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Potential impact of harvesting management measures on the reproductive parameters of the limpets *Patella aspera* and *Patella candei* from Madeira Island

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ABSTRACT

Intertidal and shallow subtidal molluscs are highly sensitive to overharvesting because of their restricted habitat, limited mobility and easy access to humans. Several parameters have been previously used to determine their exploitation status, e.g. sizes, abundances and reproductive stages. Herein the reproductive parameters of two exploited limpets, *Patella candei* and the protandrous hermaphrodite *Patella aspera* were examined. Limpets were collected "before" (1996–2006) and "after" (2007–2017) the implementation of management measures aiming to preserve limpet populations in Madeira Island (NE Atlantic Ocean). The proportion of reproductive individuals increased approximately 14% after the implementation of management measures for both species. An increase in the size and age at first maturity of both species (from 34.6 to 37.5 mm in *P. aspera* and from 33.4 to 37.4 mm in *P. candei*) also occurred after such implementation. "Before" samples of *P. aspera* showed male-biased populations (1.7:1) shifting towards a balanced sex ratio (1:1) after the regulations. No "before" nor "after" sex ratio variations were observed in *P. candei* populations. Reproductive parameters revealed feasible to determine the efficiency of the implementation of management measures and to detect a slight improvement in reproductive potential of both limpet species.

1. Introduction

Limpets are pivotal for structuring and regulating the ecological balance of intertidal communities, directly through the key process of grazing that determines macroalgal abundance, and indirectly by enhancing or inhibiting the establishment of other organisms (Jenkins et al., 2005; Coleman et al., 2006).

Limpets are common grazing marine gastropods on rocky shores and are highly vulnerable because of their restricted habitat and easy access to humans (Nakin and McQuaid, 2014). These molluscs have been used as a food resource worldwide and exploited by human since the Palaeolithic (Turrero et al., 2014). The exploitation of limpets is known to induce decreased species richness and biomass and to promote shifts on the communities' structure in rocky shores (Durán and Castilla, 1989; Lasiak, 1998; Sagarin et al., 2007; Fenberg and Roy, 2008). Exploited limpet populations show a reduction in density and shifts in population structure toward smaller sizes which can lead to a lower reproductive output since individual fecundity is size-dependent (Branch, 1975; Levitan, 1991; Tegner et al., 1996). These effects are related to the size-selective nature of limpet harvesting, with the removal of older and larger individuals (more visible and with greater commercial value) resulting in changes in demographics, life-history parameters and reproductive success of the exploited populations (Griffiths and Branch, 1997; Lindberg et al., 1998; Kido and Murray,

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2003; Fenberg and Roy, 2008; Ramírez et al., 2009).

The impact of limpet harvesting has been observed for *Patella candei* d'Orbigny and *Patella aspera* Rödin, 1798 in Madeira Island (Sousa et al., 2019), for *P. candei* and *Patella candei crenata* in the Canaries Islands (Ramírez et al., 2009; Núñez et al., 2003), *P. candei* and *P. aspera* in the Azores Islands (Martins et al., 2008) and *Patella ferruginea* Gmelin, 1791 in Algeria and Spain (Espinosa, 2009; Espinosa et al., 2009). This situation has led to the implementation of management measures including the establishment of closed seasons, species-specific daily allowable catches, and minimum size of capture. These measures aim to preserve size/age structure, maintain yields within sustainable limits, prevent significant changes in sex ratios and sperm limitation, and avoid shifts to early maturation. Additionally, the establishment of closed areas where harvest is prohibited, such as Marine Protected Areas (MPAs) have proven to be an effective key tool in marine biodiversity conservation in coastal regions (Ballantine, 1991; Zann, 1995; Halpern and Warner, 2002; Edgar et al., 2014) due to its ecosystem-level approach for exploited species (Henriques et al., 2017). MPAs promote the recovery and protect exploited marine organisms within their boundaries while sustaining fisheries at the same time. This is accomplished by re-establishing natural conditions for reproduction (Halpern, 2003; Lubchenco et al., 2003), increasing density and size leading to greater production of larvae, and enhancing adjacent fisheries through the export and settlement of larvae outside the protected zones (Branch and Odendaal, 2003; Gell and Roberts, 2003; Pelc et al., 2009).

Harvesting regulation is of paramount importance because limpets are broadcast spawners that do not exhibit external sexual dimorphism, whose reproductive success is size- and density-dependent. Therefore, changes in population structure towards a greater frequency of smaller individuals may lead to a decline in gamete production resulting in decreased reproductive fitness, as reported by Kido and Murray (2003) for *Lottia gigantea* (Sowerby, 1834).

