ELSEVIER

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares



Long-term population status of two harvested intertidal grazers (*Patella aspera* and *Patella candei*), before (1996–2006) and after (2007–2017) the implementation of management measures



Ricardo Sousa^{a,b,*}, Joana Vasconcelos^{b,c,d}, Paulo Henriques^e, Ana Rita Pinto^b, João Delgado^{b,f}, Rodrigo Riera^d

- ^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 Investigação (DSI) Direção Regional das Pescas, Estrada da Pontinha S/N, 9004-562 Funchal, Madeira, Portugal
- ^c Centro de Ciências do Mar e do Ambiente (MARE), Quinta do Lorde Marina, Sítio da Piedade 9200-044 Caniçal, Madeira Island, Portugal
- d Departamento de Ecología, Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Casilla 297, Concepción, Chile
- ^e Universidade da Madeira, Campus da Penteada, 9020-105 Funchal, Madeira, Portugal
- f Centro Interdisciplinar de Investigação Marinha e Ambiental (CIIMAR/CIMAR), Rua dos Bragas, 4050-123 Porto, Portugal

ARTICLE INFO

Keywords: Limpets Size-structure Harvesting Management measures North-eastern Atlantic

ABSTRACT

Intertidal limpets are subject to harvesting pressure in regions, e.g. oceanic islands, where marine organisms are a more accessible source of protein. These molluscs are very sensitive to human exploitation which often results on a decrease of their densities and an over-representation of immature individuals, because of the loss of large-sized reproductive specimens. Two species of exploited limpets (*Patella aspera* and *Patella candei*) were assessed throughout 21 years, before (1996–2006) and after (2007–2017) the implementation of conservation measures for their sustainable management in Madeira (North-eastern Atlantic Ocean). Different levels of anthropogenic pressure were also taken in account in this comparative study: (i) proximity to coastal settlements ("Near" vs. "Far") and (ii) accessibility to the coast (North vs. South), that may be considered surrogates of harvesting pressure on the intertidal of Madeira. The present results showed that the stocks of *P. aspera* and *P. candei* are slightly recovered after regulatory measures entered into force, with an increase of mean shell length and dominance of reproductive individuals (> 40 mm). *P. aspera* populations showed a clearer effect mainly due to the higher exploitation rate relative to *P. candei*. Conservation measures prompted a positive effect on both exploited limpet species, but further assessment studies are necessary to address the evolution of stocks over time.

1. Introduction

Limpets play a key role in regulating the ecological balance of littoral ecosystems and are of significant economic importance, being used worldwide as food since prehistoric times (Bowman and Lewis, 1986; Stearns, 1992; Gutíerrez-Zugasti, 2011). These intertidal grazers are extremely vulnerable because of their particular life-traits, restricted habitat and its accessibility to human activity (Nakin and McQuaid, 2014).

Patellid limpets are exposed to anthropogenic impacts on the littoral ecosystems such as, harvest (Martins et al., 2008; Riera et al., 2016) and habitat modification (Cole et al., 2012). The expansion of coastal

settlements resulting in the increase of human population density along the coast, has prompted a consistent decrease of limpet populations throughout the last decades worldwide (Kido and Murray, 2003; Martins et al., 2008). In several cases, this phenomenon has led to the reduction in abundance and/or shifts in size composition of their populations that result from the size-selective nature of limpet harvest, with larger specimens, with higher commercial value, being subject to higher harvesting pressure. Size reduction and abundance decreases in exploited populations of limpets have been reported for several species such as, *Patella candei crenata* (Ramírez et al., 2009) and *P. candei* d'Orbigny, 1840 (Núñez et al., 2003) in the Canaries, *P. candei* and *P. aspera* Röding, 1798 in the Azores (Martins et al., 2008), *Helcion*

E-mail address: ricardo.sousa@oom.arditi.com (R. Sousa).

^{*} Correspondence author at: Observatório Oceânico da Madeira, Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação (OOM/ARDITI) – Edifício Madeira Tecnopolo, 9020-105 Funchal, Madeira, Portugal.

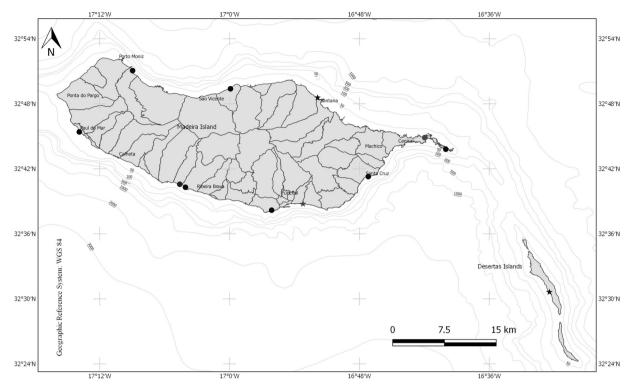


Fig. 1. Representation of sampling locations of Patella aspera and Patella candei in the Madeira archipelago (• exploited zones, ★ natural reserves).

concolor (Krauss, 1848) (Branch, 1985), and Patella ferruginea Gmelin, 1791 in Algeria (Espinosa, 2009) and Spain (Espinosa et al., 2009), as well as for the species Cymbula oculus (Born, 1778) in Southern Africa (Branch and Odendaal, 2003).

