Vanessa Freire de Carvalho

BANCOS DE RODOLITOS DO ATLÂNTICO SUL: ESTRUTURA DE COMUNIDADE E ASPECTOS FISIOLÓGICOS

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"Bancos de rodolitos do Atlântico Sul - estrutura de comunidade e aspectos fisiológicos"

Por

Vanessa Freire de Carvalho

Tese julgada e aprovada em sua forma final pelos membros titulares da Banca Examinadora (019/2018/PPGECO) do Programa de Pós-Graduação em Ecologia - UFSC.

Prof.(a) Dr.(a) Fábio Gonçalves Daura Jorge
Coordenador(a) do Programa de Pós-Graduação em Ecologia

Banca examinadora:

Dr.(a) Paulo Antunes Horta Junior (Universidade Federal de Santa Catarina)
Orientador(a)

Prof. Dr. Fábio Daura Jorge
Coordenador do PPG em Ecologia
CCB/UFSC

Dr.(a) Guilherme Henrique Pereira Filho – participação por videoconferência
(Universidade Federal de São Paulo)

Dr.(a) Alberto Lindner (Universidade Federal de Santa Catarina)

EDUARDO L H GIEHL

Dr.(a) Eduardo Luis Hettwer Giehl (Universidade Federal de Santa Catarina)

Florianópolis, 10 de agosto de 2018.

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“O mar é o vasto reservatório da natureza. Por assim dizer, foi pelo mar que o globo começou e quem sabe se não acabará por ele! Nele reina a suprema tranquilidade. O mar não pertence aos déspotas. À sua superfície podem ainda eles exercer os seus iníquos direitos, entrecombaterem-se, entredevorarem-se, nele amontoar todos os horrores terrestres. Mas a dez metros abaixo da superfície cessa o seu poder, extingue-se a sua influência, desaparece a sua força!”

(Vinte mil léguas submarinas – Jules Verne, 1870)

RESUMO

Variáveis ambientais controlam a ocorrência a abundância de diversos organismos formadores de habitat ao longo do mundo. Entre eles, os bancos de rodolitos possuem destaque, estando distribuídos desde as regiões tropicais a polares e são responsáveis por aumentar a biodiversidade local. As características destes organismos são determinadas por fatores que variam em escalas maiores e menores, como temperatura, luz, disponibilidade de nutrientes, correntes locais e profundidade. A reunião destes fatores modifica a morfologia e fisiologia dos rodolitos, bem como a composição e interação com as espécies associadas. A ampla distribuição dos bancos de rodolitos pelo Atlântico Sul está condicionada a um gradiente de fatores e a variações sazonais específicas. Com o objetivo de detectar áreas mais receptivas para o desenvolvimento de rodolitos e quais os fatores ambientais controlam a variabilidade na sua abundância e espécies associadas, o Capítulo 1 mostra a abundância total de rodolitos e macroalgas epífitas em regiões tropicais, zona de transição e temperada quente do litoral brasileiro. As variáveis ambientais utilizadas foram extraídas do Bio-Oracle e usadas na modelagem de biomassa dos bancos de rodolitos e na análise BIO-ENV para identificar as que mais contribuem para a composição de epífitas. As regiões tropicais tiveram maior abundância de rodolitos. As variáveis que mais influenciaram a sua ocorrência foram luz e temperatura, e a abundância foi nitrato, temperatura e velocidade de corrente. Não foram detectadas diferenças entre as regiões com relação à biomassa total de epífitas. No entanto, os pontos de coleta foram significativamente diferentes com relação à composição dos táxons predominantes. Os fatores ambientais que mais influenciaram a composição de epífitas foram a temperatura máxima e nitrato mínimo. Na região tropical observou-se uma maior abundância de espécies que são mais comuns em águas quentes, cuja biomassa decresceu em direção à região temperada quente. O Capítulo 2 avalia a influência dos fatores ambientais que atuam na comunidade de um mesmo banco de rodolitos ao longo de dois anos. Foram analisadas a biomassa de rodolitos e espécies associadas ao longo deste período, além de um experimento conduzido *in situ* para avaliar a produção primária dos rodolitos sozinhos e na presença das epífitas. A maior biomassa total de rodolitos ocorreu durante o inverno. *Lithothamnion crispatum* foi a espécie mais abundante no verão. As macroalgas epífitas ocorreram apenas no verão de 2015, com a predominância de *Padina gymnospora*. Com relação à fauna associada, os filos Annelida, Arthropoda e Mollusca tiveram a menor biomassa em fevereiro de 2015 e a maior em novembro de 2016. As populações de espécies-chave de peixes recifais dentro e em torno do banco de rodolitos mostraram variações significativas ao longo do tempo. A densidade de garoupas (carnívoras/piscívoras) parece aumentar com o passar do tempo, especialmente de 2015 a 2016. Por outro lado, a população de peixes predadores de macroinvertebrados apresentou um decrescimento (de 2014 a 2016). Com relação à produção primária, a fotossíntese e calcificação de *L. crispatum* foram menores na presença de *P. gymnospora*. Enquanto as condições meteo-oceanográficas parecem causar alterações na composição e abundância sazonal no banco de rodolitos, mudanças na comunidade bêntica associada parecem ser uma consequência de mudanças nas interações tróficas. Um efeito da cascata trófica causou um controle top down, estruturando a comunidade bêntica com a redução de macroalgas carnosas, como observado em diferentes sistemas recifais. A supressão da cobertura das algas epífitas parece aumentar a produção primária do banco de rodolitos.

Palavras-chave: Tropical, variáveis ambientais, rodolitos, macroalgas, calcificação, fotossíntese.

ABSTRACT

Environmental variables control the occurrence and abundance of habitat-forming organisms around the world. Among them, rhodolith beds are distributed from tropical to polar regions and harbor a wide local biodiversity. The characteristics of these organisms are drived by factors that vary in large and local scale, such as temperature, light, nutrient availability, currents and depth. The combination of these factors modify the morphology and physiology of rhodoliths, as well as the composition and interaction of associated species. The wide distribution of rhodoliths along South Atlantic coast is conditioned to a gradient of factors and seasonal variation. Chapter 1 shows the total abundance of rhodoliths and epiphytic macroalgae on tropical, warm temperate regions and transition zone in order to detect the environmental factors that drive their variability and associated species. The environmental variables used were extracted from Bio-Oracle and used in modeling of rhodolith beds and in the BIO-ENV analysis to identify their contribution the composition of epiphytes. Tropical regions had greater abundance of rhodolits. The variables that most influenced the occurrence were light and temperature and the abundance were nitrate, temperature and current velocity. No latitudinal gradient was detected with respect to total epiphyte biomass. However, the collection points were significantly different with respect to the composition of the predominant taxa. The environmental factors that most influenced the epiphyte composition were a maximum temperature and minimum nitrate. The tropical region had greater abundance of species that are more common in hot waters, whose biomass decreased towards the subtropical region. Chapter 2 evaluate the influence of environmental factors that operate in the community of the same rhodolith bank over two years. The biomass of rhodoliths and associated species was analyzed during this period, as well as an experiment conducted *in situ* to evaluate the primary production of rhodoliths alone and in the presence of epiphytes. The highest total biomass of rhodoliths occurred during winter. *Lithothamnion crispatum* was the most abundant species in the summer. The epiphytic macroalgae occurred only in the summer of 2015, with the predominance of *Padina gymnospora*. Regarding the associated fauna, the phyla Anelida, Arthropoda and Mollusk had the lowest biomass in February 2015 and the highest in November 2016. The populations of key reef fish species in and around the rhodolith bank showed significant variations over time. Groupers (carnivorous / piscivorous) density seems to increase with the passage of time, especially from 2015 to 2016. On the other hand, the macroinvertebrate predatory fish population showed a slight decrease (from 2014 to 2016). Regarding the primary production, the photosynthesis and calcification of *L. crispatum* were smaller in the presence of *P. gymnospora*. While meteo-oceanographic conditions seem to cause change in seasonal abundance and composition of rhodoliths in Arvoredo Rhodolith bed, shifts in associated benthic community were a consequence of alteration of trophic interactions. A trophic cascade effects caused a top down control structuring a benthic community with reduced abundance of fleshy macroalgae, as observed in different reef systems. Suppression of canopy or flesh algae canopy cover seems to increase potential primary production of rhodolith bed.

Keywords: Tropical, Environmental variables, rhodoliths, macroalgae, calcification, photosynthesis

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1. INTRODUÇÃO

A variabilidade das características ambientais determina a ocorrência e abundância de uma série de organismos formadores de habitat. Nesse contexto, vários estudos buscam investigar a influência dos fatores abióticos na resposta individual, populacional ou de comunidade sob uma perspectiva macroecológica, sazonal e preditiva.

Um dos ramos da macroecologia estuda como recursos ambientais que variam ao longo da latitude podem influenciar nas características de espécies formadoras de habitat, como florestas (HUANG et al., 2010; REICH et al., 2014), manguezais (ROVAI et al., 2016), recifes de corais (LAJEUNESSE et al., 2004; ULSTRUP et al., 2006), Kelps (GRAHAM et al. 2007; BERNARDES et al. 2018) e bancos de rodolitos (HERNANDEZ-KANTUN et al., 2017).

Dentre esses habitats, os bancos de rodolitos são um dos mais abundantes ao longo do mundo (FOSTER et al., 2013; RIOSMENA-RODRÍGUEZ et al., 2017) e estruturam ambientes que são descritos como recifes biogênicos, construídos por algas calcárias incrustantes de vida livre (WOELKERLING, 1988; BOSCENCE; WILSON, 2003). Segundo Steneck (1986), um espécime é classificado como “rodolito” quando mais de 50% volume total é composto por alga calcária. Estas algas fornecem habitat para diversos organismos marinhos e são responsáveis por aumentar a diversidade e abundância da flora (GUERARDHI, 2004; ORDINES et al., 2015) e fauna dos ambientes onde ocorrem (HARVEY; BIRD, 2008; KONAR et al., 2006). Algumas espécies da fauna associada parecem ser rodolito-específicas (STELLER et al., 2003), sendo influenciadas pela morfologia dos rodolitos e pelas suas espécies formadoras (HINOJOSA-ARANGO et al., 2004; SANÉ et al. 2016). Recentemente descobriu-se que os rodolitos podem abrigar estágios de vida endolíticos previamente desconhecidos de microalgas dinoflageladas de importância ecológica (KRAYESKY-SELF et al., 2017).

Estes bancos estão distribuídos desde regiões tropicais (CAVALCANTI et al., 2014) até polares (JØRGENSBYE; HALFAR, 2017) e de áreas rasas até mais de 200 metros de profundidade (AMADO-FILHO et al., 2017). Apesar da ampla distribuição, a ocorrência e abundância destas espécies estão sujeitas a fatores abióticos e bióticos que variam localmente e ao longo das estações (PASCELLI et al., 2013; MCCONNICO et al., 2017).

Além de entender padrões e processos envolvidos na estruturação dos ecossistemas, o estudo das respostas de espécies-chave a variações ambientais atuais nos permite predizer quais serão as respostas desses organismos frente a cenários futuros (SMALE; WERNBERG, 2013). Devido as crescentes alterações climáticas, alguns estudos preveem a tropicalização de ambientes de clima temperado e subtropical e o desaparecimento de várias espécies em latitudes tropicais (VERGÉS et al., 2014; WERNBERG et al., 2016; ARAÚJO et al., 2018). O aumento da acidificação e da temperatura oceânica devido à liberação de CO_2 na atmosfera causará a diminuição de organismos com carbonato de cálcio em sua composição, com consequente decrescimento de outras espécies dependentes (HOOIDONK et al., 2013; LEGRAND et al., 2017). Já alterações antrópicas de impactos locais como descarga de nutrientes e sedimentação resultarão em destruição de habitat, além do desaparecimento de espécies (STELLER et al., 2003; WILSON et al., 2004).

A seguir, será apresentada uma revisão de literatura sobre a distribuição dos bancos de rodolitos ao longo do mundo e quais os principais fatores ambientais que norteiam esses padrões. Além disso, serão apresentadas as principais vulnerabilidades desses ambientes frente às mudanças climáticas e alterações locais.

1.1. Bancos de rodolitos: distribuição global e importância ecológica.

O estabelecimento, a distribuição e a abundância dos bancos de rodolitos ao longo do mundo têm sido associadas a fatores ambientais como temperatura, luz, salinidade e correntes (WILSON et al., 2004; TEICHERT et al., 2012). Até um certo limite fisiológico, irradiância e temperatura possuem uma relação positiva com a fotossíntese e calcificação (KAMENOS; LAW, 2010; BURDETT et al., 2014), processos intimamente ligados (JOHANSEN, 1981; HILL et al., 2015). Apesar de não demandar altos valores de irradiância para atingir a taxa fotossintética máxima (Figura 1), a maior frequência da exposição de luz pode favorecer a fotossíntese e o crescimento dos rodolitos (TEICHERT; FREIWALD, 2014). Além disso, o aumento da temperatura (até 30°C), sem irradiância subsaturante, favorece uma alta taxa metabólica (VÁSQUEZ-ELIZONDO; ENRÍQUEZ, 2016; HOFFMAN et al., 2016). Assim sendo, os mares dos trópicos, por terem temperaturas mais quentes e disponibilidade de luz o ano inteiro, possuem condições ambientais mais favoráveis ao desenvolvimento dos bancos de rodolitos.

Enquanto os maiores bancos de rodolitos estão localizados nas regiões tropicais, com a maior formação contínua do Atlântico Sul situada em Abrolhos, no litoral brasileiro (AMADO-FILHO et al., 2012), há um decrescimento nos registros em direção a região ártica (Figura 2). Além disso, o banco de Abrolhos possui uma alta taxa de produção de carbonato de cálcio (1000± 700 g m^{-2} yr^{-1}: AMADO-FILHO et al., 2012) se comparada a outros bancos de rodolitos do mundo, como o de regiões temperadas (Brasil – Ilha Deserta - SC, 55 - 136.3 g CaCO$_3$ m^{-2} yr^{-1}, GHERARDHI, 2004; França - 490 g CaCO$_3$ m^{-2} yr^{-1}, Martin et al., 2007) e polares (Noruega, 200.3 g CaCO$_3$ m^{-2} yr^{-1}, TEICHERT; FREIWALD, 2014). No entanto, apesar da menor diversidade e abundância dos bancos de rodolitos em regiões polares, as espécies formadoras são adaptadas a condições de baixas temperaturas e restrição de luz em boa parte do ano, além de serem fundamentais do ponto de vista ecológico (TEICHERT; FREIWALD, 2014).

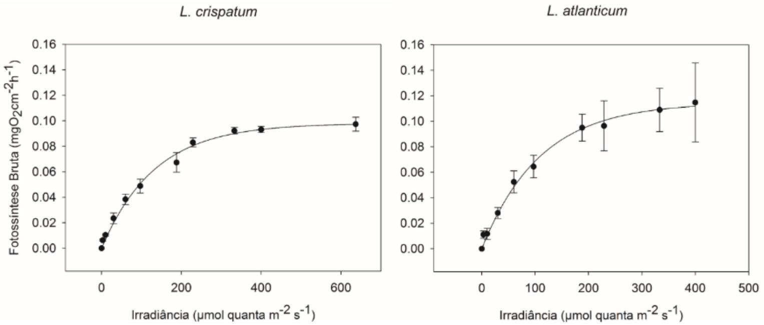

Figura 1. Curvas PI (n = 4, ±SE) das espécies formadoras de rodolitos *Lithothamnion crispatum* (esquerda) e *Lithophyllum atlanticum* (direita), realizadas a uma temperatura de 24°C. A Análise de regressão não-linear foi realizada no programa Sigma Plot 10.0, usando a equação y = a*(1-exp(-b*x)).

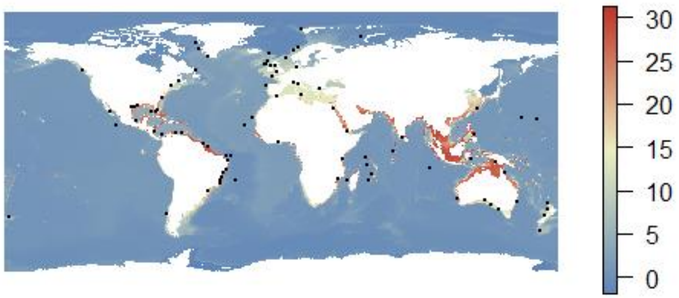

Figura 2. Distribuição dos bancos de rodolitos registrados ao longo do mundo. A escala se refere à temperatura média de fundo (°C, extraída do Bio-ORACLE). Os dados de ocorrência de espécies formadoras de rodolitos foram extraídos dos sites das organizações "*Ocean Biogeographic Information System* (www.iobis.org)" e "*Global Biodiversity Information Facility* (www.gbif.org)" e confirmados por publicações científicas.

A pequena quantidade de bancos de rodolitos registrados para as regiões árticas estão situados na Noruega (FREIWALD; HENRICH, 1994; TEICHERT et al. 2012; TEICHERT et al., 2014), Groelândia (JØRGENSBYE; HALFAR, 2017), Canadá (GAGNON et al., 2012) e no Alasca (KONAR et al., 2006). Na Noruega, as algas calcárias *Lithothamnion glaciale* Kjellman e *Phymatolithon tenue* (Rosenvinge) Düwel & Wegeberg ocorrem sob a forma de rodolitos entre as profundidades de 27 a 50 metros, na forma incrustante de 70 a 80 metros e fornecem habitat para uma fauna bentônica composta por 59 espécies (TEICHERT et al., 2012; TEICHERT et al., 2014). Esta distribuição se deve principalmente à disponibilidade de luz, já que em profundidades de > 80 metros é insuficiente para a fotossíntese das algas incrustantes e em < 30 metros é alta o suficiente para o desenvolvimento de algas filamentosas vermelhas de rápido crescimento, que poderiam competir com os rodolitos (TEICHERT et al., 2012). Nos outros três pontos de ocorrência do Ártico a composição dos rodolitos é ainda mais restrita, com apenas *Clathromorphum compactum* (Kjellman) Foslie compondo quase a totalidade dos rodolitos na Groenlândia (e poucas áreas cobertas por *L. glaciale*) e apenas *Phymatolithon calcareum* (Pallas) W.H.Adey & D.L.McKibbin ex Woelkering & L.M.Irvine para o Alasca (KONAR et al., 2006; JØRGENSBYE; HALFAR, 2017) e *L. glaciale* para o Canadá (GAGNON et al., 2012).