Also, several species of limpets, such as *Patella vulgata* Linnaeus, 1758, *P. ferruginea* and *P. aspera* are known protandrous hermaphrodites (Le Quesne and Hawkins, 2006; Rivera-Ingraham et al., 2011; Martins et al., 2017). In these species the size-selective harvesting is of particular concern, since after reaching sexual maturation a fraction of males changes to females, thus the removal of larger individuals will target primarily females (Martins et al., 2017). There are also evidences that harvesting leads to decreases in both shell size and size at sex change, suggesting a shift to earlier sex change in exploited populations (Fenberg and Roy, 2012). Even though sex change is thought to be determined genetically, occurring mainly after the first maturation period (Fretter et al., 1998), external cues are involved in the timing of sex change of many protandrous hermaphrodite gastropods (Guallart et al., 2013). Among those cues, greater abundance of large females delays or inhibits sex change in males (Hoagland, 1978), while conversely size-selective harvesting targets the larger females which may promote sex change in protandrous hermaphrodites. In fact, in highly exploited populations of protandrous hermaphrodite limpets, such as *P. aspera* and *P. vulgata*, sex change tends to occur at an earlier size/age (Martins et al., 2017; Borges et al., 2016).

Another effect of heavy exploitation of hermaphrodite species is the occurrence of disruptions in the population sex ratio, often skewing towards the sex that matures at smaller size/age. Therefore, the sex ratio of populations subject to size-selective exploitation will be biased, resulting in reproductive failure in harvested populations (Alonzo and Mangel, 2004; Hamilton et al., 2007).

In the Madeira archipelago, limpets are harvested since the early years of colonization, dating back to the early 15th century (Silva and Menezes, 1921). Currently, limpets are landed in a mixed exploitation of *P. aspera* and *P. candei*, representing approximately 1.5% of the total of the fisheries of the region and reaching an average value of 4 € per Kg (Sousa et al., 2019). In 2017, the commercial landings in weight reached annual catches of up to 111 tonnes yielding a first value of *ca.*

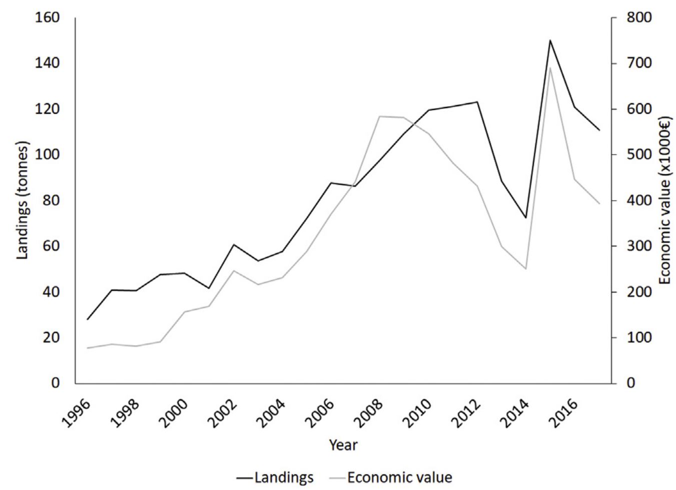

Fig. 1. Representation of landings (tonnes) and economic value (thousand euros) of limpets from 1996 to 2017 in the archipelago of Madeira.

0.4 M€ (Fig. 1). This long-term continuous exploitation is likely to have changed the reproductive dynamics of *P. aspera* and *P. candei* in the Madeira archipelago. In the present study, the status of exploited populations is represented by data gathered before the implementation of harvesting management measures in 2006. Subsequently, continuous monitoring of the exploited stocks provided data for a comparative study to analyse the effects of harvesting regulations on the species targeted by this locally important socioeconomic activity.

The present study assessed whether the implementation of those management measures improved the reproductive parameters in exploited populations of *P. aspera* and *P. candei*, namely in terms of: i) the proportion of reproductive individuals in the populations, which is hypothesised to increase in both species after the implementation of management measures; ii) the size at first maturity, which is expected to increase after the introduction of harvesting regulations and iii) the sex ratio of the populations, particularly in *P. aspera* (a protandrous hermaphrodite), since the establishment of the minimum catch size is expected to positively impact the proportion of females in the larger size classes.

2. Material and methods

2.1. Sampling surveys and data collection

From 1996 to 2017 specimens *of P. aspera* and *P. candei* were randomly collected from inter- and subtidal rocky shores in Madeira Island, north-eastern Atlantic (Fig. 2) by snorkelling during 30 min without selecting species or specimen size. A total of nine sampling areas throughout Madeira Island, six in the south coast (Calheta, Ponta do Sol, Ribeira Brava, Funchal, Santa Cruz and Machico) and three in the north coast (Porto Moniz, São Vicente and Ponta de São Lourenço) of Madeira were sampled all year round, including during the legally established closed season from December to March.

All specimens were measured (total shell length, L) using a Vernier caliper (0.1 mm) and weighed (total weight, W) on a digital balance (0.01 g). Individuals were sexed according to gonad pigmentation, pale white or pink in males and brown to red in females. The dissection of individuals and macroscopic examination of the gonads allowed assigning each specimen to a maturation stage, determined according to the progression of the gonadal volume in the haemocoel, based on an adaptation of Orton et al. (1956) as described by Sousa et al. (2017).

