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# Colonization and growth of crustose coralline algae (Corallinales, Rhodophyta) on the Rocas Atoll

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## ABSTRACT

Crustose coralline algae play a fundamental role in reef construction all over the world. The aims fo this study were to identify and estimate the abundance of the dominant crustose coralline algae in shallow reef habitats, measuring their colonization, growth rates and productivity. Crusts sampled from different habitats were collected on leeward and windward reefs. Discs made of epoxy putty were fixed on the reef surface to follow coralline colonization and discs containing the dominant coralline algae were fixed on different habitats to measure the crusts' marginal growth. The primary production experiments followed the clear and dark bottle method for dissolved oxygen reading. *Porolithon pachydermum* was confirmed as the dominant crustose coralline alga on the Rocas Atoll. The non-cryptic flat form of *P. pachydermum* showed a faster growth rate on the leeward than on the windward reef. This form also had a faster growth rate on the reef crest (0.05 mm.day$^{-1}$) than on the reef flat (0.01 mm.day$^{-1}$). The cryptic protuberant form showed a trend, though not significant, towards a faster growth rate on the reef crest and in tidal pools than on the reef flat. Colonization was, in general, very slow as compared to that presented by other reef studies. *P. pachydermum* was a productive crust both in non-cryptic and cryptic habitats.

## RESUMO

As algas calcárias incrustantes exercem um papel fundamental na construção de recifes ao redor do mundo. Neste trabalho os objetivos foram: identificar e estimar a abundância da alga calcária incrustante dominante nas partes rasas do recife, verificando suas taxas de colonização, crescimento e produtividade. Crostas de diferentes habitats foram estudadas em locais a barlavento e sotavento. Discos feitos com massa epóxi foram fixados na superfície do recife para acompanhar a colonização das algas calcárias e discos contendo a alga calcária dominante foram fixados em diferentes habitats para medir o crescimento de suas margens. Os experimentos de produtividade seguiram o método de frascos claros e escuros para leitura de oxigênio dissolvido. *Porolithon pachydermum* foi confirmado como a espécie de alga calcária incrustante dominante no recife do Atol das Rocas. O local abrigado apresentou maior crescimento da forma plana e típica de crista de *P. pachydermum* em relação ao exposto. Esta forma também teve um crescimento maior na crista recifal (0,05 mm.dia$^{-1}$) do que no platô (0,01 mm.dia$^{-1}$). A forma protuberante e típica de fendas de *P. pachydermum* apresentou tendência, não significativa, para maior crescimento na crista e poça em relação ao platô. A colonização apresentou baixas coberturas quando comparada a outros estudos recifais. *P. pachydermum* é uma planta produtiva tanto em ambientes ensolarados como sombreados.

Descriptors: Crustose coralline alga, Growth rates, Rocas Atoll.
Descritores: Alga calcária incrustante, Taxas de crescimento, Atol das Rocas.

## INTRODUCTION

Crustose coralline algae (Corallinales, Rhodophyta) have been found in the fossil record ever since the beginning of the Paleozoic as important constructors of biological reefs (Bosence, 1983), and continue so to act in the shallow and turbulent water of contemporary reefs (Adey & Vassar, 1975). The variation in shape and growth of framework building coralline algae and their role in reef structure is directly related to hydrodynamic energy (Steneck, 1986; Gherardi & Bocense, 2001). Leeward sites favor fast vertical growth, characterized by protuberant and branched shapes, whereas at windward sites the growth of coralline algae is slower, flat and compact shapes are favored and thick crusts form dense constructions (Adey, 1978; Bosence, 1983; Gherardi & Bosence 1999; 2001).

The crustose coralline algae that cover much of the living surface of many reefs in the Atlantic and Pacific Oceans are a fundamental element in the contemporary construction of these reefs, serving as a consolidated substratum, favoring the establishment and the development of other benthic organisms (Morse, 1992). In the Abrolhos archipelago, Brazil, the abundance of crustose coralline algae accounts for from 30 to 50% of the living surface of the reefs (Villaça & Pitombo, 1997; Figueiredo *et al*., 1997, 2000). In St. Croix, in the Caribbean Sea, crustose coralline algae occupy nearly 30% of the living surface (Adey, 1975). On the Great Barrier Reef, the covering of crustose coralline algae varies from 36 to 55% (Fabricius & De'ath, 2001). On the reefs of Waikiki, Oahu Island, Hawaii, these algae cover 39% of the surface and exceed other organisms in abundance.

