


## RESEARCH ARTICLE

WILEY

# The protection effects of marine protected areas on exploited molluscs from an oceanic archipelago

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## Funding information

ARDITI-OOM, Grant/Award Number: OOM/2016/010 (M1420-01-0145-FEDER-000001- OOM); FCT, Grant/Award Number: SFRH/BSAB/143056/2018; MARE, Grant/Award Number: UID/MAR/04292/2019; RAM; UE FEDER, Grant/Award Number: MARISCOMAC (MAC/2.3d/097), MACAROFOOD (MAC/2.3d/015); Universidad Católica de la Santísima Concepción, Grant/Award Number: FAA 01/2019

## Abstract

1. Limpets are one of the most successful intertidal algal grazers in the north-eastern Atlantic. They provide valuable ecosystem services, playing a pivotal role in maintaining rocky shore ecological balance and have an important economic value, being subject to high levels of exploitation in several oceanic archipelagos. Limpets represent one of the most profitable economic activities of small-scale fisheries in the Madeira archipelago. However, limpets are extremely vulnerable to anthropogenic impacts, such as overharvesting, habitat fragmentation, and pollution.
2. The protection effects and the effectiveness of marine protected areas (MPAs) on the population dynamics of two historically highly exploited limpet species, *Patella aspera* and *Patella candei*, were analysed through a comparative study of size, reproduction, and biomass in the Madeira archipelago.
3. The effects of protection from MPAs on limpet populations resulted in a differential increase on size at first maturity, shell size, and capture per unit effort according to the degree of protection.
4. Old and enforced MPAs showed the best-preserved limpet populations in the study area, and both variables (age and enforcement) best explained the observed variability among the MPAs studied.
5. A thorough and multidisciplinary study is necessary to obtain a reliable picture of commercial stocks of the two targeted species (*P. aspera* and *P. candei*). Genetic analysis and studies on the food source of limpets may shed light to develop integrative conservation strategies.

## KEYWORDS

conservation evaluation, harvesting, Atlantic Ocean, intertidal, invertebrates

## 1 | INTRODUCTION

Human exploitation of organisms on rocky shores is an important cause of disturbance of intertidal communities that has been occurring since prehistoric times (Boer & Prins, 2002; Bustamante & Castilla, 1990; Martins, Jenkins, Hawkins, Neto, & Thompson, 2008). Human activities often lead to the reduction of densities and maximum sizes of several species around the world (Moreno, Sutherland, & Jara, 1984). Among the rocky shores organisms, molluscs are one of the most exploited worldwide (Roy, Collins, Becker, Begovic, & Engle, 2003; Sagarin et al., 2007), being extensively harvested in several geographic regions (Keough, Quinn, & King, 1993; Moreno et al., 1984). Currently, the exploitation of these organisms involves recreational, subsistence, and commercial activities (Moreno et al., 1984; Siegfried, 1994) and depends on factors such as human demography, tradition, and economy (Rius & Cabral, 2004).

The removal of organisms for food, bait, aquariums, and shell collection for decorative purposes are human activities that most affect the mollusc populations in coastal zones (Ramírez, Tuya, & Haroun, 2009), resulting in direct and indirect disturbance of intertidal populations (Addressi, 1994; Kingsford, Underwood, & Kennelly, 1991; Lindberg, Estes, & Warheit, 1998). These disturbances essentially focus on the abundance, size structure, and alterations on the reproductive output and replenishment of the exploited populations as a result of the size-selective nature of harvesting (Kido & Murray, 2003; Lindberg et al., 1998; Martins et al., 2017; Riera et al., 2016; Sousa et al., 2019). Larger specimens are the more attractive, visible, and prone to be caught, adding to their higher commercial value (Kido & Murray, 2003; Lindberg et al., 1998; Ramírez et al., 2009). This preferential removal of the larger and older specimens leads to a decrease in the reproductive success of the exploited population. Also, a decrease in the effective population size leads to lower reproductive output and could culminate in the disappearance of local populations from extensive intertidal areas, as occurred for the limpets *Cellana sandwicensis* (Pease, 1861), *Cellana exarata* (Reeve, 1854), and *Cellana talcosa* (Gould, 1846) in Hawaii (Valledor, 2000); or they could even become highly threatened, such as *Patella ferruginea* Gmelin, 1791 (Espinosa, 2009), and in extreme cases lead to extinction (Guerra-García, Corzo, Espinosa, & García-Gómez, 2004; Núñez, Brito, Riera, Docoito, & Monterroso, 2003). Furthermore, the effects of harvesting pressure may extend to the whole ecosystem through cascading trophic effects (Scheffer, Carpenter, & Young, 2005).

The exploitation of rocky shore molluscs in the archipelago of Madeira dates back to the 15th century and focuses mainly on limpets (*Patella candei* d'Orbigny, 1840 and *Patella aspera* Röding, 1798) and topshells (*Phorcus sauciatus* (Koch, 1845)) (Silva & Menezes, 1921; Sousa, Delgado, González, Freitas, & Henriques, 2018). This activity has been traditionally carried out by the coastal populations in the intertidal zone and commercially in the subtidal zone by snorkellers. The sharp decrease of intertidal limpet populations has forced the harvesters to target subtidal populations in the Madeira archipelago (Delgado et al., 2005). Even though, the stocks of *P. aspera* and *P. candei* are not overexploited, they are being exploited near their

maximum sustainable yield. Their slow growth rate and long life contribute to these species being extremely vulnerable to exploitation. As such, the enforcement of existing harvest regulations is essential to prevent future overexploitation of these keystone species (Henriques et al., 2012; Sousa et al., 2019; Sousa, Delgado, Pinto, & Henriques, 2017).

The conservation of exploited limpet populations is of concern, especially in coastal isolated areas, where no adjacent populations are present to supply larvae for settlement and recruitment (Cowen, Lwiza, Sponaugle, Paris, & Olson, 2000). The implementation of marine protected areas (MPAs) is considered a key tool for the conservation of marine biodiversity in coastal areas (Ballantine, 1991; Henriques, Delgado, & Sousa, 2017; Zann, 1995). Marine reserves defined as no-take zones are a popular alternative to traditional management measures of marine resources (Halpern & Warner, 2002). The exploited marine organisms, as a rule, reach higher density, biomass, and size in MPAs (Halpern, 2003; Hockey & Bosman, 1986; Keough et al., 1993). Reserves also act as a source of larvae that could eventually contribute to settlement and recruitment outside of the reserves (Pelc, Baskett, Tanci, Gaines, & Warner, 2009; Rakitin & Kramer, 1996), as evidenced by Christie et al. (2010), who showed larval connectivity between marine reserves and unprotected areas.