The loss of large individuals produces cascading effects on the biology of limpets in exploited populations, including changes in lifehistory parameters, demographics, reproductive success, genetics, as well as changes in ecological interactions and limpet behaviour (Fenberg and Roy, 2008; Espinosa et al., 2009; López et al., 2012; Henriques et al., 2017). In the most extreme cases, harvesting pressure is recognized to have led to the high fragmentation of limpet assemblages as occurred for P. candei crenata and P. aspera in the Canaries (Riera et al., 2016) and even to the disappearance of populations of P. ferruginea, an endemic and endangered species from the Mediterranean Sea (Espinosa, 2009), and of the endemic species Cellana sandwicensis (Pease, 1861), Cellana exarata (Reeve, 1854) and Cellana talcosa (Gould, 1846) in Hawaii (Valledor, 2000). Local extinction events are particularly worrying in oceanic islands due to the low connectivity existing between insular limpet populations (Bird et al., 2007; Goldstien et al., 2009).

In Madeira, the harvesting targeted limpets are P. aspera and P. candei representing one of the most profitable commercial activities on small-scale fisheries, reaching annual catches of up 150 t in 2015 yielding a total first sale value of ca 0.7 M€ (Henriques, 2010; Sousa et al., 2017). Therefore, harvesting pressure is one of the greatest concerns for limpet conservation in Madeira since their high economic value, reaching in average ca. 4 € per Kg in 2017, together with their biological characteristics could lead to the decline of populations and conduct to the overexploitation of the stocks. To prevent this situation, regulators established several management measures enforcing the maximum allowable commercial catch of 15 kg/person/day or 200 kg/ boat/day, a minimum catch size of 40 mm and the obligation of harvesting licenses (Regional Legislative Decree N.° 11/2006/M, 18 April 2006). A closed season was also implemented between December and March to avoid limpet harvest during the reproductive season (Henriques et al., 2017). Several studies have shown that limpet populations respond positively to implemented management measures, as long as the enforcement of those measures is adequately accomplished by the responsible authorities and more particularly when there is an active participation of the local communities (Fenberg et al., 2012; Coppa et al., 2016; Henriques et al., 2017).

Herein the effects of anthropogenic pressure on the size structure and abundance of populations of *P. aspera* (white-footed limpet) and *P. candei* (black-footed limpet) in Madeira (North-eastern Atlantic Ocean) are analysed. We hypothesized that the proximity to human settlements will result in a decrease in mean limpet size and lower abundance in "near" stations (< 1 km from human settlements) compared to "far" stations (> 3 km from human settlements). Additionally, we hypothesized that accessibility to limpet populations also affects negatively the size structure and abundance of the more accessible populations (South coast) compared to least accessible populations (North coast). Moreover, a comparative study was carried out considering two timeseries, "before" (1996–2006) and "after" (2007–2017) the implementation of management measures in order to verify their effectiveness along the Madeira coast.

2. Materials and methods

Fresh samples of *P. candei* and *P. aspera* were collected in the rocky shores of Madeira, NE Atlantic, in the framework of the European Fisheries Research Projects 'Programa Nacional de Recolha de Dados da Pesca' and MARISCOMAC- MAC/2.3d/097.

A total of 9 coastal settlements throughout the South (6) (Calheta, Ponta do Sol, Ribeira Brava, Funchal, Santa Cruz and Machico), and North coasts (3) (Porto Moniz, São Vicente and Ponta de São Lourenço) of Madeira were sampled all year round between 1996 and 2017. Three natural reserves, where limpet commercial harvest is not allowed, were also sampled as control areas (Garajau, Rocha do Navio and Desertas) (Fig. 1). At each locality, a minimum of 2 sites were selected according to the classification of Riera et al. (2016) as "near", < 1 km from the nearest human settlement, and "far", > 3 km from the nearest human settlement. Accessibility to the coast was grouped into "North", the

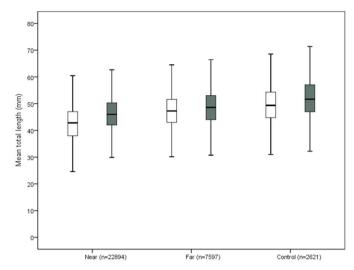


Fig. 2. Mean total length according to proximity to human settlements for white and black footed limpets. White bars represent *Patella aspera* and dark grey bars represent *Patella candei*. Box-plot showing median (black line) and upper and lower quartiles of the data.

least accessible due to rough seas, and "South", as more accessible due to milder conditions. Sampling was randomly performed at the subtidal by snorkelers in several dives over a period of 30 min without selecting for size or species. All individuals were measured (total shell length, TL, mm) using a Vernier caliper (0.1 mm) and weighted (total weight, TW, g) on an electronic scale with 0.01 g accuracy.