Water temperature, desiccation, availability of light and intensity of grazing by herbivores are the main factors that influence the rates of crustose coralline algal growth (Adey, 1970; Littler & Doty 1975; Littler & Littler 1984; Steneck, 1990, 1997; Figueiredo *et al*., 2000). Some coralline algae exhibit a cell sloughing that occurs naturally as part of the growing and aging processes and also when there is a thick epiphyte cover. Possibly, this is a physical anti-fouling mechanism, giving corallines a competitive advantage over fouled organisms (Keats *et al*., 1994; Figueiredo *et al*., 1997; Steneck, 1997; Villas Bôas & Figueiredo, 2004). Thus it is that crustose coralline algae are able to dominate on some reefs.

Little is known about the colonization, growth rates and productivity of crustose coralline algae in tropical reef environments. Adey & Vassar (1975) studied their colonization and growth rates on the reefs of the Caribbean St. Croix, and Figueiredo (1997) on reefs in the Brazilian Abrolhos archipelago. Matsuda (1989) measured their growth rates on the subtropical reefs of Ryukyu Islands. Littler & Littler (1984) tested inhibition and saturation levels for photosynthesis on reefs in the Atlantic Ocean, while Littler & Doty (1975) measured the productivity of *Porolithon* crusts on tropical Pacific reefs.

According to Gherardi & Bosence (2001) the Rocas Atoll differs from other reefs situated in the Caribbean Sea and Indo-Pacific Ocean because it is mainly composed of crustose coralline algae and does not present evidence of the joint activity of coralline algae and corals as constructors of the reef. On this reef, the coralline alga *Porolithon cf. pachydermum* is a dominant organism and the primary reef constructor, being the basis for the development of secondary constructors such as vermetid gastropods and encrusting foraminifera, mainly *Homotrema rubrum* (Gherardi & Bosence, 1999). The Rocas Atoll is a Marine Biological Reserve that presents a pristine physical and biological environment. The crustose coralline algae of this reef have been little studied and are thus deserving of detailed research, not only in terms of taxonomy but also as regards their ecology, so as to enrich our understanding of their life forms, dynamics and influence on the structure of the reef community. This study had as its objectives: 1) The confirmation of the identification of the dominant species of crustose coralline algae on the Rocas Atoll and a brief description of the specimens studied; 2) Adescription of the relative abundance of the organisms that compose the surface layer at two reef sites and 3) An estimate of the rates of algal colonization, growth and productivity.

## MATERIALS AND METHODS

### The Study Area

Rocas Atoll is the only Atoll situated in the South Atlantic Ocean, at 144 nautical miles from the city of Natal, Rio Grande do Norte, Brazil (3°51'S. and 33°49'W) (Fig. 1). The reef is composed of two arches, the reef-crest on the windward arch being well developed and continuous, and the leeward arch, less developed and with a discontinuous crest (Kikuchi & Leão, 1997). The relative constancy in the direction and speed of the trade winds and waves results in intense hydrodynamic energy on both the windward and leeward arches (Gherardi & Bosence, 1999). The tide regime has a maximum range of 3.8 m and causes very strong tidal currents over the reef (Kikuchi & Leão, 1997, Gherardi & Bosence, 1999).

Two sites were chosen for this study: one situated on the windward arch, on the southeast of the reef, exposed to the winds and constant waves during most of the year, and the second, situated on the leeward arch on the west of the reef and sheltered from most of the wave action (Fig. 1). The reef habitats studied within each site were: 1) the reef crest, which has an irregular surface highly exposed to light during long periods of low tides, though constant wave action keeps this environment damp; 2) the reef flat, which is 30 m from the reef crest, towards the inner part of the reef and which waves do not reach at low tide; 3) reef crevices, including cracks, holes and grooves forming channels that maintain the water circulation inside the reef even at low tide; 4) a tidal pool, found within the leeward reef-flat and which remains constantly full of water even at low tide, and 5) the reef pool edges, which are on the lowest part outward from the reef crest. Fieldwork took place between June and July of both 2002 and 2003.

### Coralline Algae Taxonomy

Cryptic and non-cryptic forms of coralline algal samples were collected and preserved in formaldehyde 4% in seawater, decalcified in 10% nitric acid, dehydrated in alcohol series, embedded in hystoresin, sectioned with a microtome and stained for Optical Microscopy analysis (Moura *et al*., 1997). Taxonomic identification of coralline algae was based on Woelkerling (1988), Penrose & Woelkerling (1988), Womersley (1996) and Littler & Littler (2000).