The effectiveness of marine reserves depends on their size, with the protection benefits of marine reserves increasing directly with their size; as such, larger reserves may be required to achieve the proposed objectives (Halpern, 2003). Additionally, Christie et al. (2010) highlighted the importance of considering oceanographic and ecological variables, as well as genetic information, when determining larval connectivity between populations. More recently, Edgar et al. (2014) showed that the conservation value in fish communities within MPAs is affected by the cumulative effects of five key features, summarized as NEOLI; that is, no take, well enforced, old, large, and isolated.

The protection effects of MPAs on the population dynamics of *P. aspera* and *P. candei* was analysed through a comparative analysis of size composition, reproduction ( $Lm_{50}$ ) and biomass in Madeira (north-east Atlantic Ocean), where these species have been historically highly exploited. To achieve this objective: (i) it was hypothesized that populations in MPAs will have a greater mean size than in exploited areas; (ii) it was assumed that limpet populations in protected areas will have greater size at first maturity than exploited populations, since this size has been previously observed as a good proxy of the stock exploitation status (Riera et al., 2016); and (iii) it was also hypothesized that the lack of harvesting pressure on limpet populations in MPAs will result in an increase in the individual biomass compared with the exploited populations in full-access areas.

## 2 | METHODS

The study was conducted on fresh specimens of *P. aspera* and *P. candei*, randomly collected from the intertidal and subtidal zones of the rocky shores of the Madeira archipelago, north-east Atlantic, by snorkelling. Each harvesting event was performed for a standard

period of 30 min by the same experienced harvesters, and all observed individuals were censused. The locations were selected based on similar abiotic and biotic conditions (i.e. type of substrate, slope of the coast, rugosity, hydrodynamic conditions, and type of community).

Sampling was performed at four MPAs (Garajau, Rocha do Navio, Desertas, and Selvagens) and 12 exploited coastal areas throughout the south (seven sites: Paúl do Mar, Madalena do Mar, Ponta do Sol, Cabo Girão, Caniço, Santa Cruz, and Ponta de São Lourenço south) and north coasts (five sites: Ponta de São Lourenço north, Porto Moniz, Ribeira da Janela, Ponta Delgada, and Ponta do Pargo) of Madeira, between 2017 and 2018 (Figure 1). MPAs were grouped based on their level of enforcement, age, and size (Table 1). For the MPA on the Selvagens Islands, only *P. aspera* was considered, since the taxonomy status of *P. candei* in this region is not fully resolved. According to Faria et al. (2017), it is very probable that *P. candei* from each Macaronesian archipelago are geographically and/or ecologically isolated populations. Hence, specimens of *P. candei* from Madeira and Desertas islands are considered in order to diminish the genetic variability among the sampling places.

All specimens were sorted by species, counted, measured to the nearest 0.01 mm (total shell length, TL, millimetres) using a Vernier calliper and weighed (total wet weight, TW, grams) on an electronic scale with 0.01 g accuracy. Individuals were dissected to inspect the gonads and then sexed according to gonad pigmentation; in males the gonads are pale white or pink, and brown to red in females (Orton, Southward, & Dodd, 1956). Individuals without visible sex characteristics were considered neuter (Martins, Santos, & Hawkins, 1987; Vale, 2016).

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 two-sample test, and homogeneity of variance was determined using Levene's statistics. ANOVA was performed considering the Brown–Forsythe *F* test, when the variance of the data was not homogeneous was used to test differences in the shell length. All statistical analyses were performed using SPSS v.24.0 (IBM Corp., 2016). For all tests, statistical significance was accepted when  $P < 0.05$ .

**TABLE 1** Category of enforcement, age and size by marine protected area in the Madeira archipelago (L, low; M, medium; H, high)

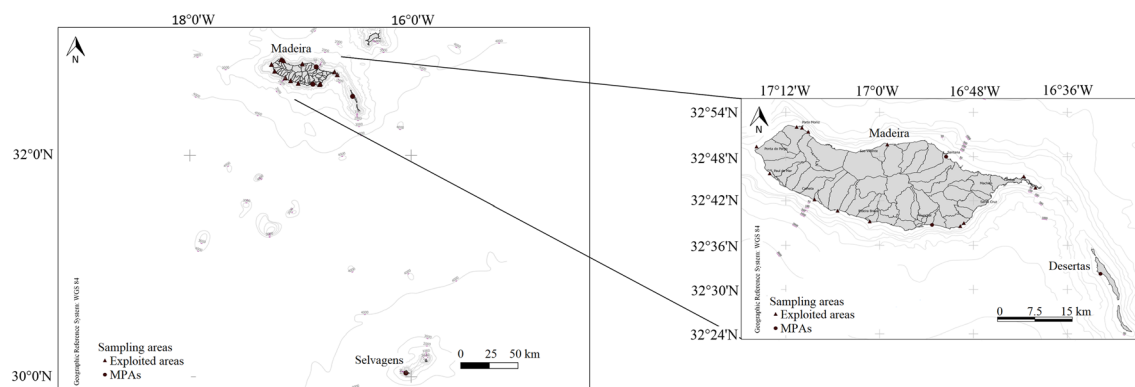
	Enforcement	Age	Size
Rocha do Navio	M	L	M
Garajau	M	M	L
Desertas	H	L	H
Selvagens	H	H	M

## 2.1 | Impact of MPAs on size-structure of *Patella aspera* and *Patella candei* populations

A comparative study to verify the effects of MPAs on length size-frequency of *P. aspera* and *P. candei* was conducted throughout the rocky shores of the Madeira archipelago, considering individuals from four MPAs and 12 exploited areas. The comparison of the impact of MPAs on limpet size was carried out using ANOVA, and the comparison of the proportion of individuals per size class between both unexploited and exploited zones was performed using a Pearson's chi-square analysis to determine any differences observed in limpet size distribution between the two zones (exploited [12 areas] and unexploited [four areas]).

## 2.2 | Impact of MPAs on the reproduction and catch per unit of effort of *Patella aspera* and *Patella candei* populations

The impact of MPAs on sexual maturation was evaluated through the analysis of size at first maturity and age at first maturity for each species, considering populations from MPAs and exploited zones. The size at first maturity  $L_{m50}$  was estimated from the relationship between the proportion of mature individuals and size (5 mm size classes), applying the balanced logistic function:  $p = 1/[1+\exp\{- (a + bL)\}]$  (Sparre & Venema, 1997), where  $p$  is the balanced probability and  $a$  and  $b$  are the equation parameters determined by the linear



**FIGURE 1** Sampling areas of *Patella aspera* and *Patella candei* in the Madeira archipelago, north-east Atlantic Ocean

least-square method, after logarithmic transformation. The mean size at first maturity was defined as the size in which 50% of the individuals from a population are mature; when  $p = 0.5$  then  $L_{m50} = -a/b$  (King, 1995).

Age at first maturity  $A_{50}$  was estimated by applying the inverse von Bertalanffy growth function (von Bertalanffy, 1938),  $A_{50} = t_0 - (1/K)\ln[1 - (L_{m50}/L_{\infty})]$  (Jennings, Kaiser, & Reynolds, 2001), where,  $L_{\infty}$  is the asymptotic shell length,  $K$  is the growth coefficient,  $t_0$  is the theoretical age at zero length of the limpet, and  $L_{m50}$  is the size at first maturity. The differences between exploited and unexploited populations of limpets was determined by testing the slopes of the maturity curves using an analysis of covariance.

