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When descriptive ecology meets physiology: a study in a South Atlantic rhodolith bed

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Abstract

This study presents two years of characterization of a warm temperate rhodolith bed in order to analyse how certain environmental changes influence the community ecology. The biomass of rhodoliths and associated species were analysed during this period and *in situ* experiments were conducted to evaluate the primary production, calcification and respiration of the dominant species of rhodoliths and epiphytes. The highest total biomass of rhodoliths occurred during austral winter. *Lithothamnion crispatum* was the most abundant rhodolith species in austral summer. Epiphytic macroalgae occurred only in January 2015, with *Padina gymnospora* being the most abundant. Considering associated fauna, the biomass of Mollusca increased from February 2015 to February 2016. Population densities of key reef fish species inside and around the rhodolith beds showed significant variations in time. The densities of grouper (carnivores/piscivores) increased in time, especially from 2015 to 2016. On the other hand, grunts (macroinvertebrate feeders) had a modest decrease over time (from 2014 to 2016). Other parameters such as primary production and calcification of *L. crispatum* were higher under enhanced irradiance, yet decreased in the presence of *P. gymnospora*. Community structure and physiological responses can be explained by the interaction of abiotic and biotic factors, which are driven by environmental changes over time. Biomass changes can indicate that herbivores play a role in limiting the growth of epiphytes, and this is beneficial to the rhodoliths because it decreases competition for environmental resources with fleshy algae.

Introduction

Physical factors such as wind, marine currents and temperature have a major influence on species physiology and community processes (Kordas *et al.*, 2011). Winds drive horizontal movement of the water, creating surface currents and vertical movements of upwelling and downwelling (Ottersen *et al.*, 2014). These movements are important in the dispersion of many species (Frith *et al.*, 1986; Treml *et al.*, 2008), determining benthic community structure (Foster, 2001) and macroalgal nutrient uptake (Neushul *et al.*, 1992; Ho & Carpenter, 2017). Moreover, changes in marine temperature affect reproduction, growth and survival of invertebrates (Levin & Creed, 1986; Randall & Szmant, 2009), fishes (Pörtner *et al.*, 2001; Herbing, 2002), fleshy algae (Fong & Zedler, 1993; Andrews *et al.*, 2014) and rhodoliths (Horta *et al.*, 2016). Rhodoliths are structures composed of red coralline algae that have an important ecological function, providing refuges for a wide diversity of flora and fauna (Bahia *et al.*, 2010; Pascelli *et al.*, 2013; Amado-Filho *et al.*, 2017). Their morphology, physiology and biomass are influenced both by abiotic factors, such as hydrodynamics, temperature and light (Figueiredo *et al.*, 2000; Steller *et al.*, 2007; Sañé *et al.*, 2016), and by biotic factors, such as the presence of associated animals and macroalgae (Guillou *et al.*, 2002; Legrand *et al.*, 2017).

Free-living rhodoliths, also known as maerl, require environmental factors such as water motion (e.g. waves and currents) and bioturbation for their dispersion and rotation on the seafloor (Steller *et al.*, 2003). If water turbulence is low, the rhodolith bed does not develop because it gets covered by sedimentation and fouling (Foster, 2001). If water motion is too high, the thalli become fragmented (Foster, 2001; Hinojosa-Arango *et al.*, 2009). In addition, these environmental drivers also play a key role in their growth and morphogenesis (Steller & Foster, 1995; Pascelli *et al.*, 2013). Water motion (e.g. tidal currents and storms) may fragment rhodoliths, reducing their structural complexity and thus, habitat heterogeneity (McConnico *et al.*, 2017). However, periodic rotation is necessary as it allows light to reach all sides of the thalli (Hinojosa-Arango *et al.*, 2009).

In addition to waves and currents, seasonal environmental factors such as changes in seawater temperature (Kamenos & Law, 2010) and irradiance (Burdett *et al.*, 2014) can affect rhodolith beds due to their direct influence on photosynthesis and calcification. These physiological processes are intimately linked. During photosynthesis, consumption of CO_2 increases the

surrounding seawater pH and carbonate saturation state, favouring calcification (Johansen, 1981). In this way, environmental factors that affect photosynthesis may also affect calcification. Available information suggests that crustose coralline algae require relatively low irradiance levels for photosynthesis (Figueiredo *et al.*, 2000), but long summer days increase photosynthesis and growth (Teichert & Freiwald, 2014). When seawater temperature increases due to seasonal fluctuations (i.e. 10–16°C in the Bay of Brest and 10–30°C in the Gulf of California), the photosynthesis also increases, which enhances the growth rate and biomass of free-living coralline algae (Martin *et al.*, 2006; Steller *et al.*, 2007).

Changes in rhodolith density, biomass and morphology can influence the local diversity of flora and fauna since they provide microhabitats to many organisms (Foster *et al.*, 2013; Neill *et al.*, 2015). Rhodoliths in the north-western Gulf of Mexico harbour microalgal life history stages residing within cells of *Lithothamnion* sp. (Krayesky-Self *et al.*, 2017; Fredericq *et al.*, 2018). These cells may act as marine biodiversity hotspots that function as seedbanks, i.e. temporary reservoirs for life history stages of ecologically important eukaryotic microalgae and macroalgae, or as refugia for ecosystem resilience (Krayesky-Self *et al.*, 2017; Fredericq *et al.*, 2018). Hence, it is necessary to investigate environmental factors that influence both rhodolith morphology and density in order to assess changes in local community structure.

Associated animals and macroalgae that have seasonal life cycles or traits can respond more quickly to environmental conditions than rhodoliths (Martin *et al.*, 2007). Movement of rhodoliths represents a potential disturbance event to the community associated with the rhodolith bed. Algal biomass and motile fauna abundances are lower under more windy conditions, while the abundance of sessile species tends to increase with wind speed (Hinojosa-Arango *et al.*, 2009). During turnover events, attached macroalgae and animals could be abraded or buried, whereas motile fauna that take shelter in the bed could be impacted by the abrasion of rhodoliths. Such disturbances can prevent the development of a stable community (Maughan & Barnes, 2000; Hinojosa-Arango *et al.*, 2009). In addition, changes in rhodolith density promoted by burial/exposure or displacement will directly influence habitat availability for associated flora and fauna. Therefore, when these rhodolith beds have higher densities, this trait will be associated with higher abundances of associated biodiversity (Pascelli *et al.*, 2013).

The presence of associated organisms determines the interspecific relations that influence the whole community structure of the rhodolith bed, since they can behave as partners or pests (Scherner *et al.*, 2010). Besides trophic relation, flora and fauna can change micro-niche chemical conditions, which are factors that play a key role in ecophysiological processes (Stachowicz & Hay, 1996; Semesi *et al.*, 2009; Legrand *et al.*, 2017). Regarding macroalgae, their presence can either be positive or negative for rhodoliths. Turf algae benefit associated coralline algae since they elevate the pH of the surrounding medium, thus facilitating calcification (Short *et al.*, 2015). Under high irradiances, the epiphytes can protect the crustose coralline algae from photoinhibition (Figueiredo *et al.*, 2000). However, associated macroalgae can also shade rhodoliths and limit the availability of light and other environmental resources, such as CO_2 and nutrients (Wahl, 2008), which cause a decrease in photosynthesis (Dodds, 1991). Furthermore, animals, such as polychaetes, crabs and molluscs, can help maintain rhodolith health by controlling epiphyte growth (Scherner *et al.*, 2010; Legrand *et al.*, 2017). For example, coralline algae are relatively rare in shallow areas with low rates of herbivory. These organisms rely on herbivory or low light levels to avoid being overgrown by competitively superior fleshy algae (Stachowicz & Hay, 1996). Some crabs clean the surface of coralline algae by consuming a wide array of epiphytic macroalgae that commonly co-occur with their host (Stachowicz & Hay, 1996). These macroalgae include chemically defended species of the genera *Halimeda*, *Dictyota* and *Laurencia*, which are usually avoided by herbivorous fishes (Stachowicz & Hay, 1996). Thus, small grazers such as amphipods, gastropods, molluscs and polychaetes remove grazer-susceptible epiphytes, thus allowing for the growth of less competitive, grazer-resistant species such as coralline red algae (Lubchenco, 1983; Hay *et al.*, 1988; Steneck *et al.*, 1991; Stachowicz & Whitlatch, 2005; Scherner *et al.*, 2010).

Since the structure and resilience of rhodolith beds are affected by environmental and biological factors, the aim of this study was to characterize the communities associated with rhodolith beds over two years and analyse the abiotic factors that could cause changes in rhodolith physiology and morphology. The biomass of rhodoliths and associated species were analysed during this period. *In situ* experiments were conducted in order to measure the primary production and calcification of rhodolith communities, focusing on the dominant species. In this experiment, we investigate how photosynthesis and calcification rates of the dominant rhodolith-forming species *Lithothamnion crispatum* Hauck respond to the presence of the dominant fleshy alga *Padina gymnospora* (Kützing) Sonder. Our hypotheses are: (1) the biomass of rhodoliths and associated communities vary according to environmental changes during the study period; (2) the growth of *P. gymnospora*, which is a result of changes in environmental factors and trophic relations, alters the physiological responses of *L. crispatum*.