### Abundance of Sessile Organisms

To identify potential competitors for space, percentage cover of sessile organisms was estimated on both leeward and windward reefs using a line transect measuring 10m in length, parallel to the reef front, with 30 random points for each habitat. Specimens were quantified and collected from the surface of the reef crest, the reef flat, crevices and tidal pools.

### Colonization, Growth and Productivity Experiments

The colonization experiment used seven flat discs, 3 cm in diameter, made with epoxy resin (Tubolit), fixed in non-cryptic areas of both leeward and windward reef-flats for a period of 40 days. To estimate percentage cover of coralline algae, a Petri dish marked with 15 random points was placed upon each colonized disc.

Growth rates were measured for crustose coralline algae from cryptic and non-cryptic habitats. Coralline algae were cleaned of epiphytes and cut into a spherical shape, and the initial size measured taking an average of two perpendicular diameters (mm). One piece of the each crust was placed onto a disc prepared with epoxy resin and numbed (n=6). Discs were fixed on reefs with epoxy resin. In the first experiment, the non-cryptic form was transplanted to both sites, crusts from the reef crest were fixed on reef-crest and crusts from the reef flat were fixed on the reef flat. A second experiment was set up on the windward site only; the cryptic form was transplanted to the reef crest, tidal pools and reef flat. After a period of 40 days the discs were retrieved and preserved in plastic bags with 4% formaldehyde. Measurements were taken to estimate the relative growth rate (RG), calculated by the difference between the logarithms of the final and initial diameters (Df and Di, respectively) of the algae, divided by the number of days the experiment lasted, by using the formula RG = (ln Df – ln Di) / day, recommended by Kain (1987).

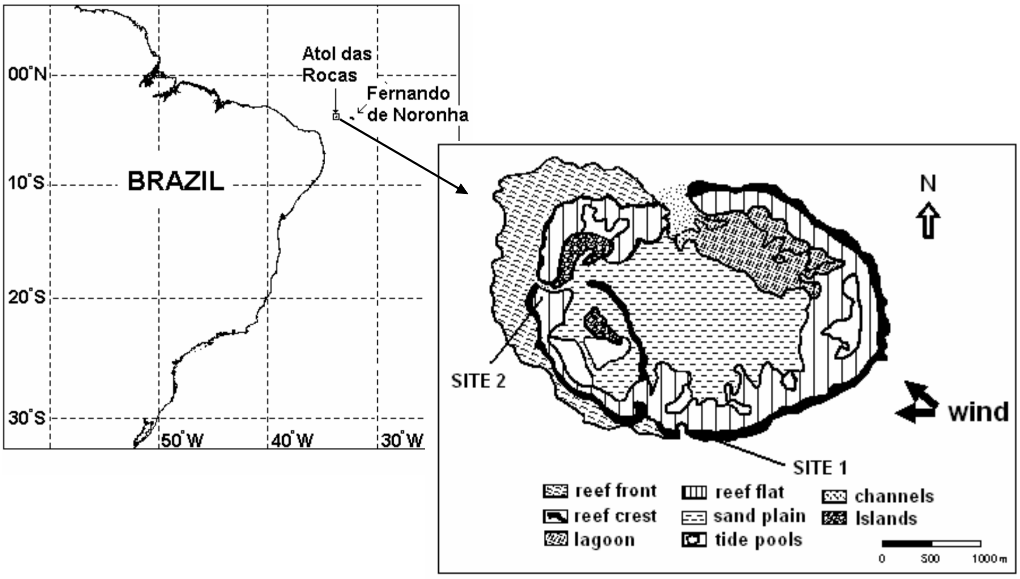


Fig. 1. Study area.

The primary production experiments followed the clear and dark bottle method for dissolved oxygen reading (Thomas, 1988). Biological Oxygen Demand (BOD) bottles of 300ml were used for sample incubation. Equivalent levels of irradiance found on the reef habitats studied were used and two different experiments were carried out for each crust form: one compared 100% and 38% and another compared 100% and 16 % of total irradiance. Clear bottles were used to measure photosynthesis under total irradiance (100%), and shaded bottles covered with a black nylon screen to measure photosynthesis under 38% and 16% of total irradiance. Dark bottles covered with aluminium foil were used to measure respiration rates. One initial bottle was kept filled with seawater only to be compensated for phytoplankton production.

