila N. Mil Fontes	37°43′18″N–8°47′34″W	Non harvested
	Portugal	Cascais	38°42′23″N–9°29″00″W	Non harvested
	Portugal	Sines	37°52′39 N–8°47′48″W	Harvested
	Portugal	Praia da Calada	39°01′53″N–9°25′10″W	Harvested
	Portugal	Ribamar	39°00′38″N–9°25′25″W	Harvested
Azores	Santa Maria	Fonte da Prainha	36°57′03″N–25°06′31″W	Non harvested

3. Results

A total of 10,480 individuals of *P. sauciatus* from mainland Portugal, Azores, Madeira, and the Canaries were analysed. Total size ranged from 2.40 mm TL in Madeira to 27.98 mm TL in Azores ($X = 15.28 \pm 3.43$ mm TL). Size–frequency distributions (Fig. 2) showed that the sampled data had a normal distribution ($Z = 2.028$, $p < 0.001$) and did not exhibit homogeneous variance for region ($W = 51.869$, $p < 0.001$) nor for exploitation status ($W = 25.034$, $p < 0.001$).

3.1. Comparative analysis of harvesting pressure among regions

The comparative analysis of the size–structure of *P. sauciatus* showed that the largest individuals were recorded in the Azores ($X = 21.09 \pm 3.31$ mm TL) and the smallest in Madeira ($X = 14.39 \pm 3.44$ mm TL). Topshell mean size in the Canaries was 17.32 ± 2.61 mm TL and 16.13 ± 3.01 mm TL in mainland Portugal (Fig. 3). Differences found in mean shell length among sampling locations were statistically significant ($F = 558.529$, $p < 0.001$) (Table 2).

In harvested populations, mean size ($X = 14.42 \pm 3.26$ mm TL) was smaller than in non-harvested ones ($X = 17.30 \pm 3.03$ mm TL). Differences found in size–structure according to population state were statistically significant ($F = 1867.26$, $p < 0.001$). The comparison of *P. sauciatus* populations from the considered locations according to harvesting pressure showed that the greatest impact of harvest on the size–structure occurred in Madeira where mean size was 13.71 ± 3.04 mm TL, followed by mainland Portugal ($X = 15.32 \pm 3.36$ mm TL) and the Canaries ($X = 16.91 \pm 2.72$ mm TL). In populations that are not subject to harvesting pressure the greatest mean size was observed in the

Table 2
Results of analysis of variance on the size–structure of *Phorcus sauciatus*, in the north-eastern Atlantic, considering the location and the exploitation status of the populations.

Factor	Sum of squares	df	Mean square	F	*p*-value
Location	17,281.291	3	5,760.30	558.529	0.000
Exploitation status	18,956.037	1	18,956.037	1827.264	0.000
Location x Exploitation status	34,259.590	6	5,709.932	656.663	0.000

Table 3
Descriptive statistics (n — sample size; Min — minimum; Max — Maximum; S.D. — standard deviation) and results of analysis of variance on the size–structure of *Phorcus sauciatus*, according to the exploitation status per region.

Region	Exploitation status	n	Shell length (mm)				F test	p-value
			Min.	Max.	Mean	S.D.		
Canaries archipelago	Non harvested	1719	6.40	25.39	18.18	2.11	5.81	0.009
	Harvested	601	7.73	26.38	16.91	2.72		
Madeira archipelago	Non harvested	2041	3.22	25.79	18.13	3.10	398.84	0.000
	Harvested	2543	2.40	25.07	13.71	3.04		
Mainland Portugal	Non harvested	2402	4.67	25.24	16.31	2.90	4.48	0.016
	Harvested	1003	5.12	23.81	15.32	3.36		
Azores	Non harvested	171	13.38	27.98	21.09	3.31	–	–

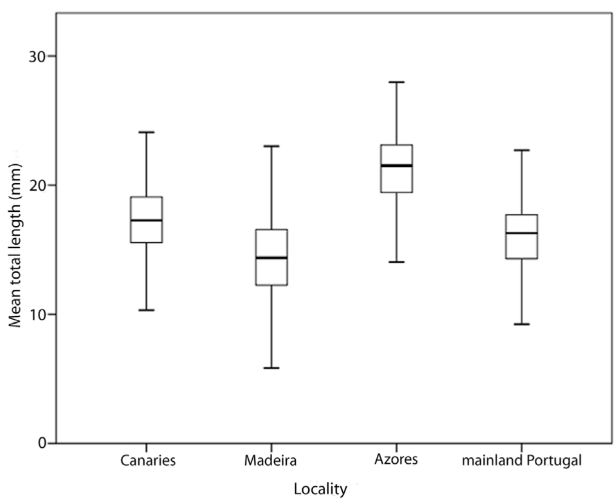

Fig. 3. Mean total length of *Phorcus sauciatus* for each sampled region. Box-plot showing median (black line) and upper and lower quartiles of the data.