Relative biomass was estimated using the catch per unit of effort by weight, corresponding to the ratio between the total weights of captured specimens by species at each harvesting set and time. The effect of MPAs was estimated through the comparison of the biomass of *P. aspera* and *P. candei* in MPAs and exploited zones by applying the Pearson chi-square statistics.

## 2.3 | Impact of enforcement, age, and size on the effectiveness of MPAs in the conservation of *Patella aspera* and *Patella candei* populations

The analysis of the impact of planning and management features on MPA effectiveness on the conservation of limpet populations was carried out considering the features enforcement, age, and size. These features were considered a reliable proxy considering the specificities of the species studied and the protected areas studied. The influence of these three features within the MPAs surveyed was categorized at three levels: low (L), medium (M), and high (H) (Table 1).

- i. Enforcement concerns the extent of compliance to the law that prohibits fishing, through policing and community support (L: little attempt at control; M: moderate control with policing attempted but with apparent infractions; and H: well enforced but poaching may occur).
- ii. Age relates to the time elapsed between the fishing restriction being implemented and the undertaking of the surveys (L: MPA with ages between 20 and 30 years; M: encompassed reserves with ages between 31 and 40 years; and H: MPAs over 40 years old);
- iii. Size of MPAs as described in the management plan (L: MPA area <5 km<sup>2</sup>; M: MPA area between 5 and 100 km<sup>2</sup>; H: MPA area >100 km<sup>2</sup>).

The influence of the aforementioned features on the size-structure, reproduction, and biomass were evaluated within each MPA. The effect of these features on population size-structure was assessed through an ANOVA, on the size at first maturity using an analysis of covariance, and on biomass by applying a Pearson's chi-square statistic for both species according to each category.

### 2.3.1 | Patterns of limpet size structure according to enforcement, age, and size of the MPA

To examine patterns of limpet size structure among the MPAs studied, a non-metric multidimensional scaling procedure was conducted based on Bray–Curtis similarity on square-root-transformed data; the multidimensional scaling was used to visualize data spatially. Only centroids (i.e. means) for each coastal MPA were plotted to facilitate visualization of multivariate patterns in the ordination space. A distance-based redundancy analysis (Legendre & Anderson, 1999) tested whether variation in the features 'enforcement' and 'age' contributed to explaining variations in limpet size structure in the MPAs studied. Multivariate multiple regression, using the DISTLM routine (Anderson, 2001), then tested the significance of these relationships by fitting a linear model based on Bray–Curtis dissimilarities from square-root-transformed biomass data. To retain variables with good explanatory power, as a result of collinearity among variables, the Akaike information criterion routine was used as a selection criterion (Legendre & Anderson, 1999). All multivariate procedures were carried out via the PRIMER v6 (Clarke & Gorley, 2006) and PERMANOVA+ (Anderson, Gorley, & Clarke, 2008) statistical package.

## 3 | RESULTS

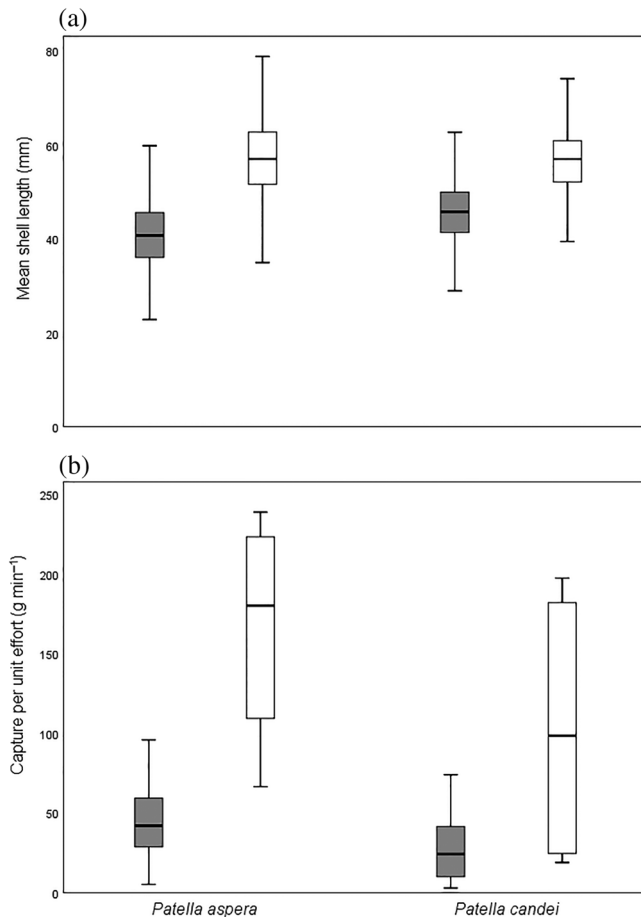
A total of 7,090 specimens from the 16 selected locations (12 from exploited areas and four MPAs) of the rocky shores of the Madeira archipelago were investigated. The mean shell length of the 4,226 sampled individuals of *P. aspera* was  $45.10 \pm 9.97$  mm, whereas for the 2,864 specimens of *P. candei* the mean shell length was  $48.56 \pm 8.22$  mm. The analysis of size-frequency showed a normal distribution of data for both *P. aspera* ( $Z = 3.966$ ,  $P < 0.01$ ) and *P. candei* ( $Z = 1.709$ ,  $P < 0.01$ ). Nevertheless, size did not show homogeneous variance for *P. aspera* ( $W = 27.728$ ,  $P < 0.01$ ), in contrast to the homogeneous variance exhibit by *P. candei* ( $W = 0.937$ ,  $P > 0.01$ ).

### 3.1 | Impact of MPAs on the size-structure of *Patella aspera* and *Patella candei* populations

The study populations of *P. aspera* were characterized by a wide range of sizes, from 3.07 to 75.22 mm in exploited zones and from 12.56 to 84.22 mm in MPAs. Differences in mean shell length of *P. aspera* were observed between zones, with smaller specimens in exploited zones than in MPAs (Table 2). The same pattern was observed for *P. candei*, with smaller individuals in exploited zones than in MPAs (Figure 2a). This species also showed a wide range of sizes, from 25.25 to 68.04 mm in exploited zones and from 14.22 to 79.63 mm in MPAs. The observed differences in mean shell length between exploited zones and MPAs were statistically significant for both *P. aspera* ( $F = 1214.030$ ,  $P < 0.01$ ) and *P. candei* ( $F = 345.701$ ,  $P < 0.05$ ).