Crust samples of standard volume of 3 to 5 ml were previously cleaned of epiphytes and boring organisms. Seawater was collected before dawn, heated to boiling point, cooled to air temperature and filtered. Samples were incubated from 12 to 17:30 h, and the average incident irradiance was measured every half hour. Seawater temperature varied from 28°C to 31°C. Six replicates were used in each treatment for the photosynthesis and three for the respiration. Dissolved oxygen readings were measured using a sensor with a stirrer linked to an oxymeter (YSI 5000) and irradiance measurements were taken with a Li-Cor light meter (LI-1000). Each coralline sample was decalcified in 10% nitric acid and oven-dried at 60°C to correct oxygen readings to dry weight (g). The net photosynthesis and respiration rates were calculated using Thomas' modified formulas (1988).

### Statistical Analysis

Cluster analysis based on the Bray-Curtis similarity coefficient (Valentin, 2000) was applied to the specific composition and abundance of sessile organisms. One-way and two-way analysis of variance (Anova) were tested for significant differences among treatments in the experiments. Samples were randomly collected and independently distributed, though normality of data was not tested because small samples can be taken from highly skewed populations (Sokal & Rohlf, 1980). Homogeneity of variances was previously verified using Cochran's test (Underwood, 1997).

## RESULTS

### Coralline Algae Taxonomy

Crusts found on non-cryptic reef habitats, such as reef-crest and reef-flat, presented a light brown color, flat surface and thick thallus, measuring on average 635 µm on reef crest and nearly half that thickness on the reef flat. Crusts found within cryptic reef habitats, such as crevices and grooves, presented a deep purple color, protuberant surfaces and thinner thallus, measuring on average 260 µm. Both cryptic and non-cryptic forms of coralline algae were of the same species.

*Porolithon pachydermum* (Foslie) Foslie 1909: 57
Basionym: *Lithophyllum onkodes* f. *pachydermum*
Foslie 1904: 5

Thallus (150) 168-358 (635) µm thick with protuberances ranging from 1-3 mm in diameter and 1-2 mm in heigth. Monomerous non-coaxial organization, trichocyst fields disposed horizontally 10-16 µm in width and 20-30 µm in heigth, both on the surface and sunken. Fusion cells and primary pit-connections were present and secondary pit-connections were absent. Conceptacles, uniporated and tetrasporic, in the internal cavity measured 120-175 µm in width and 50-80 µm in heigth (Fig. 2). Algae of crustose habit were frequently perforated by polychaetes in all the reef habitats studied and were associated with the foraminifera *Homotrema rubrum* and vermetid gastropods.

### Abundance of Sessile Organisms

On the leeward site, the reef-crest community was dominated by the crustose coralline alga *P. pachydermum* (93%) (Fig. 3a). On the reef-flat there was a dominance of the red turf alga *Digenia simplex* (Wulfen) C. Agardh, and *P. pachydermum* crust (43% and 47 %, respectively) (Fig. 3b). The tidal pool edge was dominated by *P. pachydermum* (80 %) followed by the red alga *Gelidiella setacea* (Feldmann) Feldmann & Hamel (20%) (Fig. 3c).

On the reef crest of the windward site, the *P. pachydermum* cover was higher (73 %) than that of two other macroalgae, the green *Dictyosphaeria ocellata* (M. Howe) J. L. Olsen and *D. simplex* (Fig. 3d). On the reef-flat, *D. simplex* was dominant (46%) as compared to *D. ocellata* and *P. pachydermum* (both 26 %) (Fig. 3e). The tidal pool was the richest habitat, containing the red alga *Gelidiopsis sp*., polychaete tubes, *P. pachydermum* and the green macroalga *Cladophoropsis membranacea* (C. Agardh) Börgesen (33%) (Fig. 3f).

The similarity analysis of the distribution and abundance of sessile organisms in these six reef habitats studied revealed a high degree of similarity as between the crest habitat of the two sites (RC1; RC2) and the edge of the reef pool (E) (75%). The reef-flat habitat of the two sites (RF1; RF2) formed a second group (70%). The third group distinguished the tide pool habitat (TP) (Fig. 4).