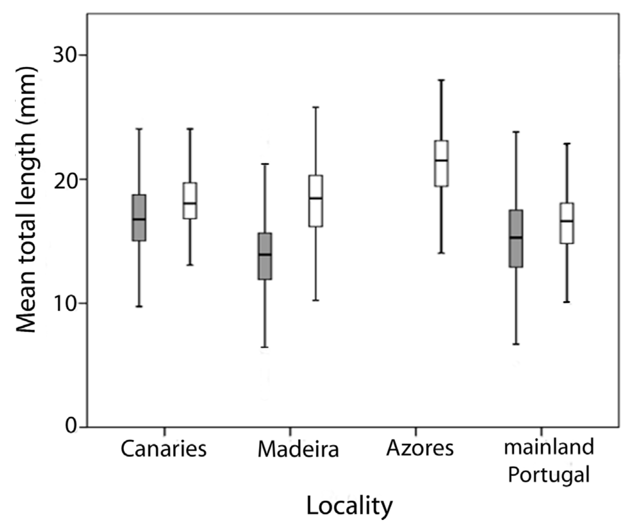

Fig. 4. Mean total length of *Phorcus sauciatus* for each sampled location according to exploitation status. Boxplot showing median (black line) and upper and lower quartiles.

Azores (X = 21.09 ± 3.31 mm TL), followed by the Canaries (X = 18.18 ± 2.11 mm TL), Madeira (X = 18.13 ± 3.10 mm TL) and mainland Portugal (X = 16.31 ± 2.90 mm TL) (Fig. 4). Differences found in topshell mean size between non-harvested and harvested population per region were statistically significant for the Canaries ($F = 5.81$, $p < 0.001$), Madeira ($F = 398.84$, $p < 0.001$) and mainland Portugal ($F = 4.48$, $p < 0.05$) (Table 3). Also, the differences among localities were statistically significant ($F = 656.66$, $p < 0.001$). *Post hoc* analysis Tamhane's T2 showed statistically significant differences between all the pairwise comparisons except for the non-harvested populations from Madeira and the Canaries ($p>0.001$).

4. Discussion

The present study showed that *P. sauciatus* from Madeira archipelago exhibited the smallest total length within the four studied locations, this may result from a high level of harvesting pressure, known to negatively affect the exploited populations by altering their population size–structure (Riera et al., 2016; Tuya et al., 2006). Recently, it was suggested that harvesting has a great impact on the population dynamics of *P. sauciatus* from Madeira archipelago with more emphasis on harvested populations that show a smaller mean size and lower proportion of reproductive individuals (Sousa et al., 2019b).

Intertidal topshells are characterized by similar exploitation rates in the Canaries and Madeira, where this species has been exploited since colonization in the early fifteenth century and is performed in an unregulated manner. The highest mean total length was observed in the Azores, where this species is not traditionally exploited since it is believed to have colonized this archipelago recently, namely the Island of Santa Maria, most likely after 2009 (Ávila et al., 2015). However, the present results from Azores need to be taken with caution since a higher number of samples are necessary to develop more reliable conclusions. *Phorcus sauciatus* from the Canaries showed intermediate values of mean total length, even though this species is pervasively exploited in some of the islands since prehistoric times (Moro and Herrera, 2000). The higher mean size in the Canaries compared to Madeira may be the result from the conservation efforts that have been undertaken in the Canaries, aiming to contribute to the stock recovery of *P. sauciatus* and *P. atratus*. This is mainly due to the implementation of a minimum capture size of 15 mm TL for both species in 2011 (González et al., 2012). The increase in the mean size of the specimens becomes more evident when comparing the results of the present study with those by Ramírez et al. (2009) and reinforces the positive role of regulation in recovering the size–structure of the exploited populations.

Contrarily in Madeira no conservation efforts were made aiming the conservation of the highly exploited *P. sauciatus* and no studies prior to 2018 are available. According to Sousa et al. (2018b) urgent conservation measures, such as landing obligation, a minimum catch size of 15 mm length, and a closed season are warranted to preserve the stocks of this species.