Data were tested for normality of distribution of samples and for the homogeneity of variance using the Kolmogorov-Smirnov test (two samples) and the Levene's statistics respectively. All analysis of variance were performed considering the Brown-Forsythe F test, when the variance of the data was not homogeneous. Proximity to human settlements and accessibility were considered with the data to determine the influence of harvesting on limpet populations.

A univariate comparison of the size of *P. aspera* and *P. candei* was performed using an analysis of variance (ANOVA) to verify the effect of each categorical variable (proximity and accessibility) on the shell length, and a two-way analysis of variance (ANOVA) was performed to examine the influence of the interaction of the two categorical independent variables (proximity and accessibility) on the continuous dependent variable (shell length).

A comparative study was conducted considering two time-series, before (1996–2006) and after (2007–2017) the implementation of the management measures. Specimens were separated in non-reproductive and reproductive considering the size at first maturity of both species, 36.70 mm for *P. candei* (Henriques et al., 2012) and 38.29 mm for *P. aspera* (Sousa et al., 2017). The comparison of limpet size from both time series was carried out using an analysis of variance (ANOVA). The size structure of the exploited populations was analysed for both periods (before and after management measures implementation) by the non-parametric Mann-Whitney test (two samples) in order to determine any differences observed in limpet's size between the two time-series when the data was not normally distributed.

All statistical analyses were performed using SPSS v.20.0 (IBM Corp., Armonk, NY). For all tests, statistical significance was accepted when p < 0.05.

3. Results

3.1. Effect of proximity and accessibility

A total of 33,112 limpets from 9 selected locations and 3 control locations of the rocky shores of Madeira were analysed. The mean shell

length of the 16,345 sampled specimens of *P. aspera* was 44.63 \pm 7.27 mm while for the 16,767 specimens of *P. candei* shell length showed a mean of 47.03 \pm 6.78 mm. The size-frequency showed that the sampled data had a normal distribution for *P. aspera* (Z = 3.095, p < 0.001) and *P. candei* (Z = 3.788, p < 0.001). However, size did not exhibit homogeneous variance in neither *P. aspera* (W = 12.196, p < 0.001) nor *P. candei* (W = 17.492, p < 0.001).

The size distribution of both species showed that larger sizes (> 40 mm length) were dominant with 75% of *P. aspera* and 86% of *P. candei* specimens. In both cases the observed size range indicates that most specimens are reproductive individuals, having reached the size at first maturity. *P. aspera* and *P. candei* assemblages were dominated by individuals ranging from 40 to 50 mm (50.53 and 53.33% of the overall abundance, respectively). However, the modal class for *P. aspera* (40–45 mm) was slightly smaller than for *P. candei* (45–50 mm).

For *P. aspera*, 10,490 specimens were caught from near sites, 3,944 from far sites and 1,911 from the control sites. Differences in mean shell length were found between the three sites, with smaller individuals in near sites (42.69 \pm 6.56 mm) than in far sites (47.26 \pm 6.99 mm). Control zones, where no commercial harvest is allowed showed the highest mean shell length (49.82 \pm 7.31 mm). The same pattern was observed for the 12,404, 3,653 and 710 sampled specimens of *P. candei* from near (46.27 \pm 6.47 mm), far (48.68 \pm 6.98 mm) and control (51.99 \pm 7.30 mm) sites, respectively. The observed differences in mean shell length between sites were significant for both *P. aspera* (F = 1,185.716, p < 0.05) and *P. candei* (F = 345.701, p < 0.05) (Fig. 2).

The effect of accessibility was observed for *P. aspera* with larger individuals on the north coast (44.09 \pm 6.53 mm) than those from the southern coast (43.07 \pm 7.55 mm). However, this trend was not observed for *P. candei* that exhibited a smaller mean shell length in the north coast (46.69 \pm 6.39 mm) than in the south coast (46.94 \pm 7.23 mm). Differences in mean shell length between the north and south coasts were significant for *P. aspera* (F = 58.807, p < 0.05) but not for *P. candei* (F = 3.763, p > 0.05) (Fig. 3).

The effect of the interaction of proximity and accessibility was observed for both species with larger specimens occurring on far sites on the north coast. Differences in mean shell length between the north and south coast, considering proximity to human settlements were statistically significant for P. aspera ($F=10.790,\ p<0.05$) and P. candei ($F=11.814,\ p<0.05$). This analysis highlights differences in mean shell length for P. candei between the north and south coast which aren't

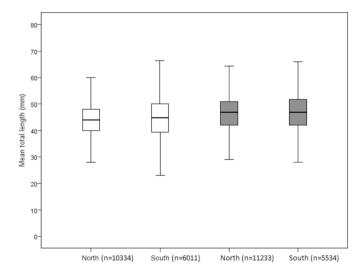


Fig. 3. Mean total length according to accessibility of white and black footed limpets populations. White bars represent *Patella aspera* and dark grey bars represent *Patella candei*. Box-plot showing median (black line) and upper and lower quartiles of the data.

evident when considering only the accessibility.