Materials and methods

Study site

The experiment was conducted in a rhodolith bed at Rancho Norte (27°17′S 48°22′W), Brazil, which is part of the 176 km^2 Marine Protected Area (MPA) called Arvoredo Marine Biological Reserve (Rebio Arvoredo), created in March 1990. The rhodolith bed extends over a sandy bottom on the north-western shore of Arvoredo Island, covering an area of ~100,000 m^2. The isobaths are between 7 m and 20 m. Average annual seawater temperature is around 22°C. Since Rebio Arvoredo is only 10 km away from the coastal zone, depending on winds and currents, the continental runoff from urban and industrial contaminants of the metropolis of Florianópolis can reach the area (Freire *et al.*, 2017). The area is influenced by the Brazilian Current (BC), which carries warm and salty tropical water from the low latitudes, and by an intense seasonal mixture of coastal, shelf and open ocean water masses from the Malvinas Current, which carries cooler and less saline water derived from the Antarctic Circumpolar Current (Matano *et al.*, 2010; Orselli *et al.*, 2018). These two opposing currents converge to form the Brazil–Malvinas Confluence Zone (Matano *et al.*, 2010). The South Atlantic Central Water (SACW) formed in this region is transported to the south of Brazil by the BC under the tropical water (Freire *et al.*, 2017). Water coming from the Brazil–Malvinas Confluence also mixes with the low salinity plume from Rio de La Plata, the Patos-Mirim Lagoon and other local sources of continental runoff (Möller *et al.*, 2008; Strub *et al.*, 2015). The influence of this plume on the region is seasonal, where in the winter, the south-westerly winds force the plume to move to lower latitudes (28° S), and in the summer, north-easterly winds lead the plume poleward (Möller *et al.*, 2008). This seasonality results in a dynamic and complex environment (Eichler *et al.*, 2008; Paquette *et al.*, 2016).

The rhodolith bed of Rancho Norte represents the southernmost limit of this habitat in the western Atlantic (Gherardi, 2004; Pascelli *et al.*, 2013). This bed provides ecosystem services,

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such as habitat for epiphytic algae (Horta *et al.*, 2008), refuge and food sources for a faunal community formed by zoanthids (*Zoanthus* sp., *Anthozoa*, *Hexacorallia*), ascidians, polychaetes, crabs, bivalves (Rocha *et al.*, 2006; Scherner *et al.*, 2010), ophiuroids, bryozoans, sponges and starfishes (Gherardi, 2004).

Environmental conditions

To investigate the variation of monthly seawater temperature between 2014 and 2016, data loggers (HOBO® Data Logger UA-002) were installed at 10 m depth, in the rhodolith bed. These data loggers were periodically changed to avoid biofouling and the temperature was recorded at an interval of 20 min. The average of a month was considered in analyses. Measurements of photosynthetically active radiation (PAR; μmol s^{-1} m^{-2}) were performed at 10 m depth where incubations took place using a LI-COR LI-1400 coupled to a hemispherical sensor.

The average wind data from six months prior to summer and winter sampling efforts were considered in the analyses of the influence of predominant wind direction (i.e. N, NE, E, SE, S, SW, W, NW (%)) and speed (m s^{-1}) on the rhodolith bed. This interval enables investigation of the history of wind changes before each collection, since the rhodolith bed's response to environmental change could be delayed. Hourly data of wind direction and speed were obtained from the online database of the National Institute of Meteorology – INMET (INMET, accessed online August 2017).

Community structure

For community structure analysis, sampling was conducted using quadrats (25 × 25 cm) that were placed randomly over the Rancho Norte rhodolith bed. All the organisms in each square were stored in plastic bags and transported to the laboratory. Quadrats were collected during the summer, in February 2015 (N = 9) and February 2016 (N = 14), late spring, in November 2016 (N = 9), and in winter, in September 2015 (N = 6) and June 2016 (N = 5). Rhodolith and epiphyte macroalgae were separated from animals and sorted by species (the identification following Woelkerling, 1988; Littler & Littler, 2000; Sissini *et al.*, 2014). For rhodoliths composed of more than one species, the species covering the majority of the surface (more than 50%) was considered. Macroinvertebrates were separated (by phylum) and weighed (in g, fresh weight). Epiphytes and rhodoliths were separated by species, dried at 60°C and then weighed (precision of ±0.001 g). To detect which rhodolith species could more easily be transported by currents, we weighed 50 unbroken samples from each species.

Since epiphytes only occurred during one summer (February/2015), only the herbivores from summer/late spring samples were analysed to compare the differences in abiotic factors that could have favoured such occurrences. However, to analyse the seasonal variations in biomass of rhodoliths, all sampling efforts were considered.

In this study, underwater visual censuses were applied to collect and quantify fish population density data (UVC: 20 × 2 m strip transects = 40 m^2). The procedure required a diver to swim along a transect 1 m above the substrate. While unrolling a measuring tape, the diver recorded all fish by species and calculated their size by placing them into 5 cm categories (Floeter *et al.*, 2007). All sampling campaigns were conducted in the morning, by the same diver, during summers.

The biomasses of fishes were calculated using the following equation (1) (published weight-length relationships):

$$W = axTL^b \quad (1)$$

in which W is the total wet weight in grams, a and b are species-specific parameters of the relationship, and TL is the total length in cm (Anderson *et al.*, 2014; Froese & Pauly, 2016).

Experimental design

Primary production, respiration and calcification were measured on the rhodolith species *L. crispatum*, and the epiphyte *P. gymnospora* alone and associated with *L. crispatum*. *In situ* physiological experiment was conducted during one summer (3–4 February 2015) at a depth of 10 m. During this period, we conducted ~2 h incubations inside closed chambers and analysed changes in dissolved oxygen concentrations (DO) and total alkalinity (TA). The following combinations were incubated (N = 5 at daylight and N = 3 at night): (1) – two specimens of *L. crispatum* alone (64.89 ± 20.20 g), (2) – two specimens of *P. gymnospora* alone (2.67 ± 0.79 g) and (3) – one specimen of *L. crispatum* and one specimen of *P. gymnospora* together (66.79 ± 30.68 g). These different combinations were placed inside transparent nylon chambers, which did not allow for gas exchange and did not influence the light quality. All chambers were filled with ~2 l of bottom seawater and sealed with a holder made of PVC tube. They were tied and suspended with a rope, just above the bottom, subjecting them to gentle movement from the current. This enabled circulation inside the chambers, thus reducing the formation of large diffusion boundary layers around the organisms and providing a homogeneous distribution of nutrients (Hurd, 2000). All combinations were incubated once at each of three different natural irradiances (Time 1, 2 and 3) and one time at night (Time 4), always using different samples (during ~2 h). PAR (μmol s^{-1} m^{-2}) was determined next to the chambers using a LI-COR hemispherical sensor throughout each incubation. Averaged PAR values (3 points) were considered for each incubation period for the productivity analyses. After the incubation, the chambers were brought to the surface to measure the parameters used to calculate productivity and calcification. The volume of seawater was measured in each chamber with a graduated beaker.

Productivity and respiration

For dissolved oxygen concentration analyses, five samples of 12 ml of seawater were taken from each chamber at the beginning and at the end of the incubation. The mean value per chamber was used in the calculations. The dissolved oxygen was measured by the Winkler method, modified by Labasque *et al.* (2004). This method enables a repeatability of 0.45% (30 samples) and a reproducibility of 0.73% near 250 μmol kg^{-1} of O_2. Although we incubated five chambers per combination at daylight, we only used four in the calculation of primary production after detecting outlier values probably caused by bubbles produced in the sample collection. In the laboratory, the organisms were dried for 48 h at 60°C and then weighed. The DO values were used to calculate the Net production (NP), Respiration (R) and Gross Production (GP) rates (in μmol O_2 cm^{-2} h^{-1}) according to Noisette *et al.* (2013) and the following equations (2) to (4):

$$NP = \frac{\Delta O_2(\mu mol\ l^{-1})(light)xV}{\Delta txA} \quad (2)$$

$$R = \frac{\Delta O_2(\mu mol\ l^{-1})(dark)xV}{\Delta txA} \quad (3)$$

$$GP = NP - R \quad (4)$$

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where: ΔO_2 = Difference between final and initial oxygen (μmol l^{-1}), A = surface area of algae (cm^2), V = chamber volume (L) and Δt = incubation time (h). Noisette *et al.* (2013) considered the dry weight in the calculation. However, the surface area of *L. crispatum* and *P. gymnospora* was considered separately instead of the dry weight in order to make the physiological results of both more comparable.