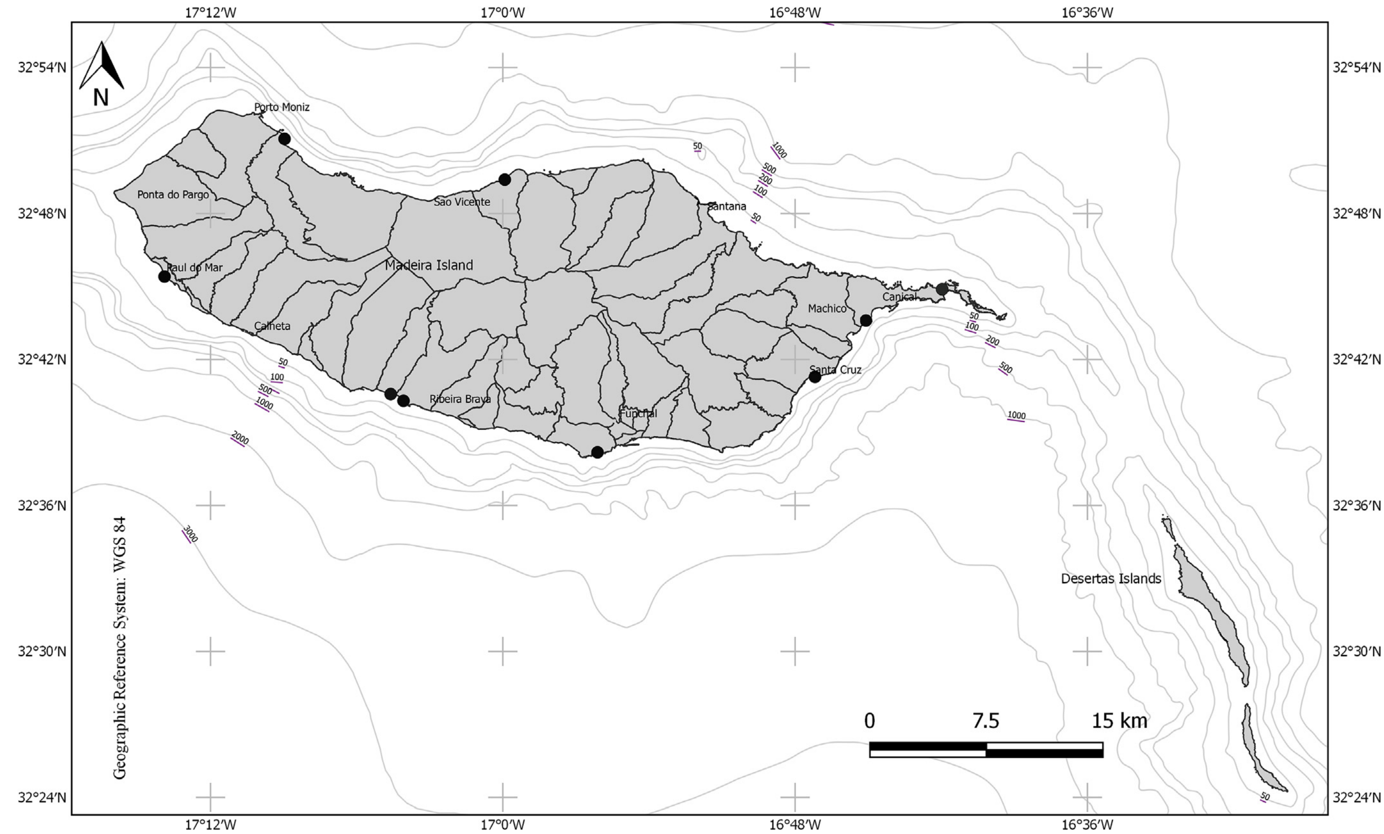

Fig. 2. Representation of sampling locations of *P. aspera* and *P. candei* in the Madeira Island.

2.2. Effect of harvesting regulations on the proportion of reproductive individuals

The proportion of reproductive individuals in the populations of *P. aspera* and *P. candei* was analysed before and after the implementation of harvesting management measures. For that purpose, specimens were classified as non-reproductive, reproductive, and resting based on the maturation scale and the estimated size at first maturity of both species.

2.3. Effect of management measures on the size at sexual maturity

The size at first sexual maturity of *P. aspera* and *P. candei* before and after the implementation of harvesting regulations were compared to determine the effectiveness of those management measures. For that purpose, the size at first maturity (Lm_{50}), was estimated from the relationship between the proportion of mature specimens and shell length, according to the balanced logistic equation: (Sparre and Venema, 1997)

$$P = {}^{1}\!/\!\left(1 + exp^{(-(a+bL))}\right)$$

where P is the balanced probability, a and b are the equation parameters determined by the linear least square method using the logarithmic transformation. The mean size at maturity was defined as the size at which 50% of the population is mature, when P = 0.5 then $Lm_{50} = {}^{(-a)}\!/_{b}$ (King, 1995).

