

Original Article

Cite this article: Sousa R, Vasconcelos J, Delgado J, Riera R, González JA, Freitas M, Henriques P (2019). Filling biological information gaps of the marine topshell *Phorcus sauciatus* (Gastropoda: Trochidae) to ensure its sustainable exploitation. *Journal of the Marine Biological Association of the United Kingdom* 99, 841–849. <https://doi.org/10.1017/S0025315418001054>

Received: 4 June 2018

Revised: 22 October 2018

Accepted: 30 October 2018

First published online: 5 December 2018

Key words:

Life history; North-eastern Atlantic; *Phorcus sauciatus*; sustainable exploitation; yield-per-recruit

Author for correspondence:

Ricardo Sousa,

E-mail: ricardo.sousa@oom.arditi.com

Filling biological information gaps of the marine topshell *Phorcus sauciatus* (Gastropoda: Trochidae) to ensure its sustainable exploitation

Ricardo Sousa^{1,2}, Joana Vasconcelos^{2,3,4}, João Delgado^{2,5}, Rodrigo Riera⁴, José A. González⁶, Mafalda Freitas^{1,7} and Paulo Henriques⁸

¹Observatório Oceânico da Madeira, Agência Regional para o Desenvolvimento da Investigação Tecnologia e Inovação (OOM/ARDITI) – Edifício Madeira Tecnopolo, Funchal, Madeira, Portugal; ²Direção de Serviços de Investigação (DSI) – Direção Regional das Pescas, Estrada da Pontinha, Funchal, Madeira, Portugal; ³Centro de Ciências do Mar e do Ambiente (MARE), Quinta do Lorde Marina, Sítio da Piedade Caniçal, Madeira Island, Portugal; ⁴Departamento de Ecología, Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Casilla 297, Concepción, Chile; ⁵Centro Interdisciplinar de Investigação Marinha e Ambiental (CIIMAR/CIMAR), Rua dos Bragas, Porto, Portugal; ⁶Ecología Marina Aplicada y Pesquerías (i-UNAT), Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria, Spain; ⁷Estação de Biologia Marinha do Funchal e Centro de Ciências do Mar e do Ambiente (MARE), Cais do Carvão, Funchal, Madeira, Portugal and ⁸Universidade da Madeira, Campus da Penteada, Funchal, Madeira, Portugal

Abstract

Topshells play a pivotal role in intertidal rocky ecosystems and are adapted to harsh thermal and hydric stress. *Phorcus sauciatus*, a common grazer in the Macaronesian region (Madeira and the Canaries), has rarely been studied due to its restricted geographic distribution compared with *Phorcus lineatus*. Monthly samples were taken throughout 2017 to analyse biological parameters and evaluate the harvesting effect on the stocks of this species in Madeira. Individuals of the first age classes (<4 years) were dominant (~89%), while immature individuals were more abundant during the summer season. The spawning season occurs between March and August, especially from March to June. The size at first maturity was 12.95 mm long (1.68 years), with a continuous recruitment pattern throughout the year. Yield-per-recruit analysis (Y/R) showed that maximum production is achieved at a fishing mortality of 1.7 year⁻¹, corresponding to a Y/R of 0.023 g. Currently, *Phorcus sauciatus* seems to be moderately exploited in Madeira, but urgent conservation measures, such as a landing obligation, the establishment of a minimum catch size of 15 mm length, and a closed season (February–May), are warranted to preserve stocks of this species in the medium to long term.

Introduction

Topshells, limpets and winkles are among the most successful intertidal algal grazers in the North-eastern Atlantic Ocean and the Mediterranean Sea (Templado & Rolán, 2012). These marine gastropod molluscs are subject to one of the most extreme and dynamic natural environments, occurring from the supratidal to the subtidal zones in rocky shores. Topshells are exposed to different levels of thermal and hydric stress that result in specific morphological and biological characteristics related to adaptations to the harsh environmental conditions on rocky shores (Ramírez *et al.*, 2005; Donald *et al.*, 2012; Henriques *et al.*, 2017). They play a pivotal role in the intertidal ecological balance and are frequently used as biological indicators of anthropogenic impacts (Sousa *et al.*, 2018).

The ecological importance of the genus *Phorcus* Risso, 1826 on the overall structure of intertidal communities, particularly their influence and control on algae, prompted intensive research over the past decades, highlighting that the removal of these grazers leads to imbalances on rocky shore communities (Creese, 1988; Branch & Moreno, 1994). However, most of the studies concerning this genus focused on *Phorcus lineatus* (da Costa, 1778), and little information is available on *Phorcus sauciatus* (Koch, 1841). Nonetheless, local information on the population structure and distribution of *P. sauciatus* is available from the north-west Iberian Peninsula (Rubal *et al.*, 2014) and the Canary Islands (Ramírez *et al.*, 2005, 2009; Alfonso *et al.*, 2015).

Phorcus sauciatus, a common temperate-subtropical grazer that inhabits extensive and gently sloping rocky shore platforms in the eastern Atlantic, including the Macaronesian archipelagos of Madeira, the Canaries and the Azores, reaches its northern boundary in the Iberian Peninsula (Rubal *et al.*, 2014; Ávila *et al.*, 2015). The life history traits of this species vary intraspecifically due to genetic differences and environmental effects. The size and age of these gastropods are positively related, thus allowing studies on population structure, reproductive strategy, growth rates, mortality and longevity (Crothers, 1998). These parameters depend on a complex combination of selective forces and are required to understand the distribution, abundance and adaptations of this species to an ever-changing environment.



Additionally, the knowledge on the life history traits of these populations will play a pivotal role in providing proper background information for effective management of this important resource.

Exploitation of *P. sauciatus* in Madeira dates back to the 15th century when the archipelago was colonized by the Portuguese and has become more intensive due to the demographic increase of human settlement of the islands' coast and the technological advances that facilitate access to the whole coast (Silva & Menezes, 1921; Sousa *et al.*, 2018).