Calcification

To analyse the calcification rates of the organisms, we measured changes in seawater total alkalinity within chambers during the incubations. At the beginning and at the end of the incubations, two samples of seawater were stored in 40 ml vials. Samples were poisoned with mercuric chloride (0.02%) and the analyses were conducted according to the open-cell protocol described by Dickson *et al.* (2007) at the LEOC laboratory in the Institute of Oceanography at the Federal University of Rio Grande (FURG). Regular analyses of Certified Reference Material (CRM) Batch 149, obtained from the Scripps Institution of Oceanography, were carried out for quality control purposes (Dickson *et al.*, 2003). The accuracy of the total alkalinity measurements was set using the CRM by applying a correction factor to the measured values that was based on the nominal CRM values. The analytical precision of the total alkalinity measurements was investigated daily through replicate analyses of a single sample and was determined to be ± 1.0 μmol kg^{-1}. The pH (pH AT-315 Alfakit, resolution 0.01 and precision ±0.01%) was measured at the beginning and end of each incubation. Before use, the pH meter was calibrated to buffer solutions (pH 4.00, 7.00 and 10.00 – NBC scale) according to commercial protocols. Light and dark calcification rates were estimated using the alkalinity anomaly technique (Smith & Key, 1975), where for each mole of $CaCO_3$ precipitated, total alkalinity (At) decreases by two equivalents: $Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + H_2O + CO_{2(aq)}$ (Johansen, 1981; Wolf-Gladrow *et al.*, 2007). The difference between initial and final alkalinity of the incubation (ΔAt) was considered to calculate calcification rates (G, μmol $CaCO_3$ cm^{-2} h^{-1}), following equations (5) and (6) below (Noisette *et al.*, 2013):

$$G_{\text{biomass}} = \frac{-(\Delta At)xV}{2x\Delta txDW} \quad (5)$$

$$G_{\text{area}} = \frac{-(\Delta At)xV}{2x\Delta txA} \quad (6)$$

For subsequent analyses, calcification normalized to biomass (G_{biomass}) was used to quantify rhodolith production of g $CaCO_3$ on the day of the experiment, and calcification normalized to surface area (G_{area}) was used to compare the metabolic rates of the rhodoliths and *P. gymnospora* occurring alone and together.

Algae surface area

The surface area of *Padina gymnospora* was calculated from photos that were analysed using Image J software and expressed in cm^2. The samples were placed individually under a white background with a scale and then photographed at a distance of 50 cm. A methodology modified from Hoegh-Guldberg (1988), was used for the rhodolith surface area estimation. Dried *L. crispatum* samples (N = 19) from the Rancho Norte rhodolith bed, with varied sizes, were weighed and then coated in a commercial blank dye (composed of resin and water). The first coat sealed the surface, reducing the porosity. After 20 min, they received another layer and were re-weighed before and after the second coat. The conversion from weight increase to the surface area was done by doing a calibration with four expanded polystyrene cubes of known area (13.6–61.45 cm^2). The relationship between the weight of the second dye coat and the surface area of the cubes was used to calculate the three-dimensional surface area of 19 dried samples ($y = 183.04x–0.458$, $r^2 = 0.9953$). Then, the regression relationship between the surface area and the weight of the samples was used to calculate the surface area of rhodoliths used in the experiment ($y = 2.5108x + 9.9264$, $r^2 = 0.9337$).

Rhodolith growth

The growth rate of rhodoliths was determined *in situ*. Random rhodoliths (N = 30) from the Arvoredo bed at 10 m depth were collected in May 2014 and taken to the laboratory and stained with an aerated 0.025% (w/v) alizarin red seawater solution for 24 h (Blake & Maggs, 2003). The specimens were tagged with nylon lines and plastic beads. Afterwards, they were taken back to the field and were recollected in November 2015. To estimate the length of the growth layer, the rhodoliths were cross-sectioned radially using a circular rock saw (Caragnano *et al.*, 2016) and then visualized under a light microscope (Leica S8AP0) (Supplementary Figure S1). Some rhodoliths with undetectable alizarin marks were left out. From each sample (N = 11), at least 20 measurements were taken. The measurements were equally distributed around the circumference.

The amount of $CaCO_3$ fixed in the rhodolith bed (g m^{-2} $year^{-1}$) was obtained by considering the growth lengths, the radii, and the dry weights of the rhodoliths of each quadrat from the biomass sampling, as described in Amado-Filho *et al.* (2012*a*). We made one modification; the weight of the rhodoliths was used instead of their volume. The rhodoliths were weighed individually and the rhodolith radii were measured according to the shortest, intermediate and largest radii. The proportion of the total rhodolith weight (W_r) relative to the growth layer weight (W_l) was calculated from the ratio of the growth length (estimated to be 0.319 ± 0.226 mm $year^{-1}$, based on measurements of rhodoliths that were left in the field) to the mean radii (R_r), as described in equation (7):

$$W_l = W_r x \frac{0.319}{R_r} \quad (7)$$

The amount of $CaCO_3$ produced by the rhodolith bed per m^2 (0.0625 m^2 per quadrat) in g m^{-2} $year^{-1}$ ($CaCO_3pr$) considered the sum of the W_l of all the rhodoliths of each quadrat (SW_l), according to the equation (8):

$$CaCO_{3pr} = \frac{SW_l}{0.0625} \quad (8)$$

Using the calcification data measured *in situ* (G_{biomass}) and normalized to weight, we calculated diel calcification (DG), expressed as μmol $CaCO_3$ g^{-1} DW day^{-1} (considering 13:11 h Light: Dark cycle), according to equation (9):

$$DG = G_{\text{light}} \times 13 + G_{\text{dark}} \times 11 \quad (9)$$

G_{light} takes the three daylight incubations into account. The DG value (converted from μmol to g) was used to calculate the $CaCO_3$ production of *L. crispatum* (R $CaCO_3pr$) of each quadrat individually, expressed in g $CaCO_3$ day^{-1} according to equation (10):

$$R\ CaCO_{3pr} = \frac{DG \times W_r}{0.0625} \quad (10)$$

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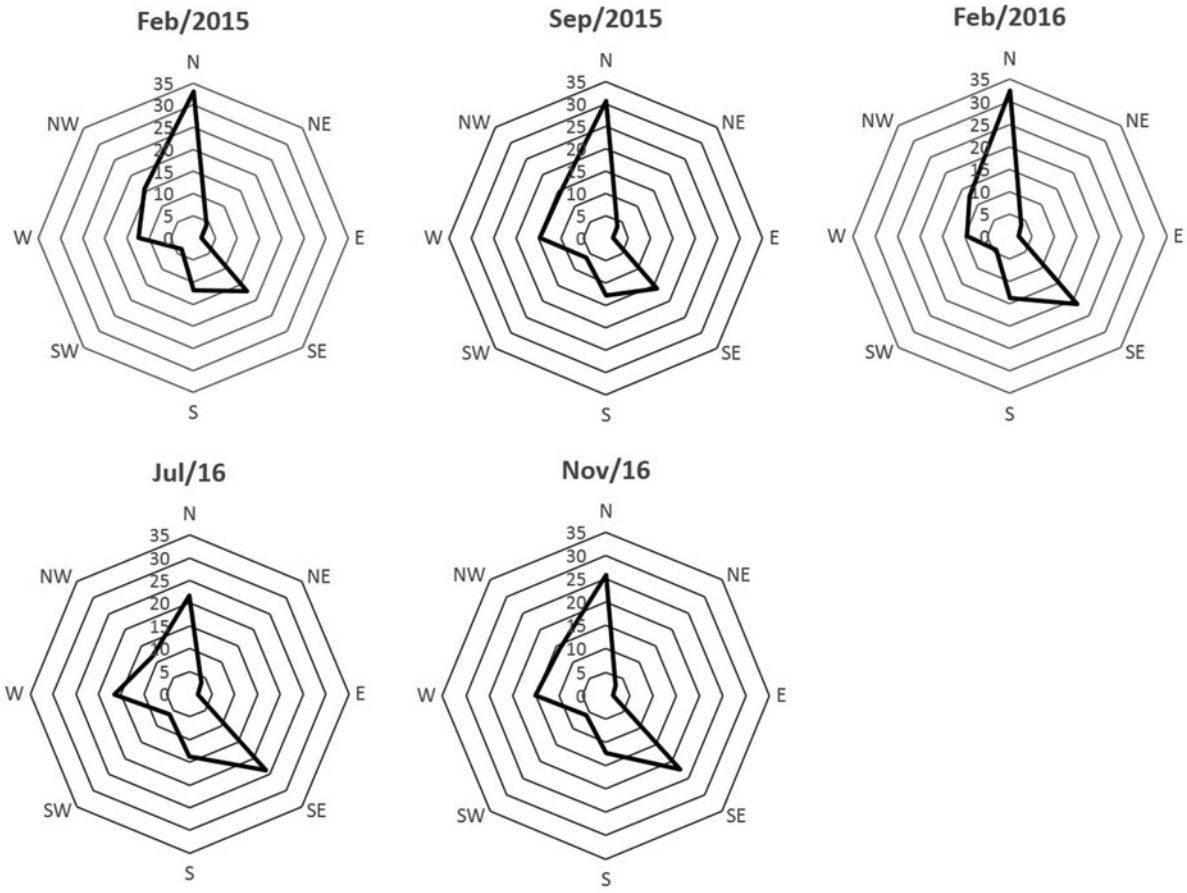


Fig. 1. Frequency (%) of wind direction in the six months prior to each month of collection. Data: INMET (Brazilian Meteorology Institute – Florianópolis/São José/A806 Station).