Diferente das regiões polares, os registros dos bancos de rodolitos das áreas de clima temperado são mais numerosos e com maior riqueza de espécies, com registros para o hemisfério Norte, na região Nordeste do Atlântico (MARTIN et al., 2007; HINOJOSA-ARANGO et al., 2009; DUTERTRE et al., 2015), Mar Mediterrâneo (SCIBERRAS et al., 2009; PEÑA et al., 2014; CABANELLAS-REBOREDO et al., 2017), Baixa Califórnia (MELBOURNE et al., 2018) e Sul, na Nova Zelândia (NEILL et al., 2015), Austrália (HARVEY; BIRD, 2008) e sudeste do Pacífico (MACAYA et al., 2014). Estes bancos podem ser compostos por uma ou várias espécies formadoras de rodolitos, algumas das quais estão presentes em regiões tropicais, como *Lithothamnion crispatum* Hauck e *Lithothamnion muelleri* Lenormand ex Rosanoff (NEILL et al., 2015). Além da elevada abundância de fauna associada, composta por invertebrados e peixes (HINOJOSA-ARANGO et al., 2009; NEIL et al., 2015), esses bancos abrigam boa parte da diversidade local de macroalgas (SCIBERRAS et al., 2009; PEÑA et al., 2014). Nas áreas mais próximas às menores latitudes, foram observadas mudanças na composição da flora associada, sendo as macroalgas tolerantes ao clima frio gradualmente substituídas pelas espécies adaptadas ao calor (PEÑA et al., 2014).

Nas regiões tropicais, os litorais do Caribe (LITTLER et al., 1991), África (BOSENCE, 1983) e, principalmente, do Brasil (FOSTER et al., 2013; AMADO-FILHO et al., 2017) se destacam pela grande quantidade de registros de bancos de rodolitos. Na costa brasileira, os bancos ocorrem desde a latitude 5°N, na região sob influência da foz do Rio Amazonas (MOURA et al., 2016) até 27°S, na costa do estado de Santa Catarina (GHERARDI, 2004; PASCELLI et al., 2013), região considerada por alguns autores como subtropical (VIEIRA-PINTO et al., 2014; ANDERSON et al., 2014) e por outros como temperada quente (HORTA et al., 2001; PASCELLI et al., 2013). Os bancos de rodolitos de Santa Catarina são referidos como o limite sul de distribuição desse tipo de ambiente para o Atlântico (PASCELLI et al., 2013).

No banco de rodolitos de Abrolhos, um dos maiores do Atlântico Sul, Brasileiro et al. (2016) identificaram 14 espécies de algas incrustantes formadoras de rodolitos, destacando-se *Hydrolithon rupestre* (Foslie) Penrose e *L. crispatum* pela predominância. Em baixas latitudes, os rodolitos abrigam uma grande diversidade de espécies de macroalgas adaptadas a altos valores de temperatura e irradiância (RIUL et al., 2009; BAHIA et al., 2010; AMADO-FILHO et al., 2012; FOSTER et al., 2013; AMADO-FILHO et al., 2017). Em latitudes médias, em profundidade de 45 a 120 metros, os bancos de rodolitos fornecem substrato para a espécie endêmica formadora de Kelp *Laminaria abyssalis* A.B.Joly & E.C.Oliveira (AMADO-FILHO et al., 2007; ROTHMAN et al., 2017). Nas latitudes mais ao sul, essas espécies se tornam raras ou são substituídas por espécies mais tolerantes a temperaturas mais frias (PASCELLI et al., 2013). Apesar das espécies tropicais dominarem esses ambientes, *L. glaciale* já foi encontrada em profundidades de 60 metros, onde as temperaturas abaixo de 15°C permitem o seu desenvolvimento (HENRIQUES et al. 2011).

Considerados "engenheiros do ecossistema" (BASSO, 2012), os bancos de rodolitos brasileiros possuem um importante papel na prestação de serviços ecossistêmicos e na conservação e proteção da biodiversidade marinha (PEREIRA-FILHO et al. 2012). No entanto, apenas alguns estão localizados em áreas de proteção ambiental, como Fernando de Noronha (AMADO-FILHO et al., 2012), Abrolhos (BRASILEIRO et al. 2016), Santa Catarina (PASCELLI et al. 2013) e na cadeia Vitória-Trindade (PEREIRA-FILHO et al. 2012), sendo esta última criada apenas recentemente sob o Decreto 9312 de 19/03/2018. De modo a fornecer subsídios para uma possível ampliação das áreas de conservação, torna-se fundamental estudar a comunidade desses habitats e os principais fatores que influenciam a sua composição, bem como a identificação de áreas onde há maior probabilidade de ocorrência de bancos ainda não mapeados.

1.2. Fatores locais e sua influência sobre os rodolitos e nas relações com a comunidade associada

Apesar da ampla ocorrência dos bancos de rodolitos em várias latitudes, fatores abióticos e bióticos de escala local também parecem ser determinantes para a formação e abundância desses habitats (HERNANDEZ-KANTUN et al., 2017). Velocidade das correntes, ondulação e profundidade estão dentre os fatores locais que mais influenciam na formação dos rodolitos (HINOJOSA-ARANGO et al., 2009; SAÑÉ et al., 2016). Sob correntes muito fracas, as algas calcárias não se desprenderiam e não rolariam. Já as muito fortes, causariam a fragmentação do talo (FOSTER, 2001; HINOJOSA-ARANGO et al., 2009). A morfologia dos rodolitos também é influenciada pelo grau de movimentação da água: em regiões mais agitadas, possuem a forma mais esférica e lisa, enquanto em regiões mais calmas, mais achatada, discoide e com reentrâncias (SAÑÉ et al., 2016; CABANELLAS-REBOREDO et al., 2018).

A intensidade das correntes e ondulações influenciam não só os rodolitos, como a comunidade associada. Regiões com maior movimentação tendem a ter menor abundância de organismos móveis e aumento dos organismos com estruturas de fixação mais fortes

(MAUGHAN; BARNES, 2000; HINOJOSA-ARANGO et al., 2009). Outros autores relataram uma diferença sazonal na cobertura de epífitas, com a sua diminuição no inverno devido as tempestades que ocorrem nesta estação (AMADO-FILHO et al., 2007; PASCELLI et al., 2013).

A influência da batimetria na abundância de rodolitos é variável, pois diferentes respostas foram reportadas na literatura. Enquanto alguns autores observam uma correlação negativa entre o tamanho dos rodolitos e a profundidade (RIUL et al., 2009; BAHIA et al., 2010; PASCELLI et al., 2013; VALE et al., 2018), outros relatam uma relação positiva (QUEIROZ et al., 2016). O grau de movimentação da água ao longo de um gradiente de profundidade pode ter maior influência na distribuição batimétrica dos bancos de rodolitos do que a penetração de luz, já que estes organismos possuem alta tolerância a diferentes intensidades luminosas (SAÑÉ et al., 2016; CABANELLAS-REBOREDO et al., 2018). A predominância de rodolitos em uma determinada profundidade pode estar relacionada ao grau de sedimentação da área (BRASILEIRO et al., 2016; VALE et al., 2018), aspecto mais explorado adiante. A composição da comunidade associada, principalmente das macroalgas, é fortemente influenciada pela batimetria. Autores reportaram o decrescimento da cobertura de algas epífitas com o aumento da profundidade, devido a diminuição de luz (RIUL et al., 2009; BRASILEIRO et al., 2016).

Além da movimentação da água, a proximidade com aportes de nutrientes também influencia a ocorrência de rodolitos e comunidade associada (BJÖRK et al., 1996; FIGUEIROA et al., 2014). Regiões próximas a descarga de rios e esgotos geram maior sedimentação (Figura 3), reduzindo a disponibilidade de luz e eficiência fotossintética dos rodolitos (MARTIN et al., 2014). Segundo Vale et al. (2018), em áreas muito próximas a pluma do Rio Amazonas, os nódulos biogênicos são, em sua maioria, constituídos por briozoários. Os autores relacionam essa composição à ausência de luz decorrente da sedimentação e excesso de nutrientes causados pelas descargas. De maneira semelhante, Brasileiro et al. (2016) apontaram a proximidade com a descarga do Rio Doce como provável causador da ausência de rodolitos em profundidades menores que 40 metros ao sul de Abrolhos. A redução na cobertura de algas calcárias em regiões com grande aporte de sedimentos pode estar relacionada a redução na fotossíntese. Um experimento mostrou que mesmo uma redução de 30% na luz causada por uma fina camada de sedimentos pode diminuir a fotossíntese dos rodolitos em 70% (RIUL et al., 2008). Outro mostra que uma cobertura de 70% da superfície do rodolito por sedimento pode causar uma redução de 30% da eficiência fotossintética de *Mesophyllum engelhartii* (Foslie) Adey e *Lithothamnion* sp. (FIGUEIREDO et al. 2015).

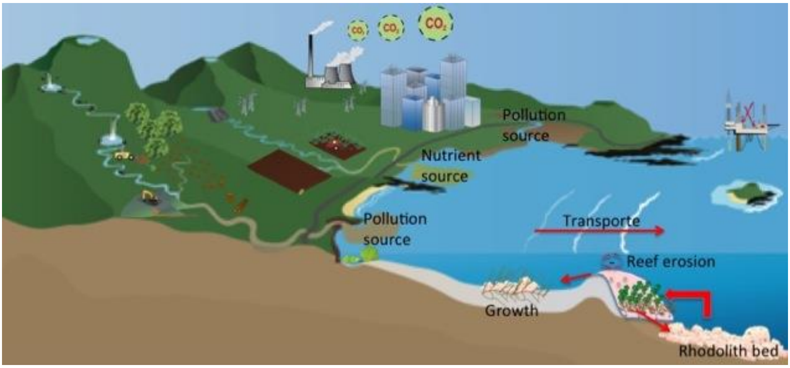

Figura 3: Fatores de origem antrópica que influenciam no processo de formação dos bancos de rodolitos.

O aumento do aporte de nutrientes oriundos de estuários ou poluentes também pode alterar a composição de epífitas, causando a proliferação de algas de rápido crescimento na superfície dos rodolitos (FONG et al., 1994; HARDISON et al., 2011; NEIL; NELSON, 2016). Algumas espécies de algas epífitas podem competir com os rodolitos por luz e nutrientes (WAHL, 2008), além de causar o sombreamento (Figura 4) absorvendo boa parte da luz disponível na superfície (DODDS, 1991). As algas calcárias incrustantes possuem estratégias que evitam o crescimento excessivo de algas epífitas na sua superfície, como a descamação de células epiteliais (HOFMANN et al., 2016) e produção de substâncias alelopáticas (GROSS, 2003; KIM et al., 2004). Além disso, alguns animais herbívoros associados, como peixes, caranguejos, poliquetas e moluscos podem ser benéficos, já que se alimentariam de esporos das algas epífitas, e controlariam o seu crescimento (SCHERNER et al., 2010; LEGRAND et al., 2017). A herbivoria é um dos fatores que mais influenciam na composição da comunidade de macroalgas (POORE et al., 2012; BONALDO; HAY, 2014; LONGO et al., 2015). Esta pode ter um papel maior na composição da comunidade de macroalgas do que outros fatores abióticos como sedimentação e ressurgência (SANGIL et al., 2011). Dessa forma, as comunidades das áreas com maior abundância de herbívoros tendem a ser colonizadas por algas que produzem defesas químicas, como os membros da ordem Dictyotales (STACHOWICZ; HAY, 1996; BIANCO et al., 2010; ARAÚJO et al., 2018b).

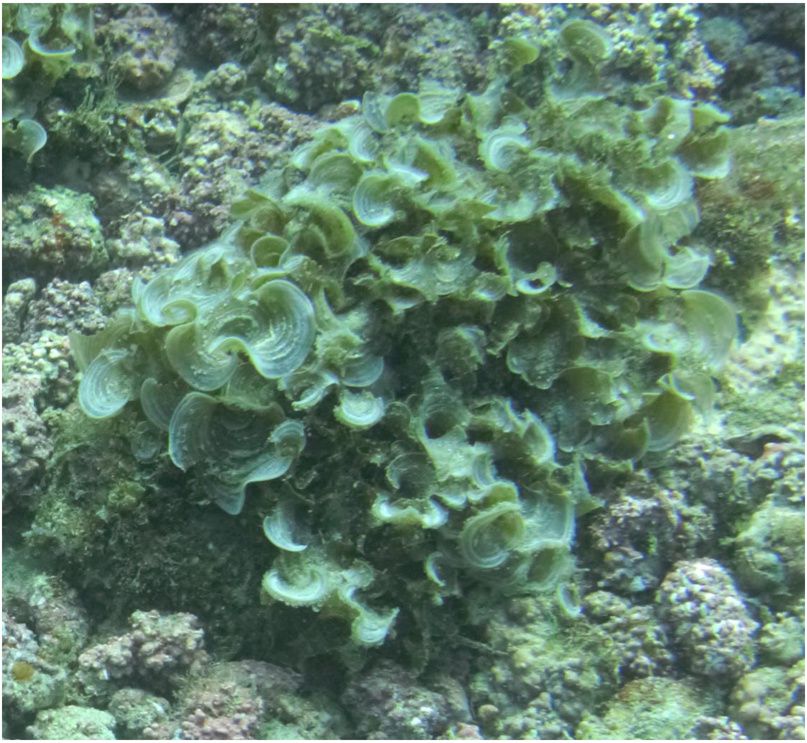

Figura 4. *Padina gymnospora* causando sombreamento em rodolitos no banco da Reserva Biológica do Arvoredo – SC. Foto tirada em Fevereiro/2015.

1.3. Vulnerabilidade dos bancos de rodolitos às mudanças climáticas e consequências para a comunidade associada

A grande importância ecológica dos bancos de rodolitos tem levado cientistas do mundo todo a pesquisarem sobre as respostas da comunidade as alterações ambientais futuras (RAGAZZOLA et al., 2016; LEGRAND et al., 2017; MUÑOZ et al., 2018). A crescente emissão de CO_2 na atmosfera tem causado um aumento na temperatura e diminuição do pH oceânicos. A estimativa para 2100 é de 4 graus a mais na média de temperatura e uma concentração de CO_2 equivalente a 1000ppm (IPCC, 2014). Esse crescente aumento da temperatura tem levado a tropicalização dos ambientes temperados e o enfraquecimento de organismos calcários formadores de habitat nas regiões tropicais (VERGÉS et al., 2014). Por ser um país tropical com grande diversidade de ecossistemas, o Brasil é um dos países que mais sofrerão com as alterações causadas pelas mudanças climáticas (HORTA et al., 2016). Alguns ecossistemas situados na plataforma continental brasileira são mais sujeitos a acidificação oceânica por estarem localizados em áreas que atuam como sumidouros de CO_2 em estações do ano específicas (KERR et al., 2016). Estas áreas incluem regiões próximas a pluma do Rio Amazonas e margem continental sudeste (~20°S a 28°S) (KERR et al., 2016).

O aumento de CO_2 no oceano causará o decrescimento na saturação de calcita, diminuindo a taxa de calcificação dos organismos calcários (NASH et al., 2016; COMEAU et al., 2016). Além disso, a temperatura além do limite térmico dos rodolitos aumenta a respiração além dos níveis compensatórios de fotossíntese (WERNBERG et al., 2016). Um experimento de curta duração (48h) mostrou um efeito negativo no desempenho fisiológico das algas calcárias *Lithothamnion crispatum* e *Sonderophycus capensis* tanto do aumento da temperatura, quanto da diminuição do pH (MUÑOZ et al., 2018). No entanto, em *Lithophyllum cabiochae* e *Porolithon onkodes*, o efeito do aumento da temperatura na produtividade primária é negativo apenas quando em conjunto com o incremento nos níveis de CO_2 (ANTHONY et al., 2008). Outros estudos mostram que, sob condições de níveis elevados de CO_2, há um incremento na fotossíntese de algas como *Phymatolithon lusitanicum* (SORDO et al., 2016) e *Lithothamnium corallioides* (NOISETTE et al., 2013), indicando a capacidade de aclimatação a esse cenário.

Alguns estudos *in situ* já tem demonstrado que a proximidade com fontes naturais de CO_2 causa o decrescimento na biomassa de algas calcárias e o aumento de macroalgas carnosas (HALL-SPENCER et al., 2008). Algas de rápido crescimento como *Gracilaria* e *Ulva* podem se beneficiar do aumento de CO_2 (YOUNG; GOBLER, 2016). Em um experimento *in situ* em uma assembleia de *maerl*, a produção primária bruta e a respiração foram maiores sob elevado valor de CO_2 durante o verão, sendo atribuído a maior biomassa de epífitas, que se beneficiaram da condição (LEGRAND et al., 2017). No entanto, o mesmo estudo mostrou uma diminuição da calcificação da comunidade, devido a resposta de *Lithothamnion corallioides* (LEGRAND et al., 2017).