The harvesting of these molluscs is not regulated in the Madeira archipelago except for coastal natural reserves where harvest is interdicted. The absence of proper harvest regulation results in the landings of this species not passing through auction, which prohibits us from knowing how much effort is exerted on the harvested populations. Knowledge gaps regarding the life traits and population dynamics of this species are one of the key factors contributing to the lack of harvest regulation (Sousa *et al.*, 2018). These gaps prompted an intensive collection of biological data in the scope of a comprehensive biological and ecological study that aimed to provide the scientific information required for the implementation of conservation measures and the proper regulation of harvesting activities.

Herein, we aim to (i) provide information on the biological parameters and exploitation rate of *P. sauciatus* in Madeira (NE Atlantic Ocean) and (ii) evaluate the effect of size at first capture on the exploited stock by applying a yield-per-recruit model. These objectives are pivotal for developing a series of conservation measures to preserve stocks of this mollusc, such as the establishment of a minimum catch size, the introduction of a closed season and the implementation of mandatory landings and first sale at auction of this commercially harvested species.

Materials and methods

Data collection

Monthly samples of *P. sauciatus* were collected from three locations throughout the coast of Madeira, located in the north-eastern Atlantic (32.00–33.05°N 15.05–18.00°W), between January and December 2017. Specimens were randomly collected from the mid-to-lower intertidal zone of the rocky shores during low tide, without selecting for size, for a period of 15 min. Shell length (L) was measured using a Vernier calliper to the nearest 0.01 mm, and total weight (W) to the nearest 0.01 g was measured using an electronic scale. Specimens were removed from the shell and dissected for sexing purposes by macro- and microscopic observation of the gonads (Desai, 1966). Macro- and microscopic inspection of the gonads allowed for the assignment of each specimen to one of the five gonad maturation stages based on an adaptation of Desai's (1966) maturation scale. In stage I, female and male gonads present pink-brown pigmentation. The germinal epithelium in both sexes are ill-defined and oocytes are ~25 µm in diameter; in stage II, females present with greenish gonads, and males present with irregularly greenish gonads. Females present a well-defined germinal epithelium with numerous oocytes, measuring up to 45 µm in diameter, in each trabecula divided by connective tissue. Males present a germinal epithelium with rounded spermatogonia; in stage III, both female and male gonads are intumescent and present uniformly greenish pigmentation. Females have a well-defined honeycomb structure of connective tissue and oocytes up to 50 µm, and males present spermatocytes and spermatids; in stage IV, both sexes present fully developed gonads. Female gonads present with intense green pigmentation, and males present with pink and yellowish gonads. Females present numerous large oocytes that are freely present in the

connective tissue. Oocytes up to 165 µm seem to remain intact when released into seawater. Males present spermatozoa; in stage V, females present with green gonads, and males present with pink and yellowish gonads. Female ovaries are filled almost exclusively with mature oocytes, and male gonads are filled with active spermatozoa. After macroscopic observation, the gonads were removed, damp-dried, weighed to 0.001 g accuracy and prepared for histological confirmation of the maturation stages. All measurements were performed on fresh samples.

The data were analysed for deviations to the parametric assumptions of analysis of variance (ANOVA). The data distribution was tested for normality using the Kolmogorov–Smirnov two-sample test. Homogeneity of variance was determined using Levene's statistics. ANOVA was used to test for differences in the shell length and total weight between the sexes (Sokal & Rohlf, 1995).

Growth and age

The shell weight-length relationship (W/L) was estimated by least-squares linear regression after the logarithmic transformation of both variables ($\log W = \log a + b \log L$) using the potential relationship $W = aL^b$ (Bagenal & Tesch, 1978), where W is the total weight (g), L is the shell length (mm), a is the intercept (condition factor) and b is the slope (relative growth rate). The coefficient of determination, r^2 , was used as an indicator of the quality of the regression. A Student's t -test (King, 1995) was used to test the hypothesis of an isometric relationship ($H_0: b = 3$; $H_1: b \neq 3$, at the 5% significance level).

Monthly length-frequency distributions were inferred through apparent shifts of the modes in the time series of the length-frequency samples by means of modal progression analysis (MPA) and used to estimate absolute growth using Bhattacharya's method, which is included in the package FISAT II (Fish Stock Assessment Tools FAO–ICLARM), VER 1.2.0 (Gayaniilo *et al.*, 2005). This method implies the identification of mean values through the decomposition of composite distributions into their components followed by the determination and linking of means perceived to belong to the same cohort, and finally, the estimation of growth parameters is determined using the growth increments and size-at-age resulting from the linking of the means. All of the identified size-age groups resulted from at least three consecutive points, and the selection of the best results was based on the separation index (SI) values (>2) for the different age groups and the number of individuals per age group. Only size-age groups with an SI greater than 2 were considered, since values below 2 are unreliable (Sparre & Venema, 1997). NORMSEP by Hasselblad & Tomlinson (1971) was applied to decompose the mixtures of normal distributions based on Hasselblad's maximum likelihood method (Hasselblad, 1966).

The von Bertalanffy growth parameters were estimated by means of the Gulland and Holt method (Gulland & Holt, 1959) for non-linear parameter estimation in the routine ELEFAN I available in FISAT II (Gayaniilo & Pauly, 1997) using the equation $L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}$ (Gulland & Holt, 1959), where L_t is the mean shell length at age t (mm), L_∞ is the asymptotic shell length (mm), K is the growth coefficient (year^{-1}), t is the age of *P. sauciatus* (years), and t_0 is the hypothetical age at which $L_t = 0$ (years).