**TABLE 2** Shell size of *Patella aspera* and *Patella candei*, according to the exploitation status in the Madeira archipelago

Species	Exploitation status	Min	Max	Mean	SD	N
<i>P. aspera</i>	Exploited	3.07	75.22	41.82	7.65	3207
	Protected	12.56	84.22	55.40	9.37	1019
<i>P. candei</i>	Exploited	25.25	68.04	45.65	6.61	1981
	Protected	14.22	79.63	55.64	7.21	883

**FIGURE 2** (a) Mean total length and (b) capture per unit effort for *Patella aspera* and *Patella candei*. Dark grey bars represent exploited zones; white bars represent MPAs. Box plot showing median (black line) and upper and lower quartiles of the data

The structure of size classes of both *P. aspera* and *P. candei* per size-class were dominated by larger individuals in MPAs than in exploited zones (*P. aspera*,  $\chi^2 = 1689.301$ ,  $P < 0.05$ ; *P. candei*,  $\chi^2 = 930.859$ ,  $P < 0.05$ ). The highest percentages of *P. aspera* specimens was observed in classes 55–60 mm (~26% of the total of the specimens) in the MPAs and 40–45 mm (~30%) in exploited zones. The same pattern was observed for *P. candei*, with the highest percentages of specimens in classes 55–60 mm (~22%) in the MPAs and 45–50 mm (~26%) in exploited zones (Figure 3).

### 3.2 | Impact of MPAs on the reproduction and catch per unit of effort of *Patella aspera* and *Patella candei* populations

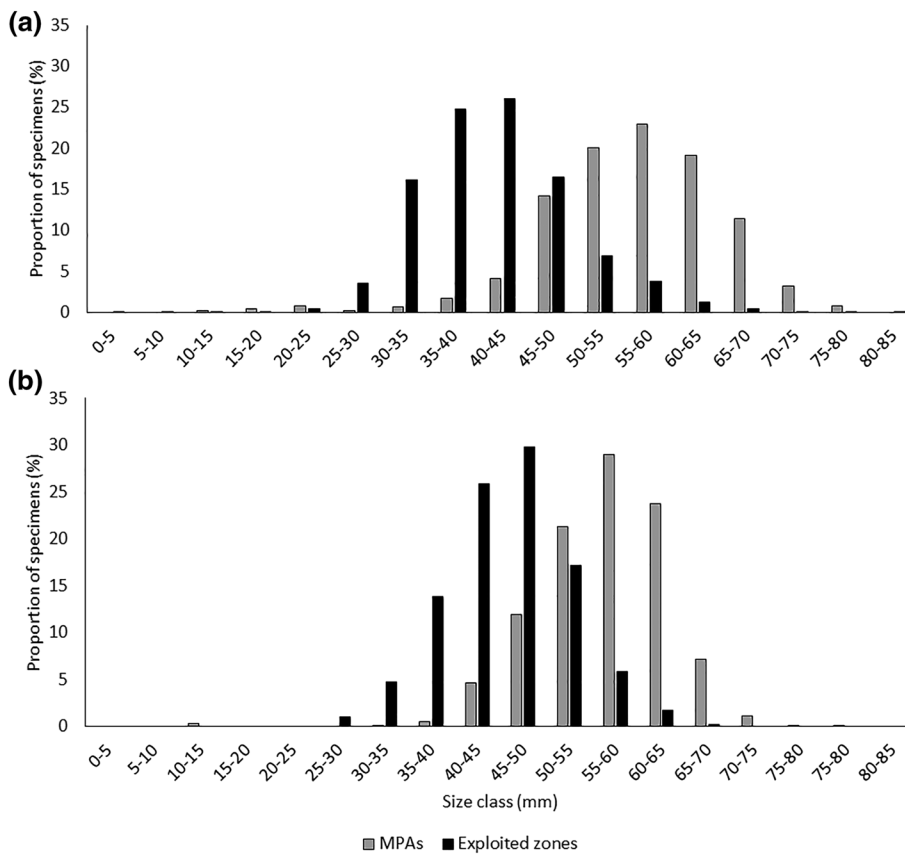
The determined mean size at first maturity exhibited higher values in MPAs for both *P. aspera* and *P. candei*. The  $L_{m50}$  increased from 37.02 mm in exploited zones to 40.47 mm in MPAs for *P. aspera*. Consequently, an increase in the estimated mean  $A_{50}$  for this species was also observed from 1.9 years (exploited zones) to 2.2 years (MPAs). Concerning *P. candei*, the  $L_{m50}$  increased from 37.14 mm (exploited zones) to 42.82 mm (MPAs), corresponding to an increase in  $A_{50}$  from 1.9 years in the exploited zones to 2.4 years in MPAs. The observed differences in  $L_{m50}$  between exploited zones and MPAs were statistically significant for *P. aspera* ( $F = 69.417$ ,  $P < 0.001$ ) and for *P. candei* ( $F = 64.116$ ,  $P < 0.001$ ).

The abundance, expressed as grams per minute, showed higher rates in MPAs than in exploited zones for both limpet species. Concerning *P. aspera*, the biomass ranged from 66.5 to 238.96 g min<sup>-1</sup> ( $166.47 \pm 37.81$  g min<sup>-1</sup>) in MPAs and from 5.28 to 95.96 g min<sup>-1</sup> ( $45.89 \pm 25.89$  g min<sup>-1</sup>) in exploited zones. Regarding *P. candei*, the biomass varied from 19.04 to 197.52 g min<sup>-1</sup> with a mean biomass of  $103.42 \pm 91.84$  g min<sup>-1</sup> in MPAs and from 2.95 to 74.07 g min<sup>-1</sup> ( $28.08 \pm 21.47$  g min<sup>-1</sup>) in exploited zones (Figure 2b).

The differences in biomass between MPAs and exploited zones were statistically significant for *P. aspera* ( $\chi^2 = 14.792$ ,  $P < 0.05$ ) and for *P. candei* ( $\chi^2 = 8.571$ ,  $P < 0.05$ ).

### 3.3 | Impact of the effectiveness of MPAs in the conservation of *Patella aspera* and *Patella candei* populations

The effect of planning and management measures on the mean shell length of the populations of *P. aspera* among MPAs was observed, with the largest specimens occurring in Selvagens ( $57.34 \pm 9.22$  mm) and Rocha do Navio showing the smallest individuals ( $51.74 \pm 10.00$  mm). The same pattern was observed for the populations of *P. candei*, where the largest individuals were in Desertas ( $58.03 \pm 7.73$  mm) and Rocha do Navio had the smallest specimens ( $53.78 \pm 6.59$  mm). Significant differences in mean shell length among MPAs were found for *P. aspera* ( $F = 18.368$ ,  $P < 0.05$ ) and for *P. candei* ( $F = 28.318$ ,  $P < 0.05$ ).