Age at median maturity (A_{50}) was calculated by the inverse von Bertalanffy growth function (von Bertalanffy, 1938): (Jennings et al., 2001)

$$A_{50} = t_0 - \left({}^{1}\!/_{K}\right)\ln\left(1 - {}^{Lm_{50}}\!/_{L_\infty}\right)$$

where, L_∞ is the asymptotic shell length, K is the growth coefficient, t_0 the theoretical age at zero shell length and Lm_{50} is the size at first maturity.

2.4. Effect of management measures in the sex ratio

To assess the impact of the implementation of harvesting management measures on the reproduction of *P. aspera* and *P. candei*, the sex ratio (male:female) of both species was investigated for the two time-series (before and after those regulations).

2.5. Statistical analyses

The effect of harvesting regulations on the proportion of reproductive individuals was analysed by comparing the proportion of reproductive individuals between time-series and among size-classes within each time-series using the Pearson's chi-square test.

The existence of differences in limpet size-at-maturity between time-series was identified by comparing the slopes of the maturity curves using an analysis of covariance (ANCOVA). This test allows comparing the size-at-maturity before and after implementation of management measures, while statistically controlling for discrepancies in size-at-maturity caused by variation in size classes.

Additionally, the existence of differences in the proportion of sexes between time-series and among sizes-classes within each time-series was tested using the Pearson's chi-square test.

Statistical analyses were performed using SPSS v.24.0 (IBM Corp, 2016) with significance level considered for $p < 0.05$.

3. Results

A total of 51,380 limpets from both *P. aspera* and *P. candei* were analysed from the rocky shores of Madeira from 1996 to 2017. The shell length of the 26,273 sampled specimens of *P. aspera* ranged from 3.1 to 82.9 mm ($\bar{x}$ = 43.2 ± 7.8 mm) while for the 25,107 specimens of *P.*