Devido a vulnerabilidade dos bancos de rodolitos do Brasil frente às crescentes mudanças climáticas e estressores locais, é necessário investigar quais fatores abióticos possuem maior influência na sua abundância e na comunidade associada em grande escala, além daqueles que atuam em menor escala, variando ao longo do tempo. Diante disso, o Capítulo 1 trará uma perspectiva macroecológica dos bancos de rodolitos do Brasil, com resultados de coletas realizadas desde a região tropical a temperada quente. Através da análise da relação entre os resultados de biomassa de rodolitos e macroalgas epífitas e os fatores abióticos extraídos de *rasters* do Bio-ORACLE que comprovadamente possuem influência na sua fisiologia, foi verificado quais são os maiores responsáveis pelas diferenças encontradas. De posse destes resultados, foi realizada uma modelagem preditiva para a costa do Brasil, com o objetivo de estimar os lugares mais favoráveis a ocorrência e quais possuem maior abundância de bancos de rodolitos, apontando quantidades expressivas para áreas ainda pouco estudadas. Os resultados abrem os horizontes para possíveis novas áreas de conservação marinha. Por outro lado, o Capítulo 2 mostrará o acompanhamento da comunidade de um banco de rodolitos da região temperada quente, situado na Reserva Biológica Marinha do Arvoredo – SC, entre os períodos de fevereiro/2015 a novembro/2016. O trabalho abordará quais fatores ambientais poderiam influenciar nas diferenças na comunidade observadas ao longo do tempo, explorando a relação entre a abundância de fauna e o aparecimento de algas epífitas. Além disso, através de um experimento *in situ*, foi demonstrando o efeito do crescimento excessivo da macroalga epífita *Padina gymnospora* (Kützing) Sonder sobre a superfície de *L. crispatum* na sua fotossíntese e calcificação.

1.4. OBJETIVO GERAL

Verificar quais variáveis ambientais são os principais condutores das diferenças nas comunidades dos bancos de rodolitos do Atlântico Sul em escala sazonal e macroecológica.

1.4.1. OBJETIVOS ESPECÍFICOS

- Identificar quais variáveis abióticas são responsáveis pelas diferenças na abundância dos rodolitos e macroalgas associadas ao longo da costa do Atlântico Sul;
- A partir das variáveis mais relevantes, realizar uma análise preditiva para a costa brasileira, identificando áreas mais sucetíveis a ocorrência de bancos de rodolitos e onde há maior abundância;
- Relacionar as diferenças na composição dos rodolitos e algas epífitas de um banco da região temperada quente no período de dois anos com as mudanças nas variáveis bióticas e abióticas;
- Avaliar, por meio de experimento *in situ*, como o crescimento de uma alga dominante na superfície de rodolitos pode alterar a produção primária e calcificação de um banco da região temperada quente.

CAPÍTULO 1

2. Environmental drivers of rhodolith beds and epiphytes community along a latitudinal gradient of SW Atlantic Coast

Vanessa F. Carvalho[1*], Jorge Assis[2], Ester A. Serrão[2], José M. Nunes[3], José B. Barufi[1], João Silva[2], Sonia M. B. Pereira[4], Paulo A. Horta[1]

[1] Laboratório de Ficologia, Departamento de Botânica, Universidade Federal de Santa Catarina, Florianópolis, Santa Catarina, Brazil.
[2]CCMar – Centre of Marine Sciences, Universidade do Algarve, Campus de Gambelas, Faro, Portugal
[3] Departamento de Botânica, Universidade Federal da Bahia, Salvador, Bahia, Brazil
[4] Departamento de Biologia, Universidade Federal Rural de Pernambuco, Recife, Brazil
*Corresponding author: carvalhovf2@gmail.com

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ABSTRACT

Environmental conditions shape the occurrence and abundance of habitat-building organisms at global scales. Among them, rhodolith beds are spread along SW Atlantic coast in Tropical and Warm temperate regions, providing hard substrate for benthic organisms, such as other macroalgae. These organisms can benefit the local biodiversity by increasing the habitat availability but can also compete with rhodoliths for light, gas and nutritional resources. Therefore, understanding the factors that shape the distribution of structuring species and associated communities along entire ranges is crucial for their conservation management in the face of environmental changes. In other to detect suitable habitat areas and the main drivers controlling their variability and associated epiphytes, this study focus in abundance data along latitudinal gradient and uses environmental predictors extracted from Bio-Oracle. Tropical regions had the highest abundance of rhodoliths. The major drivers influencing rhodolith occurrence were light availability at the bottom of the ocean and temperature, while for abundance were nitrate, temperature and current velocity. No latitudinal pattern was detected in total epiphytes abundance. However, significant differences were found between sites regarding to the composition of predominant taxa. The predictors influencing such differences were maximum temperature and minimum nitrate. The Tropical region is abundant in species with warm-water affinities, which decrease toward warm temperate. Notwithstanding, the expressive occurrence of tropical species not referred before for warm temperate beds, indicate a tropicalization event.

Keywords: Habitat-building; Marine ecology; Macroalgae;
Temperature; Light; Nitrate

2.1. INTRODUCTION

Environmental conditions drive the distribution, occurrence, patterns of community structure and population biology of globally distributed habitat-building organisms (Hillebrand, 2004; Spalding et al., 2007; Graham et al., 2007; Liuzzi et al., 2011; Freestone and Osman, 2011), such as mangroves (Rovai et al., 2016), seagrasses (Chefaoui et al., 2015), marine forests of macroalgae (Santelices and Marquet, 1998; Keith et al., 2013; Graham et al., 2007; Assis et al., 2017a; Bernardes et al., 2018) and rhodolith beds (Hernandez-kantun et al., 2017). In particular, rhodoliths occur from Tropical (Cavalcanti et al., 2014; Vale et al., 2018) to Polar Regions (Teichert, 2014). They are composed by non-geniculate red calcareous algae in free-living form (Foster et al., 2001; Pereira-Filho et al., 2011; Amado-Filho et al., 2012), which create complex three-dimensional structures providing habitats for a rich diversity and abundance of mobile (e.g. molluscs, decapods, fish) (Ordines et al., 2015) and sessile organisms (e.g. cnidarian, sponges and macroalgae) (Steller et al., 2003; 2007; Sciberras et al., 2009; Peña et al., 2014).

Some studies have focused on the effects of invertabrates and fleshy macroalgae interactions on rhodoliths (Scherner et al., 2010; Legrand et al., 2017). The fleshy macroalgae can benefit the local fauna by providing habitat and food (Neill and Nelson, 2016; Aued et al., 2018) and protect the rhodolith to excess of light in shallow water (Figueiredo et al., 2000). However, in great quantity, the epiphytes can shade the surface of host and compete for environmental resources (Drake et al., 2003; Wahl, 2008). Because of the variability of rhodolith responses in the presence of epiphytes, study the patterns of community structure of the beds and the factors that drive the differences is fundamental for conservation management in the face of environmental changes.

The community structure, morphology and abundance of rhodoliths beds are influenced by global (e.g., temperature and irradiance) (Cavalcanti et al., 2014; Caragnano et al., 2016; Jørgensbye and Halfar, 2017) and local environmental conditions (e.g., ocean currents, nutrient supply and herbivory) (Bjork et al., 1995; Sciberras et al., 2009; Hardison et al., 2011; Martin et al., 2014; Sañé et al., 2016). The variation in temperature and irradiance are linked to photosynthesis, calcification and respiration process. Until a certain physiological threshold, increasing temperatures and irradiance improve photosynthesis and calcification in calcareous algae (Martin et al., 2013; Campbell et al., 2016; Comeau et al., 2016). For instance, a previous study indicated that under 30°C and without subsaturating irradiance, rhodoliths could reach their highest metabolic rate (Vásquez-Elizondo and Enríquez, 2016; Hoffman et al., 2016). Thus, better suitable habitats for rhodolith growth are expected near tropical regions, where warmer waters with high transparency rates prevail. At local scales, current velocity allows rhodoliths to roll and keep their circular shape, and influence their vertical distribution (Foster, 2001; Cabanellas-Reboredo et al., 2018). Water motion can also influence erosive processes and the associated community structure. Several studies correlated higher species richness and epibenthic biomass with reduced frequency and intensity of storms (Amado-Filho et al., 2007). Local nutrient load can also have an effect on the abundance of macroalgae composition (Fong et al., 1994; Figueroa et al., 2014), with eutrophic regions showing beds colonized by fast growing algae (Scherner et al., 2013; Neill and Nelson, 2016; Gouvêa et al., 2017).

The environmental conditions of South Atlantic coast make this area suitable for rhodolith beds (Foster et al., 2001). At the Brazilian coast, several beds were found from 5°N (near to Amazonian river - Moura et al., 2016) to 27°S (at Santa Catarina state – Gherardi, 2004; Pascelli et al., 2013). At lower latitudes, rhodolith beds host a great biodiversity adapted to higher temperatures and irradiance (Riul et al., 2009; Bahia et al., 2010; Amado-filho et al., 2012; Foster et al., 2013; Amado-Filho et al., 2017), while at higher latitudes, species tend to be rare and replaced by cold adapted taxa (Pascelli et al., 2013). In warm temperate region, diversity of rhodolith bed is also reduced (e.g., at Marine Protected Area (MPA) of Arvoredo) (Pascelli et al., 2013). This variability suggests that large-scale environmental drivers, together with more local conditions, influence the abundance and occurrence of rhodoliths and associated macroalgae. However, the absence of standardized collected data provide weak framework to further discussions regarding the macroecological drivers.

Considering this, the present study used depth standardized sampling and macroecological modelling to explain and predict the occurrence of rhodolith beds, their biomass and that of associated epiphytes along a latitudinal gradient of Southwestern Atlantic coast. Our main hypotheses are that (1) rhodolith abundance increases from higher to lower latitudes, since tropical sites have environmental conditions that favor higher photosynthesis and calcification and (2) the epiphytes composition and biomass of tropical regions differ from warm temperate regions, with species adapted to higher-transparency and warm-water at lower latitudes.

2.2. MATERIAL AND METHODS

2.2.1. Study area

Sampling was conducted along the southwestern Atlantic Coast, encompassing the tropical, transition and warm temperate regions (according to Horta et al., 2001 and Spalding et al., 2007), between latitudes of ~3°S and 27°S. Sites are depicted in Figure 1 and sampling coordinates and years in Table 1. Horta et al. (2001) separated this coast based on phycological composition and indicated the habitat heterogeneity and temperature as the major drivers of the differences. Spalding et al. (2007) also found this classification considering other marine organisms and mentioned that the differences in species composition is due to dominant biogeographic forcing agents (e.g.: upwelling, nutrient inputs, temperature regimes, currents and bathymetry).

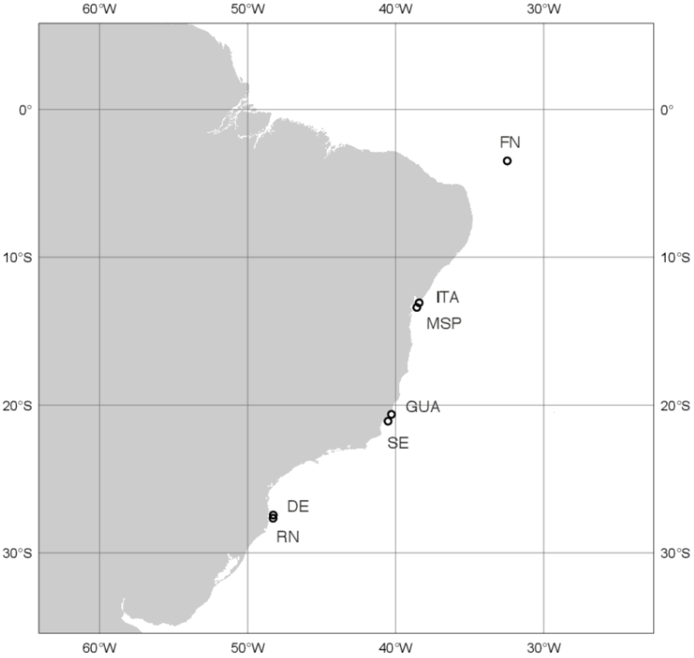

Figure 1. Collection points at Brazilian coast. FN: Rata island, ITA: Itaparica, MSP: Morro de São Paulo, GUA: Guarapari, SE: Sequim, DE: Deserta Island, RN: Rancho Norte.

Table 1. Collection points and coordinates at Brazilian coast.

City-State/Sites	Coordinates	Year of sampling
Fernando de Noronha– PE/ Rata Island (FN)	03°53’S; 32°28’W	Summer/2016
Itaparica– BA/ Itaparica Island (ITA)	13°04’S; 38°40’W	Summer/2014
Cairu– BA/ Morro de São Paulo (MSP)	13°25’S; 38°52’W	Summer/2014
Guarapari – ES/ Rasas Island (GUA)	20°40’S; 40°21’W	Summer/2014
Itaipava – ES/ Sequim (SE)	20°59’S; 40°44’W	Summer/2014
Florianópolis – SC/ Deserta Island (DE)	27°15’S; 48°19’W	Summer/2014
Florianópolis – SC/ Rancho Norte (RN)	27°16’S; 48°22’W	Summer/2015

The tropical region receives influence of Brazil Currents (BC) and North Brazil Currents (NBC) (Stramma and England, 1999). The coastal shelf of this region is relatively narrow (~70km), except for Abrolhos, where it reaches 200km offshore (Oliveira et al., 2012). The sea surface temperature (SST) varies from 25 to 29°C. Rata Island (FN), Itaparica (ITA) and Morro de São Paulo (MSP) sites are located in this region.

At the transition zone between Tropical and Warm temperate regions, BC, South Atlantic Central Water (SACW) and Coastal Water (CW) dynamic equilibrium influence the inner shelf (Castro and Miranda, 1998). Although the predominance of oligotrophic waters, a seasonal upwelling reaches the southern margin during summer (Schmid et al., 1995). The high abundance of substrates and the seasonal cold water upwelling of the transition zone favor the richest marine flora of Brazil, with occurrence of common species from the two adjacent regions (Guimarães, 2003; Amado-Filho et al., 2007). The SST vary from 21 to 27°C. Guarapari (GUA) and Itaipava (SE) sites are located this region.

The warm temperate region is influenced by the Brazil 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 Malvinas Current, a cooler and less saline water derived from the Antarctic Circumpolar Current (Matano et al., 2010; Orselli et al., 2018). The South Atlantic Central Water (SACW) formed in this region is transported southward by BC under the tropical water

(Stramma and England, 1999). Beyond SACW, waters coming from the Brazil-Malvinas Confluence mix with the low salinity and nutrient-rich plume added from the La Plata river, Patos-Mirim Lagoon, and other local sources of continental runoff (Möller et al., 2008; Strub et al., 2015). The SST varies from 16 to 27°C. Deserta (DE) and Rancho Norte (RN) are located in this region, within the Marine Protected Area (MPA) Arvoredo Marine Biological Reserve (Rebio Arvoredo). These rhodolith beds represent the southernmost limit of this habitat in the western Atlantic (Guerardhi, 2004; Pascelli et al., 2013).

2.2.2. Sampling and processing

The collections were conducted in rhodolith beds at a standardized depth of 10 ± 1m. This depth was chosen because the abundance of rhodolith and associated macroalgae is higher in shallow than deeper waters (Riul et al. 2009, Amado-Filho et al. 2007, Pascelli et al. 2013). Rhodoliths and associated epiphytes were collected within 5-15 quadrats of 0.0625 m^2, 2 meters distant from each other, randomly disposed along the bed. After each collection, all the content of each quadrat was taken to the laboratory and preserved at -20 ^{o} C until separation and identification at the species level, following standard methods (Joly, 1967; Cordeiro-Marino, 1978; Littler and Littler, 2000). Rhodoliths and epiphytes were then dried at 60ºC for 48 hours and weighted (balance precision of $1x10^{-3}$g). The genera *Neosiphonia*, *Polysiphonia, Ceramium* and *Centroceras* frequently occurred together on turf assemblage. Because of this, they were weight together and considered as Filamentous Red Algae in the following analyses. All rhodoliths from each quadrat were further disposed in a beaker filled with water to estimate their volume by water displacement (Pascelli et al., 2013). The relation between weight (g DW) and volume (cm^3) of rhodoliths was used to calculate the density (g DW. cm^{-3}) of the entire quadrat.

2.2.3. Statistical analyses

The differences between volume, density and biomass of rhodoliths and epiphytes between sampling sites were analyzed by Kruskal-Wallis test and multiple comparisons of mean ranks, using the software Statistica 13.3.

Models explaining and predicting the potential occurrence and biomass of rhodolith beds were developed using a delta-lognormal statistical approach. This fitted environmental predictors against the occurrence of rhodoliths (i.e., binomial response variable), separately from biomass (i.e., lognormal variable), and combined both approaches with a product function (reviewed by McGill et al., 2007). To this end, the machine-learning algorithm Boosted Regression Trees (BRT) was used since it handles non-linear relationships and complex interactions, while avoiding overfitting (i.e., the fit describing random noise) by forcing predictors to have positive or negative monotonic responses on the models, and by optimizing the number of diagrams, diagram complexity and learning rate (Elith, et al., 2008). A cross-validation framework using independent latitudinal bands was implemented to tune these three parameters (i.e., Neiva et al., 2015; Assis et al., 2016, 2017a).

The environmental predictors used in the analyses were selected considering the current ecological knowledge of coralline algae (e.g., Martin et al., 2014; Sañé et al. 2016) and were extracted from Bio-Oracle (Tyberghein et al. 2012, Assis et al. 2018), an open source dataset with information for the mean depth of the ocean at a spatial resolution of 30 arcmin (~9.2 km at the equator). Considering the high correlation found between nitrates and phosphates (0.94; Figure S1), we discarded the latter from analyses because it showed an higher correlation with maximum temperatures (0.97; Figure S1).

The binomial model used detailed georeferenced presence data gathered from Global Biodiversity Information Facility (GBIF) (http://data.gbif.org) and the available literature (Table S1), alongside with pseudo-absences generated with a three-step technique for improved species distribution modelling (see Senay et al., 2013 for details). The lognormal model used the mean biomass of each site, considering all samples.

True skill statistics (TSS) and the area of the receiver operating characteristic curve (i.e., AUC) were used to assess the performance of the binomial model while deviance explained was used for the lognormal model. The ecological significance of both models was investigated by determining the contribution of each environmental predictor to their performance and by developing partial dependency plots for each predictor, while fixing all alternative predictors onto their average (Elith et al., 2008).