**FIGURE 3** Size distribution of (a) *Patella aspera* and (b) *Patella candei* sampled in exploited coastal areas (exploited zones) and marine protected areas (MPAs)

*Patella aspera* showed a higher proportion of specimens in the size-class 50–55 mm in Rocha do Navio (~26%) and Garajau (27%), in the size-class 55–60 mm in Selvagens (~24%) and in the 60–65 mm size-class in Desertas (~22%) (Figure 4a). Concerning *P. candei*, the highest proportion of specimens was observed in the size-class 55–60 mm for Rocha do Navio (~29%) and in the size-class 60–65 mm for Desertas (~31%) and Garajau (~29%) (Figure 4b). Differences in the proportion of specimens per size classes between MPAs were significant for *P. aspera* ( $\chi^2 = 132.489$ ,  $P < 0.001$ ) and for *P. candei* ( $\chi^2 = 98.834$ ,  $P < 0.001$ ).

The estimated values of the mean size at first maturity for *P. aspera* showed a progressive increase from Rocha do Navio (38.27 mm) to Selvagens (44.52 mm). The same pattern was observed for *P. candei*, with an increase from 38.15 mm (Rocha do Navio) to 44.84 mm (Desertas). The observed differences in  $L_{m50}$  between MPAs according to the protection measures were statistically significant for *P. aspera* ( $F = 151.174$ ,  $P < 0.001$ ) and for *P. candei* ( $F = 95.144$ ,  $P < 0.001$ ).

The biomass rates of *P. aspera* showed the lowest values in the Rocha do Navio MPA (66.55 g min<sup>-1</sup>) compared with the more effectively protected Selvagens MPA (238.96 g min<sup>-1</sup>). Regarding *P. candei*, the highest biomass was reported in Garajau with 197.52 g min<sup>-1</sup>. The differences in biomass between MPAs were significant for *P. aspera* ( $\chi^2 = 863.000$ ,  $P < 0.001$ ) and for *P. candei* ( $\chi^2 = 728.000$ ,  $P < 0.001$ ).

### 3.3.1 | Enforcement

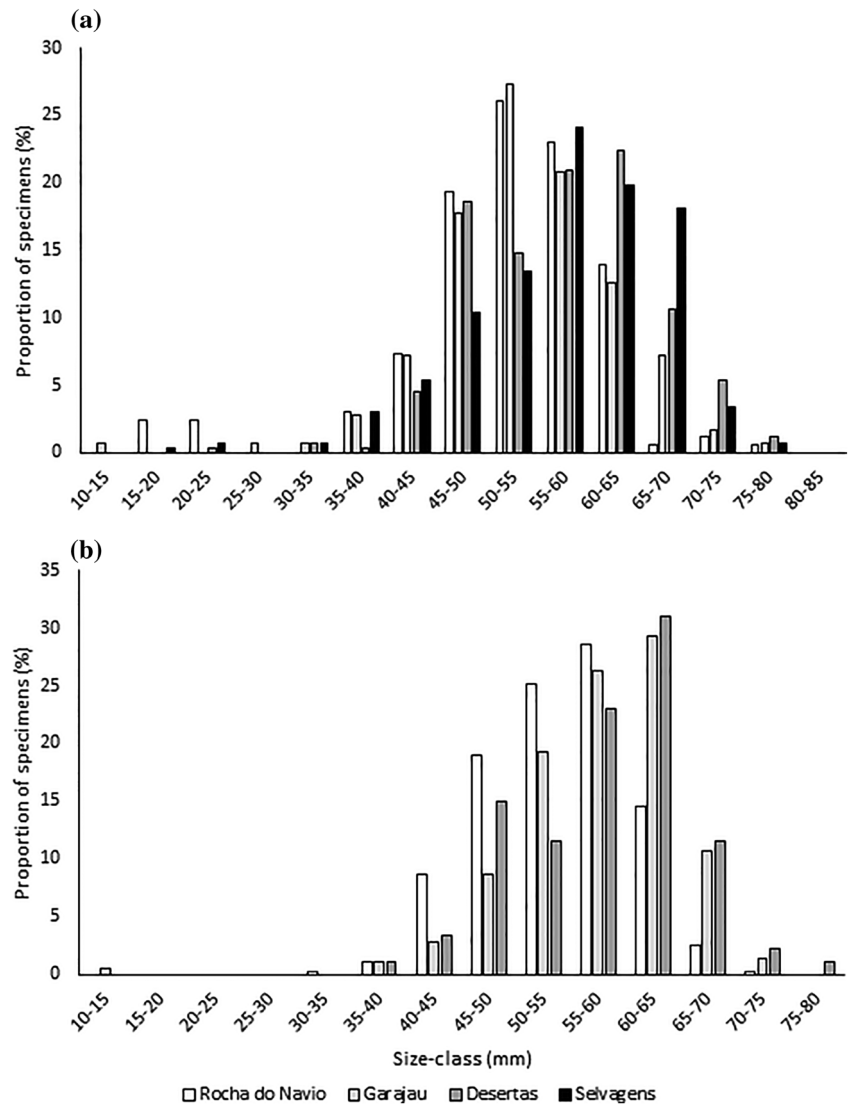
The impact of the MPAs enforcement on the mean shell size was observed for *P. aspera* ( $F = 46.691$ ,  $P < 0.05$ ) and for *P. candei* ( $F = 61.655$ ,  $P < 0.05$ ). Larger specimens of *P. aspera* were observed in the well-enforced MPAs of Desertas and Selvagens (mean size  $\pm$  SE: 57.24  $\pm$  8.43 mm) compared with the moderately enforced reserves of Rocha do Navio and Garajau (53.15  $\pm$  9.37 mm). The same pattern was observed for the populations of *P. candei*, which showed larger individuals in the well-enforced MPA of Desertas (58.03  $\pm$  8.40 mm) relative to the moderately enforced MPAs of Rocha do Navio and Garajau (55.38  $\pm$  8.07 mm). Additionally, the proportion of specimens per size class was also significantly different for *P. aspera* ( $\chi^2 = 75.404$ ,  $P < 0.001$ ) and for *P. candei* ( $\chi^2 = 23.711$ ,  $P < 0.001$ ) between moderate and well-enforced MPAs.

The estimated values of  $L_{m50}$  showed a progressive increase from the MPAs with moderate control to well-enforced MPAs for both limpet species. An increase was also observed in the estimated mean  $A_{50}$  for both limpet species. The observed differences in  $L_{m50}$  between MPAs were statistically significant for *P. aspera* ( $F = 35.255$ ,  $P < 0.001$ ) and for *P. candei* ( $F = 100.226$ ,  $P < 0.001$ ).

The biomass rates followed the same pattern as size and  $L_{m50}$ , with higher values in well-enforced MPAs. The differences in biomass between MPAs according to the degree of enforcement of the protected area were statistically significant for *P. aspera*



**FIGURE 4** Size distribution of (a) *Patella aspera* and (b) *Patella candei* sampled inside each marine protected area in the Madeira archipelago



( $\chi^2 = 863.000$ ,  $P < 0.001$ ) and for *P. candei* ( $\chi^2 = 728.000$ ,  $P < 0.001$ ).