The average *R* $CaCO_3$*pr* of the individual quadrats (Total *R* $CaCO_3$*pr*) was used to calculate the $CaCO_3$ production of *L. crispatum* per area during *in situ* incubations.

Data analyses

The photosynthetic, respiratory and calcification rates of the macroalgae were analysed using parametric statistics. After evaluating the normality (Shapiro–Wilk test) and homoscedasticity (Levene's test) of the data, a two-way ANOVA was performed to test the significant differences of photosynthesis and calcification data under different light levels and the effects of individual *vs* combined species. For the respiration data, one-way ANOVAs were performed using incubation data at dark. The Newman–Keuls *post hoc* test was applied when significant differences were observed ($P < 0.05$). ANOVA assumptions were not met for the total biomass of rhodoliths and fauna, so these data were analysed using a Kruskal–Wallis test followed by pairwise multiple comparisons. The correlation between the total biomass of rhodoliths and the mean values of wind direction/velocity from six months prior to each collection was analysed with a Spearman correlation and was considered significant when $P < 0.05$. The analyses were performed in Statistica 13.0.

Linear Models (LM) and subsequent Analyses of Variance (ANOVA) were used to test the effect of season on the biomass of rhodolith species and the effect of time on the fish density inside the Arvoredo MPA. Total densities and species biomass were used as dependent variables, whereas time (years) was used as a factor (Underwood, 1981; Chatfield, 1989; Snedecor & Cochran, 1989). When significant differences were found, the Tukey HSD post-hoc test was used to verify sources of variation. Assumptions of normality and homoscedasticity were assessed with Kolmogorov–Smirnov/Lilliefors and Bartlett's tests (Underwood, 1981; Snedecor & Cochran, 1989; Zar, 1999). Analyses were run in the R environment package 'Agricolae' (de Mendiburu, 2013).

Results

Environmental conditions

During the six months before each of the summer/late spring collections, the north winds were predominant. The highest frequency was during the semester before February 2015 (33.19%), followed by February 2016 (32.42%) and November 2016 (25.89%) (Figure 1). However, the speed of the wind six months before February 2015 was the lowest among the summer collections (Figure 2). Regarding the winter collections, the north wind was higher during the semester before September 2015 (30.61%), whereas in the months before July 2016, the south-east wind prevailed (23.82%).

The values of monthly seawater temperature from May 2014 to December 2016 varied between 16.6°C in winter and 26.1°C in summer (Figure 3). The seawater temperature at the rhodolith bed during the physiological experiment varied between 25.6 and 26.9°C. The mean PAR values measured at each incubation time were, in order of execution, 35 µmol photons m^{-2} s^{-1} at Time 1, 472 (± 20.64) µmol photons m^{-2} s^{-1} at Time 2, 119 (±0.68) µmol photons m^{-2} s^{-1} at Time 3 and 0 µmol photons m^{-2} s^{-1} at Time 4. Salinity varied between 33 and 34.

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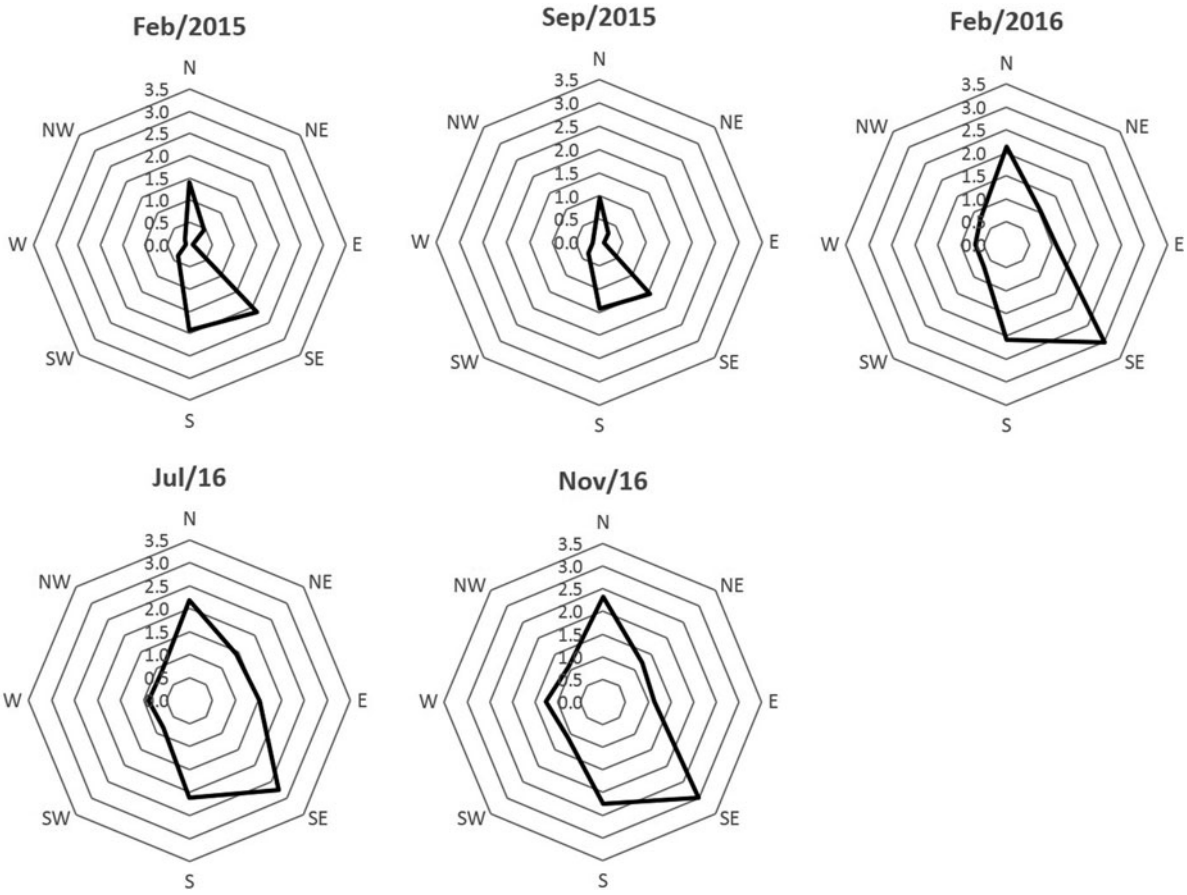


Fig. 2. Mean wind speed ($m\,s^{-1}$) of six months prior to each month of collection. Data: INMET (Brazilian Meteorology Institute – Florianópolis/São José/A806 Station).

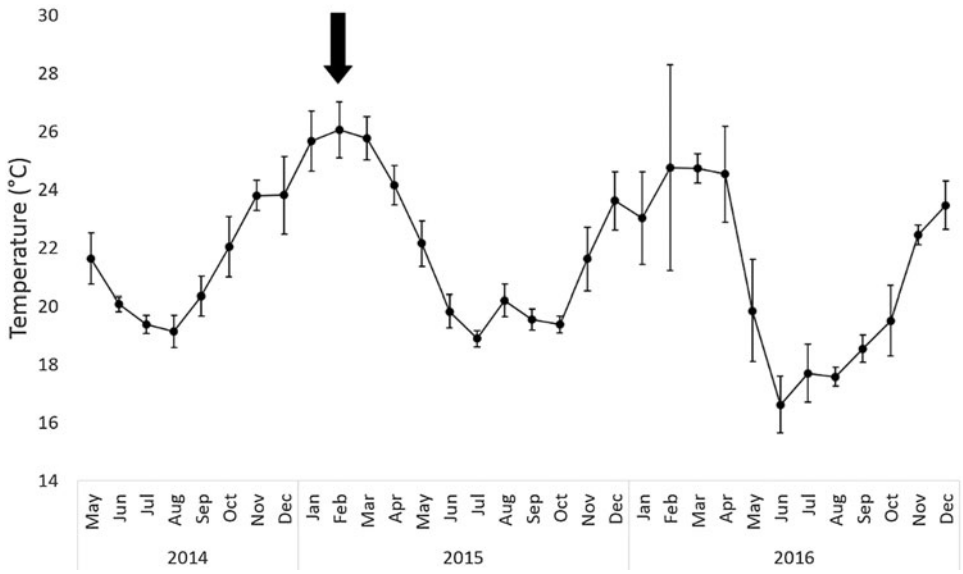


Fig. 3. Variation of mean (±SE) monthly seawater temperature at 10 m depth from May 2014 to December 2016 at the Marine Protected Area (MPA) of Arvoredo, Brazil. The black arrow indicates the month of *in situ* physiological experiment.