3.2. Effects of management measures on the stock of P. aspera and P. candei

The assemblages of *P. aspera* and *P. candei*, before the implementation of management measures (1999–2006), were characterized by a wide range of sizes, from 11.00 to 68.00 mm and 16.00 to 76.00 mm respectively. In the period following the regulation of limpet harvesting (2007–2017) an increase in size range was observed for *P. aspera*, ranging from 3.10 to 82.86 mm. For *P. candei* this effect was less pronounced with sizes ranging from 25.46 to 78.31 mm. The mean size of *P. aspera* increased from 43.53 \pm 6.23 mm before regulation to 45.38 \pm 7.82 mm after, these differences between time-series were statistically significant (F = 281.295, p < 0.05). An increase in size was also observed for *P. candei* from a mean shell length of 46.26 \pm 6.34 mm before regulation to 47.89 \pm 7.14 mm after, this difference in mean size was also significant (F = 240.469, p < 0.05).

The proportion of size classes was slightly right-skewed after implementation of management measures for P. aspera, with the highest percentages in classes 40 to 45 mm before and 45 to 50 mm after. Limpets smaller than 10 mm and larger than 70 mm were only observed following regulation. Specimens of P. aspera with mean shell length between 25 and 35 mm and from 50 to 85 mm were predominant after regulation (Fig. 4). However, the observed differences in size classes between the two time-series were not significant (U = 121.000, p > 0.05). The proportion of reproductive individuals (> 38.29 mm) remained unaltered for P. aspera before and after implementation of management measures.

For *P. candei*, the proportion of size classes remained mostly similar before and after implementation of management measures, the size class with the highest percentages was the same for both time-series (45–50 mm). Specimens of *P. candei* with mean shell length between 50 and 85 mm were slightly more abundant after regulation (Fig. 5). Differences in size classes between the two time-series were not significant (U = 141.000, p > 0.05). As occurred for *P. aspera* no changes in the proportion of reproductive individuals for *P. candei* (> 36.70 mm) were observed.

4. Discussion

Anthropogenic activities affect negatively populations of marine gastropods of commercial interest, such as limpets, namely by altering

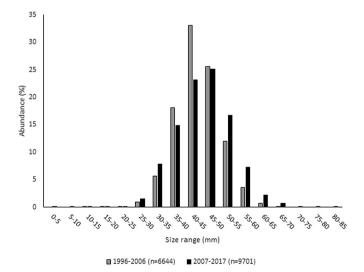


Fig. 4. Variation of size ranges of *Patella aspera* before (1996–2006) and after (2007–2017) the implementation of management measures in Madeira archipelago.

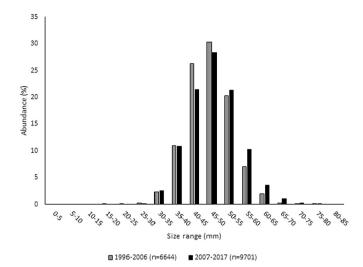


Fig. 5. Variation of size ranges of *Patella candei* before (1996–2006) and after (2007–2017) the implementation of management measures in Madeira archipelago.

population structure of the affected species, resulting in decreased abundance, and altered size structure (Tuya et al., 2006). Management measures are thought to preserve age structure, maintain sex-ratios, prevent sperm limitation, enhance yield, and restrict evolutionary changes in response to fishing or harvesting, such as shifts to early maturation (Alonzo and Mangel, 2004; Baskett et al., 2005; Heppell et al., 2006; Hamilton et al., 2007). Limpet harvesting is a traditional activity in Madeira archipelago, dating back to the early years of colonization (Silva and Menezes, 1921). Since 2006, this activity has been regulated, following the guidelines obtained from the first stock assessment performed on the stocks of both species (Delgado et al., 2005). The implementation of management measures is of utmost importance considering the harvesting pressure resulting from the importance of limpets in the local gastronomy, both for locals and tourists' consumption.

The overall results of this study indicate that the size composition of the populations of P. aspera and P. candei in Madeira, are going through a slight recovering phase as a result of the implementation and enforcement of management measures on limpet harvesting. The populations are currently characterized by the increase in mean shell length and by the dominance of individuals with larger sizes in both species. Most of the specimens are adults (> 40 mm) with high reproductive potential and as such, main contributors to the fitness of the exploited populations. This pattern is more evident in P. aspera where the consolidation on the recruitment is also evident by the current increase of specimens in the smaller size classes when comparing the "before" (1999-2006) and "after" (2007-2017) time-series. The small differentiation observed in the recovery of the exploited populations is more evident in P. aspera due to the fact that this species is thought to be more heavily exploited than P. candei and as such the effect of the management measures is more noticeable for this species.