### 3.3.2 | Age

The age of the MPA was also an important factor on the populations of *P. aspera* and *P. candei*, with the largest individuals occurring in the oldest MPA of Selvagens (>40 years) and the smallest specimens in the younger MPAs of Rocha do Navio and Desertas (<30 years). The differences in mean shell length between old and new MPAs were significant for *P. aspera* ( $F = 10.613$ ,  $P < 0.05$ ) and for *P. candei* ( $F = 33.886$ ,  $P < 0.05$ ), as was the proportion of specimens per size class (*P. aspera*,  $\chi^2 = 82.675$ ,  $P < 0.001$ ; *P. candei*,  $\chi^2 = 58.347$ ,  $P < 0.001$ ).

The estimated  $L_{m50}$  exhibited a progressive increase from the younger to the older MPAs for both limpet species. Subsequently, an increase in the estimated mean  $A_{50}$  was also observed. The observed differences in  $L_{m50}$  between MPAs according to the size of the

protected areas were statistically significant for *P. aspera* ( $F = 119.067$ ,  $P < 0.001$ ) and for *P. candei* ( $F = 103.542$ ,  $P < 0.001$ ).

The biomass rates increased progressively from the younger to the older MPAs for both limpet species. The differences in biomass between MPAs according to the age of the protected area were statistically significant for *P. aspera* ( $\chi^2 = 1726.000$ ,  $P < 0.001$ ) and for *P. candei* ( $\chi^2 = 863.000$ ,  $P < 0.001$ ).

### 3.3.3 | Size

The populations of both species were characterized by a wide range of sizes in the three MPA size categories analysed. Both species showed a pattern of increase in the mean shell length from the smallest MPA, Garajau, to the largest MPA, Desertas. Differences in mean shell length were observed between MPAs for *P. aspera* ( $F = 8.396$ ,  $P < 0.05$ ) and *P. candei* ( $F = 28.318$ ,  $P < 0.05$ ) according to the size of the MPA. The differences in the proportion of specimens per size classes according to the size of the MPAs were statistically

significant for *P. aspera* ( $\chi^2 = 65.530$ ,  $P < 0.05$ ) and for *P. candei* ( $\chi^2 = 98.834$ ,  $P < 0.05$ ).

Mean size at first maturity and age at first maturity presented an increase from the smaller to the larger MPAs for both *P. aspera* and *P. candei*. The observed differences in  $L_{m50}$  between MPAs according to the size of the protected areas were statistically significant for *P. aspera* ( $F = 118.779$ ,  $P < 0.001$ ) and for *P. candei* ( $F = 114.995$ ,  $P < 0.001$ ).

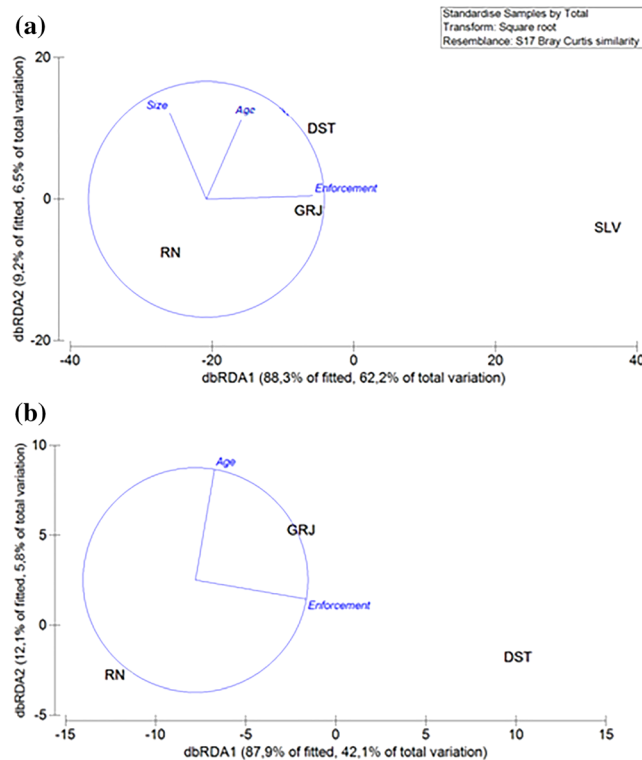
The biomass rates increased from the smaller to the larger MPAs for *P. aspera*. With regard to *P. candei*, the biomass was higher in the

medium-sized MPAs. The differences in biomass between MPAs considering the reserve size were statistically significant for *P. aspera* ( $\chi^2 = 863.000$ ,  $P < 0.05$ ) and for *P. candei* ( $\chi^2 = 728.000$ ,  $P < 0.05$ ).

### 3.3.4 | Patterns of limpet size structure according to enforcement, age, and size of the MPA

Limpet size structure varied among the MPAs studied. Selvagens was clearly separated from the others due to the greater proportion of larger size-class individuals (>60 mm). Also, a high variation in limpet size was observed within Desertas, relative to the high similarity among within-replicates from the other MPAs (i.e. Rocha do Navio and Garajau).

The first two axes of the distance-based redundancy analysis explained approximately 68% of overall variation in *P. aspera* size structure (Figure 5a). Two MPA features, enforcement and age, contributed significantly to explain the observed variability on *P. aspera* size classes. Age was the most important variable, followed by enforcement, explaining 48% and 18% of the populations' variability respectively (Table 2). For *P. candei*, the Selvagens MPA was not included due to taxonomic discrepancies concerning the identification of this species in this small archipelago. For this species, the first two distance-based redundancy analysis axes explained 48% of total variability of the size structure (Figure 5b). Enforcement was the most important variable explaining the observed variability of *P. candei* among sites, being responsible for 35%. Age was also responsible for the observed variability (12%), but not significantly (Table 3). Hence, these two variables were important drivers explaining patterns in limpet size structure regardless of the limpet species.



**FIGURE 5** Distance-based redundancy analysis (dbRDA) biplot of first and second axes relating environmental variables that affected significantly (see Table 2) the size structure of targeted limpet species for (a) *Patella aspera* and (b) *Patella candei*. Centroids for each distance are plotted. DST: Desertas; GRJ: Garajau; RN: Rocha do Navio; SLV: Selvagens

## 4 | DISCUSSION

The effects of protection from the MPAs on limpet stocks are not only restricted to an increase of abundance inside non-harvested sites but also an increase of size at first maturity and shell size, albeit at different rates. Differences among MPAs were mainly explained by two features (age and enforcement), though an improvement of the marine ecosystem and population health for both limpet species was

**TABLE 3** Results of multivariate multiple regression testing the relationship between the age and enforcement (Table 1) and limpet size structure of both species

Species	Variable	SS (trace)	Pseudo-F	P	Proportion of explained variation
<i>Patella aspera</i>	Age	4,713.40	10.336	<b>0.0012</b>	0.484
	Enforcement	1,819.10	5.690	<b>0.002</b>	0.187
<i>Patella candei</i> <sup>a</sup>	Enforcement	731.19	4.385	<b>0.009</b>	0.354
	Age	257.15	1.670	0.188	0.124

SS: sum of squares.