The growth performance index (ϕ') is generally considered a better tool for comparing growth dynamics between species, phylogenetically related groups and intraspecific areas. The estimated parameters L_∞ and K were used to determine ϕ' through the application of the equation $\phi' = \log_{10}(K) + 2 \log_{10}(L_\infty)$ (Pauly & Munro, 1984).

The inverse von Bertalanffy growth equation, $t = t_0(1/K) \ln(1 - L_t/L_\infty)$, was used to determine the age at length of *P. sauciatus*

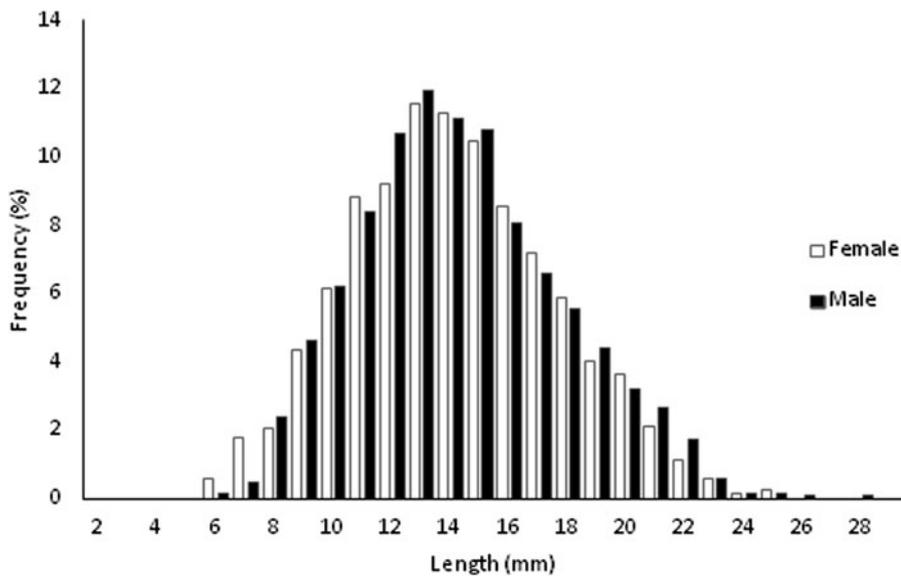


Fig. 1. Length-frequency distributions for females and males of *Phorcus sauciatus*, collected from January to December 2017.

(King, 1995), and the potential longevity ($A_{0.95}$) was estimated from the equation $A_{0.95} = t_0 + 2.996/K$ (Taylor, 1958).

Reproduction and recruitment

The sex ratio of *P. sauciatus* was determined, and the existence of differences in the proportion of sexes was tested using the chi-square goodness-of-fit statistic. A Pearson's χ^2 test was applied to test for the presence of differences in sexual proportions between months. The gonadosomatic index (GSI) was estimated according to $GSI = (\text{wet gonad weight}/\text{total body wet weight}) \times 100$. Differences in the mean GSI values between sexes among months were tested through ANOVA, considering a significance level of 0.05. To estimate the spawning season, the proportion of immature/mature specimens per month was plotted; all immature individuals between stages 1 and 3 and all mature individuals in stages 4 or 5 of gonadal development were considered (Desai, 1966). The existence of a correlation between monthly sea surface temperature (SST) and the GSI was determined using the Pearson correlation.

The size at first maturity (i.e. the size at which 50% of all specimens in a stock are mature, L_{m50}) was estimated from the correlation between the proportion of mature individuals and length according to the logistic equation: $P = 1/(1 + \exp^{-(a+bL)})$ (Sparre & Venema, 1997), where P is the balanced probability, and a and b are the equation parameters estimated by the linear least square method using a 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 $L_{m50} = (-a)/b$ (King, 1995). The lengths at which 25% (L_{m25}) and 75% (L_{m75}) of the topshells were mature was also determined.

The recruitment pattern was determined through the projection of the length-frequency data backwards on the time axis using the estimated growth parameters (Moreau & Cuende, 1991), and a normal distribution of this pattern was obtained by the NORMSEP routine (Pauly & Caddy, 1985) in FISAT.

Mortality, exploitation rate, probability of capture and yield-per-recruit

Total mortality (Z) was estimated using the length-converted catch curve procedure, where the percentage of samples in the length groups are pooled to simulate a steady-state population. The natural mortality rate (M) was determined by Pauly's empirical model: $\log_{10}M = -0.0066 - 0.279 (\log_{10}L_{\infty}) + 0.6543 (\log_{10}K) +$

$0.4634 (\log_{10}T)$ (Pauly, 1980), where L_{∞} is the asymptotic shell length (mm), K is the growth coefficient (year^{-1}), and T is the annual mean environmental temperature, which was 20.5°C for the habitat of *P. sauciatus* in the study area. Harvesting mortality (F) was calculated as the difference between Z and M , and the exploitation rate (E) was estimated from $E = F/Z$ (Gulland, 1971).

The probability of capture for *P. sauciatus* was calculated by using a logistic transformation of the probabilities obtained from the small topshells using the ascending left arm of the length-converted catch curve by plotting the cumulative probability of capture against the middle point of the length class intervals. The length at first capture (i.e. the cumulative probability of 50%, L_{c50}) was obtained from the resulting curve according to the equation: $S_L = 1/[1 + \exp(S1 - S2 \times L)]$ (Sparre & Venema, 1997), where S_L is the logistic curve, $S1$ and $S2$ are constants in the equation for the length-based logistic curve, and L is the topshell length. The lengths that correspond to the cumulative probabilities of 25% (L_{c25}) and 75% (L_{c75}) were also estimated.