Consistent differences were found in limpet size structure when considering the effect of proximity to human settlements, with larger individuals being more abundant in distant sites. This trend was observed for both limpets (*P. aspera* and *P. candei*) with smaller individuals being more common in sites closer to human settlements than in more distant sites. When considering the control sites, where no harvesting has been allowed for over 20 years it is evident that these populations are in balance by the highest mean shell length and abundances obtained at the three considered sites.

The observed recovery pattern in the exploited populations of both limpets agreed with Martins (2009) that observed the same correlation between limpets' abundances and the proximity to coastal settlements

in Azores (NE Atlantic). Also, when considering the control sites, these results are concurrent with López et al. (2012) that observed that sites where harvesting is not allowed, e.g. marine protected areas (MPAs), assemblages had larger individuals and higher abundances, and also an increase of their populations was observed. In general, the implementation of MPAs results in direct improvements for the protected populations in terms of size structure, abundance, and population density and indirect effects regarding reproductive output of these broadcast spawners (Carr, 2000; Claudet et al., 2011). Therefore, these areas should be used as complementary tools for the recovery of depleted ecosystems as well as for the management and protection of the exploited resources (Jenkins and Hartnoll, 2001).

The accessibility to P. aspera populations was shown to also affect negatively the size structure and abundance of these populations on the south coast which are more accessible than the populations in the north coast. Nevertheless, this pattern was not observed for P. candei since there were no significant differences in the size structure and abundance when considering the factor accessibility. The differences in how accessibility affects these two species are likely related to the greater harvesting pressure that P. aspera is subject to, or to specific characteristics of this species that confer greater vulnerability and/or a more pronounced effect to its size structure, such as the fact that this species is a protandrous hermaphrodite (Martins et al., 2017). In fact, the size selective nature of harvest would more than likely contribute to a decrease in the percentage of females (more common in larger size classes), hindering the reproductive success of this species making it more vulnerable to harvesting. Therefore, the implementation of the minimum size of catch (40 mm) was pivotal to ensure a sufficient percentage of the population reaches sexual maturity, thus increasing the reproductive output of these populations. Despite the effect of accessibility being less pronounced in P. candei, when considering the interaction of accessibility and proximity the differences in mean shell length of *P. candei* were also significant, even though less marked than in P. aspera. This might imply that the effect of accessibility on P. candei is related also to the proximity to human settlements with smaller sizes occurring in near sites in the south coast (more accessible) where harvesting pressure, habitat loss and pollution are higher.

The effects of regulation on the recovery of the exploited populations of limpets in Madeira were characterized by an increase in the range of sizes and in the mean shell length. This pattern was more pronounced in P. aspera, with individuals smaller than 10 mm and larger than 70 mm were only observed following the introduction of harvest regulation. Concerning P. candei, this effect was mainly observed by the increase in the percentages of larger specimens (> 50 mm) after the regulation. The implementation of harvesting regulation for P. aspera in Madeira seems to have been effective in not only allowing individuals to reach larger sizes, but also to guarantee that these specimens reproduce and contribute to recruitment of new individuals into the exploited populations, thus increasing the proportion of smaller individuals. For P. candei, these measures have allowed the exploited populations to recover mainly in terms of the abundance of larger specimens, but no effect is expected to have occurred in terms of its reproductive success since the proportion of reproductively active specimens is similar before and after the implementation of the management measures. Even though the implementation of harvesting regulations has resulted in a slight recovery of the exploited populations, a greater effect was expected to be evident after 11 years since its introduction. This could be explained by poaching which is known to occur during the closed season, without abiding the minimum catch size and the maximum allowable catch weight. This could be mitigated by raising awareness of the fishery and restauration communities to the need of conservation of these species and by actively involving them in the conservation effort, namely by not commercialising limpets during the closed season. Also, the increase of population density along the coast, the technological advances introduced in methods of processing and storage of limpets as well as a booming tourism activity is likely to add pressure to the exploited populations.

Martins et al. (2011) showed the legislation and current levels of enforcement were insufficient to protect the exploited limpet populations in Azores. Thus, they proposed that greater levels of enforcement should be considered, through the establishment of physical barriers and other protective strategies. Co-management has been observed to have positive results for conservation of exploited stocks (Costello et al., 2008), taking into consideration the need to enhance ownership of conservation areas and to involve all interested parties in the development of management schemes (Baxter, 2001; Thompson et al., 2002). Riera et al. (2016) showed that limpet harvesting has led to a sharp decrease in the mean size of both P. aspera (7 mm) and P. candei crenata (5 mm) in Tenerife (Canary Is.), together with a low representation of reproductive individuals (> 35 mm). Even though limpet harvesting is controlled by regulations, the obtained results highlighted the low viability of limpet populations at medium and longterm in Tenerife as a consequence of ineffective surveillance due to a lack of means, coupled with a high human population density in coastal areas (Riera et al., 2016).