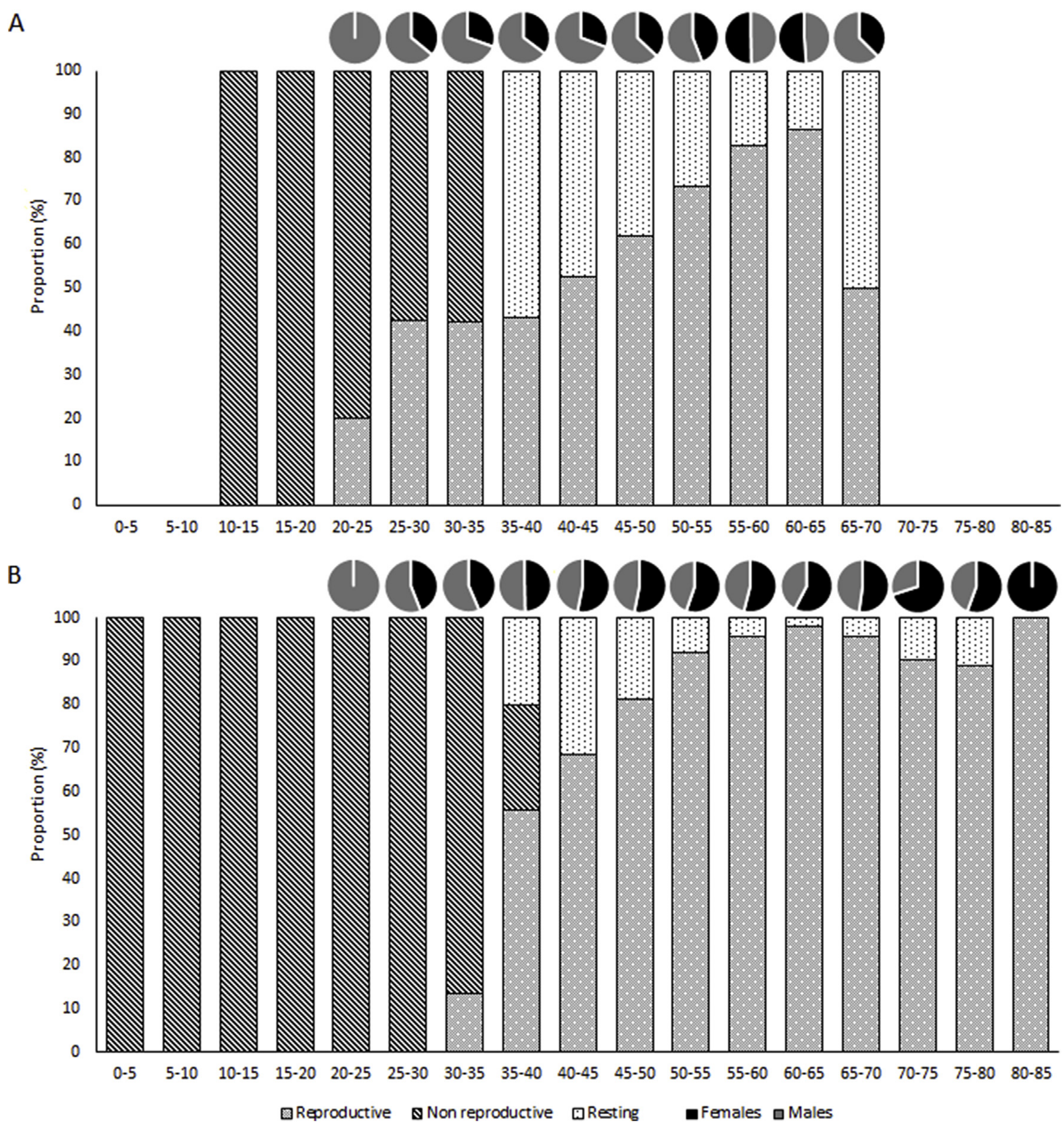

Fig. 3. Relative proportions of non-reproductive, reproductive, and resting individuals by size-class (bars) and sexual proportion (pie) of *P. aspera*: a) before (1996–2006) and b) after (2007–2017) the implementation of harvesting management measures in Madeira Island.

candei shell length varied from 6.0 to 81.8 mm ($\bar{x}$ = 46.7 ± 7.9 mm).

3.1. *Proportion of reproductive individuals before and after harvesting regulations*

Before the implementation of management measures in 2006, of the total *P. aspera* analysed, 3.9% were non-reproductive, 56.4% reproductive and 39.7% resting. After the implementation of those measures (2007–2017), an increase in the proportion of non-reproductive (12.8%) and reproductive (70.5%) and a decrease in the resting individuals (16.7%) was observed. In *P. candei*, of the specimens sampled between 1996 and 2006, 1.2% were non-reproductive, 69.5% reproductive and 29.3% in resting stage. Similarly to *P. aspera*, following the implementation of management measures *P. candei* displayed an increase in the proportion of non-reproductive (4.4%) and reproductive (83.5%) and a decrease in resting specimens (12.1%).

Regarding the size distribution, non-reproductive individuals of *P. aspera* were dominant (> 50%) between 10 and 35 mm L, reproductive specimens predominated in the larger size-classes (40–65 mm L) and resting individuals prevailed between 35 and 40 mm before the implementation of management measures (Fig. 3A). The time-series after the management measures was characterized by a broader range of size-classes, with the predominance of non-reproductive specimens in the smaller classes (0–35 mm L) and the prevalence of reproductive individuals in the remaining classes (35–85 mm L) with more than 80% in the size-classes from 40 to 85 mm L (Fig. 3B). The differences in the proportions within each time-series were statistically significant before (χ^2 = 4141.763, $p < 0.05$) and after (χ^2 = 12,106.199, $p < 0.05$) the implementation of management measures. The differences between the two sampling periods (1996–2006 *vs.* 2007–2017) were also statistically significant (χ^2 = 1554.921, $p < 0.05$).

Similarly, non-reproductive individuals of *P. candei* were predominant in the smaller size-classes (15–30 mm L), reproductive individuals in the larger classes (35–80 mm L) and resting specimens more abundant between 35 and 40 mm L (45%) during the period before management measures (Fig. 4A). These differences in the proportion of non-reproductive, reproductive, and resting individuals were statistically significant (χ^2 = 5206.493, $p < 0.05$). Concerning the