Estimates of the relative yield-per-recruit (Y/R) and the harvesting mortality corresponding to the maximum production (F_{MAX}) were estimated according to Beverton & Holt's (1957) length-based method:

$$\frac{Y}{R} = Fe^{(-M(T_c - T_r))} w_{\infty} \left\| \frac{1}{Z} - \frac{3S}{Z + K} + \frac{3S^2}{Z + 2K} - \frac{S^3}{Z + 3K} \right\|,$$

where Y/R is the catch in weight, w_{∞} , K and t_0 are growth parameters, T_c is the age at first capture, T_r the age at recruitment, F the harvesting mortality, M the natural mortality, Z the total mortality and $S = e^{(-K(T_c - T_r))}$.

To assess the effect of harvesting smaller and larger specimens on harvesting mortality and Y/R , the sizes of capture estimated previously (L_{c25} , L_{c50} and L_{c75}) were applied to the Y/R model to simulate the effect of size.

Results

A total of 5480 specimens, 56.48% females and 43.52% males, were sampled throughout the study (Figure 1). Individual size varied between 6.09 and 29.25 mm L ($\bar{x} = 14.64 \pm 3.55$ mm L) in females and between 6.73 and 28.78 mm L ($\bar{x} = 14.74 \pm 3.50$ mm L) in males. The total weight ranged from 0.11 to 6.08 g ($\bar{x} = 1.06 \pm 0.79$ g) in females and from 0.13 to 5.68 g ($\bar{x} = 1.11 \pm 0.84$ g) in males. The smallest sample specimen was collected in

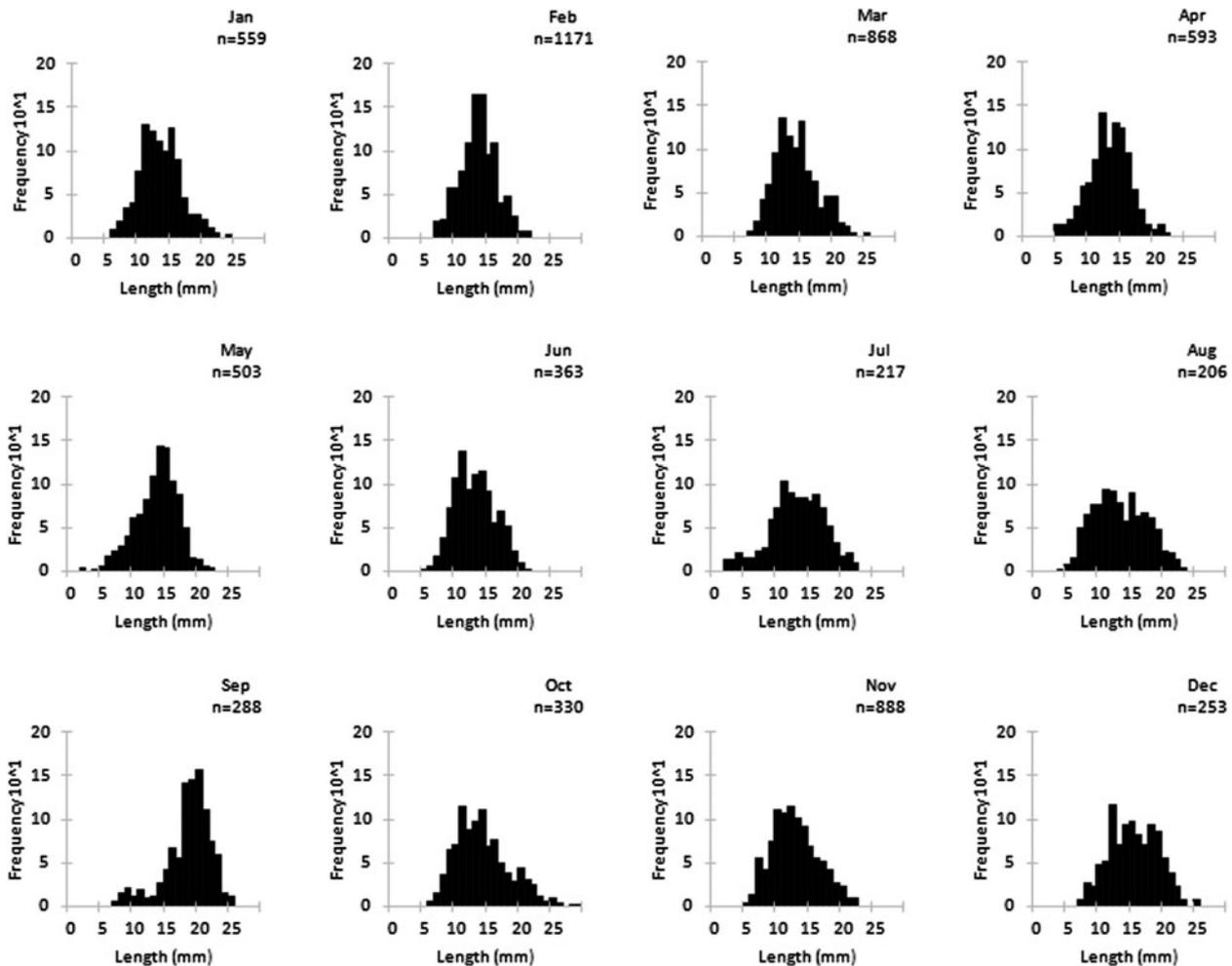


Fig. 2. Monthly length-frequency for *Phorcus sauciatus*, collected from January to December 2017.

July at 2.34 mm *L*, and the largest specimen was collected in October at 29.25 mm *L*.

Growth and age

Phorcus sauciatus size-frequency showed a normal distribution ($Z = 1.861$, $P < 0.05$) and a homogenous variance between the sexes ($W = 0.145$, $P > 0.05$); the same pattern was observed regarding weight, with a normal distribution ($Z = 7.946$, $P < 0.05$) and a homogenous variance between the sexes ($W = 3.659$, $P > 0.05$). No significant differences were found in the mean length ($F = 0.749$, $P > 0.05$) or in the mean weight ($F = 2.668$, $P > 0.05$) between females and males; thus, monthly length and weight frequency estimates were combined.