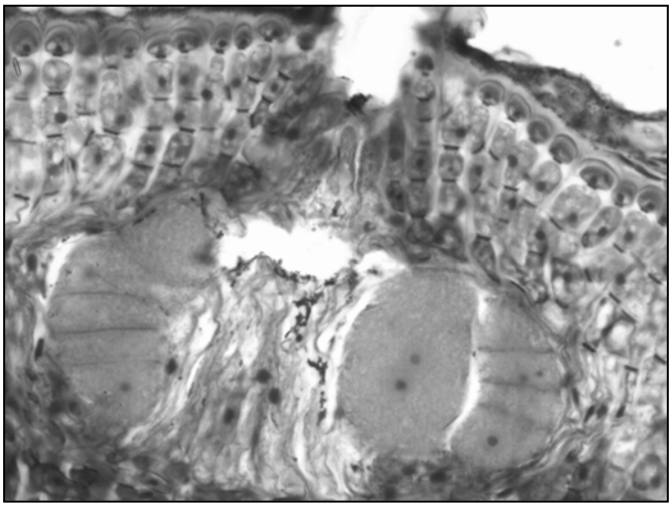


Fig. 2. Uniporate tetrasporic conceptacle of *P. pachydermum* (400x).

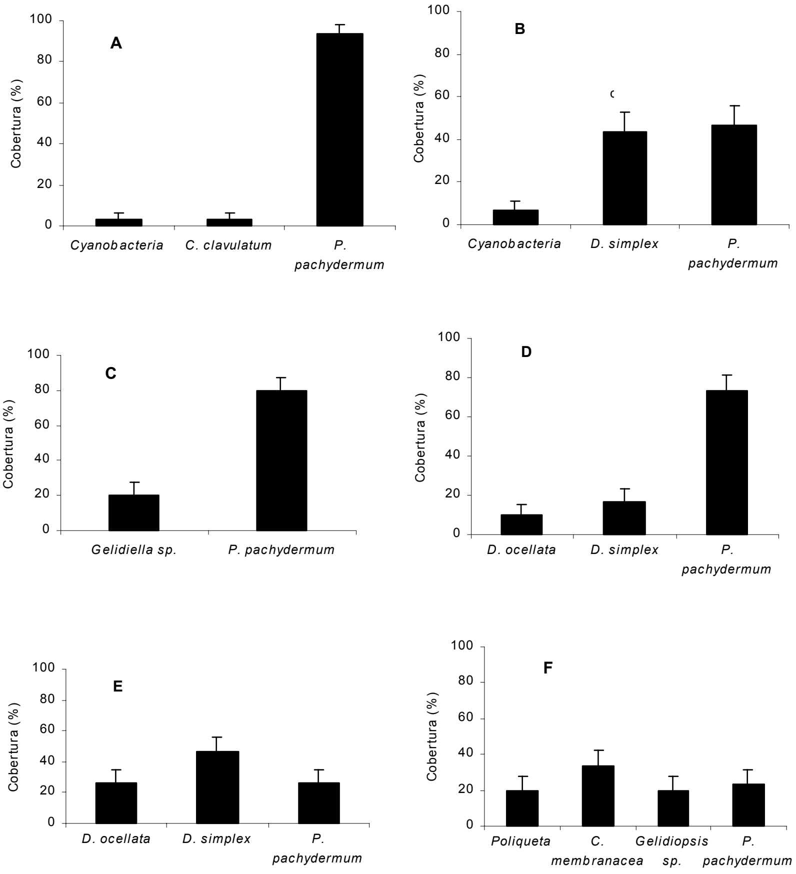


Fig. 3. Abundance of sessile organisms on reef habitats: (A) reef crest, (B) reef flat and (C) reef pool edge of the windward arch and (D) reef crest, (E) reef flat and (F) tide pool of the leeward arch..