The differences between the three regions with respect to community composition of epiphytes were analyzed using PERMANOVA, based on Bray-Curtis dissimilarities using 999 permutations (Anderson, 2001). The BIO-ENV procedure (Clarke and Ainsworth, 1993) used to identify which combination of the environmental variables extracted from Bio-Oracle best explained variations in community structure of epiphytes (Clarke and Ainsworth, 1993). SIMPER analysis was conducted to identify the species that most contributed to Bray–Curtis dissimilarity between regions (Clarke, 1993). The results of the BIO-ENV procedure were represented through in Non-metrical multidimensional scale (nMDS) ordinations of the states based on each composition of epiphytes (Bray–Curtis dissimilarities) and the associated best subset of explanatory environmental variables (Euclidean dissimilarities). Non-parametric Spearman test were also used to determine correlations between environmental predictors. These statistical analyses were performed using R software and packages “vegan”.

2.3. RESULTS

2.3.1. Rhodoliths abundance

The biomass, volume and density of rhodoliths from each sampling site were significate different (H=56.80461, p <0,001; H=32.43684, p<0.001; H=54.07191, p<0.001, respectively). The highest biomass and volume corresponded to the tropical site FN (36,476.3 [±10,295.9] and 26,080 [±8,077.2] gDW/m^2, respectively) and the lowest to warm temperate DE (11,121.4 [±2,930.7] and 11,729.2 [±3,936.0] gDW/m^2) and transition site SE (9,652.8 [±3,558.0] and 10,858.6 [±5,475.1] gDW/m^2, Figure 2A, 2B). With respect to density (Figure 2C), the results were more homogeneous. The higher density corresponded to tropical sites MSP (1.44[±0.22]), ITA (1.39[±0.06]) and FN (1.40[±0.09] gDW/m^2).

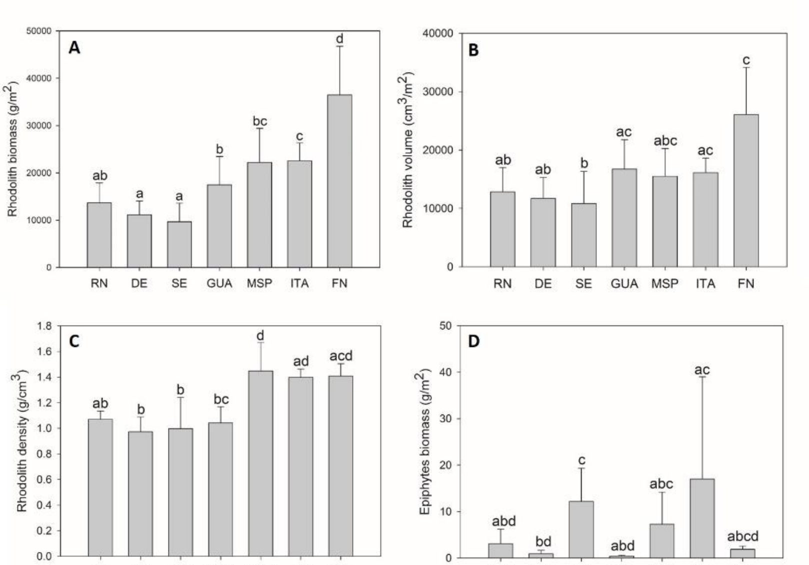

Figure 2. Biomass (A), volume (B) and density (C) of rhodoliths and biomass of epiphytes (D) from seven collections points along Brazilian coast (±SD bars). RN: Rancho Norte/ Florianópolis – SC; DE: Deserta Island/ Florianópolis – SC; SE: Sequim/ Itaipava – ES; GUA: Rasas Island/ Guarapari – ES; MSP: Morro de São Paulo/ Cairu– BA; ITA: Itaparica Island/ Itaparica– BA; FN: Rata Island/ Fernando de Noronha– PE. Letters above bars indicate results of Kruskall-Wallis multiple comparisons test (p<0.05).

2.3.2. Environmental drivers of rhodolith beds

The ecological models developed to explain and predict the occurrence of rhodoliths retrieved high performance (TSS: 0.90, AUC 0.95). In the same way, the model for biomass showed little deviation (deviance explained: 0.90) between observations and predictions (average difference of 2519 ± 2086 g/m^2; Figure 5; S2). The contribution of predictors to the models showed the occurrence of rhodolith beds (at the scales of our study) being mainly determined by maximum and minimum temperatures, as well as light availability at the bottom of the ocean (contributions > 10%; Figure 3). The partial dependency plots showed suitable habitats between ~16.0 and ~28.8ºC, although with higher probability between ~17.5ºC and ~26.5ºC, and light availability above ~3 E . m^{-2} . yr^{-1} (Figure 4). Where rhodoliths occur, biomass was largely explained by nitrate availability, and on a lower degree, by current velocity and minimum ocean temperatures (Figure 3). Higher levels of biomass were explained by temperatures above 23.3ºC, nitrates above 2 mmol.m^{-3} and current velocity above 0.22 m.s^{-1}. The integration of both models (i.e., delta-lognormal approach) predicted 229,718 km^2 of suitable habitats distributed between Rio Grande do Sul and Amapá States (Brazil) and between 1 to 149m (Figure S3), with a total potential overall biomass of 4,560 x 10^6 ton.

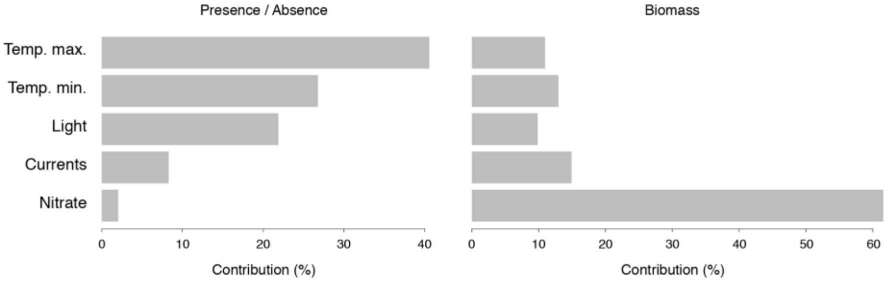

Figure 3. Relative contribution of climate predictors to the models developed for (left panel) presence / absence and (right panel) from biomass.

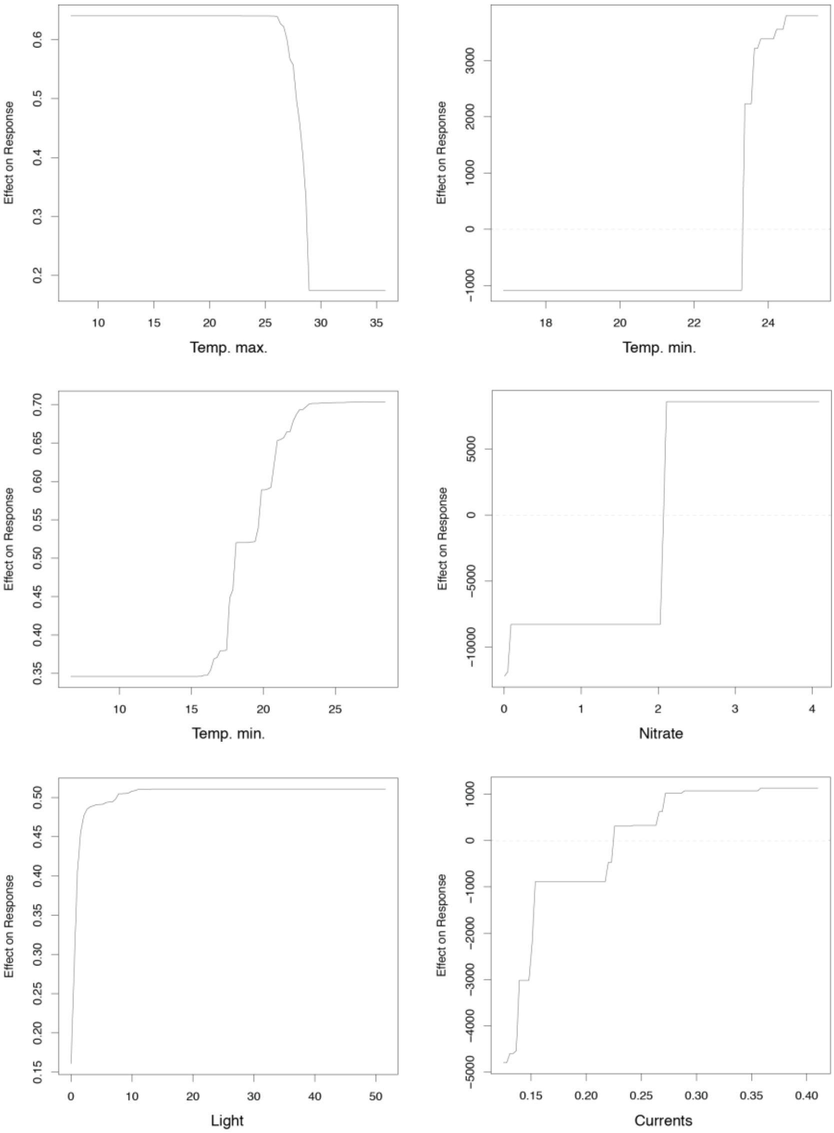

Figure 4. Partial dependency functions depicting the effect of the most important climate predictors on the models of (left panels) presence / absence and (right panel) biomass.

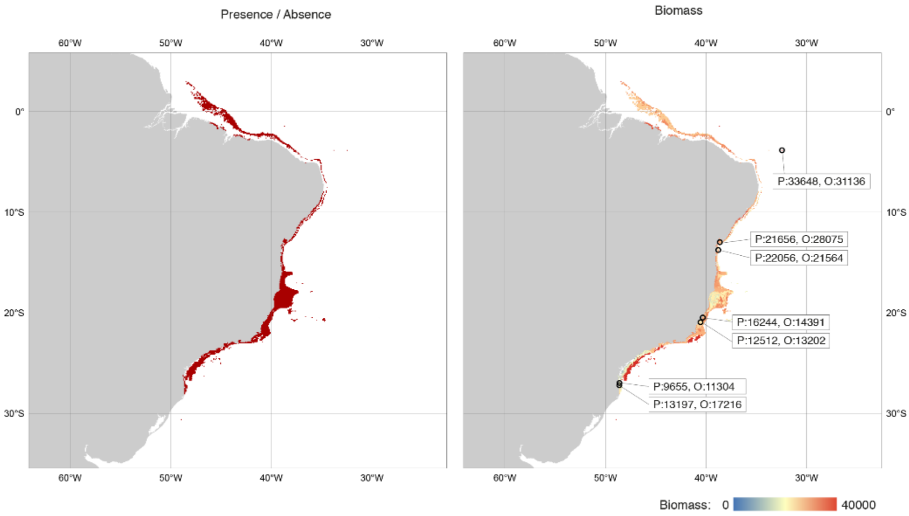

Figure 5. Potential (left panel) distribution and (right panel) biomass of Rhodolith beds (g/m^2). Black circles (right panel) depict sampling sites and boxes the correspondent predicted (P) and observed (O) biomass (g/m^2).

2.3.3. Epiphytes abundance

The total epiphytes biomass was significantly different among sites (H=45.54, p<0.001), but there was no clear latitudinal pattern (Figure 2D). ITA had the highest biomass, with 17 (±22) gDW/m^2 and GUA the lowest, with 0.412 (±0.240) gDW/m^2. With respect to the composition of epiphytes species, there were significant differences (F=8.77, p<0.001) between tropical, warm temperate and transition regions with respect to epiphytes of rhodolith beds, which are represented in Figure 6. SIMPER analyses indicate that the macroalgae that mainly contributed to differences between tropical/warm temperate was *Dictyopteris jolyana*, with 31.17%, while *Caulerpa pusilla* contributed to differences of tropical/transition with 12.58% and warm temperate/transition, with 17.10% (Table S4). The BEST analysis of BIO-ENV procedure indicated that the setting of epiphytes that most contributed differences in overall community was composed by Filamentous Red Algae group, *Hypnea spinella*, *Jania* spp, *Dictyota bartayresiana*, *Canistrocarpus cervicornis*, *Dictyopteris jolyana*, *Sargassum* sp. and *Padina gymnospora* (correlation = 0.67) (Figure 6). Regarding to environmental variables that explain variations in community structure, the best set was composed by maximum temperature and minimum nitrate (correlation = 0.26).

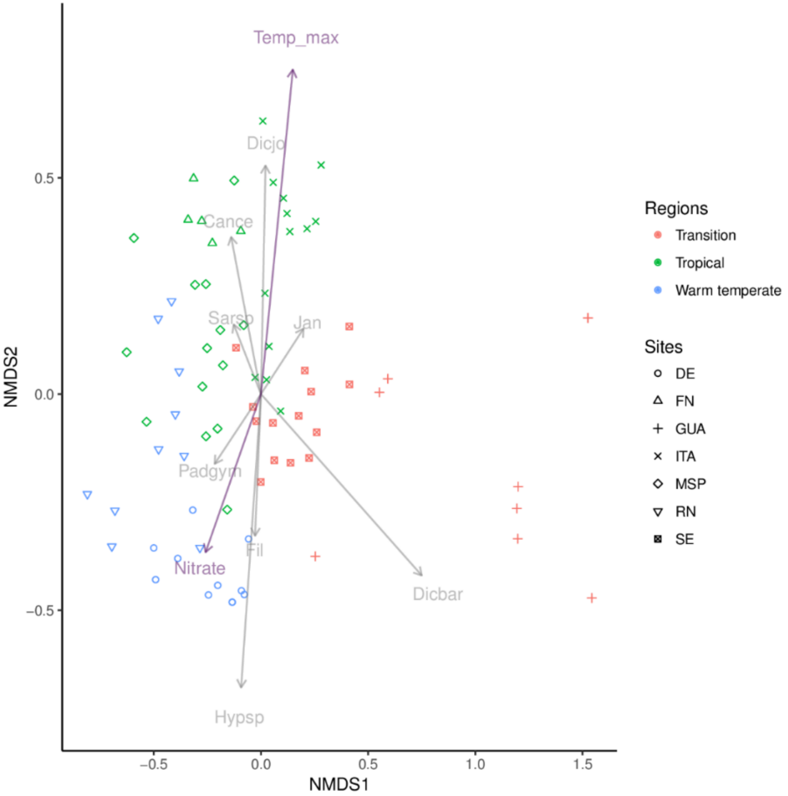

Figure 6. nMDS (stress = 0.161) representing groups of epiphytes community of rhodolith beds from Sites at Brazilian Regions highlighted in different colors ($p<0.001$). Gray arrows indicate species that most contributed to differences among communities (Codes: Padgym = *Padina gymnospora*, Dicjo = *Dictyopteris jolyana*, Jan = *Jania* sp., Dicbar = *Dictyota bartayresiana*, Hypsp = *Hypnea spinella* and Fil = Filamentous red algae, Sarsp = *Sargassum* sp., Cance = *Canistrocarpus cervicornis*). Purple arrows indicate environmental variables correlated with each species composition.

2.4. DISCUSSION

Studies focusing on the occurrence and composition of rhodolith beds have become increasingly available during the last years, however, this is the first to focus on abundance and associated community structure along a broad latitudinal gradient. By combining standardized sampling with macroecological modelling, it shows a clear latitudinal pattern of rhodolith abundance, which is mainly explained by nutrients, current velocity temperatures and light. With respect to total biomass of associated macroalgae, there was no evidence for a latitudinal gradient; however, the differences found in species composition corroborate with biogeographical regions (Horta et al. 2001), explained by higher temperature and irradiance of tropical regions or higher nutrient load of warm temperate province. According to the results, although the abundance of rhodoliths tended to increase with temperature, the limit of 28°C is yet preferable for occurrence, threshold corroborated by ecophysiological evaluations of tropical species (Diaz-Pulido et al. 2012, Vásquez-Elizondo et al. 2016, Scherner et al. 2016). The suitable area for these bioengineers of the Brazilian coast, comparable to the global coral reef (Jones et al., 2015), as well as the potential total biomass, reinforce the importance of rhodolith beds of Brazil, calling attention to further discussion regarding their conservation and eventual management.

2.4.1. Rhodolith abundance

The variation of abundance and density of rhodoliths followed the explored latitudinal gradient, with higher values in tropical sites decreasing towards warm temperate. The higher biomass in the tropics indicate a larger potential of this region for carbonate production and habitat building (Steller et al., 2003; Amado-Filho et al., 2012b; Foster et al., 2013) and the higher density suggests more robust and heavy individuals than in warm temperate areas. These characteristics may protect them from potential breaks caused by strong water movement and favor the stability of the bed (Marrack, 1999; Hinojosa-Arango and Riosmena-Rodríguez, 2004; Amado-Filho et al., 2007). The ecological models indicated that their occurrence is driven by increasing temperatures (until 28°C) and by light availability, while nutrients are the main predictor explaining abundance. While the effect of temperature on calcification and photosynthesis of coralline algae are not yet well known at global scales, they have been reported for tropical (Comeau et al., 2016), temperate (Martin et al., 2013) and polar environments (King and Schramm, 1982). For instance, the calcification in *Lithophyllum kotschyanum* increased linearly with temperature during spring, except when exposed to a thermal maximum of 31.5 °C (Comeau et al., 2016), a threshold close to that inferred in our study. Moreover, the gross photosynthesis in the Mediterranean crustose coralline algae *Lithophyllum cabiochae* was about two to threefold higher in summer than in winter, while calcification was four to eightfold higher in summer than in winter (Martin et al., 2013). In the Baltic Sea, the calcification of *Phymatolithon calcareum* increased linearly from 10 to 24 µg $CaCO_3$ g^{-1} h^{-1} between 0 and 20 °C (King and Schramm, 1982). The positive physiological response of coralline algae to temperature increase (until a certain limit) indicates that warm tropical sites are more suitable to rhodolith bed growth. In the same way, the high transparency of tropical waters seem to favor the occurrence and biomass of rhodolith beds. Increasing irradiance until a certain limit improves photosynthetic rates, which consequently enhanced calcification (Martin et al., 2013). Crustose coralline algae can exhibit a metabolic control of surface pH through photosynthesis and light-inducible H^+ pumps, which play an important role in biological processes related to inorganic carbon uptake and calcification (Hofmann et al., 2016). In Polar Regions, light is the important factor to $CaCO_3$ increment, followed by temperature (Teichert and Freiwald, 2014). In *Lithothamnion glaciale*, the summer growth seems to depend on the effect of previous winter cloud cover (Burdett et al., 2010).