Interspecific competition for substrate between *P. sauciatus* and *P. lineatus* in mainland Portugal may explain the smaller mean size observed compared to the Canaries and Azores, particularly considering that topshells are subject to lower harvesting pressure in mainland Portugal than in the Canaries. The obtained results in mainland Portugal are in agreement with those obtained by Rubal et al. (2014). It is known that high densities of *P. lineatus* result in slower growth rates and consequently smaller individuals (Williamson and Kendall, 1981; Rubal et al., 2014). Thus, it is expected that the coexistence in sympatry of these two species in mainland Portugal has a limiting effect on growth of *P. sauciatus*, explaining the smaller mean size obtained in the present study. In fact, it is known that interspecific competition in gastropods may result in differences in shell shape associated with resource usage (Heller, 1987; Emberton, 1995) or in niche differentiation through changes in body size (Ritchie and Olff, 1999).

The importance of Marine Protected Areas (MPAs) is steadily increasing since the evidence of overexploitation is pervasive worldwide (Coll et al., 2008). Moreover, recent studies showed that recovery rates following depletion of stocks is lower than expected (Lotze et al., 2011). Various processes are responsible of this trend: (i) failure to prevent stock exploitation, e.g. illegal harvesting; (ii) reduced reproductive success of depleted populations (Allee effects); (iii) ecosystem shifting, e.g. habitat degradation or loss; (iv) species interactions, e.g. predator–prey interactions, bottom-up and top-down effects; (v) genetic loss and increased sensitivity to disturbance (Micheli et al., 2008). Hence, the creation of a net of MPAs is pivotal to recover pre-harvesting conditions of the overexploited intertidal species. We herein observed that regardless the region, MPAs returned individuals with the highest mean sizes supporting their effectiveness in preserving the size–structure of this species. The differences found between size of harvested and non-harvested populations in mainland Portugal and the Canaries were smaller than those observed in Madeira archipelago. This is related to the lack of regulation in Madeira, with uncontrolled total catch of this species (Sousa et al., 2019b). Also, the lack of widespread traditional harvest of topshells in mainland Portugal results in less marked differences between harvested and non-harvested areas.

The results of the present study need to be taken with caution, since there were differences in sampling effort among locations, and hence, the collection of samples was uneven, but still a differentiation was made among the areas with and without harvesting pressure. During the last years, extensive intertidal field work has been carried out in Madeira, particularly focused on the characterization of commercially-exploited species, i.e. limpets (*Patella* spp.) and topshells (*Phorcus sauciatus*) (Sousa et al., 2018a,b, 2019a,b,c). Unfortunately, this effort has been performed mostly in the Canaries and the Azores in the 1990s and during the first decade of this century (Núñez et al., 2003; Ramírez et al., 2009; Riera et al., 2016), but no current data on the harvest of *Phorcus* are available with the exception of those herein provided. This situation is also reported from mainland Portugal, but the interest on the study species still remains overlooked. Most of the studies on *P. sauciatus* are concerning the geographic distribution of the species along the Iberian coast (Fischer-Piétte, 1963; Rubal et al., 2014).

As previously shown, most of the results may be explained by the differences in harvesting pressure, and herein only two treatments were considered, i.e. harvested and non-harvested. Several areas may be subjected to "partial" harvesting pressure, e.g. sites suffering exploitation in certain times of the year, for example, summer season or bank holidays from non-local harvesters, or areas with restricted geographically access that may act as "geographic MPAs" that preserve *Phorcus* stocks from the harvesting pressure. We herein did not consider this differentiation of "partial" harvesting pressure, since it needs to be monitored throughout the year. However, most of the coastal harvested sites are subjected to constant harvesting throughout the year, with a high frequency of walks from harvesters searching for newly-settled or previously-hidden *Phorcus* (authors pers. obs.).

The herein results highlight the importance of regulating the harvest of *P. sauciatus* in Madeira archipelago and mainland Portugal, as well as the implementation of management measures aiming at the sustainable exploitation and conservation of this species at medium and long-term. Current field observations and experimental approaches constitute the first step to get a thorough understanding of intertidal ecosystem processes, especially in the current fast-changing environmental scenarios.

CRediT authorship contribution statement

Ricardo Sousa: Conceptualization, Methodology, Data curation, Formal analysis, Validation, Writing - review & editing. **Joana Vasconcelos:** Conceptualization, Methodology, Validation, Writing - original draft. **Rodrigo Riera:** Conceptualization, Supervision, Validation, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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