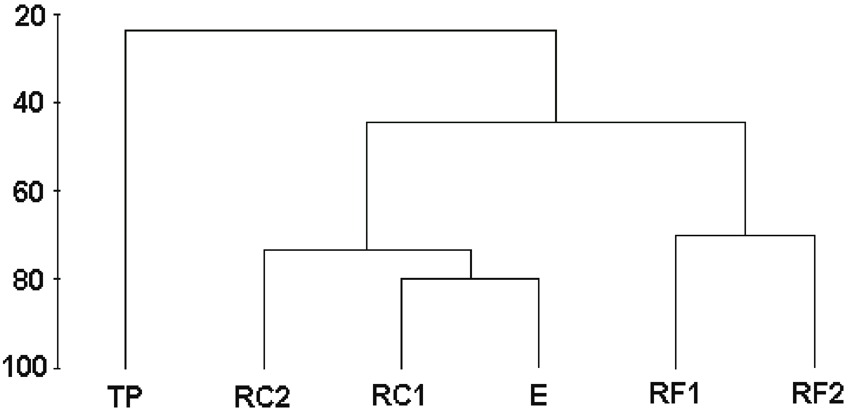


Fig. 4. Similarity between the distribution and abundance of sessile organisms on the reef habitats. (RC1) reef crest, (E) reef pool edge and (RF1) reef flat of the windward arch and (RC2) reef crest; (RF2) reef flat and (TP) tide pool of the leeward arch.

### Colonization, Growth and Productivity of Coralline Algae

At the windward site, the colonization discs did not have any sessile organisms visible on their surfaces after 40 days. In contrast, at the leeward site crustose coralline algae were the only colonizers on discs, 7.22 % of the total disc areas.

The relative growth of the non-cryptic form of *P. pachydermum* showed no significant interaction between the effects of sites and habitats. When the sites were compared, crusts on the leeward site were found to have a significantly faster growth rate than those on the windward site, regardless of habitat. In relation to habitats, the growth rate on the reef-crest was significantly faster than that on the reef flat, regardless of site (Fig. 5, Table 1). However, the cryptic form of *P. pachydermum* did not show any significantly different growth rates as among habitats (Anova, p=0.12) (Fig. 6).

Productivity of the non-cryptic form of *P. pachydermum* was not found to have any significant difference as between 100% and 38% of the incident irradiance, presenting, respectively, 1376 and 522 µmol.m$^{-2}$.s$^{-1}$ (Anova, p=0.66). The following productivity experiment with the non-cryptic form of *P. pachydermum* had negative $O_2$ production under the low irradiance of 228 µmol.m$^{-2}$.s$^{-1}$ as compared to the control of 1431 µmol.m$^{-2}$.s$^{-1}$, respectively, at 16 % and 100 % of incident irradiance, thus showing a significant difference (Anova, p<0.001) (Fig. 7).

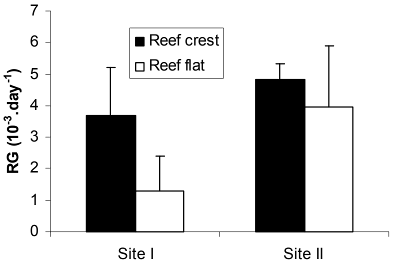


Fig. 5. Marginal growth of the non-cryptic form of *P. pachydermum* on the reef crest and reef flat of the windward (site I) and leeward archs (site II) (RG = relative growth).

Table 1. Analysis of variance of the relative growth of the cryptic form of *P. pachydermum* on reef crest and reef flat habitats of windward and leeward sites.

| Sources of variation | DF | MS | F | P |
|---|---|---|---|---|
| Sites (S) | 1 | 1,31x10$^{-5}$ | 7,934076 | 0,02 |
| Habitat (H) | 1 | 9,4x10$^{-6}$ | 5,686909 | 0,04 |
| S x H | 1 | 3,02x10$^{-6}$ | 1,829509 | 0,21 |
| Error | 8 | 1,65x10$^{-6}$ | | |

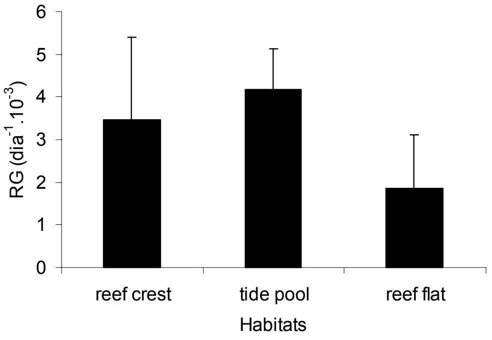
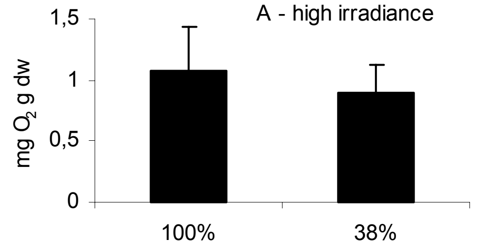


Fig. 6. Marginal growth of the cryptic form of *P. pachydermum* on the reef crest, reef flat and tide pool at windward (site I) (RG = relative growth).