Regarding the nutrients, the positive correlation of nitrates with biomass agrees with Dutertre et al. (2015) that also reported an increase in percentage of maerl cover near areas with higher nitrate concentration. In the same way, additional experiment showed the growth of the coralline algae *Lithophyllum yessoense* positively correlated with nitrate concentrations (Ichiki et al., 2000). However, Bjork et al. (1995) reported no significant effect of nitrate or ammonia on coralline algae calcification, while Vale et al. (2018) reported a reduction of rhodoliths near areas with high organic matter loads near Amazon River. However, our model showed no probability of occurrence in that area related to reduce light availability, and not due to increasing nutrients. This may also explain the lower observed and predicted biomass adjacent to the coast of Santa Catarina (at higher latitudes), which receive nutrient-rich waters coming from the plume from Rio de La Plata, Central Water of South Atlantic and, eventually, from the Malvinas Current, alongside with other local sources of continental runoff (Möller et al., 2008; Strub et al., 2015). In this region, higher biomass of rhodoliths were predicted 60km offshore, likely due to irradiance availability on deeper areas and favorable temperature and nutrient levels.

Currents were also important to explain the biomass of rhodoliths, although on a lower extent. Regions exposed to intense currents provide necessary movement to avoid epiphytes and fauna overgrowth, which could cover the rhodolith surface and disturb the acquisition of resources. Martin et al. (2014) suggest that flat and coarse-grained areas with strong bottom currents tends to be suitable habitats to rhodolith beds in the Mediterranean Sea, since that reduces sedimentation. Moderate hydrodynamics are preferable to rhodoliths than lower and higher (Cabanellas-Reboredo et al., 2018; Melbourne et al., 2018). Low hydrodynamics favors sedimentation, disrupts gas exchange, and enables overgrowth of epiphytic organisms under rhodolith surface (Steller and Foster, 1995; Sañé et al., 2016). Similarly, a more active hydrodynamic regime may also increase rhodolith density. The greater solidity of *Spongites fruticulosus* rhodoliths has been attributed to wave action that polishes the edges of this nucleated species (Steller and Foster, 1995; Cabanellas-Reboredo et al., 2018).

2.4.2. Epiphytes abundance

The differences in epiphytes community composition observed in Figure 6 is due to predominance of species with tropical and warm temperate preferences. The species that composes the community of tropical region seems to be driven by higher temperatures. The species relevant to the community in this region were *D. jolyana* and *C. cervicornis*. Dictyotales members were previously referred as abundant in tropical region (Sangil et al., 2011; Brasileiro et al., 2016). They can grow in places with higher light levels, since this enhance photosynthetic efficiency, irradiance of saturation and non-photochemical quenching for chlorophyll fluorescence (Celis-Plá et al., 2015).

At warm temperate sites, the abundance of tropical genera decreases and tends to be replaced by species that have cold-water affinities. A latitudinal variation in seaweed communities was also reported for NE Atlantic, with warm-tolerant species in south and cold and low-light-tolerant species in north (Peña et al., 2014). As indicated in Figure 6, *Hypnea spinella* and Filamentous red algae were relevant in community of this region and were positive correlated with minimum nitrate. Studies with *Hypnea* species, indicate that these algae can tolerate high nutrient concentration and act as biofilters of nitrogen and phosphorus (Martins et al., 2009; Ribeiro et al., 2013, Whitehouse and Lapointe, 2015). Moreover, phosphate, which was correlated with nitrate (Figure S1), has a role in metabolic processes related to nitrate reductase activity, responsible to catalyze the reduction of nitrate to nitrite, which is an important factor in regulation of growth and protein production (Martins et al., 2009). In general, previous studies observed that algae with higher surface-area/volume ratio tend to have more nutrient requirement and faster growth than thicker algae (Taylor et al., 1998; Piazzi et al., 2011).

Due to the peculiarities of ES state, it was referred as a transition zone between Tropical and Warm temperate regions of Brazil with respect to macroalgae flora (Horta et al., 2001; Guimarães et al., 2008; Amado-Filho et al., 2010) and other marine organisms (Spalding et al., 2007; Teixeira et al., 2013; Vila-Nova et al., 2014). The encounter of BC and SACW leads to this region tropical waters from the north and a seasonal influence from cold and high rich nutrient waters from south, enabling the co-occurrence of organisms of warm and cold tolerant waters (Guimarães, 2003). A similar pattern was observed in the present results. *D. bartayresiana* was the algae more relevant to this transition region community due to the predominance in GUA site. However, the alga that most contributed to this region being different from tropical and warm temperate was *C. pusilla*. This alga was previously referred for rhodolith beds of this region during Summer in Amado-Filho et al. (2010). Some articles with another species of *Caulerpa* reveled that they can survive in a large range of temperatures (10-30°C, Terrados and Ros, 1992 or 15-30°C, Ukabi et al., 2013) and persist under high nutrient load (Lapointe and Bedford, 2010), environmental conditions similar to reported for the transition region in summer.

Besides the predominance of the tropical *P. gymnospora* in the warm temperate site (RN), expressive biomass of other Dictyotales algae such as *Canistrocarpus cervicornis* and *Dictyota delicatula* reinforce some tropical affinities (Table S2). These species were not referred for RN rhodolith bed by Pascelli et al. (2013), who highlighted the low diversity of macroalgae of this region, relating this to warm temperate climate of the region. Therefore, these shifts in flora composition suggest a response to an environmental change, which turn this area more similar to tropical region for a temporary time. The tropicalization process due to climate change have been described for subtropical and temperate regions (Vergés et al., 2014; Wernberg et al., 2016; Araújo et al., 2018). The sampling at RN in the summer/2015 coincided with the occurrence of El Niño event, reflecting substantial environmental changes such as altered rain regimes, winds and marine currents, which influence the seawater temperature (Freire et al., 2017). Moreover, Gouvêa et al. (2017) registered a strong heatwave at warm temperate coast in Spring 2014, which could cause the shifts in community structure of summer/2015. These events have been more frequent and intense due to climate changes (Wernberg et al., 2013; 2016). Consequently, tropicalization of warm temperate region ecosystems is an ongoing process and management measures are necessary to protect these environments.

Although several publications cited in this study highlight the importance of different abiotic characteristics of tropical and warm temperate environments to macroalgae growth, the correlation with the best environmental variable predictors was weak (0.26). This can indicate that faster and local-scale environmental changes not considered here could drive the abundance of these fast growth organisms (Riul et al., 2009; Pascelli et al., 2013; McConnico et al., 2017). Even though this study avoids the seasonal factor changes related with time scale by conducting all collections in summer, environmental changes along seasons and years should add additional light in the discussion about environmental drivers of macroalgal community (Gatti et al., 2015).

Besides abiotic factors, herbivory is one of the major drivers of macroalgal composition (Littler et al., 1995; Poore et al., 2012; Bonaldo and Hay, 2014; Longo et al., 2015). The action of herbivores along latitudinal gradient seems to vary according to the organisms considered. The herbivory by fishes tends to increase towards the tropics, due to higher temperatures (Floeter et al.,2004; Ferreira et al., 2004; Longo et al., 2014). The abundance of invertebrates (which include herbivores) increases at latitudes higher than 20° in the southeastern Atlantic (Aued et al., 2018). Carvalho et al. (2018, unpublished data) observed the disappearance of epiphytes at RN rhodolith bed along time, following the increase in invertebrates. However, Poore et al. (2012) analyzed experiments with fishes and invertebrate herbivores exclusion and concluded that there was no latitudinal gradient of herbivory, but it depends on the taxonomic (with major impact on brown algae) or morphological group, with major impacts on leathery macrophytes and foliose algae. The dominant species found in tropical sites are Dictyotales members that can produce chemical defenses when subjected to herbivory (Stachowicz and Hay, 1996; Bianco et al., 2010; Araújo et al., 2018b), which suggest that herbivores could have an important role in structuring macroalgal community in this region.

Finally, the positive influence of higher temperatures on tropical Dictyotales abundance shows that these faster growth species could benefit from a possible temperature increment, and so does rhodoliths abundance. Although this study focused only on the abundance of these algae on rhodolith beds, they were reported for tropical shallower environments that experience temperatures above 28°C (Nunes and Paula, 2006; Scherner et al., 2013). However, the oc currence of the beds is limited under temperatures higher than 28°C. This indicates that if ocean temperatures increase due to climate changes, this could limit the occurrence of rhodoliths in tropical regions and restrict it to higher latitudes, as suggested for other marine environments (Hooidonk et al., 2014; Wernberg et al., 2016; Vinagre et al, 2018). The vulnerability of tropical rhodoliths and the probably future increase in competition with epiphytes suggest that monitoring and conservation measures are fundamental in the face of environmental changes.

2.5. Conclusions

Temperatures, nutrients, current velocity and water transparency are among the main environmental drivers of rhodoliths and associated epiphytic assemblage. The higher biomass at 10 m depth was observed in tropical sites, while the suitable sites were more abundant in transition and warm temperate regions. The predictive model indicates high biomass of rhodoliths 60km off Paraná and São Paulo coast, a region that was not well explored yet. With respect to epiphytes, temperature and nitrate seems to be the major drivers controlling the composition of species, with warm-water adapted species in tropical region and cold-water and higher nutrient adapted species in warm temperate. Although in low abundance, tropical species not referred before for warm temperate beds appeared in summer 2015,which can indicate a tropicalization event.

2.6. Author contributions

VC, JS, JN, SB and PH planned the sampling design of the study. VC and JA performed the modelling and statistical analysis. PH, JS and JN were responsible for field collections and financial support. VC analyzed the field samples and wrote the first draft of the manuscript; JA, ES, JN, SB, JB and PH wrote sections of the manuscript. All authors contributed to manuscript discussion and revision.

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Supplementary materials

Table S1. Dataset of occurrences of rhodolith-forming species in Brazil used in presence/absence model.

Species	Lon	Lat	RecordUserID
Harveylithon rupestre	-49.924	4.4294	Vale et al. 2018
Lithophyllum gr. pustulatum	-49.924	4.4294	Vale et al. 2018
Sporolithon sp.	-49.924	4.4294	Vale et al. 2018
Rhodoliths Unid.	-49.92	4.37	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Sporolithon sp.	-48.492	3.003	Vale et al. 2018
Lithophyllum sp	-48.492	3.003	Vale et al. 2018
Sporolithon sp.	-46.779	1.401	Vale et al. 2018
Lithophyllum gr. prototypum	-46.779	1.401	Vale et al. 2018
Rhodoliths Unid.	-46.78	1.3	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Rhodoliths Unid.	-46.84	1.32	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithothamnion crispatum	-46.48	1.165	Vale et al. 2018
Rhodoliths Unid.	-46.5	1.1	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithothamnion crispatum	-46.61	0.806	Vale et al. 2018
Rhodoliths Unid.	-46.64	0.2	Laboratorio de Ficologia, Universidade Federal de Santa

			Catarina, http://lafic.ufsc.br/
Rhodoliths Unid.	-45.56	0.11	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Harveylithon rupestre	-44.807	-0.245	Vale et al. 2018
Lithophyllum gr. pustulatum	-44.807	-0.245	Vale et al. 2018
Lithoporella sp	-44.807	-0.245	Vale et al. 2018
Sporolithon sp	-44.807	-0.245	Vale et al. 2018
Rhodoliths Unid.	-44.81	-0.27	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Rhodoliths Unid.	-32.29	-3.59	Presente trabalho
Hydrolithon rupestre	-32.4	-3.81	Amado-Filho et al. 2012
Lithophyllum corallinae	-32.4	-3.81	Amado-Filho et al. 2012
Lithothamnium crispatum	-32.4	-3.81	Amado-Filho et al. 2012
Sporolithon episporum	-32.4	-3.81	Amado-Filho et al. 2012
Sporolithon ptychoides	-32.4	-3.81	Amado-Filho et al. 2012
Mesophyllum engelhartii	-32.4	-3.81	Amado-Filho et al. 2012
Mesophyllum erubescens	-38.4	-3.566667	GBIF.org (25 May 2018) GBIF Occurrence
Lithothamnion superpositum	-32.393333	-3.815833	GBIF.org (25 May 2018) GBIF Occurrence
Mesophyllum erubescens	-32.416667	-3.833333	GBIF.org (25 May 2018) GBIF Occurrence
Lithothamnion superpositum	-33.855278	-3.846944	GBIF.org (25 May 2018) GBIF Occurrence
Lithothamnion superpositum	-32.470833	-3.866389	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum corallinae	-32.466389	-3.885278	GBIF.org (25 May 2018) GBIF Occurrence
Rhodoliths Unid.	-35.26	-4.98	Testa and Bosence 1999
Rhodoliths Unid.	-35.13	-4.96	Testa and Bosence 1999

Lithophyllum	-35.32	-5.1	Testa and Bosence 1999
Mesophyllum	-35.32	-5.1	Testa and Bosence 1999
Rhodoliths Unid.	-35.25	-5.19	Testa and Bosence 1999
Lithothamnion occidentale	-36.5169	-5.9177	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Mesophyllum erubescens	-36.5169	-5.9177	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Sporolithon episporum	-34.76	-6.96	Riul et al. 2009
Lithophyllum	-34.76	-6.96	Riul et al. 2009
Lithothamnion	-34.76	-6.96	Riul et al. 2009
Sporolithon episporum	-34.73	-7	Riul et al. 2009
Lithophyllum	-34.73	-7	Riul et al. 2009
Lithothamnion	-34.73	-7	Riul et al. 2009
Sporolithon episporum	-34.74	-7.07	Riul et al. 2009
Lithophyllum	-34.74	-7.07	Riul et al. 2009
Lithothamnion	-34.74	-7.07	Riul et al. 2009
Lithophyllum stictaeforme	-34.75	-7.5666	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithothamnion occidentale	-38.2203	-8.3753	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithothamnion superpositum	-38.2203	-8.3753	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Mesophyllum erubescens	-38.2203	-8.3753	Laboratorio de Ficologia, Universidade Federal de Santa

			Catarina, http://lafic.ufsc.br/
Lithophyllum corallinae	-35.838178	-9.768831	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum frondosum	-41.2362	-11.5207	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum johansenii	-41.2362	-11.5207	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum stictaeforme	-41.2362	-11.5207	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithothamnion occidentale	-41.2362	-11.5207	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithothamnion superpositum	-41.2362	-11.5207	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Mesophyllum erubescens	-38.3724	-12.959166	GBIF.org (25 May 2018) GBIF Occurrence
Lithothamnion brasiliense	-38.3725	-12.959167	GBIF.org (25 May 2018) GBIF Occurrence
Lithothamnion superpositum	-38.370278	-12.966944	GBIF.org (25 May 2018) GBIF Occurrence
Sporolithon	-38.6331	-13.0041	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum depressum	-38.637778	-13.005889	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum corallinae	-38.86	-14.901944	GBIF.org (25 May 2018) GBIF Occurrence

Lithophyllum corallinae	-38.86	-14.901944	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum corallinae	-38.86	-14.901944	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum frondosum	-39.711944	-16.398333	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-39.711944	-16.398333	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum frondosum	-38.869444	-16.905833	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-38.869444	-16.905833	GBIF.org (25 May 2018) GBIF Occurrence
Lithothamnion superpositum	-38.869444	-16.905833	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-39.1826	-17.1136	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Mesophyllum erubescens	-39.1826	-17.1136	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum stictaeforme	-39.2174	-17.2554	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Mesophyllum erubescens	-39.2174	-17.2554	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Sporolithon yoneshigueae	-38.1841	-17.6458	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithothamnion superpositum	-37.916389	-17.900556	GBIF.org (25 May 2018) GBIF Occurrence
Mesophyllum erubescens	-38.6833	-17.95	Laboratorio de Ficologia, Universidade Federal de Santa

			Catarina, http://lafic.ufsc.br/
Lithothamnion superpositum	-38.695278	-17.9625	GBIF.org (25 May 2018) GBIF Occurrence
Lithothamnion occidentale	-38.7	-17.9666	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Mesophyllum erubescens	-38.7	-17.9666	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum depressum	-38.674267	-17.973533	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum frondosum	-38.890833	-18.1525	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-38.890833	-18.1525	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum frondosum	-38.723333	-18.185555	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-38.723333	-18.185555	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum frondosum	-38.768333	-19.539722	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-38.768333	-19.539722	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum depressum	-40.5929	-19.5966	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum johansenii	-40.5929	-19.5966	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum stictaeforme	-40.5929	-19.5966	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithothamnion superpositum	-40.5929	-19.5966	Laboratorio de Ficologia, Universidade

			Federal de Santa Catarina, http://lafic.ufsc.br/
Sporolithon yoneshigueae	-39.45	-19.6167	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithothamnion superpositum	-40.101389	-19.920833	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum corallinae	-40.137	-19.9378	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum stictaeforme	-40.137	-19.9378	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithothamnion superpositum	-40.137222	-19.973056	GBIF.org (25 May 2018) GBIF Occurrence
Rhodoliths Unid.	-48.49	2.95	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Sporolithon yoneshigueae	-30.1	-20.48	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum depressum	-29.334194	-20.489472	GBIF.org (25 May 2018) GBIF Occurrence
Sporolithon yoneshigueae	-34.7711	-20.5783	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Mesophyllum erubescens	-40.366667	-20.666667	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum espiritosantense	-40.5689	-20.8842	Laboratorio de Ficologia, Universidade Federal de Santa