The correlation between shell length and total weight showed a negative relationship, and the parameters of the regression were estimated as $W = -3.325 + L^{2.815}$, $r^2 = 0.95$, $P < 0.05$. The b coefficient returned values less than 3, and statistical differences were highly significant ($t = 21.762$, $P < 0.05$).

The monthly length-frequency distributions of *P. sauciatus* are shown in Figure 2. The von Bertalanffy growth parameters were obtained for the best fit with $L_{\infty} = 31.90$ mm *L* and $K = 0.31$ year⁻¹. The growth performance index (ϕ') was calculated as 2.50. *Phorcus sauciatus* showed a predominance of individuals in the first age classes, with 88.94% of all specimens from the studied population being <4 years. The most representative age class was 2 years, representing 54.71% of the studied specimens. Potential longevity, assuming $t_0 = 0$, was determined to be 9.66 years.

Reproduction and recruitment

Phorcus sauciatus does not exhibit observable external sexual dimorphism. The overall sex ratio favoured females (1:1.30). The Chi-square goodness-of-fit test showed that the observed differences were significant ($\chi^2 = 57.791$, $P < 0.05$). Monthly sex ratio analysis showed that females were predominant all year, except in February, when males were predominant ($\chi^2 = 64.605$, $P < 0.05$).

Immature and mature specimens were found all year (Figure 3). Immature specimens were more abundant in summer, and mature individuals were more abundant in the remaining seasons. The highest proportion of immature specimens occurred in August (54.92%), and the lowest proportion occurred in February (24.12%). Mature individuals were predominant (~61%) from September to May, with the highest proportion found in February (75.88%) and the lowest in August (45.08%).

GSI values only showed significant differences between sexes in March ($F = 5.763$, $P < 0.05$) and April ($F = 6.764$, $P < 0.05$) and monthly differences within females ($F = 18.291$, $P < 0.05$) and males ($F = 22.053$, $P < 0.05$) (Figure 4). Monthly proportions revealed an increase from October to March for both sexes. The highest GSI values occurred in March for both sexes, with 6.78% for females and 7.42% for males. After the observed peak in March, there was a decrease until August for both sexes, suggesting that the spawning season of *P. sauciatus* occurs between March and August with higher values from March to June. The observed monthly variations in the GSI were in accordance with the observed proportions of immature and mature individuals, increasing when the proportion of mature specimens was higher but

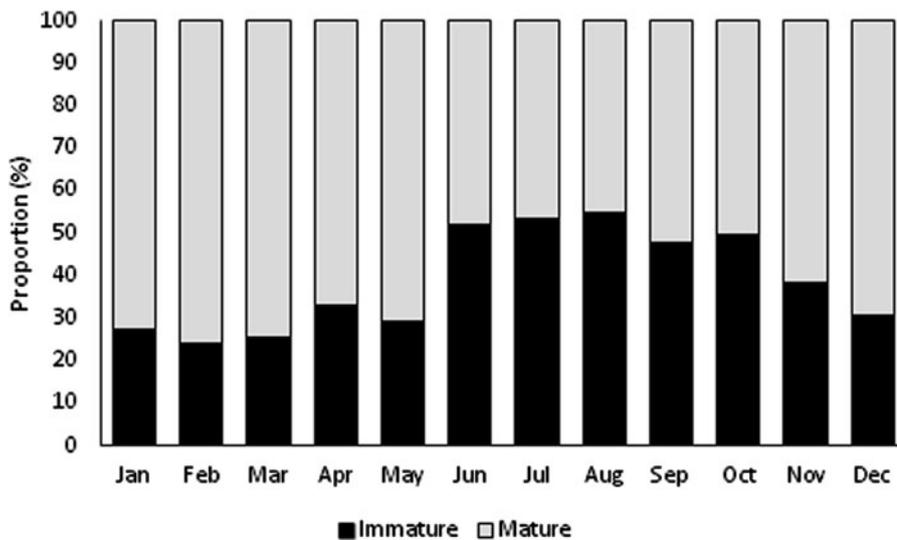


Fig. 3. Monthly distribution of immature and mature individuals of *Phorcus sauciatus* from Madeira archipelago, collected from January to December 2017.

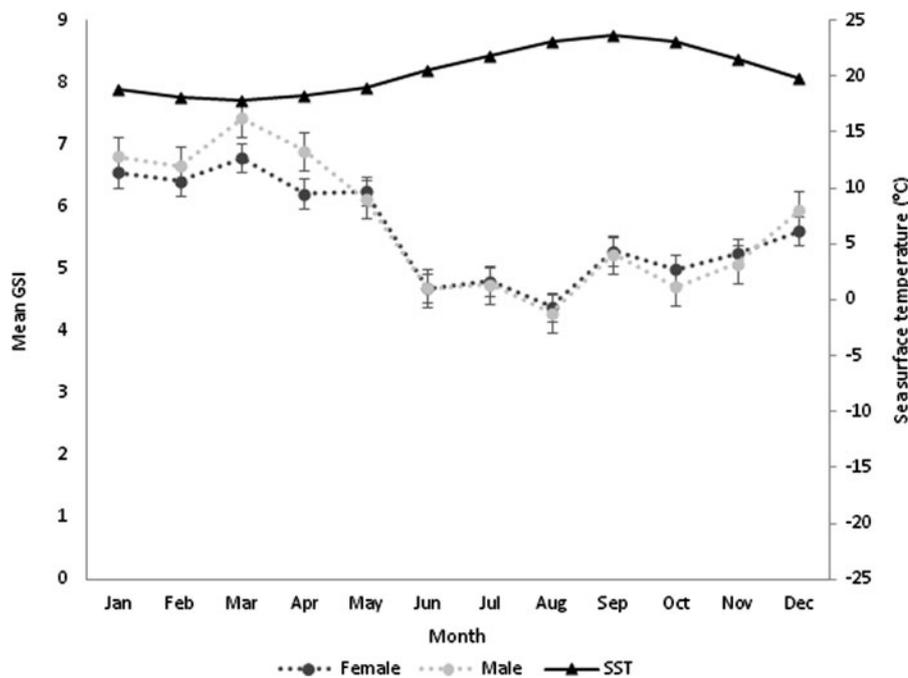


Fig. 4. Monthly variation in sea surface temperature and seasonal changes in gonadosomatic index (GSI) for females and males of *Phorcus sauciatus* from the Madeira archipelago collected from January to December 2017.