The scenario in Madeira seems to be more favourable, with the implemented measures having contributed to a slow but steady recovery of the exploited limpet populations. However, continuous monitoring of both species is required to address the evolution of the stocks over time, and to ensure the sustainable exploitation of these coastal resources. In the future, monitoring surveys should be accomplished using non-destructive methods in order to minimize the pressure exerted on these species. For that end, survey samplings should be performed in field, and after measuring, weighing and sexing, specimens should be returned to their habitat. The most adequate method for sexing specimens without killing them would be taking a biopsy of the gonad with a hypodermic needle (Baxter, 1982; Wright and Lindberg, 1979; Le Ouesne and Hawkins, 2006).

One major difficulty in the management of these species in Madeira is to accurately quantify the landings of each species since they are landed together, as such it would be fruitful to implement obligatory species-specific landings, to allow for a more accurate monitoring of the exploited stocks. Other anthropogenic pressures have also to be considered, proximity to and accessibility of limpet populations not only increases their vulnerability to harvest but also to habitat loss and pollution among other factors that negatively impact these still fragile populations. The overall improvement of the exploited populations will have greater benefits in the medium- and long- term if management measures are fully fulfilled and involve the local community, thus assuring the sustainability of these species. Additionally, genetic studies should complement the continuous monitoring of these species, particularly in defining whether these limpets represent a metapopulation or segregated populations, allowing to adapt the management measures to the particularities of the exploited populations.

Acknowledgements

The authors are grateful to the Fisheries Research Service (DSI) from the Regional Directorate of Fisheries of the Autonomous Region of Madeira. We also acknowledge to Dr.^a Antonieta Amorim for providing the Map with the stations, used in this research and also grateful to the technicians of DSI (Filipe Andrade, Jorge Lucas, José Aires Brites, José Luís Figueira and Nélia Nóbrega) for their help during this work, namely in biological sampling and harvesting surveys and to Dr.^a 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 natural reserve areas. The first author (RS) was supported by a grant from ARDITI OOM/2016/010 (M1420-01-0145-FEDER-000001-Observatório Oceânico da Madeira-OOM). This study had also the support of FCT, through the strategic project UID/MAR/04292/2013 granted to MARE, the UE FEDER in the framework of the Project MARISCOMAC- MAC/

2.3d/097 and the Regional Government of Madeira.

Declaration of interest

None.

Authors' contributions

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

Funding source

The first author (RS) was supported by a grant from ARDITI-OOM/2016/010 (M1420-01-0145-FEDER-000001-Observatório Oceânico da Madeira-OOM).

References

- Alonzo, S.H., Mangel, M., 2004. The effects of size selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. Fish. Bull. 102, 1–13.
- Baskett, M.L., Levin, S.A., Gaines, S.D., Dushoff, J., 2005. Marine reserve design and the evolution of size at maturation in harvested fish. Ecol. Appl. 15, 882–901. https:// doi.org/10.1890/04-0723.
- Baxter, J.M., 1982. Population dynamics of *Patella vulgata* in Orkney. Neth. J. Sea Res. 16, 96–104. https://doi.org/10.1016/0077-7579(82)90021-7.
- Baxter, J.M., 2001. Establishing management schemes on marine special areas of conservation in Scotland. Aquat. Conserv. Mar. Freshwat. Ecosyst. 11, 261–265. https://doi.org/10.1002/agc.465.
- Bird, C.E., Holland, C., Bowen, B.W., Toonen, R.J., 2007. Contrasting phylogeography in three endemic Hawaiian limpets (*Cellana* spp.) with similar life histories. Mol. Ecol. 16, 3173–3186.
- Bowman, R.S., Lewis, J.R., 1986. Geographical variation in the breeding cycles and recruitment of *Patella* spp. Hydrobiologia 142, 41–56. https://doi.org/10.1007/BF00026746.
- Branch, G.M., 1985. Limpets: their role in littoral and sublittoral community dynamics.
 In: Moore, P.G., Seed, R. (Eds.), The Ecology of Rocky Coasts. Hodder & Stoughton,
 London, pp. 97–116.
- Branch, G.M., Odendaal, F., 2003. The effects of marine protected areas on the population dynamics of a south African limpet, Cymbula oculus, relative to the influence of wave action. Biol. Conserv. 114, 255–269. https://doi.org/10.1016/S0006-3207(03) 00045-4.
- Carr, M.H., 2000. Marine protected areas: challenges and opportunities for understanding and conserving coastal marine ecosystems. Environ. Conserv. 27, 106–109.
- Claudet, J., Guidetti, P., Mouillot, D., Shears, N.T., Micheli, F., 2011. Ecological effects of marine protected areas: conservation, restoration and functioning. In: Claudet, J. (Ed.), Marine Protected Areas: Effects, Networks and Monitoring – A Multidisciplinary Approach. Cambridge University Press, Cambridge. https://doi. org/10.1017/CB09781139049382.005.
- Cole, V.J., Johnson, L.G., McQuaid, C.D., 2012. Effects of patch-size on populations of intertidal limpets, Siphonaria spp., in a linear Landscape. PLoS ONE 7 (12), e52076. https://doi.org/10.1371/journal.pone.0052076.
- Coppa, S., De Lucia, G.A., Massaro, G., Camedda, A., Marra, S., Magni, P., Perilli, A., Di Bitetto, M., García-Gómez, J.C., Espinosa, F., 2016. Is the establishment of MPAs enough to preserve endangered intertidal species? The case of *Patella ferruginea* in the Mal di Ventre Island (W Sardinia, Italy). Aquat. Conserv. Mar. Freshwat. Ecosyst. 4, 623–638. https://doi.org/10.1002/aqc.2579.
- Costello, C., Gaines, S.D., Lynham, J., 2008. Can catch shares prevent fisheries collapse? Science 321, 1678–1681. https://doi.org/10.1126/science.1159478.
- Delgado, J., Alves, A., Góis, A.R., Faria, G., Henriques, P., Correia, J., Brites, J., 2005. Exploração Comercial de Lapas na Madeira: Estudo Biológico e Contributo Para a Gestão do Recurso. (Relatórios DBPO 01/2005). Direção Regional de Pescas, Funchal.
- Espinosa, F., 2009. Populational status of the endangered mollusc *Patella ferruginea* Gmelin, 1791 (Gastropoda, Patellidae) on Algerian islands (SW Mediterranean). Anim. Biodiv. Conserv. 32 (1), 19–28.
- Espinosa, F., Rivera-Ingraham, G., García-Gómez, J.C., 2009. Gonochorism or protandrous hermaphroditism? Evidence of sex change in the endangered limpet *Patella ferruginea*. J. Mar. Biol. Assoc. Biodiv. Rec. 2 (e153), 1–3. https://doi.org/10.1017/S1755267209990790.
- Fenberg, P.B., Roy, B., 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Mol. Ecol. 17, 209–220. https://doi.org/10. 1111/j.1365-294X.2007.03522.x.
- Fenberg, P.B., Caselle, J.E., Claudet, J., Clemence, M., Gaines, S.D., García-Charton, J.A.,