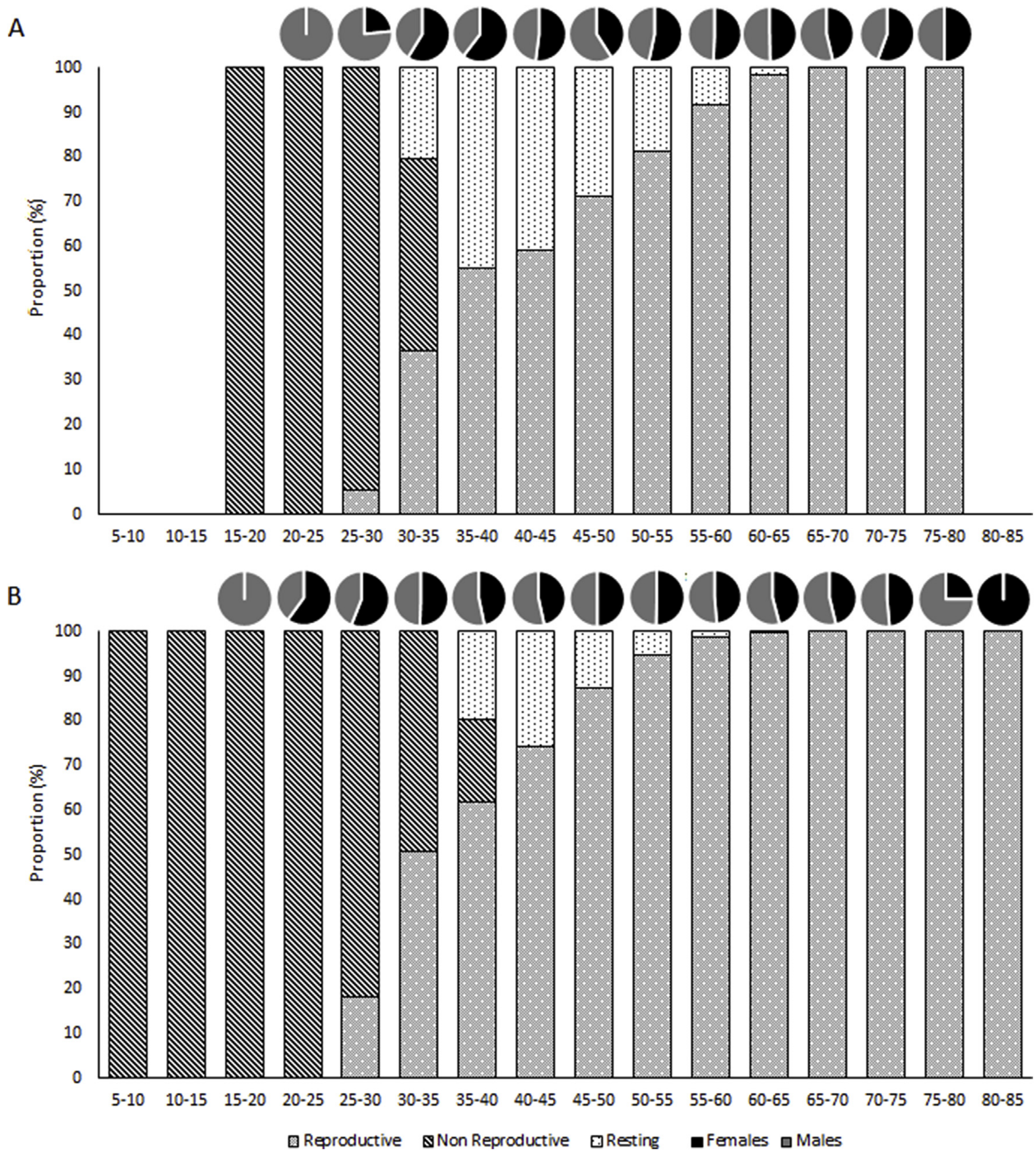

Fig. 4. Relative proportions of non-reproductive, reproductive, and resting individuals by size-class (bars) and sexual proportion (pie) of *P. candei*: a) before (1996–2006) and b) after (2007–2017) the implementation of harvesting management measures in Madeira Island.

period after implementation of harvesting regulations, *P. candei* presented a wider range of size-classes, with non-reproductive specimens more abundant from 25 to 35 mm L and completely dominant in the smaller classes (0–25 mm). Reproductive specimens prevailed between 40 and 85 mm, with more than 75% from 45 to 85 mm L (Fig. 4B). The differences among size classes were statistically significant ($\chi^2 = 6440.242$, $p < 0.05$), as well as those between the two sampling periods ($\chi^2 = 1155.485$, $p < 0.05$).

3.2. Impact of management measures in size at first sexual maturity

The mean size at first maturity (Lm_{50}) of both *P. aspera* and *P. candei* increased with the implementation of management measures. The Lm_{50} in *P. aspera* increased from 34.6 mm during the period 1996–2006 to 37.5 mm during the period 2007–2017. The estimated mean A_{50} of *P. aspera* increased gradually from 1.8 to 2.0 years between 1996-2006 and 2007–2017. Concerning to *P. candei*, Lm_{50} increased from 33.4 mm L (1996–2006) to 37.4 mm L (2007–2017), corresponding to an increase in A_{50} from 1.7 years before to 2.0 years after the implementation of harvesting regulations. These slight differences in Lm_{50} between time-series were not statistically significant neither for *P. aspera* ($F = 0.020$, $p = 0.889$) nor for *P. candei* ($F = 0.116$, $p = 0.735$).

3.3. Effect of management measures in the sex ratio

From the sexed individuals of *P. aspera*, in the period before the implementation of the harvesting regulations (1996–2006), 63.5% were males and 36.5% females, whereas in *P. candei* 53.2% were males and 46.8% females. During the period after the implementation of regulations (2007–2017) 47.6% of the sexed specimens of *P. aspera* were males and 52.4% females, whereas *P. candei* presented 48.9% males and 51.1% females.

The sex ratio (male:female = 1.7:1) was male-biased for *P. aspera* during 1996–2006 and displayed an inverse trend during 2007–2017 (male:female = 1:1). The differences in sex ratio between time-series were statistically significant ($\chi^2 = 296.127$, $p < 0.05$). Before the implementation of the management measures the sexual proportion among size-classes was in favour of males in all size-classes (20–70 mm L), with a totality of males (100%) in the 20–25 mm L size-class (Fig. 3A). These differences in the sexual proportion among size-classes were statistically significant during 1996–2006 ($\chi^2 = 52.941$, $p < 0.05$). After the implementation of the management measures the populations presented an increase in the size-range of the individuals and a shift in the sex ratio. In this period, females predominated in the larger size-classes (40–85 mm L) and males in the smaller classes (20–35 mm L) (Fig. 3B). The differences in the sex ratio among size-classes during this period (2007–2017) were also statistically significant ($\chi^2 = 59.821$, $p < 0.05$).