decreasing when the proportion of immature specimens increased. The Pearson correlation factor ($r^2 = 0.86$) showed that the mean GSI of *P. sauciatus* was correlated with SST ($F = 298.433$, $P < 0.05$).

The mean size at first maturity (L_{m50}) was 12.95 mm *L*, corresponding to 1.68 years. The size at which 25 and 75% of the study population reached sexual maturity was estimated at 12.17 and 13.73 mm *L*, respectively. The recruitment pattern was continuous throughout the year, reaching higher values between April (10.51%) and August (16.18%) and peaking in June (16.73%). Individuals with <5.00 mm shell length were only collected from April to August.

Mortality, exploitation rate, probability of capture and yield-per-recruit

Total (Z) and natural mortality (M) were estimated at 1.61 and 0.71 per year, respectively. Harvesting mortality (F) was 0.90 per year, and the exploitation rate (E) was estimated to be 0.56. The length at first capture for the combined sexes (LC_{50}) was estimated as 13.19 mm *L*, corresponding to 1.72 years. The analysis of yield-per-recruit (Y/R) showed that, at the current exploitation

rate, maximum production is achieved at F_{MAX} of 1.7 per year, corresponding to a Y/R of 0.023 g. The simulation of Y/R varying the length-at-capture resulted in a decrease in the harvesting effort allowed to maintain a sustainable yield, with an F_{MAX} of 1.1 per year. The simulation also showed a decrease in maximum production that can be achieved, with a Y/R of 0.021 g for LC_{25} ; for LC_{75} , even though the harvesting effort can be maximized to an F_{MAX} of 2.0 per year, the gains in maximum production are negligible, with a Y/R of 0.024 g (Figure 5).

Discussion

Information on the life history traits of *P. sauciatus* provides significant knowledge, which is required to explain and understand the adaptations of this species to an ever-changing environment and to perceive how human activities such as fisheries, habitat disturbance or natural causes affect their abundance and population dynamics (Sousa *et al.*, 2018).

The size distribution estimated for *P. sauciatus* from the Madeira archipelago is in accordance with what was previously

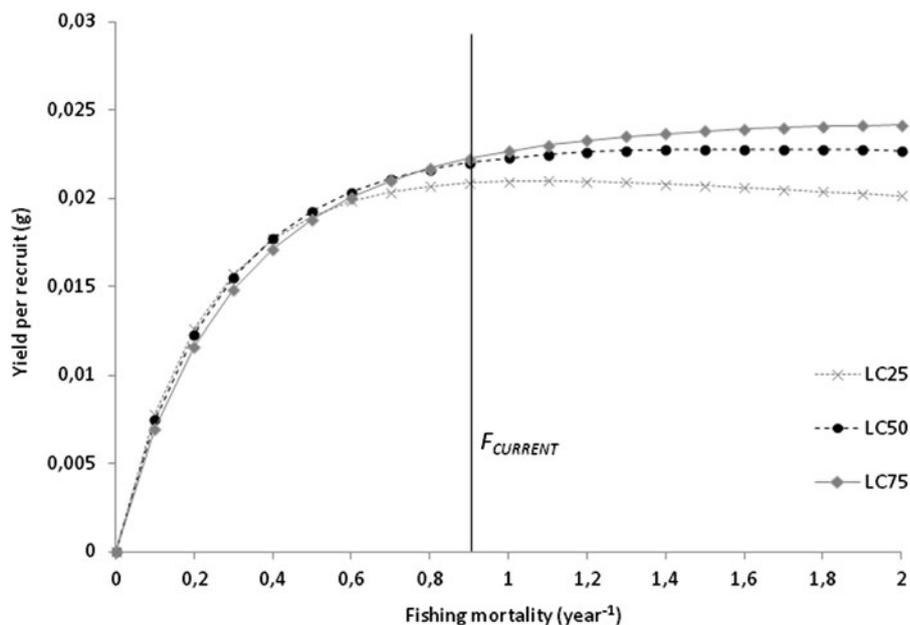


Fig. 5. Beverton-Holt yield-per-recruit curves on F for *Phorcus sauciatus*, considering LC_{25} , LC_{50} and LC_{75} .

reported for this species in the Canary Islands (Ramírez *et al.*, 2009). The relative growth coefficient obtained for the combined sexes revealed a negative allometric growth for this gastropod, which implies a disproportional increase in total weight in relation to the increase in individual shell growth. Thus, this species allocates more energy to growth than to reproduction in this geographic area. The value of the b parameter obtained for this species in the Madeira archipelago is well within the range of values usually obtained in other geographic areas (2.5–3.5) (Bagenal & Tesch, 1978; Froese, 2006), indicating normal growth dimensions and/or the well-being of the studied population (Carlander, 1969; Bagenal & Tesch, 1978; King, 1995).