Community structure

Four species of rhodoliths were found: *Lithothamnion crispatum*, *Lithophyllum atlanticum* Vieira-Pinto, M.C.Oliveira & P.A.Horta, *Mesophyllum erubescens* (Foslie) Me.Lemoine and *Lithophyllum margaritae* (Hariot) Heydrich (Figure 4). The total biomass of rhodoliths was significantly different between seasons (H: 24.51; $P < 0.01$, Supplementary Table S1, for all statistical results), with the highest value in winter, in September 2015, and the lowest in February 2016 and November 2016 (Figure 5). *Lithothamnion crispatum* was the most abundant species in the summer (F: 3.32; $P < 0.01$) at all collections, followed by *L. atlanticum* (Figure 6). However, the biomass of *L. atlanticum* increased in the winter (F: 3.32; $P < 0.01$). *Lithophyllum margaritae* only occurred in low abundance in February 2015 and July 2016. *Lithophyllum atlanticum* and *M. erubescens* specimens had similar weights and were significantly heavier than *L. crispatum* (Figure 7). The growth rates of rhodoliths from Arvoredo were 0.035–0.566 mm $year^{-1}$.

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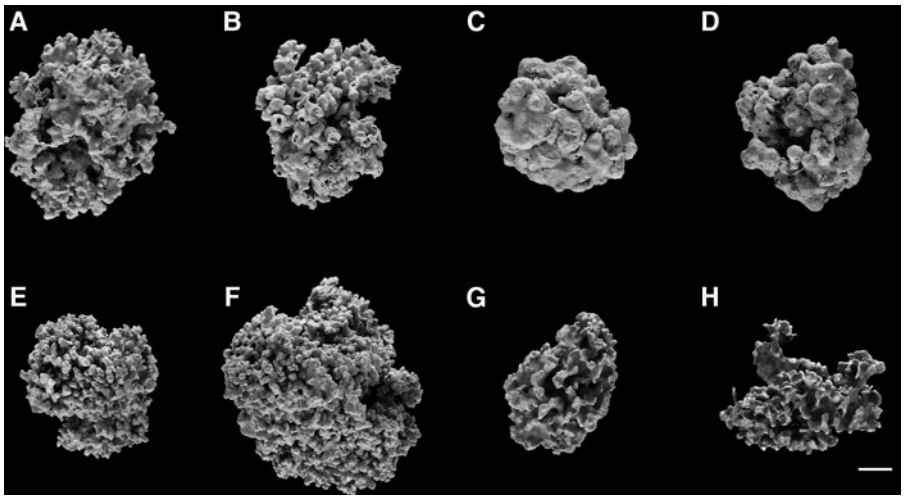


Fig. 4. Morphology of rhodoliths collected at Arvoredo (MPA), Brazil. Letters A–B: *Lithothamnion crispatum*; C–D: *Lithophyllum atlanticum*; E–F: *Mesophyllum erubescens*; G–H: *Lithophyllum margaritae*. Scale bar: 1 cm.

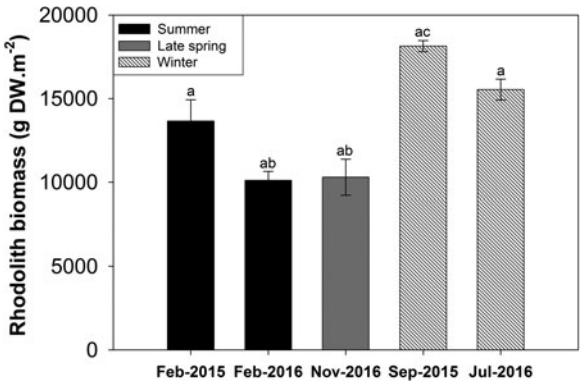


Fig. 5. Total biomass of rhodolith in g m^{-2} in summer (black bars, February 2015 (N = 9) and 2016 (N = 15)), late spring (grey bar, November 2016 (N = 14)) and winter (striped bars, September 2015 (N = 6) and July 2016 (N = 5)) at Arvoredo (MPA), Brazil. Letters indicate results of Kruskal–Wallis multiple comparisons ($P < 0.01$).

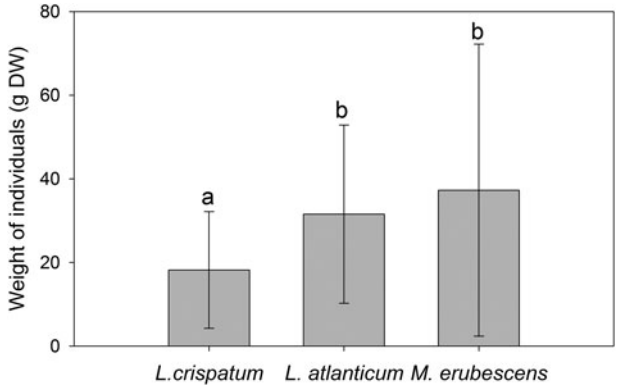


Fig. 7. Mean weight (±SE) per individual (N = 50) of three rhodolith species from Arvoredo MPA, Brazil. Letters indicate results of Kruskal–Wallis multiple comparisons ($P < 0.01$).

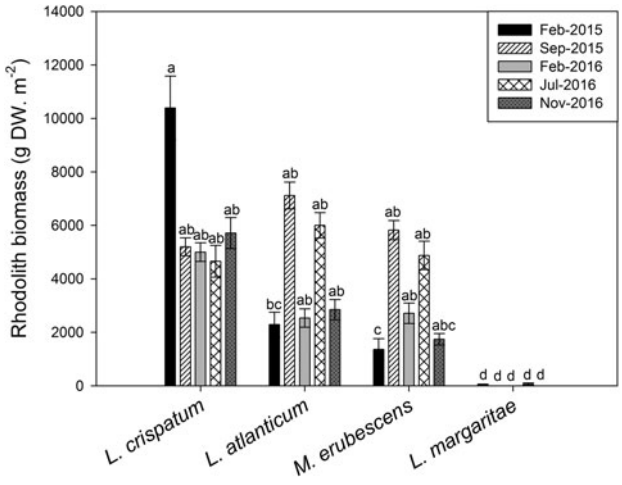


Fig. 6. Mean biomass (±SE) of rhodolith species in summer/late spring months (black and grey bars) and winter (white bars) at Arvoredo (MPA), Brazil. Letters indicate the results of Tukey test.

The mean annual rate of net $CaCO_3$ production was estimated to be 105.97 (±49.26) g m^{-2} $year^{-1}$ and ranged from 44.90 to 193.94 g m^{-2} $year^{-1}$.

Spearman test results indicate negative correlations between total rhodolith biomass and wind speed from all directions except east (Table 1). Biomass of *L. crispatum* was negatively correlated with wind speed from all directions and with the frequency of wind from south quadrants (SE, S and SW). However, it was positively correlated with winds from the north (N and NE). There were no significant correlations between *L. atlanticum*, *M. erubescens* and *L. margaritae* and wind speed for the majority of response variables ($P > 0.05$).

In relation to associated organisms, epiphytic macroalgae occurred only in January 2015, with *Padina gymnospora* presenting major cover with 36.44 (±14.42) g m^{-2}, followed by *Amphiroa fragilissima* (Linnaeus) J.V.Lamouroux with 3.90 (±1.54) g m^{-2} and *Canistrocarpus cervicornis* (Kützing) De Paula & De Clerck with 1.57 (±0.83) g m^{-2} (Supplementary Table S2). Invertebrates increased from February 2015 to November 2016 (Figure 8). However, only the biomass of Annelida ($H = 10.22$; $P < 0.01$) and Mollusca ($H = 10.21$; $P < 0.01$) presented significant differences.

Grouper (macrocarnivores) density varied significantly throughout the survey. Densities increased from 2015 to 2016 ($P < 0.05$, Tukey HSD). No significant difference was found on their biomass ($P > 0.05$, Tukey HSD) (Figure 9).

Grunts (macroinvertebrate feeders) densities showed significant differences considering the factor time ($P < 0.05$, Tukey HSD). Otherwise, biomass did not show significant differences ($P > 0.05$, Tukey HSD). Considering both population descriptors (density and biomass), populations of grunts show a modest decrease throughout the survey (from 2014 to 2016) (Figure 9).