The overall sex ratio of *P. candei* was slightly male-biased (1.1:1) before the implementation of management measures (1996–2006). During this period, *P. candei* populations were characterized by the predominance of males on the first size-classes (20–30 mm L), on the remaining size-classes males and females were balanced, except for the 70–75 mm size-class where the females prevailed (63%) (Fig. 4A). In the period following the harvesting regulations, the sex ratio (male:female = 1.05:1) was similar to the previous time-series with an increase in the size range towards smaller size-classes (15–20 mm L) with only males, an inversion of the proportion of females (> 55%) in the size-classes from 20 to 30 mm L and higher homogeneity in the sexual proportion between 30 and 75 mm (Fig. 4B). The differences in the proportion of sexes between the two time-series were significant ($\chi^2 = 6.990$, $p < 0.05$), but not among size-classes for 1996–2006 ($\chi2 = 16.946$, $p = 0.109$) nor 2007–2017 ($\chi^2 = 21.155$, $p = 0.098$).

4. Discussion

The establishment of an effective stock management strategy of marine gastropods requires a combined approach considering the traditional tools of stock assessment, such as abundance and size structure, together with the reproductive potential of the exploited populations. In that sense, reproductive parameters like proportion of reproductively active individuals, sex ratio and size at first maturity should be taken into consideration when establishing management measures.

In the present case, the protective effects of the implemented management measures on limpet stocks was evident through the increased proportion of reproductive individuals, more balanced sex ratio and larger size at first maturity.

The reproductive potential of an exploited population of limpets is affected by the reduction in abundance and mean size (Oliva and Castilla, 1986), resulting in a decreased reproductive output of these broadcast spawners. This is due to the fact that reproductive success in limpets is dependent of the quantity of gametes released into the water column and that larger limpets produce more gametes than smaller individuals. Moreover, in protandrous hermaphrodite species the removal of larger females may induce skewed sex ratios.

Several management measures were implemented in 2006 in order to prevent harvesting pressure from causing a decline of limpet populations in Madeira Island, namely the establishment of the maximum allowable commercial catch of 15kg/person/day or 200 kg/boat/day, aimed at reducing the overall harvesting effort, and the minimum catch size of 40 mm, to allow adults to contribute to the reproductive fitness, as well as the establishment of a closed season from December to March to avoid disturbance during the reproductive season (Henriques et al., 2017).

Highly exploited populations of limpets are characterized by smaller size ranges, reduced abundances, individuals maturing at smaller sizes and younger ages, reduced proportion of reproductive individuals, reduced maximum life-span and, in the case of protandrous hermaphrodites, male-biased populations and earlier sex change (Hamilton et al., 2007). Prior the implementation of management measures, the reproductive parameters of *P. aspera* and *P. candei* populations from Madeira Island were consistent with these features.

The overall results show that *P. aspera* larger than 70 mm were absent in the populations sampled prior to 2007, while for *P. candei* the full-size spectrum was found. This might result from different levels of exploitation of these species, with the preferential target species (*P. aspera*) suffering a greater reduction in mean size than *P. candei*, which is similar to what occurs in most exploited stocks (Oliva and Castilla, 1986; Pombo and Escofet, 1996; Fenberg and Roy, 2012). Additionally, the fact that *P. aspera* is a protandrous hermaphrodite makes it more vulnerable to overexploitation, since it reaches sexual maturity as males and changes to females later in life, consequently the size-selective nature of limpet harvest will target mostly females leading to male-biased populations (Martins et al., 2017).

The sex ratio by size-class in *P. aspera* prior to the implementation of management measures was male biased, which is frequent in protandrous patellids (Branch, 1974; Creese et al., 1990). After the implementation of harvesting regulations, the species sex ratio shifted towards a ratio 1:1, although males were still more abundant than females in the smaller size classes and females became more abundant in the larger size classes.

One expected impact of limpet harvesting in protandrous hermaphrodite species is the decrease of the size at which the sex change occurs as a compensation for the removal of the larger females due to size-selective harvesting, as observed for *P. vulgata* in mainland Portugal and *P. aspera* in the Azores Islands (Borges et al., 2016; Martins et al., 2017). Prior the establishment of management measures in Madeira Island, *P. aspera* reached the size of sex-change earlier than after those regulations, suggesting a possible recovery of the exploited stock, since this species potentially changed sex at larger sizes during the period 2007–2017. Even though the regulations apparently had a positive effect on the exploited populations, these stocks could still benefit from the enforcement of a maximum size of capture, allow a more effective protection of larger females, safeguarding the renewal of the exploited populations.