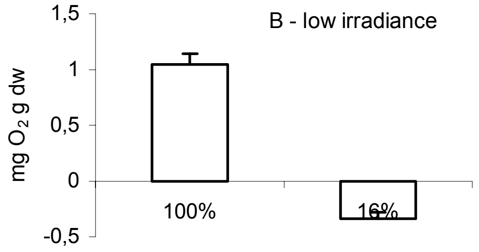
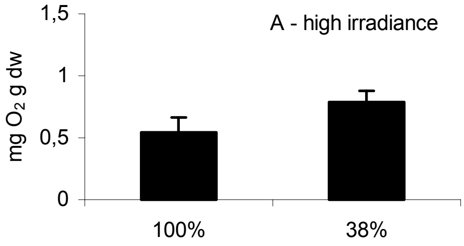


Fig. 7. Productivity of the non-cryptic form of *P. pachydermum* at different levels of irradiance: (A) 38% and 100%; (B) 16% and 100% of incident irradiance (DW= dry weight).

The primary production of the cryptic form of *P. pachydermum* showed no significant difference as between 100 % and 38 % of incident irradiance (Anova, p=0.16), which corresponded to levels of 1387 and 527 μmol.m$^{-2}$.s$^{-1}$, respectively. Although the average net photosynthesis was negative when irradiance was reduced to 16%, there was no significant difference between this and the 100 % irradiance levels, respectively, at 169 and 1062 μmol.m$^{-2}$.s$^{-1}$ (Anova, p=0.07) (Fig. 8).



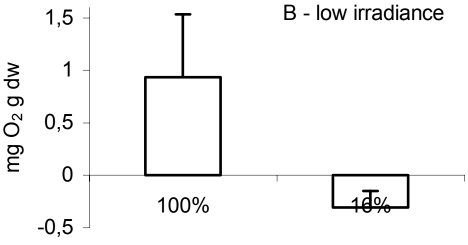


Fig. 8. Productivity of the cryptic form of *P. pachydermum* at different levels of irradiance: (A) 38% and 100%; (B) 16% and 100% of incident irradiance (DW= dry weight).

## DISCUSSION

Gherardi & Bosence (2001) listed *Porolithon cf. pachydermum*, *Lithophyllum* sp., *Lithoporella* sp. and *Sporolithon* sp. as species of coralline algae that occurred on the Rocas Atoll. The identification of *Porolithon* species has been confirmed by the present study. Generally, its thallus characteristics agree with those described for this species in the Caribbean (Littler & Littler, 2000). This taxon may be distinguished from *Hydrolithon* and *Spongites* by the presence of trichocysts distributed horizontally in various parts of the thallus (Penrose & Woelkerling, 1988).

Initially, cryptic and non-cryptic forms of coralline algae were treated as different taxonomic groups, but histology has revealed that they do in fact, belong to the same species. Variety of external morphology is commonly observed in crustose coralline algae and may reflect environmental conditions (Irvine & Chamberlain, 1994). The protuberant thallus may result from adaptations to the degree of exposure to wave energy (Steneck, 1986), thus protuberant crusts were found, in this study, to be restricted to cryptic habitats.

This study has confirmed that *P. pachydermum* is the dominant crustose coralline alga species on the living cover of the Rocas Atoll, as suggested by Gherardi & Boscence (1999). On the highly disturbed reef-crests, the dominance of *P. pachydermum* may be due to its crustose form, since strongly adherent thalli are adapted to intense wave exposure (Steneck, 1986), and erect macroalgae are limited as regards settling and growing, (Steneck & Dethier, 1994). In fact, a high degree of similarity was found as between the reef crest habitats of the two sites.

The leeward and windward reef flats had fewer *P. pachydermum* crusts, and an increasing abundance of *D. simplex*. This alga forms dense turfs, with a thick disc-like base (Littler & Littler, 2000) and may overgrow crusts, thus competition by interference is likely to occur (Olson & Lubchenco, 1990). The reef flat is distant from the wave breaking line, but is exposed to high desiccation. However, macroalgae that form a dense entangled turf may hold water among their branches, thus avoiding desiccation (Norton, 1991; Airoldi *et al*., 1996). Consequently, reef flat communities at the sites studied presented a high degree of similarity. Tidal pools differ from these habitats due to their constant submersion and exposure to extreme salinity and temperature variations, thus opportunistic and fast growing algae are to be expected.