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Table 1. Summary of Spearman correlation results (r) between wind direction and speed and the biomass of rhodoliths. Bold numbers indicate significant values ($P < 0.05$)

	Results of Spearman correlation				
	Total biomass of rhodolith	*L. crispatum*	*M. erubescens*	*L. atlanticum*	*L. margaritae*
N%	−0.042368	**0.508569**	**−0.376957**	**−0.466979**	−0.146253
NE%	0.057138	**0.416837**	−0.251020	**−0.358144**	0.075502
E%	−0.174058	−0.182531	0.085902	−0.172970	0.058079
SE%	**−0.364363**	**−0.375014**	−0.075640	−0.035682	0.193772
S%	−0.061025	**−0.618959**	**0.486569**	0.298285	0.146253
SW%	0.248532	**−0.521163**	**0.581722**	**0.639093**	0.146253
W%	**0.305593**	−0.092043	0.199401	**0.432463**	0.257130
NW%	0.267189	**0.606365**	−0.281804	−0.126171	−0.146253
N ($m\,s^{-1}$)	**−0.492788**	**−0.315776**	−0.219458	−0.158355	0.060719
NE ($m\,s^{-1}$)	**−0.364363**	**−0.375014**	−0.075640	−0.035682	0.193772
E ($m\,s^{-1}$)	−0.273875	**−0.535934**	0.147782	0.170015	0.146253
SE ($m\,s^{-1}$)	**−0.682161**	**−0.333190**	−0.234694	**−0.417381**	−0.146253
S ($m\,s^{-1}$)	**−0.492788**	**−0.315776**	−0.219458	−0.158355	0.060719
SW ($m\,s^{-1}$)	**−0.492788**	**−0.315776**	−0.219458	−0.158355	0.060719
W ($m\,s^{-1}$)	**−0.402300**	**−0.476696**	0.003965	0.047343	0.013200
NW ($m\,s^{-1}$)	**−0.402300**	**−0.476696**	0.003965	0.047343	0.013200

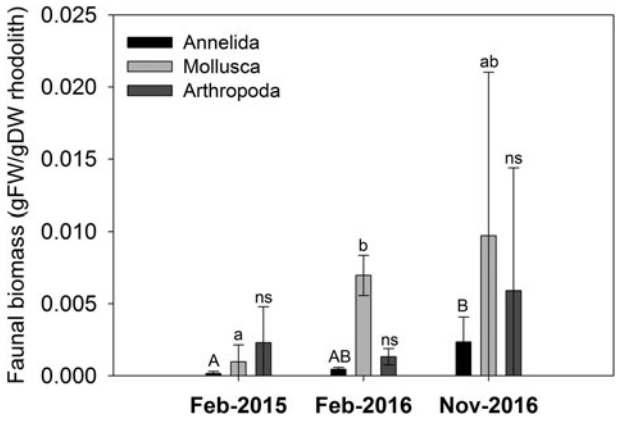


Fig. 8. Mean biomass (±SE) of Annelida, Mollusca and Arthropoda in gFW/gDW in February 2015 (N = 9), February 2016 (N = 3) and November 2016 (N = 3) at Arvoredo MPA, Brazil. Letters indicate results of Kruskal–Wallis multiple comparisons ($P < 0.01$).

Productivity and respiration

The mean rates (±SD) of gross production (GP) in *L. crispatum* varied between 0.112 (±0.056) and 0.554 (±0.149) µmol O_2 $cm^{-2}\,h^{-1}$, while in *P. gymnospora* they ranged from 0.078 (±0.033) to 0.324 (±0.017) µmol O_2 $cm^{-2}\,h^{-1}$ (Figure 10). Significant differences were detected in GP and respiration between species and times of incubation (F: 9.57; $P < 0.01$, Supplementary Table S1). *Lithothamnion crispatum* alone had the highest values of GP and respiration at all light levels. However, *L. crispatum* and *P. gymnospora* together (L + P) had the lowest values of GP, reaching only 0.214 (±0.077) µmol O_2 $cm^{-2}\,h^{-1}$.

Calcification

All light net calcification rates were positive and all dark net calcification rates were negative in all treatments (Figure 11). Significant differences in light and dark net calcification rates were detected in all species and at all times of incubation (Supplementary Table S1). Light net calcification rates of rhodoliths alone were the highest values at all light levels, reaching 0.293 (±0.014) µmol $CaCO_3$ $cm^{-2}\,h^{-1}$, while *P. gymnospora* reached only 0.063 (±0.014) µmol $CaCO_3$ $cm^{-2}\,h^{-1}$ (Figure 11). The net calcification rates of *L. crispatum* and *P. gymnospora* together were similar to the values for *P. gymnospora* alone. Net dissolution in the dark was significantly higher in *L. crispatum*, reaching 0.071 (±0.005) µmol $CaCO_3$ $cm^{-2}\,h^{-1}$. The diel net $CaCO_3$ precipitation of *L. crispatum* was 8.7 ± 2.9 g $CaCO_3$ $m^{-2}\,d^{-1}$.

Discussion

While variations in hydrodynamic conditions seem to cause the change in seasonal abundance and composition of rhodoliths in the Arvoredo rhodolith bed, the genesis of associated benthic community variability seems to be more complex. Integrated analysis indicates changes in the abundance of macroalgae and animals which may have an impact on community trophic structure. Trophic cascade effects caused a top-down control, structuring a benthic community with a reduced abundance of fleshy macroalgae, as was observed in different reef systems (Littler *et al.*, 1995; Stachowicz & Hay, 1996; Scherner *et al.*, 2010). Suppression of fleshy algae canopy cover seems to increase primary production potential, which contradicts the functional group theory (Steneck & Dethier, 1994).

Community structure

The rhodolith bed at Arvoredo represents the southernmost limit of rhodolith bed distribution in the tropical South Atlantic. *Lithothamnion crispatum*, the most abundant rhodolith species in summer, is frequently cited for Brazilian beds (Amado-Filho *et al.*, 2012*b*, 2017; Pascelli *et al.*, 2013; Cavalcanti *et al.*, 2014). Its associated flora was reduced to zero after 2015 and had a

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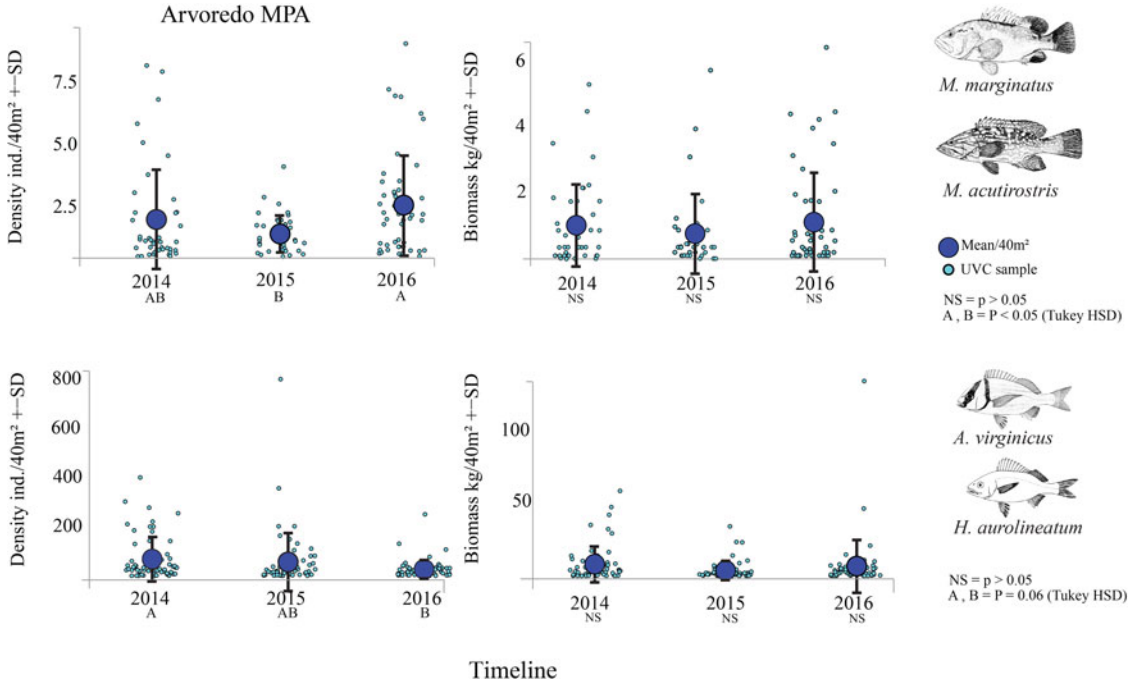


Fig. 9. Arvoredo MPA densities and biomass of Carnivores (A) and Invertebrate feeders (B).