To retain variables with explanatory power, the adjusted  $R^2$  procedure was chosen as model selection criterion using sequential tests. Bold denotes significant differences.

<sup>a</sup>No *P. candei* specimens from the Selvagens marine protected area were considered.



observed in all MPAs. However, it was evident that old (i.e. Selvagens) and well-enforced (i.e. Selvagens and Desertas) MPAs showed highly balanced populations, compared with the other two MPAs (i.e. Rocha do Navio and Garajau) and the exploited zones, due to the higher representation of adult specimens in the overall limpet populations. The present results showed that old and well-enforced MPAs harbour a high representation of large adults and more balanced populations of both *P. aspera* and *P. candei*. However, this needs to be taken with caution, since very few small individuals, mostly juveniles, were sampled. Hence, the limpet populations studied were skewed to adult-size specimens regardless of their protection regime (i.e. MPAs or exploited areas).

The implementation of MPAs has been steadily increasing worldwide only in recent years (Lubchenco & Grorud-Colvert, 2015). This is probably due to the conventional belief that the ocean was a limitless source of resources and the perception that anthropogenic activity is not a cause of extinction of marine organisms is slowly changing (Roberts & Hawkins, 1999), being increasingly evident that fishing activity affects the target species as well as the entire ecosystem through the trophic cascade effect (Castilla, 1999). The impact of anthropogenic activities is complex in biological systems (Lindberg et al., 1998), and the effect of exploitation on the upper trophic levels is difficult to predict. The islands have marine biological systems less diverse than those observed in the corresponding continental habitats (Paulay, 1994). Hence, overexploitation on the islands could lead to irreversible impacts such as local extinctions, substantial decreases, or even a total elimination of the ecosystem function provided by the exploited species through the alteration of the food web (Martins et al., 2008).

In the Madeira archipelago, *P. candei* and *P. aspera* are subject to high levels of exploitation, representing one of the most profitable economic activities of small-scale fisheries, and reported to reach an annual catch of up to 111 t in 2017, yielding a total first sale value of ~€0.38 M (Regional Directorate of Fisheries). The direct effects of intensive harvesting pressure on the exploited resources are the reduction of biomass and shifts in limpet size structure, because of the preferential harvesting of larger specimens (Griffiths & Branch, 1997). The loss of larger and older specimens due to selective harvesting influences multiple cascading effects on the biology of the target species and populations, including changes in life history, demographics, breeding success, and ecological interactions (Fenberg & Roy, 2008).

The results showed that the impact of commercial harvesting of limpets in the Madeira archipelago negatively affects the biomass, size, and reproduction of both species (*P. candei* and *P. aspera*). These molluscs are significantly less abundant, have lower sizes, and early maturation in exploited zones. Similar patterns of size decrease and biomass reduction, specifically the depletion of large adults, were reported for *P. candei* (Núñez et al., 2003) and *P. candei crenata* (Ramírez et al., 2009) in the Canary Islands, and *P. candei* and *P. aspera* in the Azores archipelago (Martins et al., 2008, 2017). This pattern has also been observed in South Africa for *Patella concolor* Krauss, 1848 (Branch, 1975) and on the Mediterranean coast of Spain for

*P. ferruginea* (Espinosa, 2009; Espinosa, Guerra-García, Fa, & García-Gómez, 2006), and even in other limpet genera, such as *Cymbula oculus* Born, 1778 in South Africa (Branch & Odendaal, 2003), *Lottia gigantea* Gray in G.B. Sowerby I, 1834 in Mexico (Pombo & Escofet, 1996) and southern California (Sagarin et al., 2007), and other species of harvested molluscs, such as *Fissurella* spp. in Chile (Moreno et al., 1984), South Africa (Hockey & Bosman, 1986), Australia (Keough et al., 1993), and Tanzania (Newton, Parkes, & Thompson, 1993).

Limpets have relatively high longevity and slow growth rates (e.g. Núñez, Brito, Riera, & Docoito, 2004), and thus are extremely vulnerable to the effect of selective harvesting of larger specimens (Henriques et al., 2012; Kido & Murray, 2003; Lindberg et al., 1998; Ramírez et al., 2009; Sousa et al., 2017). Additionally, the illegal harvesting of limpets in the Madeira archipelago, which are marketed directly to the consumer, also contributes to changes in size-structure of the limpet populations. The decrease in the biomass of higher size-class specimens leads to the illegal harvesting of specimens with smaller sizes than the minimum catch size (<40 mm) established by regulators. These catches are unreported, and hence the real impact of the limpet exploitation is underestimated, as has been previously observed in the Azores (Martins et al., 2008).

The scarcity of larger specimens, with the highest reproductive potential, may lead to a subsequent decrease in population size due to the decrease in reproductive success as previously observed in the populations of *P. candei* and *P. aspera* in the Azores (Martins et al., 2008). *Patella aspera* is a protandrous hermaphrodite (Delgado et al., 2005; Hawkins, Côrte-Real, Pannacciulli, Weber, & Bishop, 2000), being particularly susceptible to changes in its population structure that favour the decrease of the frequency of larger individuals. This situation leads to the reduction of females, which under natural conditions are more abundant in the larger size classes, with a reversal of the sex ratio in the larger size classes for this species in exploited areas in the Madeira archipelago (unpublished data), as also verified for *L. gigantea* in southern California (Kido & Murray, 2003). Hence, management measures promoting the protection of larger adults are pivotal for the replenishment of exploited populations, and concomitantly an increase of effective population size of *P. aspera*; these measures are urgently needed in the Madeira archipelago. The fact that larger specimens show a greater contribution to the population reproductive effort (Keough et al., 1993) implies that the harvesting impact on larger specimens in *P. candei* must not be overlooked. This biased harvesting will negatively affect the breeding success, as occurs in *P. ferruginea* (Espinosa et al., 2006), and may culminate in the population collapse (Guerra-García et al., 2004; Núñez et al., 2003). For example, the Canarian populations of *P. candei* showed a marked decline due to overexploitation (Navarro et al., 2005), suggesting that even this species could be susceptible to the population decline resulting from intensive exploitation. Both *P. candei* and *P. aspera* are Macaronesian endemisms, and only local populations contribute to the total recruitment, thus becoming more vulnerable and reducing the reproductive success of local populations (Martins et al., 2008).