- Gonçalves, E.J., Grorud-Colvert, K., Guidetti, P., Jenkins, S.R., Jones, P.J.S., Lester, S.E., McAllen, R., Moland, E., Planes, S., Sørensen, T.K., 2012. The science of European marine reserves: status, efficacy, and future needs. Mar. Policy 36, 1012–1021. https://doi.org/10.1016/j.marpol.2012.02.021.

 Goldstien, S.J., Gemmell, N.J., Schiel, D.R., 2009. Colonisation and connectivity by in-
- Goldstien, S.J., Gemmell, N.J., Schiel, D.R., 2009. Colonisation and connectivity by intertidal limpets among New Zealand, Chatham and Sub-Antarctic Islands. I. Genetic connections. Mar. Ecol. Prog. Ser. 388, 111–119.
- Gutíerrez-Zugasti, I., 2011. Coastal resource intensification across the Pleistocene-Holocene transition in Northern Spain: evidence from shell size and age distributions of marine gastropods. Quat. Int. 244, 54–66.
- Hamilton, S.L., Caselle, J.E., Standish, J.D., Schroeder, D.M., Love, M.S., Rosales-Casian, J.A., Sosa-Nishizaki, O., 2007. Size-selective harvesting alters life histories of a sexchanging fish. Ecol. Appl. 17, 2268–2280. https://doi.org/10.1890/06-1930.1.
- Henriques, P., 2010. Contribuição para o conhecimento da biologia, status taxonómico e estado de conservação de Patella candei ordinaria Mabille, 1888 e Patella aspera Röding, 1798 no arquipélago da Madeira (M.Sc. Thesis). University of Madeira, Funchal.
- Henriques, P., Sousa, R., Pinto, A.R., Delgado, J., Faria, G., Alves, A., Khadem, M., 2012. Life history traits of the exploited limpet *Patella candei* (Mollusca: Patellogastropoda) of the northeastern Atlantic. J. Mar. Biol. Assoc. UK 92 (1), 1–9. https://doi.org/10.1017/S0025315411001068.
- Henriques, P., Delgado, J., Sousa, R., 2017. Patellid limpets: An overview of the biology and conservation of keystone species of the rocky shores. In: Ray, S. (Ed.), Organismal and Molecular Malacology. Intech, Croatia, pp. 71–95. https://doi.org/10.5772/ 67862.
- Heppell, S.S., Heppell, S.A., Coleman, F.C., Koenig, C.C., 2006. Models to compare management options for a protogynous fish. Ecol. Appl. 16, 238–249. https://doi. org/10.1890/04-1113.
- Jenkins, S.R., Hartnoll, R.G., 2001. Food supply, grazing activity and growth rate in the limpet *Patella vulgata*: a comparison between exposed and sheltered shores. J. Exp. Mar. Biol. Ecol. 258, 123–139.
- Kido, J.S., Murray, S.N., 2003. Variation in owl limpet Lottia gigantea population structures, growth rates and gonadal production on southern California rocky shores. Mar. Ecol. Prog. Ser. 257, 111–124. https://doi.org/10.3354/meps257111.
- Le Quesne, W.J.F., Hawkins, S.J., 2006. Direct observations of protandrous sex change in the patellid limpet *Patella vulgata*. J. Mar. Biol. Assoc. UK 86, 161–162. https://doi. org/10.1017/S0025315406012975.
- López, C., Poladura, A., Hernández, J.C., Martín, L., Concepcion, L., Sangil, C., Clemente, S., 2012. Contrasting effects of protection from harvesting in populations of two limpet species in a recently established marine protected area. Sci. Mar. 76, 799–807.