			Catarina, http://lafic.ufsc.br/
Lithophyllum stictaeforme	-40.5689	-20.8842	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum corallinae	-40.582876	-20.886705	GBIF.org (25 May 2018) GBIF Occurrence
Lithothamnion superpositum	-40.756389	-20.919444	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum corallinae	-40.9175	-21.034444	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum johansenii	-40.713056	-21.034444	GBIF.org (25 May 2018) GBIF Occurrence
Lithothamnion superpositum	-40.296944	-21.048611	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum frondosum	-40.296944	-21.049444	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-40.296944	-21.049444	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum johansenii	-40.763055	-21.075833	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum johansenii	-40.704444	-21.082778	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum corallinae	-40.5025	-21.104722	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum corallinae	-40.590833	-21.250278	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum frondosum	-40.926111	-21.259444	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-40.926111	-21.259444	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum corallinae	-40.524722	-21.296667	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum frondosum	-40.524722	-21.296667	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum johansenii	-40.524722	-21.296667	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-40.524722	-21.296667	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum frondosum	-40.512222	-21.303333	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-40.512222	-21.303333	GBIF.org (25 May 2018) GBIF Occurrence

Lithothamnion superpositum	-48.366667	-27.266667	GBIF.org (25 May 2018) GBIF Occurrence
Mesophyllum erubescens	-48.366667	-27.266667	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum margaritae	-48.368319	-27.288747	GBIF.org (25 May 2018) GBIF Occurrence
Lithophyllum stictaeforme	-48.3666	-27.2916	Laboratorio de Ficologia, Universidade Federal de Santa Catarina, http://lafic.ufsc.br/
Lithophyllum margaritae	-48.653961	-27.742453	GBIF.org (25 May 2018) GBIF Occurrence

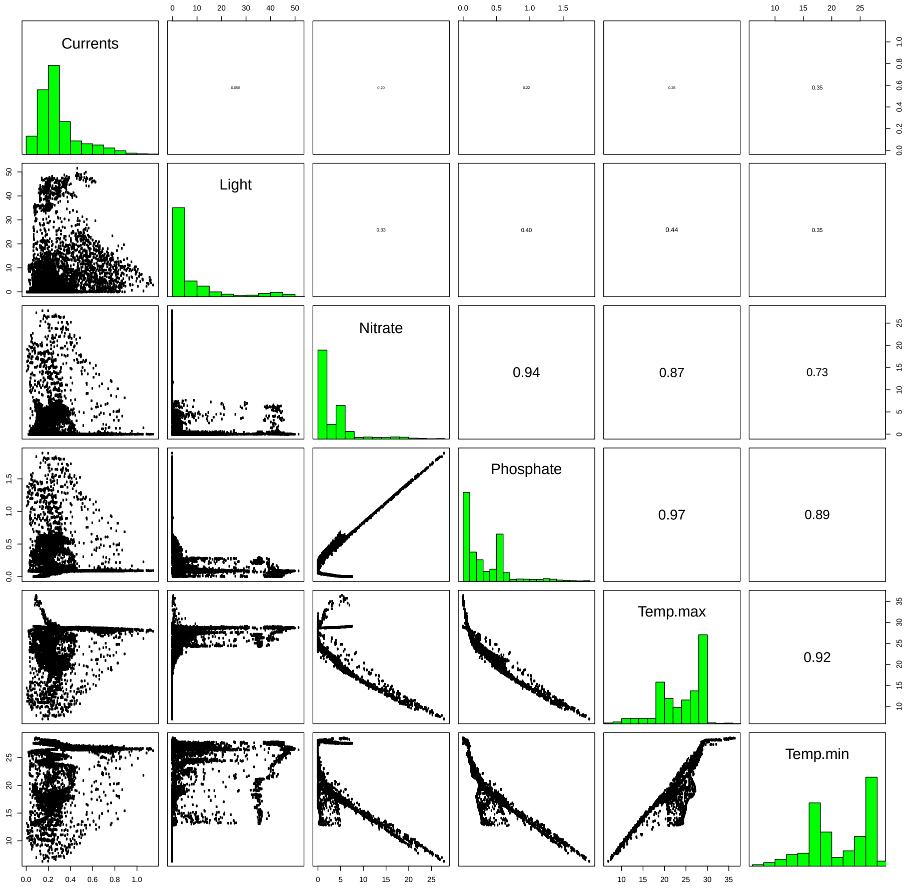

Figure S1. Plots of correlation between environmental variables used in models.

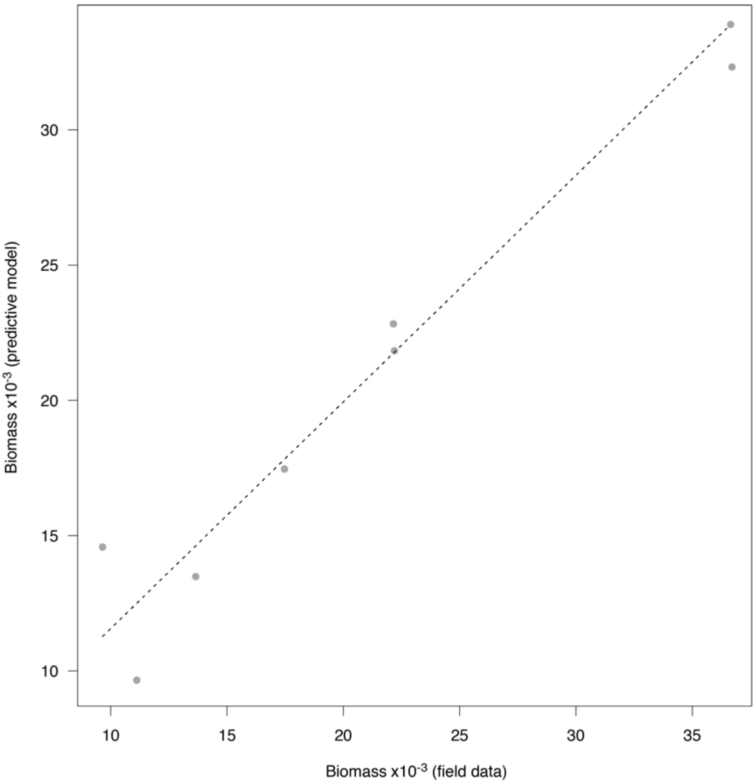

Figure S2. Relationships between the actual biomass of Rhodolith beds (field samples) and predicted biomass retrieved from the Delta-log normal approach.

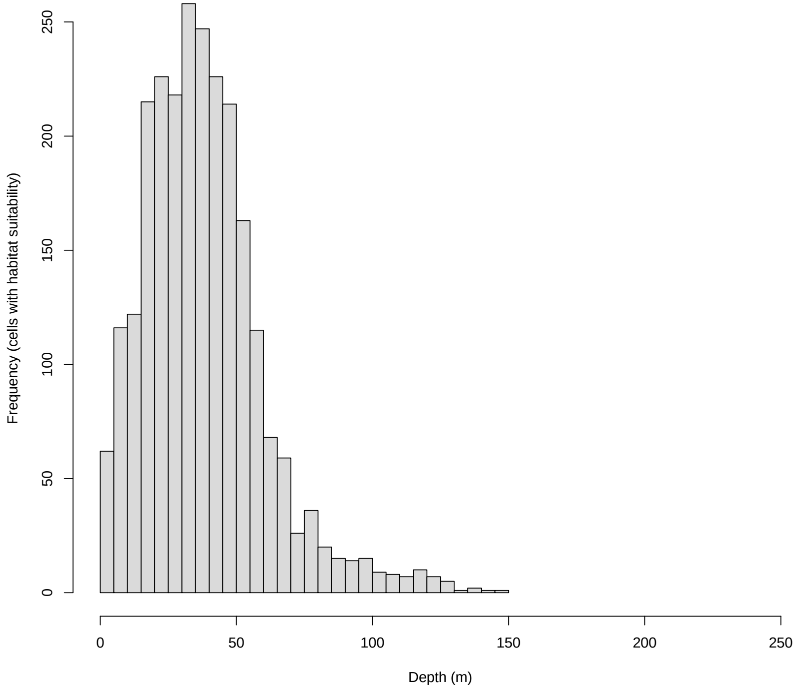

Figure S3. Distribution of the suitable habitats (presence / absence model) for Rhodolith beds as a function of depth.

Table S2. Presence/Absence of epiphytes species from collection Points.

Species	**Collection points**						
	RN	**DE**	**SE**	**RI**	**MSP**	**IT**	**FN**
Rhodophyta							
Amphiroa beauvoisii J.V.Lamouroux	0	0	1	1	0	0	1
Amphiroa fragilissima (Linnaeus) J.V.Lamouroux	1	0	0	0	0	0	0
Amphiroa rigida J.V.Lamouroux	0	0	1	0	0	0	0
Centroceras clavulatum (C.Agardh) Montagne	0	1	0	0	0	0	0

Ceramium brasiliense A.B.Joly	0	0	1	0	0	0	0
Ceramium dawsonii A.B.Joly	0	0	0	0	1	0	0
Champia parvula (C.Agardh) Harvey	1	1	1	0	0	0	0
Chrysymenia enteromorpha Harvey	0	0	1	0	0	0	0
Dasya brasiliensis E.C.Oliveira Filho & Y.Y.Braga	0	0	1	0	0	0	0
Dasya elongata Sonder	0	0	1	0	0	0	0
Dichotomaria marginata (J.Ellis & Solander) Lamarck	0	0	0	0	0	1	0
Dichotomaria obtusata (J.Ellis & Solander) Lamarck	0	0	0	0	1	0	0
Dictyurus occidentalis J.Agardh	0	0	1	0	0	0	0
Gelidium crinale (Hare ex Turner) Gaillon	1	1	0	0	1	0	0
Gracilaria sp	0	0	0	0	1	1	0
Gelidiopsis intricata (C.Agardh) Vickers	1	0	0	0	0	0	0
Hypnea musciformis (Wulfen) J.V. Lamouroux	1	0	0	0	0	0	0
Hypnea spinella (C.Agardh) Kützing	1	1	0	0	0	0	0
Jania adhaerens J.V.Lamouroux	1	1	1	0	1	0	0
Jania capillacea Harvey	0	0	1	0	0	0	1
Jania cubensis Montagne	0	0	1	0	0	0	0
Jania pumila J.V.Lamouroux	0	0	0	0	0	1	0
Jania subulata (Ellis & Solander) Sonder	0	0	1	0	1	0	0
Liagora ceranoides J.V.Lamouroux	0	0	1	0	0	0	0
Neosiphonia sphaerocarpa	0	1	0	0	0	0	0

(Børgesen) M.-S.Kim & I.K.Lee							
Neosiphonia tepida (Hollenberg) S.M.Guimarães & M.T.Fujii	0	0	1	1	0	0	0
Peyssonnelia simulans Weber-van Bosse	0	0	0	0	1	0	0
Plocamium brasiliense (Greville) M.Howe & W.R.Taylor	0	0	1	0	0	0	0
Polysiphonia denudata (Dillwyn) Greville ex Harvey	0	0	1	0	0	0	0
Polysiphonia howei Hollenberg	0	0	1	0	0	0	0
Rhodymenia pseudopalmata (J.V.Lamouroux) P.C.Silva	0	0	0	0	1	0	0
Tsengia sp	0	0	1	0	0	0	0
Ochrophyta: Class Phaeophyceae							
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck	1	0	1	0	1	1	1
Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier	0	0	1	0	0	0	0
Dictyota bartayresiana J.V.Lamouroux	0	0	0	1	0	0	0
Dictyota ciliolata Sonder ex Kützing	0	0	1	0	0	0	0
Dictyota mertensii (C.Martius) Kützing	0	0	1	0	1	1	0
Dictyota pulchella Hörnig & Schnetter	0	0	0	0	0	0	1
Dictyota sp.	0	0	1	0	0	0	0
Dictyopteris delicatula J.V.Lamouroux	1	0	0	0	1	1	1
Dictyopteris jolyana E.C.Oliveira & R.P.Furtado	0	0	1	0	0	1	0

Dictyopteris justii J.V.Lamouroux	0	0	0	0	0	0	1
Dictyopteris plagiogramma (Montagne) Vickers	1	0	0	0	1	1	1
Lobophora variegata (J.V.Lamouroux) Womersley ex E.C.Oliveira	0	0	1	0	1	1	0
Padina gymnospora (Kützing) Sonder	1	0	1	0	0	1	0
Rosenvingea sanctae-crucis Børgesen	1	0	1	0	0	0	0
Sargassum furcatum Kützing	0	0	1	0	0	0	0
Sargassum sp.	0	0	0	0	1	0	0
Stypopodium zonale (J.V.Lamouroux) Papenfuss	0	0	1	0	0	0	0
Chlorophyta							
Anadyomene lacerata D.S.Littler & Littler	0	0	1	0	0	0	0
Bryopsis plumosa (Hudson) C.Agardh	0	1	0	0	0	0	0
Caulerpa mexicana Sonder ex Kützing	0	0	1	0	0	0	0
Caulerpa pusilla (Kützing) J.Agardh	0	0	1	0	0	0	0
Cladophora vagabunda (Linnaeus) Hoek	1	1	0	0	1	0	0
Cladophora rupestris (Linnaeus) Kützing	1	1	0	0	0	0	0
Codium isthmocladum Vickers	0	0	0	0	1	0	0
Ernodesmis verticillata (Kützing) Børgesen	1	0	0	0	0	0	0
Halimeda discoidea Decaisne	0	0	1	0	0	1	0
Udotea cyathiformis Decaisne	0	0	1	0	0	0	0
Udotea unistratea D.S.Littler & Littler	0	0	1	0	0	0	0
Total	**15**	**9**	**35**	**3**	**16**	**11**	**6**

Table S3. Biomass of Epiphytes species from collection Points (±SD) .

Species	RN	DE	SE	GUA	MSP	ITA	FN
Rhodophyta							
Amphiroa beauvoisii	0	0	0.238 (±0.048)	0.069 (±0.014)	0	0	0
Amphiroa fragilissima	0.268 (±0.032)	0	0	0	0	0	0
Amphiroa rigida	0	0	0.187 (±0.019)	0	0	0	0
Champia parvula	0.004 (±0.001)	0.003 (±0.0004)	0.0001 (±0.00001)	0	0	0	0
Chrysymenia enteromorpha	0	0	0.001 (±0.0004)	0	0	0	0
Dasya brasiliensis	0	0	0.003 (±0.0009)	0	0	0	0
Dasya elongata	0	0	0.0008 (±0.0002)	0	0	0	0
Dichotomaria marginata	0	0	0	0	0	0.060 (±0.017)	0
Dichotomaria obtusata	0	0	0	0	5.644 (±0.437)	0	0
Dictyurus occidentalis	0	0	0.008 (±0.002)	0	0	0	0
Filamentous red algae	0.025 (±0.002)	0.181 (±0.015)	0.201 (±0.010)	0.007 (±0.002)	0.049 (±0.004)	0.197 (±0.034)	0.005 (±0.001)
Gelidium crinale	0.031 (±0.008)	0.006 (±0.001)	0	0	0.005 (±0.001)	0	0
Gracilaria sp.	0	0	0	0	0.004 (±0.001)	0.004 (±0.001)	0
Gelidiopsis intricata	0.007 (±0.001)	0	0	0	0	0	0
Hypnea musciformis	0.008 (±0.002)	0	0	0	0	0	0
Hypnea spinella	0.017 (±0.004)	0.751 (±0.062)	0	0	0	0	0
Jania spp.	0.013 (±0.003)	0.001 (±0.0003)	1.113 (±0.081)	0.022 (±0.005)	0.102 (±0.012)	0.096 (±0.009)	0.017 (±0.006)
Liagora ceranoides	0	0	0.301 (±0.048)	0	0	0	0
Peyssonnelia simulans	0	0	0	0	0.214 (±0.057	0	0
Plocamium brasiliense	0	0	0.006 (±0.001)	0	0	0	0
Rhodymenia pseudopalmata	0	0	0	0	0.006 (±0.001)	0	0
Tsengia sp.	0	0	0.879 (±0.203)	0	0	0	0
Ochrophyta: Class Phaeophyceae							
Canistrocarpus cervicornis	0.108 (±0.018)	0	0.196 (±0.043)	0	0.092 (±0.007)	0	0.446 (±0.042)

Colpomenia sinuosa	0	0	0.03 (±0.005)	0	0	0	0
Dictyota bartayresiana	0	0	0	0.314 (±0.029)	0	0	0
Dictyota ciliolata	0	0	0.002 (±0.001)	0	0	0	0
Dictyota mertensii	0	0	0.017 (±0.004)	0	0.033 (±0.006)	0.0003 (±0.00008)	0
Dictyota pulchella	0	0	0	0	0	0	0.050 (±0.009)
Dictyota sp.	0	0	0.014 (±0.003)	0	0	0	0
Dictyopteris delicatula	0.075 (±0.018)	0	0	0	0.039 (±0.009)	0.028 (±0.003)	0.0305 (±0.009)
Dictyopteris jolyana	0	0	0.016 (±0.003)	0	0	16.176 (±1.694)	0
Dictyopteris justii	0	0	0	0	0	0	0.107 (±0.028)
Dictyopteris plagiogramma	0.001 (±0.0003)	0	0	0	0.003 (±0.0004)	0.094 (±0.008)	1.242 (±0.115)
Lobophora variegata	0	0	0.038 (±0.005)	0	0	0.199 (±0.044)	0
Padina gymnospora	2.506 (±0.305)	0	0.423 (±0.062)	0	0	0.0004 (±0.0001)	0
Rosenvingea sanctae-crucis	0.001 (±0.0004)	0	0.209 (±0.028)	0	0	0	0
Sargassum furcatum	0	0	1.694 (±0.449)	0	0	0	0
Sargassum sp.	0	0	0	0	0.0004 (±0.00007)	0	0
Stypopodium zonale	0	0	0.031 (±0.005)	0	0	0	0
Chlorophyta							
Anadyomene lacerata	0	0	0.003 (±0.001)	0	0	0	0
Bryopsis plumosa	0	0.0003 (±0.0005)	0	0	0	0	0
Caulerpa mexicana	0	0	0.005 (±0.001)	0	0	0	0
Caulerpa pusilla	0	0	4.014 (±0.279)	0	0	0	0
Cladophora spp.	0.004 (±0.0005)	0.002 (±0.0002)	0	0	0.001 (±0.0002)	0	0
Codium isthmocladum	0	0	0	0	1.078 (±0.169)	0	0
Ernodesmis verticillata	0.004 (±0.001)	0	0	0	0	0	0
Halimeda discoidea	0	0	0.512 (±0.056)	0	0	0.147 (±0.027)	0
Udotea cyathiformis	0	0	2.029 (±0.249)	0	0	0	0
Udotea unistratea	0	0	0.005 (±0.001)	0	0	0	0

Table S4. Results of SIMPER analyses between epiphytes community of states. The table shows only species with significant contribution to dissimilarities ($p<0.05$).