On Rocas, colonization discs showed very little recruitment. On the windward reef-flat, discs were not colonized by any macroalgae after 40 days, but the discs on the leeward reef had some slight colonization of crustose coralline algae (7%). There were, however, biofilms present at both sites. Because coralline crust propagules are short-lived (Dethier *et al*., 2003), newly recruited crusts might not resist long periods of desiccation on a reef flat that emerges for 8 h at low tide. In addition, the absence of epiphytes covering coralline crusts, in the early life stages, did not protect the crusts from desiccation (Figueiredo *et al*., 2000; Coleman, 2003).

The maximum absolute daily horizontal growth of the non-cryptic form of *P. pachydermum* was 0.05 mm on the windward reef crest and the minimum was 0.01 mm on the leeward reef flat. Adey & Vassar (1975) described a marginal growth rate of between 0.03 and 0.07 mm per day for crustose coralline algae, such as *P. pachydermum*, on the St. Croix reefs in the Caribbean Sea. These values are close to those found on Rocas in this study and on the Abrolhos reefs in Brazil (absolute growth rate was divided by two to express only one crust margin, modified in accordance with Figueiredo, 1997). It is important to note that some Brazilian and Caribbean reef tops have been built essentially by crustose coralline algae, mainly *P. pachydermum* (Adey, 1975; Kikuchi & Leão, 1997, Leão *et.al*. 2003).

The windward arch showed greater horizontal growth of the non-cryptic form of *P. pachydermum* than to the crusts on the leeward arch. This fact may be related to the differences in age as between the two arches. The leeward reef is the most recent one in the reef construction process (Kikuchi & Leão, 1997; Gherardi & Bosence 2001) and may offer better growth conditions for coralline algae than does the higher windward reef, which is more exposed to desiccation at low tide. On the windward reef the non-cryptic crusts were twice as thick and grew faster on the reef crest than on the reef flat. It is likely that non-cryptic crusts were thinner and grew slower on the reef flat because they were subject to stress. The relationship expected between crust thickness and growth rates (Steneck *et al*., 1991) were not found in the area studied, where desiccation may interfere with it.

The coralline algae in the reef crest habitat presented a higher growth rate than that found on the reef flat, a fact which corroborates the hypothesis that crustose coralline algae grow faster where there is less desiccation. On Rocas, the reef-crest is constantly washed by waves at low tide and crusts are dark in color, possibly because they do not suffer from desiccation, as compared with the crusts on the reef flat 30 meters from the crest, which are pale in color. Differences in algal pigmentation depend not only on light intensity, but also on desiccation stress, which may cause coralline death depending on the duration of the exposure to the air (Figueiredo *et al*., 2000).

In sunlit habitats, the non-cryptic form of *P. pachydermum* is likely to be highly productive. On Rocas, this crust form had similar levels of $O_2$ production at both 38 and 100% of irradiance, and photosynthetic saturation and inhibition are expected at both irradiance levels. Littler & Littler (1984) showed that this species saturates above 522 $\mu$mol $m^{-2}$ $s^{-1}$ in shallow tropical reefs. Littler & Doty (1975) also mentioned that *Porolithon* dominates in sunlit environments. Indeed, this crust form presented negative $O_2$ production under lower irradiance, suggesting that its growth may be limited in low light environments.

By contrast, no diference was found between the $O_2$ production of the cryptic form of *P. pachydermum* for 38% and 100 % irradiances, demonstrating that it is well adapted to living in either of the high irradiance environments. In view of the fact that these crusts live in crevices, a habitat where irradiance is much lower, they were expected to produce more under low irradiance. However, cryptic-crusts presented negative production under low irradiance and also did better off at high irradiance levels, close to their saturation and inhibition points, as the non-cryptic crusts.

Intertidal reef habitats on Rocas were poor in benthic macroalgae, except for the crustose coralline alga *P. pachydermum* that dominates the living cover in both non-cryptic and cryptic habitats. This study showed very low recruitment of crustose coralline algae during a short period at one time of the year; however, more studies are needed at other times of the year and for longer periods to understand recruitment patterns. The non-cryptic coralline crusts of *P. pachydermum* were thicker and grew faster on the reef crest than on the reef flat and had a higher growth rate on the leeward reef than on the windward reef, possibly because they were less exposed to desiccation. *P. pachydermum* was a productive crust both in non-cryptic and cryptic habitats.

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