Many studies worldwide have reported changes in maturation dynamics of heavily exploited stocks, namely smaller size and younger age at which individuals start reproducing and the decreasing spawning biomass (Trippel, 1995; Law, 2000; Sharpe and Hendry, 2009). Size at first maturity and age at median sexual maturity are important reference points in fishery management (Hilborn and Walters, 1992), whose shifts are mainly attributed to overfishing that leads to a decrease in stock density and to changes in environmental factors (Trippel, 1995; Gerritsen et al., 2003; Domínguez-Petit et al., 2008).

The present trend of increasing size and age at first maturity after the implementation of management measures for both limpet species in Madeira Island should be analysed with some caution since, poaching still represents a serious threat that can undermine the success of the implemented management measures. Nevertheless, this slight increase likely results from an improved reproductive potential of the exploited populations, due to measures that ensure higher reproductive output, such as the closed season during the main spawning season and the prohibition of harvesting specimens smaller than 40 mm. The increase in the size at first maturity corroborates the increase in the asymptotic length (L_∞) estimated at 71.80 mm for *P. aspera* and 77.98 mm for *P. candei* before the management measures (Delgado et al., 2005) and at 84.2 mm for female and 80.5 mm for male *P. aspera* after regulations (Sousa et al., 2017) and 80.81 mm for *P. candei* (Henriques et al., 2012).

One consequence of size-selective harvesting is the removal of larger, reproductively active individuals from the target populations. In fact, for the 1996–2006 time-series both limpet species in Madeira Island exhibited smaller proportions of reproductive individuals, which was more evident in *P. aspera* (*ca.* 56%) than in *P. candei* (*ca.* 70%). After the implementation of management measures an improvement of approximately 14% in the proportion of reproductive individuals was observed for both species. These similar results are likely related to the close size at first maturity of both species and to the fact that management measures are equal for all harvested limpets. In *P. aspera* not only the proportion of reproductive individuals increased but also the size range, with specimens larger than 70 mm being only sampled in the time-series 2007–2017. Additionally, in both species the increased proportion of non-reproductive individuals, coupled with smaller specimens being sampled in the period post implementation of management measures, suggests an improvement of the reproductive potential of the harvested populations.

The opposite trend was reported for *Patella candei crenata* and *P. aspera* in the Canaries where populations were characterized by highly fragmented assemblages dominated by non-reproductive specimens (Riera et al., 2016). This scenario was observed even after implementation of management measures, due to ineffective surveillance and increasing human population in coastal areas. The poor recovery of these species resulted from intense harvesting and showed the low viability of limpet populations at medium and long-term in this region (Riera et al., 2016). The same has been observed for *P. candei* in the Azores Islands by Martins et al. (2011), who stated that the efficiency of the established measures was insufficient to ensure the recovery of exploited populations, mostly due to illegal harvesting linked to lack of enforcement of regulations.

The present parameters on the reproductive potential of exploited populations of *P. aspera* and *P. candei* are valid indicators of the efficiency of the management measures implemented, when these parameters are considered in the establishment of harvesting regulations, as occurred for these species in Madeira. In fact, the present results indicate a slight improvement in the reproductive potential of these heavily exploited limpets, although the implementation of management measures could have resulted in greater improvements because their efficiency directly depends on a thorough enforcement of the regulations. Occasional poaching is still a threat to these species, together with ecosystem disturbances related to other anthropogenic activities, such as pollution and habitat removal (reviewed in Henriques et al., 2017). To enhance the positive impacts of the implemented legislation, continuous monitoring of the exploited stocks is paramount and the establishment of a maximum size of capture should be considered aiming to ensure higher reproductive outputs. Overall the improvements in reproductive potential of *P. aspera* and *P. candei* result from a successful management strategy, although the enforcement of regulations needs to be reinforced to protect these species from illegal harvesting, while the involvement of the local population in the conservation effort is of pivotal importance to achieve this goal.

Several genetic studies including both *P. aspera* and *P. candei* were carried out in the past decades (Ridgway et al., 1998; Koufopanou et al., 1999; Weber and Hawkins, 2002). Recently, molecular tools using microsatellites were developed for conservation genetics of both species (Faria et al., 2015, 2016). Local applications of those tools are recommended in order to clarify whether these limpet populations represent a single stock or a network of smaller local stocks, with consequences on their future management. Also, studies regarding the impact of the various marine protected areas existent in Madeira, would allow a better understanding of their effect on the recovery of exploited stocks.

Overall, the present results suggest a slight improvement on the exploited limpet stocks in Madeira Island, however further development requires continuous monitoring of harvesting activities, effective vigilance of no-take areas and during the closed season to prevent poaching, further awareness and engagement of local communities on promoting a sustainable fishery, and if needed, more specific regulations, such as a maximum size of capture for *P. aspera*, to counter the negative effects of size-selective harvesting in this protandrous hermaphrodite species.

Authors' contributions

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

Conflicts of interest

The authors declare that they have no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.106264.

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