MPAs are one of the most important tools in the conservation of coastal marine biodiversity (Ballantine, 1991; Halpern & Warner, 2002; Edgar et al., 2014; Zann, 1995). MPAs also play an important role in the natural replenishment of stocks (Manríquez & Castilla, 2001). The effectiveness of the response of species to the protection provided by MPAs depends greatly on the degree of exploitation to which the species are subject. Species subject to high levels of exploitation are more likely to respond rapidly when recruitment occurs at sufficient levels, because of the removal of fishing activity that limited the population size and demographics of the species (Carr & Reed, 1993; Lotze, Coll, Magera, Ward-Paige, & Airoidi, 2011; Polacheck, 1990; Rowley, 1994). The position on the trophic chain also plays an important role in the species recovery, since it is correlated with its life history parameters. For marine invertebrates with high longevity and slow growth, temporal responses to preserve protection are assumed to be slower (Halpern & Warner, 2002). *Patella candei* and *P. aspera* are moderate long-lived organisms with slow growth rates (Henriques et al., 2012; Núñez et al., 2004; Sousa et al., 2017). They seem to be extremely vulnerable to the selective harvesting of larger specimens and have a slower temporal response to the protection in reserves.

According to Halpern (2003), the mean values of different biological variables are 20–30% higher in protected zones than in exploited zones and regardless of MPA size, indicating that small reserves can produce high values. The increase observed in the size of *P. candei* and *P. aspera* from protected areas suggests a positive effect of the MPAs in the populations of both species. The fact that the reserves' ages ranged from 21 years (Rocha do Navio) to 47 years (Selvagens) resulted in a marked differentiation in the composition of sizes in both *Patella* species between exploited and protected zones. An increase of approximately 14 mm in mean shell size for *P. aspera* and 10 mm in mean shell size for *P. candei* in the MPAs shows the key role of protected zones on the recovery of the populations of these important intertidal grazers in the Madeira archipelago. This trend becomes more pronounced when considering well-enforced and old MPAs, with an increase of approximately 16 mm and 13 mm in mean shell length for *P. aspera* and *P. candei* respectively. The pattern obtained results mainly from the removal of the greater anthropogenic impact, i.e. the harvesting activity, in protected areas that results in the recovery of the balance in the population size structure of *P. candei* and *P. aspera* in the Madeira archipelago, which agrees with the observations for *P. ferruginea* in the Alborán Sea (Mediterranean Sea) (Guerra-García, Corzo, & García-Gomez, 2003).

The progressive increase in mean size of the specimens in MPAs may result mostly from the biological characteristics of these species (i.e. slow growth, late maturity, and high longevity) together with the occurrence of illegal harvesting, especially on Garajau and Rocha do Navio. Additionally, the harvesting regulatory measures were implemented in 2006 and they have contributed to a slight recovery of the exploited populations stocks in this region and a reduction of the differences in size between exploited zones and MPAs (Sousa et al., 2019).

In the Canaries, a similar pattern was obtained for *P. candei* in Fuerteventura (Núñez et al., 2003, 2004), and also for the remaining

limpet species (*P. candei crenata*, *P. aspera*, and *Patella rustica*) in the Canaries (Ramírez et al., 2009) with better preserved populations, in terms of biomass and size structure, in areas with reduced anthropogenic impact. The effectiveness of protected zones has been reported for the black abalone (*Haliotis picta* Röding, 1798) in Tasmania (Edgar & Barret, 1999) showing declines of small-sized individuals and consistent increases of large-sized adults within one MPA relative to full-access sites. Micheli et al. (2008) showed recovery of exploited abalone populations (*Haliotis rufescens* Swainson, 1822 and *Halioti cracherodii* Leach, 1814) on California coasts. However, high natural mortality and illegal harvesting may be responsible for no signs of recovery comparable to preceding levels of stock collapse. A plausible explanation of size increases within MPAs may be related to the role of protected areas on natural replenishment of targeted populations, as observed for the abalone *Concholepas concholepas* (Bruguière, 1789) on south-east Pacific coasts (Manríquez & Castilla, 2001).

We have explored the protection effects of MPAs using several variables (i.e. size structure [size], reproduction [ $L_{m50}$ ], and biomass [CPUE]) of the most important coastal invertebrates targeted by harvesters. The limpet assemblages in old and well-enforced MPAs were dominated by adults, with a good representation of large-sized specimens (i.e. >60 mm long). Surprisingly, no recruits were censused during field surveys, but possibly were overlooked since they mimic the environment. The presence of recruits in the MPAs studied happens with certainty because their settlement is driven by cues associated with adult habitat. The MPAs play a paramount role in increasing the conservation benefits and to achieve their desired conservation value. In addition, the understanding and commitment of local communities, management regulators, policymakers, and stakeholders, based on information and education are pivotal to the effective management of MPAs and to ensure the sustainability of these commercial species and ecosystems in the medium and long term.

This study constitutes a first step in characterizing the current condition of exploited limpet assemblages in the study area. We provide a more general understanding of the processes that promote spillover of these commercial sessile species to various coastal sites with varying levels of protection (MPAs and full-access zones). Age and enforcement were the most important factors in an MPA's efficiency to protect both the commercial limpet species. This is demonstrated by populations with a high representation of adult-sized individuals in old and well-enforced MPAs. MPAs were shown to be a feasible tool for the conservation of stocks of these commercial species in the Madeira archipelago. Future management plans need to integrate the already-established MPAs into a net of MPAs where connectivity of limpet metapopulations should be taken into consideration.

## ACKNOWLEDGEMENTS

We are grateful to the Fisheries Research Service (DSI) of the Regional Directorate of Fisheries of the Autonomous Region of Madeira. We acknowledge Dr Antonieta Amorim for providing the map with the stations used in this work and are also grateful to Filipe Andrade and Jorge Lucas, namely in biological sampling and harvesting surveys, and to Dr Carolina Santos and the IFCN (Instituto

das Florestas e Conservação da Natureza da RAM) for allowing and collaborating in the collection of limpets in the protected areas. RS was supported by a grant from ARDITI OOM/2016/010 (M1420-01-0145-FEDER-000001- Observatório Oceânico da Madeira-OOM), JV by a grant from Fundação para a Ciência e Tecnologia-FCT (SFRH/BSAB/143056/2018), and RR partially funded by UCSC (FAA 01/2019). This study was also supported by the UE FEDER in the framework of the Projects MARISCOMAC (MAC/2.3d/097) and MACAROFOOD (MAC/2.3d/015), the Regional Government of Madeira, and by FCT through the strategic project UID/MAR/04292/2019 granted to MARE.

## AUTHORS' CONTRIBUTIONS

RS: study design, data acquisition, statistical analysis, data interpretation, writing the paper; RR: study design, statistical analysis, critical analysis, revision of the paper; JV: data interpretation, writing the paper; ARP: biological sampling and writing the paper; JD: critical analysis, revision of the paper; PH: study design, data acquisition, statistical analysis, data interpretation, writing the paper. All authors read and approved the final manuscript.

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**How to cite this article:** Sousa R, Henriques P, Vasconcelos J, Pinto AR, Delgado J, Riera R. The protection effects of marine protected areas on exploited molluscs from an oceanic archipelago. *Aquatic Conserv: Mar Freshw Ecosyst*. 2020;30: 717–729. <https://doi.org/10.1002/aqc.3285>