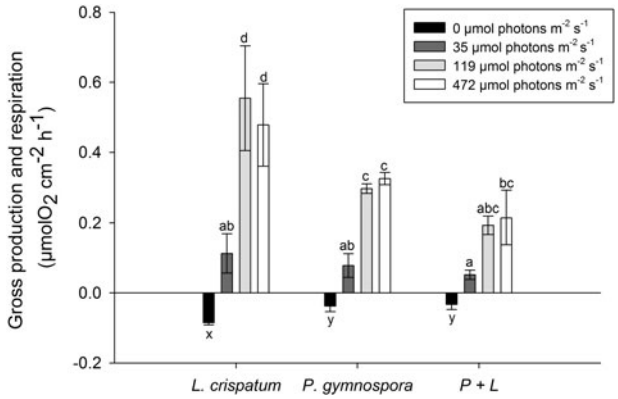


Fig. 10. Mean (±SE) gross production (N = 4) and respiration (N = 3) of *L. crispatum*, *P. gymnospora* and *P. gymnospora* and *L. crispatum* together (L + P) in summer at Arvoredo MPA, Brazil. Shades of grey indicates mean PAR values. Letters indicate results of Newman–Keuls *post-hoc* test ($P < 0.01$).

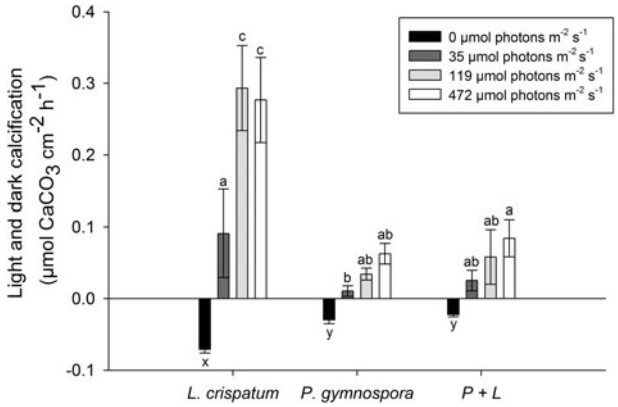


Fig. 11. Mean (±SE) light (N = 5) and dark (N = 3) calcification of *L. crispatum*, *P. gymnospora* and *P. gymnospora* and *L. crispatum* together (P + L) in summer at Arvoredo MPA, Brazil. Shades of grey indicates mean PAR values. Letters indicate results of Newman *post-hoc* test ($P < 0.01$).

lower abundance compared with other tropical formations (i.e. Amado-Filho *et al.*, 2007; Riul *et al.*, 2009; Bahia *et al.*, 2010). The annual production of the Arvoredo bed (106 g m^{-2} $year^{-1}$) is lower than reported values of tropical beds, such as in Abrolhos (1000 g m^{-2} $year^{-1}$: Amado-Filho *et al.*, 2012*a*). However, it is similar to the neighbour bed in Deserta Island, for *Lithophyllum* sp. (55–136.3 g m^{-2} $year^{-1}$) (Gherardi, 2004), and close to reported values for temperate beds (490 g m^{-2} $year^{-1}$ in Martin *et al.*, 2007; 200 g m^{-2} $year^{-1}$ in Teichert & Freiwald, 2014).

Rhodolith species composition

Total biomass of rhodoliths was higher in winter months. However, rhodoliths grow slowly and do not respond as rapidly to environmental factors as faster growing macroalgae (Wilson *et al.*, 2004; Francini-Filho *et al.*, 2013). Despite their slow growth (Basso, 2012), there is no evidence that rhodoliths lose a significant amount of biomass annually. Therefore, major changes in their abundance must be related to local dynamics and rhodolith displacement. To analyse the influence of environmental factors on their development, it is necessary to consider data from the previous season. Thus, the mean values of wind direction and speed during the six-month window prior to each collection were used. The correlation analyses between these data and total rhodolith biomass indicate a negative correlation with wind speed, which suggests that stronger currents generated by winds could cause scattering of most rhodoliths. The same results were also found in *L. crispatum*, which is lighter, more fragile and more branched than the other three species. Pascelli *et al.* (2013) performed sampling in the summer and winter at Rebio Arvoredo and reported a reduction in rhodolith diameter in winter, suggesting that storms in this season could have caused breakage. Here, the history of wind course before the period of collections revealed that wind changes are not restricted to seasons and even so, rhodolith biomass is responsive.

In relation to wind direction, *L. crispatum* was positively correlated with north quadrants and negatively correlated with south quadrants, whereas *L. atlanticum* had the opposite response.

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When the frequency of winds from the north quadrant is higher, the lighter, more fragile and branched rhodoliths (i.e. *L. crispatum*) tend to accumulate at the sampling site in the north portion of Arvoredo Island. In contrast, *L. crispatum* had the highest biomass in February 2015, and the previous months had a lower wind speed in all quadrants. Plausible mechanisms of seasonal rhodolith abundance changes may include the displacement of lighter rhodoliths in the north portion of the island, or the selective burial of heavier and sleeker morphotypes, *L. atlanticum* and *M. erubescens*. When the south wind returns, lighter rhodoliths were scattered and heavier rhodoliths unearthed. Even if rhodolith composition is correlated with wind direction and speed, other environmental factors such as bottom currents and depth could influence it as well (Sañé *et al.*, 2016). Due to this, we suggest future monitoring of other environmental changes alongside community composition observation.

Associated fauna

The faunal biomass had lower values for Mollusca in February 2015 when the mean wind speed of previous months was lower and local currents consequently decreased. These results oppose those of previous studies, which found that higher current velocity disturbs the settlement of motile animals (Maughan & Barnes, 2000; Hinojosa-Arango *et al.*, 2009). This suggests that other abiotic or biotic factors could be related to the decrease in faunal biomass. Reef fish are key players that directly and indirectly influence the dynamic balance of marine food webs (Dunne *et al.*, 2004; Bellwood *et al.*, 2017). Their biology (e.g. feeding behaviours, functional roles/trophic affinities) can influence variations in biomass and density levels of populations in the trophic web of rocky and coral reef systems (Dunne *et al.*, 2004; Bellwood *et al.*, 2017). The significant increase in invertebrate community biomass detected after 2015 raised two hypotheses regarding the probable influence of reef fish. (1) Top-down control (Worm & Myers, 2003; Begon *et al.*, 2006; Baum & Worm, 2009): population increase mediated by predators in the studied area over time (2015–2016). (2) Top-down control associated with the 'fear effect' (Worm & Myers, 2003; Côté *et al.*, 2014; Heupel *et al.*, 2014): both are mediated by the presence of a recently detected alien predator inhabiting the rhodolith beds in the studied area (more details below).

Considering the first hypothesis, the modest increase in predator populations in the Arvoredo MPA during the past three years may have reduced densities and biomass of fish populations of subjacent levels in the trophic web, such as grunts (i.e. Haemulidae). These reef fish feed mainly on macroinvertebrates (e.g. annelids, molluscs and crustaceans) and their population decrease may have caused an increase in their prey's densities and biomass ('prey release effect') (Friedlander & DeMartini, 2002; Heithaus *et al.*, 2008). However, populations of grunts in the Arvoredo MPA are still much higher than groupers, which leads us to assume that predator–prey interactions may not have been the indirect cause of the increase in invertebrate populations. Moreover, considering fish biogeography, fish populations inhabiting thresholds of distribution, such as the Arvoredo MPA (Anderson *et al.*, 2015; Anderson, 2017), tend to have more pronounced fluctuations in their populations caused by stochastic mechanisms (e.g. oscillations in temperature during harsh winters) (Almada & Faria, 2004; Anderson, 2017).

In regards to the second hypothesis, the presence of an alien species may cause a dramatic effect in local populations over a short period of time (Anderson, 2017; Andradi-Brown *et al.*, 2017). In the summer of 2015, the black-spotted snake eel *Quassiremus ascensionis* (Studer, 1889) was first recorded for the Southern Atlantic, inhabiting the rhodolith bed of Rancho Norte, Arvoredo MPA (Anderson *et al.*, 2015). In 2016, *Q. ascensionis* was detected in all parts of the Arvoredo MPA (Arvoredo Is., Deserta Is. and Galé Is.). This species is a cryptic predator (e.g. it preys with its body buried in the substrate and only the head showing), preying mainly on small fish and invertebrates (Froese & Pauly, 2016). The presence of a new predator may have influenced fluctuations in populations of small serranids, blennies and gobies (e.g. *Serranus baldwinni*, *Diplectrum radiale*, *Parablennius marmoreus*, *Parablennius pilicornis*, *Hyplerochilus fissicornis*, *Coryphopterus glaucofraenum*) and thus, a subsequent increase in density and biomass of their prey (annelids, molluscs and crustaceans).