Regions	**Species**	**Average Contribution (%)**	**Cumulative contribution (%)**	**p value**
Subtropical_ Transition	*Caulerpa pusilla*	17.10	17.46	***
	Padina gymnospora	14.01	31.77	***
	Hypnea spinella	12.76	44.79	***
	Udotea cyathiformis	9.40	54.38	***
	Dictyota bartayresiana	9.39	63.99	***
	Jania spp.	6.99	71.13	***
	Filamentous red algae	4.19	75.38	**
	Tsengia sp.	3.93	79.39	***
	Amphiroa beauvoisii	3.42	82.89	***
	Amphiroa fragilissima	2.86	89.27	**
	Halimeda discoidea	2.22	91.56	**
	Rosenvingea sanctae-crucis	1.42	94.74	***
	Liagora ceranoides	1.37	96.11	***
	Amphiroa rigida	1.00	97.13	***
	Stypopodium zonale	0.19	98.91	***
	Cladophora	0.18	99.10	**
	Colpomenia sinuosa	0.18	99.28	***
	Champia parvula	0.16	99.47	**
	Dictyota sp.	0.05	99.77	**
	Plocamium brasiliense	0.03	99.85	***
	Dictyurus occidentalis	0.03	99.88	**
	Udotea unistratea	0.02	99.91	**
	Caulerpa mexicana	0.02	99.93	**
	Anadyomene lacerata	0.01	99.95	**
	Dasya brasiliensis	0.01	99.96	**
	Dictyota ciliolata	0.01	99.97	**
	Chrysymenia enteromorpha	0.01	99.99	**

Subtropical_ Tropical	*Dictyopteris jolyana*	31.17	31.53	***
	Dichotomaria obtusata	23.99	55.79	**
	Dictyopteris plagiogramma	6.70	81.61	**
	Canistrocarpus cervicornis	3.30	88.37	*
	Dictyopteris delicatula	0.97	95.88	*
	Dictyopteris justii	0.48	98.38	*
	Dictyota pulchella	0.25	99.50	*
	Sargassum sp.	0.01	99.99	*
Tropical_ Transition	*Caulerpa pusilla*	12.58	56.50	***
	Udotea cyathiformis	6.85	63.46	*
	Jania spp.	5.28	68.83	*
	Halimeda discoidea	1.84	90.10	*
	Liagora ceranoides	0.94	95.01	*
	Amphiroa rigida	0.71	96.68	*

CAPÍTULO 2

3. Causes and consequences of rhodolith bed primary productivity: when descriptive ecology meets physiology

Carvalho VF[a,*], Silva J[b], Kerr R[c], Anderson AB[d], Bastos E[a], Cabral D[a], Gouvêa LP[a], Peres L[a], Martins CD[a], Silveira-Andrade VM[a], Sissini MN[a], Horta PH[a]

a Departamento de Botânica, CCB, Universidade Federal de Santa Catarina (UFSC), 88010-970 Florianópolis, SC, Brazil

b CCMar – Centre of Marine Sciences, Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

c Laboratório de Estudos dos Oceanos e Clima (LEOC), Instituto de Oceanografia, Universidade Federal do Rio Grande (FURG), 96203-900, Rio Grande, RS, Brazil.

d Marine Macroecology and Biogeography Lab, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, 88010-970 Florianópolis, SC, Brazil.

*Corresponding author: carvalhovf2@gmail.com

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ABSTRACT: This work present two years of characterization of a warm temperate rhodolith bed to analyze how environmental changes could influence the community ecology. The biomass of rhodolith and associated species were analyzed during this period and conducted *in situ* experiments to evaluate the community production/consumption balance. The highest total biomass of rhodoliths occurred during Austral winter. *Lithothamnion crispatum* was the most abundant species in Austral summer. Epiphytic macroalgae occurred only in January 2015, with *Padina gymnospora* having the major cover. Considering associated fauna, the biomass of Annelida, Arthropoda and Mollusca had lower values in February 2015 and higher values in November 2016. Reef fish key species populations densities inside and around the rhodolith beds showed significant variations in time. Groupers (carnivores/piscivores) densities seem to be increasing in time, especially from 2015 to 2016. On the other hand, grunts (macroinvertebrates feeders) had a modest decrease in time (from 2014 to 2016). Other parameters such as oxygen production and calcification of *L. crispatum* were higher under enhanced irradiance and 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 along time. Biomass changes can indicate that herbivores have a hole in epiphytes overgrowth, which is beneficial to rhodolith because avoid competition with fleshy algae for environmental resources. These results foster further studies related to climate change impacts, as well as long-term monitoring programs and *in situ* experiments to improve the knowledge about how community structure of rhodolith bed responds to local and global stressors.

KEYWORDS**:** Rhodoliths; Photosynthesis; Epiphytes; Herbivory; Carbonate System

3.1. Introduction

Physical factors like winds, marine currents and temperature have a major influence on marine life (Kordas et al., 2011). Winds drive horizontal movement of the water, creating surface currents and vertical movements of upwelling and downwelling (Ottersen et al., 2004). 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 macroalgae nutrient uptake (Ho and Carpinter, 2017). Moreover, changes in marine temperature have effects on reproduction, growth and survival of invertebrates (Levin and Creed, 1986; Randall and Szmant, 2009), fishes (Pörtner et al., 2001; Herbing, 2002), fleshy algae (Fong and Zedler, 1993; Andrews et al., 2014) and rhodoliths (Horta et al., 2016).

Rhodoliths, also known as maërl, require environmental factors, such as water motion (e.g., waves and currents) and bioturbation, to disperse and maintain their unattached and unburied state (Steller et al., 2003). If water turbulence is small, the rhodolith bed do not develop because they will be covered by sedimentation and fouling. If it is too high, the thalli are affected by erosion (Foster, 2001; Hinojosa-Arango et al., 2009). In addition, these environmental drivers also play a key role into their growth and morphogenesis (Steller and Foster 1995; Pascelli et al., 2013). The thallus movement can result in less structurally complex niche, due to breakage of rhodolith and the loss of 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 and Law, 2010) and irradiance (Burdett et al., 2014), can affect the rhodolith bed due to theirdirect influence on photosynthesis and calcification process. These physiological processes are intimately linked. During photosynthesis, the production of dissolved inorganic carbon (DIC) creates a high pH environment, in which calcification occurs (Johansen, 1981). At calcification process, precipitation of one mole of calcium carbonate ($CaCO_3$) decreases DIC by one mole and total alkalinity by two moles: $Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + H_2O + CO_{2(aq)}$ (Johansen, 1981). The carbon dioxide (CO_2) released in this process can be used in photosynthesis or the soluble bicarbonate (HCO_3^-) form can be converted into insoluble carbonate (Hill et al., 2015). In this way, environmental factors that affect photosynthesis can also affect calcification. Available information suggests that rhodoliths require relative low irradiance levels to photosynthesis (Figueiredo et al., 2000), but long summer days increase photosynthesis and growth (Teichert and Freiwald, 2014). When seawater temperature increase due to seasonal fluctuations, respiration and photosynthesis also increase, which enhance growth rate and biomass of rhodolith (Martin et al., 2006; Steller et al., 2007).

Changes in rhodolith density, biomass and morphology can influence local fauna and flora diversity, once they provide microhabitats to many organisms (Foster et al., 2013; Neill et al., 2015). Physical conditions that increase structural complexity and available refuge among the rhodolith branches (Steller and Foster, 1995; Pascelli et al., 2013) enhance local species richness and abundance (Steller et al., 2003). Hence, it is necessary to investigate environmental factors that influence both rhodolith physiology, morphology, and density to investigate changes in local community structure.

Associated animals and macroalgae, which have seasonal lifecycle or traits, can respond more quickly to environmental conditions than rhodoliths. Periodic rotation represents a potential disturbance event to the community associated with the bed. Algal biomass and mobile 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, while motile fauna impacted by abrasion of rhodolith. Such disturbances can prevent the development of a stable community (Maughan and Barnes, 2000; Hinojosa-Arango et al., 2009). In addition, changes in rhodolith density promoted by burial/exposition or displacement will directly influence substrate/niche availability to associated fauna and flora. Therefore, when these mobile reefs present higher densities, this trait will be associated with higher abundances of associated biodiversity (Pascelli et al., 2013).

The presence of these associated organisms determine the interspecific relations which influence the whole rhodolith bed community structure, once they can behave as partners or pests. Besides trophic relation, fauna and flora can change micro-niche chemical condition, factors with a key role in ecophysiological processes (Stachowicz and Hay, 1996; Semesi et al., 2009; Legrand et al., 2017). Regarding macroalgae, their presence can be either positive or negative to rhodolith. Turf algae benefit associated coralline algae once they elevate the surrounding medium pH facilitating calcification (Short et al., 2015). Moreover, under high irradiances, the epiphytes can protect the crustose coralline algae from photoinhibition (Figueiredo et al., 2000). On the other hand, associated macroalgae can also shade the rhodoliths and limit the available light and others environmental resources, such as CO_2 and nutrients (Wahl, 2008), which cause a decrease in photosynthesis (Dodds, 1991). In relation to animals, like polychaetes, crabs and mollusks, they can help the maintenance of rhodolith health by controlling the epiphytes' growth (Scherner et al., 2010, Legrand et al., 2017). 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 and Hay, 1996). Some crabs clean the surface of coralline algae by consuming a wide array of macroalgae that commonly co-occur with their host (Stachowicz and Hay, 1996). These macroalgae include chemically defended species of the genera *Halimeda*, *Dictyota*, and *Laurencia*, which are usually avoided by herbivorous fishes (Stachowicz and Hay, 1996). Thus, small grazers like amphipods, gastropods, mollusks and polychaetes act removing grazer-susceptible epiphytes, thus allowing growth of less competitive, grazer-resistant species as coralline red algae (Lubchenco, 1983; Hay et al., 1988; Steneck et al., 1991; Stachowicz and Whitlatch, 2005; Scherner et al., 2010).

Since the structure and resilience of rhodolith bed are affected by environmental and biological factors, the aim of this work was to characterize the community of rhodolith bed along two years and analyze changes of winds and temperature that could cause changes on rhodolith physiology and morphology. The biomass of rhodolith and associated species were analyzed along this period. Our hypothesis is that the biomass of associated community changed according to environmental changes along the study period. *In situ* experiments were conducted in order to measure the production of community, focused on dominant species of rhodolith bed. In this experiment, we investigate how photosynthesis and calcification rates of dominant rhodolith forming *Lithothamnion crispatum* Hauck responds to the presence of dominant fleshy algae *Padina gymnospora* (Kützing) Sonder.

3.2. Material and methods

3.2.1. Study sites

The experiment was conducted in a rhodolith bed at Rancho Norte (27°17’S 48°22’W), that is a part of the 176 km^2Marine Protected Area (MPA) named Arvoredo Marine Biological Reserve (Rebio Arvoredo) created in March 1990. The rhodolith bed extends over a sandy bottom in the northwestern shore of Arvoredo Island, covering an area of approximately 100,000 m^2. The isobaths are between 7 m and 20 m. Seawater annual temperature is around 22°C. As Rebio Arvoredo is only 10 km distant from coastal zone, depending on winds, currents, the continental runoff of Florianópolis metropolis, urban, industrial and chemical contaminants, can reach the area (Freire et al., 2017). The area is influenced by the Brazil 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 Malvinas Current, a cooler and less saline water derived from Antartic 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 BC under the tropical water (Freire et al., 2017). Beyond SACW, waters coming from the Brazil-Malvinas Confluence mix with the low salinity plume added from Rio de La Plata, Patos-Mirim Lagoon, and other local sources of continental runoff (Möller et al., 2008; Strub et al., 2015). The influence of this plume at the region displays seasonal characteristics: in winter, the southwesterly winds force the plume to lower latitudes (28°S), while summer northeasterly winds lead the plume poleward (Moller et al., 2008). Because of this seasonal mixture, a dynamic and complex environment is established (Eichler et al., 2008; Paquette et al., 2016).

The rhodolith bed of Rancho Norte represent the southernmost limit of this habitat in western Atlantic (Guerardhi, 2004; Pascelli et al., 2013). This bed provides ecosystems services, such as habitat for epiphytic algae (Horta et al., 2008), refuge and food source 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 (Guerardhi, 2004).

3.2.2. Environmental conditions

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

The average data of six months prior to sampling efforts, which occurred in summer and winter, was considered in the analyses of the influence of predominant wind direction (i.e., N, NE, E, SE, S, SW, W, NW [%]) and velocity (m/s) on rhodolith bed. This interval enables to investigate the historicity of wind changes before each collection since rhodolith bed could respond slowly to environmental change. Data per hour of wind direction and speed were obtained at the online database of the National Institute of Meteorology - INMET (available at www.inmet.gov.br).

3.2.3. Community structure

For community structure analysis, sampling was conducted using squares with dimensions of 25x25 cm placed randomly over the Rancho Norte rhodolith bed. All the organisms in each square were stored in plastic bags and transported to the laboratory. Squares were collected during summer, in January 2015 (n=9), February 2016 (n=14), late spring, in November 2016 (n=9) and 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 and Littler, 2000; Harvey et al., 2005; Sissini et al., 2014). In rhodoliths composed by more than one specie, the one with the major cover (more than 50%) wereconsidered.Macroinvertebrates were separated (by phylum) and weighted (in g, fresh weight). Epiphytes and rhodoliths were separated by species, dried at 60°C and then weighted (precision of ±0.001 g). To detect which rhodolith species had the heaviest individuals, was weighed 50 unbroken samples from each species.

As epiphytes only occurred in one summer (February/2015), only herbivores from another summer/late spring samples were analyzed to compare the differences in abiotic factors that could have favored such occurrences. However, to analyze the seasonal variations in biomass of rhodolith, all sampling efforts were considered.

Carnivorous and invertebrate feeders fish data were extracted from Anderson (2017). In the study, underwater visual censuses were applied to collect and quantify reef fishes populations density data (UVC: 20 × 2 m strip transects = 40 m2) (see Floeter et al., 2007 and Anderson, 2017 for further regarding UVC techniques). All sampling campaigns were conducted in the morning, during Austral summers.

The biomass of fishes was accessed using the following Eq. (1): $W = a \times TL^b$ (published weight-length relationships) 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 size in cm (Anderson et al., 2014; Froese and Pauly, 2016).

3.2.4. **Experimental design**

To analyze the primary production and respiration of *L. crispatum* and *P. gymnospora* alone and together, *in situ* incubations were conducted (10 m) to measure changes in dissolved oxygen values and total alkalinity inside closed chambers after ~2 h incubations. The combinations of five replicates of each kind of association were used: 1 - two specimens of *L. crispatum* alone, 2 - two specimens of *P. gymnospora* and 3 - one specimen of *L. crispatum* and another of *P. gymnospora* together. These different combinations were placed inside transparent nylon bags chambers, which did not allow gas exchanges, and did not influence the light quality. The chamber volume was ~2 L, filled with bottom water. All the chambers were 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 by currents. This enabled the circulation inside the chambers, reducing the formation of large diffusion boundary layers around the organisms and provided a homogenous distribution of nutrients (Hurd, 2000). The incubations were conducted with five replicates, in three times under daylight and one time during the night. Throughout each incubation, the PAR (μmol s^{-1} m^{-2}) was determined next to chambers using a LI-COR hemispherical sensor. The averaged PAR values (3 points) was considered for each incubation period for the productivity analyses.

3.2.5. **Productivity and respiration**

For dissolved oxygen analyses, five samples were taken samples of 12 mL of seawater from each chamber at the beginning and at the end of the incubation. The dissolved oxygen was measured by the Winkler method, modified by Labasque et al. (2004),0.73% for reproducibility near 250 µmol kg $^{-1}$. After incubation, the organisms were dried for 48 h at 60°C and then weighted. Net production (NP), Respiration (R), and Gross Production (GP) were calculated according to Noisette et al. (2013) and following the Eqs. (2) to (4):

$NP = \Delta O_2$ (µmol/L)(light) x $V/\Delta t$ x A (2)
$R = \Delta O_2$ (µmol/L)(dark) x $V/\Delta t$ x A (3)
$GP = NP - R$ (4)
Where: ΔO_2= Difference between final and initial oxygen (µmol/L), A = surface area of algae (cm^2), V = chamber volume (L) and Δt = incubation time (h).