- Martins, G.M., 2009. Community Structure and Dynamics of the Azorean Rocky Intertidal: Exploitation of Keystone Species. Ph.D. Thesis. University of Plymouth,
- Martins, G.M., Thompson, R.C., Hawkins, S.J., Neto, A.I., Jenkins, S.R., 2008. Rocky intertidal community structure in oceanic islands: scales of spatial variability. Mar. Ecol. Prog. Ser. 356, 15–24. https://doi.org/10.3354/meps07247.
- Martins, G.M., Jenkins, S.R., Hawkins, S.J., Neto, A.I., Medeiros, A.R., Thompson, R.C., 2011. Illegal harvesting affects the success of fishing closure areas. J. Mar. Biol. Assoc. UK 91 (4), 929–937. https://doi.org/10.1017/S0025315410001189.
- Martins, G.M., Borges, C.D.G., Vale, M., Ribeiro, P.A., Ferraz, R.R., Martins, H.R., Santos, R.S., Hawkins, S.J., 2017. Exploitation promotes earlier sex changes in a protandrous patellid limpet, *Patella aspera* Röding, 1798. Ecol. Evol. 7, 3616–3622. 10.1002-ecs3.
- Nakin, M.D.V., McQuaid, C.D., 2014. Marine reserve effects on population density and size structure of commonly and rarely exploited limpets in South Africa. Afr. J. Mar. Sci. (3), 1–9. https://doi.org/10.2989/1814232X.2014.946091.
- Núñez, J., Brito, M.C., Riera, R., Docoito, J.R., Monterroso, Ó., 2003. Distribución actual de las poblaciones de *Patella candei* D'Orbigny, 1840 (Mollusca, Gastropoda) en las islas Canarias. Una especie en peligro de extinción. Bol. Inst. Esp. Oceanogr. 19 (1–4), 371–377.
- Ramírez, R., Tuya, F., Haroun, R., 2009. Efectos potenciales del marisqueo sobre moluscos gasterópodos de interés comercial (Osilinus spp. y Patella spp.) en el Archipiélago Canario. Rev. Biol. Mar. Oceanogr. 44 (3), 703–714. https://doi.org/10.4067/S0718-19572009000300016.
- Riera, R., Pérez, O., Álvarez, O., Simón, D., Díaz, D., Monterroso, O., Núñez, J., 2016. Clear regression of harvested intertidal mollusks. A 20-year (1994-2014) comparative study. Mar. Environ. Res. 113, 56–61. https://doi.org/10.1016/j.marenvres.2015.11. 003
- Silva, F.A., Menezes, C.A., 1921. Elucidário Madeirense I Volume A-E. Tipografia Esperanca, Funchal.
- Sousa, R., Delgado, J., Pinto, A.R., Henriques, P., 2017. Growth and reproduction of the North-Eastern Atlantic keystone species *Patella aspera* (Mollusca: Patellogastropoda). Helgol. Mar. Res. 71 (8), 1–13. https://doi.org/10.1186/s10152-017-0488-9.
- Stearns, S.C., 1992. The Evolution of Life Histories, 1st ed. Oxford University Press, Oxford.
- Thompson, R.C., Crowe, T.P., Hawkins, S.J., 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. Environ. Conserv. 29, 168–191. https://doi.org/10.1017/S0376892902000115.
- Tuya, F., Ramírez, R., Sánchez-Jerez, P., Haroun, R.J., González-Ramos, A.J., Coca, J., 2006. Coastal resources exploitation can mask bottom-up mesoscale regulation of intertidal populations. Hydrobiologia 553, 337–344. https://doi.org/10.1007/ s10750-005-1246-6.
- Valledor, A., 2000. La especie suicida. El peligroso rumbo de la humanidad. Díaz de Santos, Madrid.
- Wright, W.G., Lindberg, D.R., 1979. A non-fatal method of sex determination for patellacean gastropods. J. Mar. Biol. Assoc. UK 59, 803. https://doi.org/10.1017/S0025315400045793.