Further investigations and long-term monitoring are necessary to understand the mechanism involved in population dynamics of organisms inhabiting the rhodolith beds of southern Brazil. Beyond trophic dynamics, temperature changes can also influence faunal abundance. In summer 2015, the mean seawater temperature registered at Rebio Arvoredo was the highest it had been in three years (Figure 3), whereas the coolest was in winter 2016. This could be related to the El Niño in 2015/2016, resulting in substantial environmental changes. This event could cause altered rain regimes, winds and marine currents, which could consequently influence temperature (Freire *et al.*, 2017). In 2015, the mean summer temperature was 26°C and the winter had few cold fronts when compared with the other years (Freire *et al.*, 2017). This value is much higher than the mean seawater temperature (22°C) of this region (Gherardi, 2004; Pascelli *et al.*, 2013). Climate changes and temperature increase can cause a reduction in survivorship of invertebrates and fishes (Vinagre *et al.*, 2018). The survival, body size and larval production of the polychaeta, *Streblospio benedicti* Webster, are higher in winter–spring than summer–autumn conditions (Levin & Creed, 1986). Marine heatwaves have also caused a decrease in abundance of the large gastropod, *Lunella* off the west coast of Australia (Smale *et al.*, 2017). McConnico *et al.* (2017) reported an increase in molluscs in the summer following an increase in macroalgal biomass in a rhodolith bed off Baja California, Mexico. Here, the opposite occurred. The variable responses of faunal behaviour to temperature and wind indicate that experiments involving the faunal community and larger replication are necessary. This will improve our knowledge of the environmental conditions that influence the local faunal biomass and explain the observed temporal changes. Further investigations on the dynamics of species composition by phylum in addition to biomass would contribute additional important information about community function.

Associated macroalgae

The occurrence of epiphytes only in February 2015 could indicate that higher temperature and lower wind speed, and thus, lower hydrodynamics, favoured fleshy algal growth, particularly *Padina gymnospora*. This species can grow in tropical temperatures similar to the ones that we recorded in the summer (Scherner *et al.*, 2016). Lower hydrodynamics have been associated with an increase in abundance and richness of biomass of maerl-associated algal species (Hily *et al.*, 1992; Hinojosa-Arango *et al.*, 2009). However, although smaller in quantity, previous data of total epiphyte biomass from February 2002 ($11.41\ g \times m^{-2}$ Horta, 2002, unpublished data) and February and July of 2008 (0.9 and $0.16\ g \times m^{-2}$, Pascelli, 2009) show that the occurrence of epiphytes before February 2015 was not so rare (Supplementary Figure S2).

Coralline algae can adopt strategies to reduce the growth rate and recruitment potential of fleshy macroalgae (Vermeij *et al.*, 2011), aside from producing allelopathic substances (Gross,

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2003; Kim *et al.*, 2004). Suzuki *et al.* (1998) suggested that an allelopathic non-polar substance produced by *Lithophyllum* spp. destroys zoospores of the brown alga *Laminaria religiosa* Miyabe, which contributes to the predominance of this crustose coralline alga in the coastal region of the Northern Japan Sea. However, the abrupt decrease after 2015 indicates a combination of climate events referred to above and an increase in invertebrate biomass that possibly played roles in the control of epiphytes.

The association with macroinvertebrates can benefit rhodoliths because some of these animals feed on epiphytes (Legrand *et al.*, 2017). The limpet *Patella longicosta* Lamarck has a mutualistic relationship with the crustose alga *Ralfsia verrucosa* (Areschoug) Areschoug that prevents the overgrowth of *Ulva* sp. and other grazers (McQuaid & Froneman, 1993). Mesograzers such as polychaetes and gastropods have herbivorous members and have been related to biomass control at the Rebio Arvoredo bed (Scherner *et al.*, 2010). Snails can be advantageous for macrophytes, reducing the density of bacteria and epiphytic algae that may be potentially deleterious to the host due to shading of the thallus and increased competition for resources (Underwood *et al.*, 1992; Stachowicz & Whitlatch, 2005). Some animals can even feed on rhodoliths without causing mortality. The chiton *Choneplax lata* Guilding grazes on the coralline alga *Porolithon pachydermum* (Foslie) Foslie and stimulates new meristematic activity, and also removes sporelings of competitive epiphytes (Littler *et al.*, 1995).

Community production/consumption balance

In this study, the association of rhodoliths with herbivorous invertebrates probably benefits the rhodoliths. Experimental results showed that the interaction between *Padina gymnospora* and *L. crispatum* caused a decrease in photosynthetic and calcification rates when compared with the treatments where these organisms were incubated alone. However, photosynthesis of *L. crispatum* alone had the highest value. A comparative study showed that red algae experience increased photosynthetic rates compared with green and brown algae at depths down to 10 m, which indicates that they are better adapted chromatically to photosynthesize in this range (Dring, 1981). This could be related to the fact that red coralline algae are found in a wide range of depths and irradiances, from shallow tropical coral reefs (PAR >1500 µmol photons m^{-2} s^{-1}) (Burdett *et al.*, 2014) to great depths (>200 m PAR = 0.0015 µmol photons m^{-2} s^{-1}) (Littler *et al.*, 1986). Light and dark calcification results display a pattern similar to the one observed for gross photosynthesis and respiration.

Epibiosis is usually considered harmful to the host alga because of the competition for light and nutrients, which results in a decrease in growth and reproduction (Amsler, 2008). Competition among algae for one or more limited resources may be direct (interference competition) or indirect, through the depletion of a resource (exploitative competition), and may occur within or between algal species (Reiskind *et al.*, 1989). *Padina gymnospora* may shade the rhodolith and thus decrease the light availability for photosynthesis. In earlier studies, the effects of light reduction generated by sedimentation caused a decrease in *L. crispatum* abundance (Riul *et al.*, 2008). Moreover, numerous epiphytic organisms generally colonize rhodolith beds (Grall *et al.*, 2006; Peña *et al.*, 2014). Epiphytes modify the interface between the hosting seaweed and the external environment, creating greater heterogeneity at the seaweed surface (Wahl, 2008). This may create a physical barrier for light absorption (Drake *et al.*, 2003) and carbon uptake (Sand-Jensen, 1977). Light absorption by epiphyte pigments lowered the photosynthetic rate of *Cladophora glomerata* (Linnaeus) Kützing when irradiance was below 200–500 µmol photons m^{-2} s^{-1} (Dodds, 1991). Rohde *et al.* (2008) reported that epiphytes modified the surface of the *Fucus* thallus, creating a barrier for nutrient uptake and gas exchange.

The presence of *P. gymnospora* not only caused a decrease in photosynthesis, but also in calcification. This suggests that the shade caused by *P. gymnospora* damaged rhodolith calcification. The calcification of the alga *Hydrolithon reinboldii* was 29% greater in high (650 µmol quanta m^{-2} s^{-1}) than in low (150 µmol quanta m^{-2} s^{-1}) irradiance (Comeau *et al.*, 2014). The net dissolution that occurred at night confirmed the importance of light in the calcification process of *L. crispatum*. Approximately 50% of carbon fixed in photosynthesis is lost in dark respiration (Borowitzka & Larkum, 1987). Calcification and inorganic carbon uptake predominately occur in the light (Cornwall *et al.*, 2017). Although calcification is correlated to photosynthesis, there are also metabolically controlled photosynthesis-independent ion pumps and channels with the efflux of Ca^{2+} and H^{+} outside the cells in the dark and influx under light (Hofmann *et al.*, 2016). The proton pumps in light are important to pH regulation at the thalli surface and calcification under ocean acidification (McNicholl *et al.*, 2019).

The experiment showed the negative effect of overgrowth of *P. gymnospora* on the rhodolith surface, which coincided with a decrease in invertebrates. In the following years, an opposite pattern was observed. Epiphytes disappeared, the biomass of invertebrates increased, but invertebrate feeders slightly decreased. These effects on the rhodolith bed community are probably the result of environmental changes that occurred during the years of this study. Changes in temperature and wind regimes were detected, which not only can cause altered food webs, but also changes in rhodolith composition and biomass. The variation in characteristics of the community during these two years and the environmental changes make us aware of how climate change events can affect ecosystems.

Conclusion

We conclude that environmental factors, such as wind and temperature, as well as biological factors, can cause differences in community structure over time. As a consequence of these changes, the biomass of macroinvertebrate feeders decreases, which increases the biomass of their prey. As a result, these organisms (in the major part herbivores) can feed on rhodoliths, which could possibly be one of the causes of the disappearance of macroalgae after 2015. The growth of *P. gymnospora* on *L. crispatum* detected in summer 2015 caused a decrease in photosynthetic and calcification rates of the rhodolith. These results reinforce the importance of the association with herbivores for the control of epiphytic organisms on the rhodolith surface. More long-term experiments are necessary to improve the knowledge about the role of environmental changes on rhodolith bed communities and the response of associated sessile and motile organisms. Finally, this study suggests that a healthy trophic structure with abundant top predators can indirectly increase rhodolith fitness, and potentially their resilience to climate change and local threats.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315420000284.

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