Intertidal gastropods from different geographic areas in temperate seas frequently show intraspecific variation in shell size and shape (Reimchen, 1982) as a result of adaptations to predation and wave action (Preston & Roberts, 2007) or to the conditions of their preferred habitats (Boulding *et al.*, 1999). The negative growth pattern obtained for *P. sauciatus* might be explained by the harvesting pressure on this resource, which leads to lower population densities. The reduction in population density results in an increase in food and substrate availability, promoting an increase in the population density of other intertidal gastropods, such as *Patella aspera* Röding, 1798 and *Patelloida alticostata* (Angas, 1865) (Black, 1977; Sousa *et al.*, 2017). This pattern may also result from the instability of the intertidal conditions, since *P. sauciatus* is highly vulnerable to sea temperature, wave action and desiccation (Thompson, 1979).

Growth in molluscs is influenced by several biotic factors (e.g. predation, competition and population density) (Haven, 1973) and abiotic factors (e.g. temperature, insolation, photoperiod and food availability) (Crothers, 2001, 2012). Moreover, it seems that molluscs have a strategy of diverting energy to reproduction or to growth according to the organisms' requirements, and this life history strategy will influence the growth rates of these organisms (Haven, 1973; Branch, 1974; Underwood, 1979; Clarke *et al.*, 2004). Growth in molluscs is generally conditioned by the allocation of the majority of their energy to shell production; once they reach sexual maturity, molluscs divert most of their energy to reproduction (Crothers, 1994).

The estimated asymptotic length of 31.90 mm L for *P. sauciatus* from Madeira is consistent with the length of the largest sampled specimen (29.25 mm L). This species had a moderately low growth rate of 0.31 year⁻¹, which may be partially explained

by the oligotrophic nature of the coastal waters of Madeira (Caldeira *et al.*, 2002). Similar growth rates were observed in other intertidal gastropods, such as *Patella candei* d'Orbigny, 1840 (Henriques *et al.*, 2012) and *P. aspera* (Sousa *et al.*, 2017), in the same geographic area.

Phorcus sauciatus in Madeira have a median lifespan of 9.66 years, meaning the population is moderately long-lived, which is in contrast to its congeneric species, *P. lineatus*, which may reach an age of 15 years at its northern/eastern limits in Great Britain (Crothers, 1998). The shorter lifespan observed for *P. sauciatus* in Madeira is in accordance with Clarke *et al.* (2004), who stated that molluscs in colder regions grow more slowly and reach a larger maximum size, thus achieving a longer lifespan than molluscs inhabiting warmer regions.

Phorcus sauciatus does not exhibit observable external sexual dimorphism in the studied populations, similarly to other topshells, such as *P. lineatus*, *Steromphala umbilicalis* (da Costa, 1778) and *Steromphala cineraria* (Linnaeus, 1758) (Desai, 1966; Underwood, 1972; Crothers, 2001), and British trochids (Fretter & Graham, 1962); the sexes of *P. sauciatus* are only distinguishable by gonadal observation.

The gonadal cycle of *P. sauciatus* was established based on the monthly variation of the GSI, which reflects the periods of accumulation before the ripening and release of gonadal material during spawning as well as the use of stored energy reserves (Toro *et al.*, 2002). *Phorcus sauciatus* seems to be reproductively active all year in Madeira, with mature and partially spawned individuals present throughout the year. The obtained results also showed a synchronous gametogenesis cycle between the sexes of *P. sauciatus*, with females and males exhibiting a similar pattern all year, with minor differences in the proportion of mature specimens. The reproductive cycle of this species seems to involve two key periods, namely, development and spawning. The gonadal development phase lasts from September to February when an increase in the GSI values and in the number of mature individuals can be observed. The main spawning pulse begins in March, when the highest GSI values for both sexes were found, indicating maximum development of the gonads, which consistently decreased until August, when the lowest GSI values for both sexes were observed; this finding agrees with the reduction in the proportion of ripe individuals. During this phase, gametes are released into the sea where fertilization occurs (Crothers, 2001). The occurrence of a noticeable spawning pulse between March and June

indicates that, for this species, the majority of spawning occurs in the spring and extends more subtly throughout the summer. The observed reproductive cycle did not exhibit a resting phase, agreeing with Bode *et al.* (1986) for *P. lineatus* in northern Spain. These results are contrary to those observed from the northernmost populations in England, which exhibit a resting phase between the spawning phase and the gonadal development phase, which is typically shorter (Desai, 1966; Underwood, 1972). This is probably related to differences in sea surface temperature; it is known that reproduction cycles in marine gastropods are influenced by temperature, with populations inhabiting colder habitats developing a more pronounced spawning period and a shorter development phase, while in warmer conditions, the phases of the reproductive cycle tend to be less pronounced (Crothers, 2001).

Underwood (1972) observed that *P. lineatus* spawns throughout the summer and early autumn in England. Bode *et al.* (1986) verified that this period could be extended up to November for some individuals of the same species in Spain. In Madeira, the majority of *P. sauciatus* spawning seems to occur earlier in spring, suggesting that variations in reproductive seasons and in the duration of these periods are likely related to the geographic region, mainly due to the influence of temperature.

In Madeira, the spawning pulse of *P. sauciatus* is synchronized with the increase in seawater temperature, which is in concordance with Crothers (2001), who stated that effective spawning appears to require an environmental trigger leading to gamete release at the same time with cascading effects but with sharp differences in the extent of the spawning seasons, with the northern populations characterized by short, mid-summer breeding periods and the southernmost populations with lengthened breeding periods that extend in some cases throughout much of the year but with little or no activity during mid-summer (Lewis, 1986).

Within the same geographic region, other environmental factors, such as high wind speed allied to stimulation by wave action and the increase in phytoplankton concentrations, seem to act as triggers on the intertidal limpet species *P. aspera* (Sousa *et al.*, 2017) and *P. candei* (Henriques *et al.*, 2012), which are winter breeders, suggesting that the trigger that stimulates reproduction is different between limpets and the topshells in Madeira.

The estimated length at first maturity for *P. sauciatus* in Madeira was 12.95 mm *L*, corresponding to 1.68 years. More than 60% of the sampled population was sexually mature. In the Canaries, the size at first maturity was estimated to be 9.50 mm (González *et al.*, 2012). The differences in abiotic conditions between the two archipelagos may explain the larger size at first maturity estimated for the population of Madeira. It is well known that a decrease in growth rate can be related to a decrease in temperature, resulting in delayed sexual maturation at larger sizes (Berrigan & Charnov, 1994). Another explanation may be due to the exploitation level of this species in the Canaries, where it is considered overexploited (González *et al.*, 2012). Additionally, since *Phorcus* harvest is size-dependent, as larger individuals are more visible and are thus more prone to being harvested, it is likely that the difference in the size at maturity between archipelagos is influenced by the different exploitation pressures. In overexploited populations, size at first maturity may suffer shifts as a result of changes in the population size structure, resulting in smaller sizes at first maturity (Fenberg & Roy, 2008).

The recruitment pattern of *P. sauciatus* was continuous throughout the year, as indicated by the presence of immature individuals all year, but with higher levels of new recruits occurring during the main recruitment season from April to August. In the present study, recruits (2–5 mm *L*) were detected on rocky shores from April to August. Crothers (2001) stated that

settlement occurs when individuals reach lengths >1 mm *L* and verified that most settlement for *P. lineatus* in Great Britain occurs in early September, and by the end of that month, recruits could grow to 3 mm and even 4 mm. The recruitment trend obtained for *P. sauciatus* in Madeira is most likely a consequence of warmer temperatures, which result in continuous reproductive activity throughout the year with a period of intense reproduction. Therefore, the entrance of new recruits in the adult population follows the same trend, with a more prominent recruitment period occurring within a few months following the reproductive peak.

The analysis of the mortality rates estimated for *P. sauciatus* from Madeira suggests that harvesting mortality applies a high pressure on this resource compared with natural mortality. A combination of traditional and commercial fishing methods put harvesting pressure on the stocks of this topshell in the study area, which also occurs for the limpet *P. candei* (Henriques *et al.*, 2012) and for *P. sauciatus* in the Canary Islands (Alfonso *et al.*, 2015). The relatively high total mortality together with the moderate slow growth rate estimated suggest that its biomass is maximized at an early age (King, 1995), which is supported by the fact that ~89% of the sampled specimens were <4 years old. The low frequency of specimens in the age classes between 4 and 9 years (~11%) seems to be a consequence of intensive size-selective exploitation of the larger topshells, resulting in a decrease in the reproductive output. The reproduction of this species is gamete density-dependent, as occurs in other gastropods, such as the patellids *Patella candei crenata* and *P. aspera* (Riera *et al.*, 2016; Sousa *et al.*, 2017).

The catch selectivity analysis resulted in a shell length of 13.19 mm for the length at first capture, corresponding to an individual of 1.61 years old and indicating that most individuals are harvested after *P. sauciatus* achieves sexual maturity. The yield-per-recruit analysis suggests that this species' stock is being moderately exploited in Madeira, considering the current levels of mortality are <1.7 year⁻¹, which returns a yield of 0.023 g. The data showed that even if the harvesting effort is doubled, there will only be a slight increase of 0.001 g in the yield, and since the relationship between mortality and yield is essentially asymptotic, the harvesting effort required to take approximate mortality to F_{MAX} would most likely be excessive for a profitable yield.

The simulation of the effect of size at first capture on the yield-per-recruit showed that the F_{MAX} is 1.1 year⁻¹ at LC_{25} , indicating that this fishery is vulnerable to the harvest of smaller specimens that will result in a decrease in yield, which is most likely due to lower levels of recruitment because of the lower reproductive output of smaller individuals. Increasing the size at first capture to LC_{75} (F_{MAX} increases to 2.0 year⁻¹) would produce negligible benefits in terms of yield.

Knowledge of the life history parameters on stocks of exploited marine species is one of the major contributors to the identification and implementation of harvesting management policies for sustainable exploitation. The present study showed that the urgent implementation of management measures is required to preserve the commercial stock of *P. sauciatus* in the medium and long term. As such, the data reported here will contribute to the establishment of a properly regulated harvest that is both profitable and sustainable. The recommended conservation measures are the following: (i) the definition of different harvesting typologies (e.g. non-commercial harvesters with catches for personal use and professional harvesters for commercialization) with the establishment of maximum catches per day (we suggest no more than 2 kg per day for non-commercial use and 20 kg per day for professionals); (ii) the implementation of landing obligations and first sale at auction of *P. sauciatus* in Madeira to gain exact knowledge about the

status of the commercial catches and to monitor the harvesting effort by local authorities; (iii) the establishment of a minimum catch size of 15 mm shell length to ensure that a sufficient proportion of mature individuals contributes to the reproductive effort of the exploited population, and (iv) the establishment of a closed season between February and May to prevent all types of harvesting during the main spawning pulse.

Finally, the data provided in the present study come from a single time period, and some yearly variations may occur because of the particularities of abiotic and biotic conditions, e.g. temperature and turbidity. As such, the continuation of the monitoring of exploited populations and further studies focused on the reproduction of *P. sauciatu*s are warranted to verify whether the observed patterns are consistent throughout time.

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 Jorge Lucas and André Pinto for their support, namely, in biological sampling and the fishing surveys.

Financial support. The first author was supported by a grant from ARDITI OOM/2016/010 (M1420-01-0145-FEDER-000001-Observatório Oceânico da Madeira-OOM). The present study was also supported by the Fundação para a Ciência e Tecnologia – FCT through the strategic project UID/MAR/04292/2013 granted to MARE and the European Regional Development Fund in the framework of the Project MARISCOMAC (MAC/2.3d/097) and the Regional Government of Madeira.

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