3.2.6. **Calcification**

To analyze the calcification of the organisms, the changes were measured in total alkalinity produced by the organisms during the incubation. At the beginning and at the end of the incubations, two samples of seawater were stored in vials of 40 mL. Samples were poisoned with mercury chloride (0.02%) and the analyses were conducted following the open-cell protocol described by Dickson et al. (2007) at the LEOC laboratory at the Institute of Oceanography of the Federal University of Rio Grande (FURG). Regular analyzes of Certified Reference Material (CRM) Batch 149, obtained from the Scripps Institution of Oceanography, were carried out for a 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 ±1%) was measured at the end and beginning of each incubation. The light and dark calcification fluxes were estimated using the alkalinity anomaly technique (Smith and Key, 1975), in which for each mole of $CaCO_3$ precipitated, total alkalinity (At) decreases by two equivalents (Wolf-Gladrow et al., 2007). The difference between final and initial alkalinity of the incubation (ΔAt) was considered to calculate calcification rates, following the Eqs.(5) and (6) below (Noisette et al., 2013):

$$G_{biomass} = -(\Delta At) x V/2\ x\ \Delta t\ x\ DW \qquad (5)$$

$$G_{area} = -(\Delta At) x V/2\ x\ \Delta t\ x\ A \qquad (6)$$

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

3.2.7. Algae surface area

The surface area of *Padina gymnospora* was calculated from photos that were analyzed in 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 50cm. A methodology modified from Hoegh-Guldberg (1988), was used for the rhodoliths area estimation. Dried *L. crispatum* samples (n=19) from Rancho Norte rhodolith bed, with varied sizes, were weighted and then coated in a commercial blank dye (composed of resin and water). The first coat sealed the surface, reducing the porosity. After 20 minutes, they received another layer and were re-weighted before and after the second coat. The transformation 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 area of rhodoliths used in the experiment ($y = 2.5108x + 9.9264$, $r^2=0.9337$).

3.2.8. Rhodolith Growth

Growth rates of rhodoliths were 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 and Maggs, 2003).Afterward, the specimens were taken back to the field and were recollected in November 2015. The rhodoliths were sectioned to measure the length of growth layer under a light microscope (Leica S8AP0) (Supplementary Fig.1). 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} yr^{-1}) was obtained considering the growth length, the radii, dry weight of the rhodoliths of each quadrat from the biomass sampling, as described in Amado-Filho et al. (2012a), with a slight modification: the weight of the rhodoliths were used instead of their volume. The rhodoliths were weighted 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 (W_l) was calculated from the ratio of radii (R_r) and the growth length (estimated in 0.319 ± 0.226 mm yr^{-1}, based on measurements of rhodoliths that were left in the field), as described in Eq. (7):

$$W_l = W_r x\ 0.319/R_r \qquad (7)$$

The amount of $CaCO_3$ production of the rhodolith bed per m^2 (0.0625 m^2 per quadrat) in g m^{-2} yr^{-1} ($CaCO_3pr$), considered the sum of the growth layer weight of each quadrat of rhodolith (SW_l), according to the Eq. (8):

$$CaCO_3pr = SW_l/0.0625 \qquad (8)$$

Using the calculification data measured *in situ* ($G_{biomass}$) normalized by g, was calculated the daily calcification (DG) expressed in µmol $CaCO_3$ g^{-1} DW day^{-1} (considering 13:11 h Light:Dark cycle), according to the Eq. (9):

$$DG = Mean\ G_{light} * 13 + G_{dark} * 11 \qquad (9)$$

Mean G_{light}consider the three incubations under daylight.The DG value (converted from µmol to g) was used to calculate the $CaCO_3$ production of *L. crispatum* (R $CaCO_3pr$) of each quadrant individually, expressed in g $CaCO_3$ d^{-1} according to the Eq. (10):

$$R\ CaCO_3pr = (DG\ xWr)/0.0625 \qquad (10)$$

The average of R $CaCO_3$*pr* of the individual quadrants (Total R $CaCO_3$*pr*) was used to calculate the $CaCO_3$ production per area of *L. crispatum* at the day of experiment.

3.2.9. Data analyses

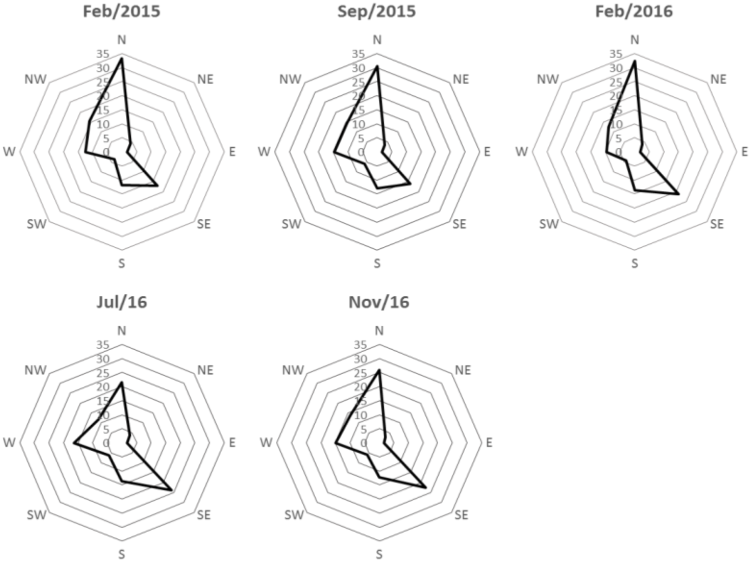
The photosynthetic, respiratory and calcification rates of the macroalgae were analyzed using parametric statistics. After evaluating the normality of the data by the Shapiro-Wilk test, a two-way ANOVA was performed to test the significant differences of photosynthesis and calcification data under different light levels and the effects of individual versus combined species. For the respiration data, we performed a one-way ANOVA was performed between incubation data at dark using a different combination of species. The Newman-Keuls *post hoc* test was applied when significant differences were observed ($p<0.05$). As ANOVA assumptions were not reached, the biomass of rhodolith and fauna was analysed with Kruskal-Wallis test followed by pairwise multiple comparisons. The correlation between rhodolith biomass and mean values of wind direction/velocity data from six months prior to each collection were analyzed according to Spearman correlation and was considered significative when $p<0.05$. The analyzes were performed in Statistica 13.0.

Linear Models (LM) and subsequent Analysis of Variance (ANOVA) were used to test the effect of time on the densities of fishesinside Arvoredo MPA. Total densities and biomass of species were used as dependent variables, time (years) as factors (Underwood, 1981; Chatfield, 1989; Snedecor and William, 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 and William, 1989; Zar, 1999). Analyses were run in R environment package “Agricolae” (de Mendiburu, 2013).

3.3. Results

3.3.1. Environmental conditions

At six months prior to summer/late spring collections, the North winds were predominant , with higher level in previous semester of February 2015 (33.19%), followed by February 2016 (32.42%) and November 2016 (25.89%) (Fig. 1). However, the velocity of wind six months prior to February 2015 was the lowest of summer collections (Fig. 2). In winter collection, the North wind was higher in previous semester of September 2015 (30.61%) while at previous months to July 2016, the southeast wind prevailed (23.82%).



Feb/2015

Sep/2015

Feb/2016

Jul/16

Nov/16

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).

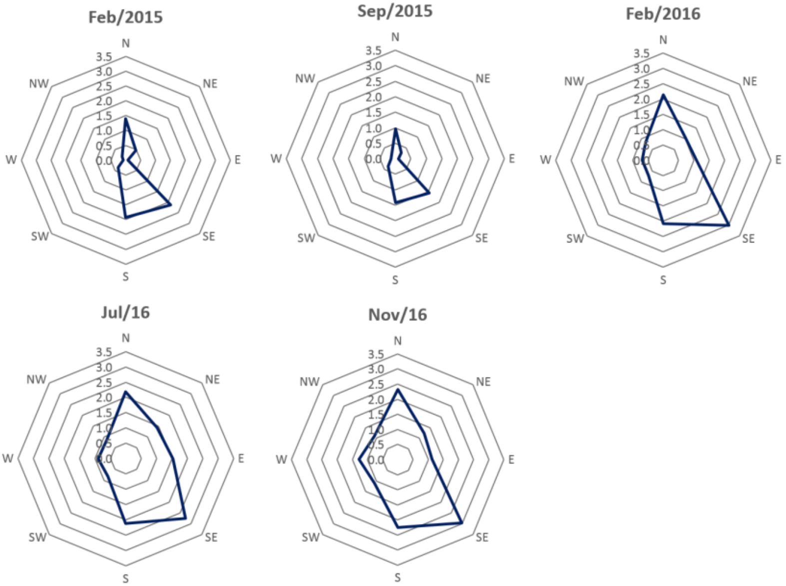


Fig. 2. Mean Velocity (m/s) of wind of six months prior to each month of collection. Data: INMET (Brazilian Meteorology Institute – Florianópolis/São José/A806 Station).

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 (Fig. 3). The temperature at the rhodolith bed during the experiment varied between 25.6 and 26.9°C. The mean PAR values measured at each incubation time were, in order of execution, 35 in Time 1, 472 (± 20.64) in Time 2, 119 (± 0.68) in Time 3 and 0 µmol photons m^{-2} s^{-1} in Time 4. Salinity varied between 33 and 34.

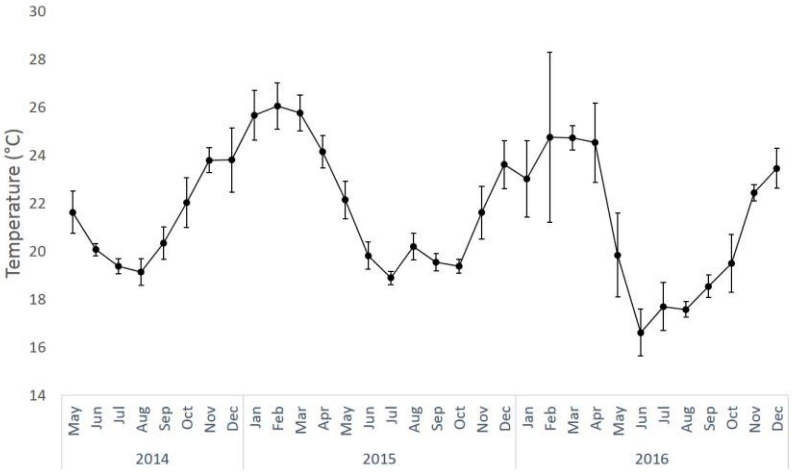


Fig. 3. Variation of mean (±SE) monthly seawater temperature at 10 m depth from May 2014 to December 2016 at the Marine Protected Area (MPA) of Arvoredo, Brazil.

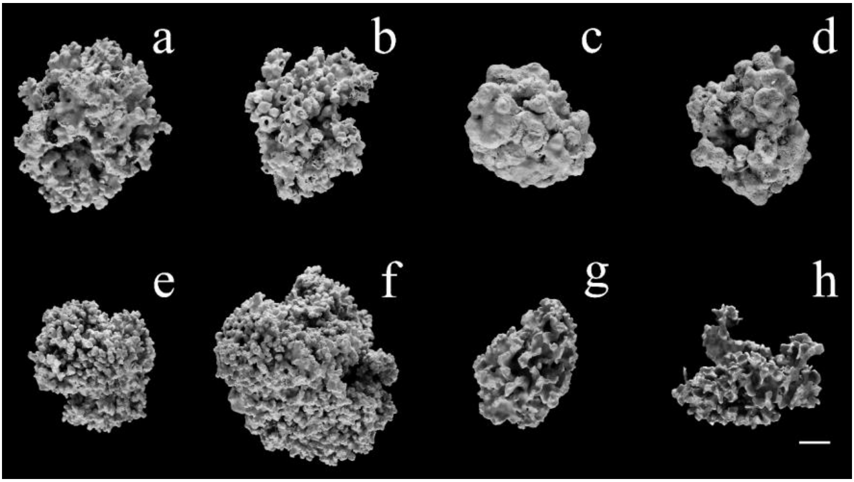


Fig. 4. Morphology of rhodoliths collected at Arvoredo (MPA), Brazil. Letters a-b: *Lithothamnion crispatum*; c-d: *Lithophyllum atlanticum*; e-f: *Mesophyllum erubescens*; g-h: *Lithophyllum margaritae*. Scale bar: 1cm.

3.3.2. Community structure

Four species of rhodolith was found: *Lithothamnion crispatum, Lithophyllum atlanticum* Vieira-Pinto, M.C.Oliveira & P.A.Horta, *Mesophyllum erubescens* (Foslie) Me.Lemoine and *Lithophyllum margaritae* (Hariot) Heydrich (Fig. 4). The total biomass of rhodoliths was significate different between season (Supplementary Table 1, for all statistical results), with the highest value in winter, in September 2015, and the lowest in February 2016 and November 2016 (Fig. 5). *L. crispatum* was the most abundant species in summer at all collections, followed by *L. atlanticum* (Fig. 6). However, the biomass of *L.atlanticum* increased in winter, followed by *M. erubescens*. *L. margaritae* occurred only in February 2015 and July 2016, in low abundance. *L.atlanticum* and *M. erubescens* specimens had similar weights and were significantly heavier than *L. Crispatum* (Fig. 7). Growth rates of rhodoliths from Arvoredo were 0.035–0.566 mm yr^{-1}. The annual mean rate of net $CaCO_3$ production was estimated in 105.97 (±49.26) g m^{-2} yr^{-1} and ranged from 44.90 to 193.94 g m^{-2} yr^{-1}.

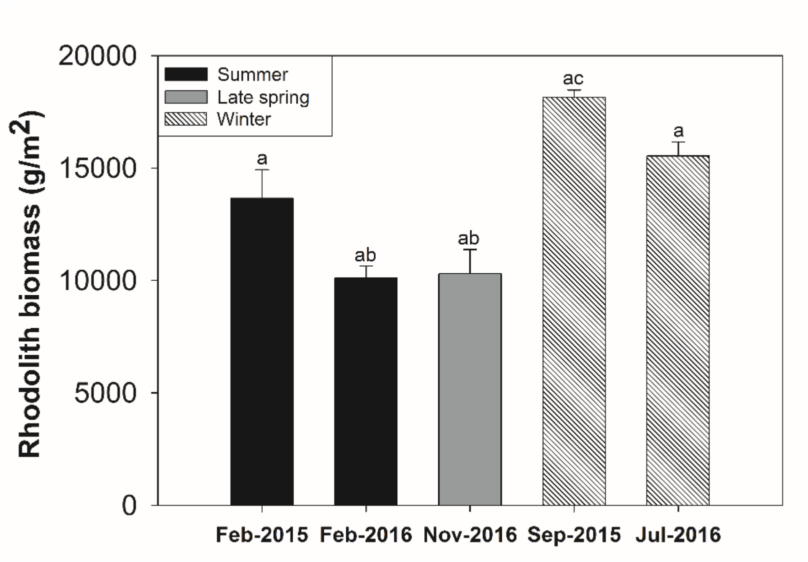


Fig. 5. Total Biomass of Rhodolith in g/m^2 in summer (black bars, February 2015 [n=9] and 2016 [n=15]), late spring (gray bar, November 2016 [n=15]) and winter (striped bars, September 2015 [n=6] and July 2016 [n=5]) at Arvoredo (MPA), Brazil. Letters indicate results of Kruskal-Wallis multiple comparisons ($p < 0.01$).

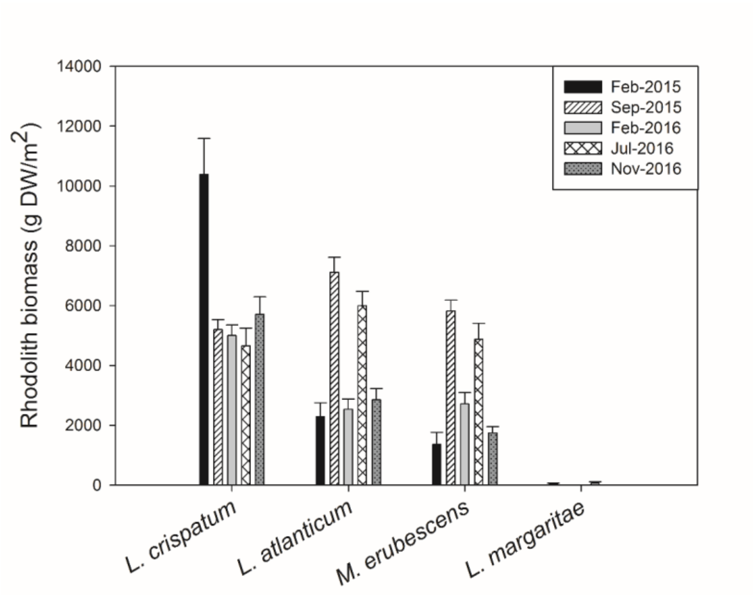


Fig. 6. Biomass of Rhodolith species in g/m^2 in summer/late spring months (black and gray bars) and winter (white bars) at Arvoredo (MPA), Brazil.

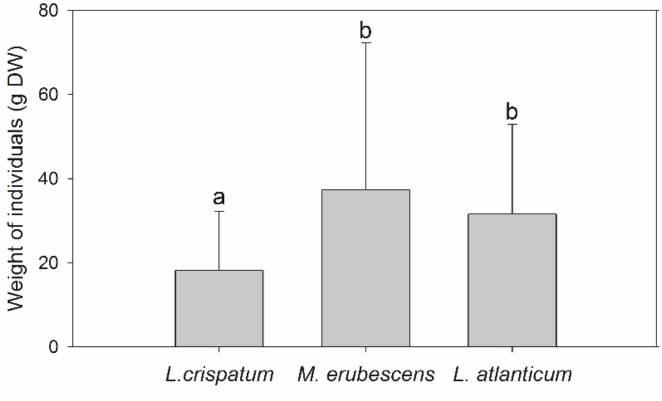


Fig.7. Weight of individuals (n=50) of three rhodolith species from Arvoredo MPA, Brazil. Letters indicate results of Kruskal Wallis multiple comparisons ($p < 0.01$).

Results of Spearman test indicates negative correlations of total biomass with the wind velocity of most of the directions (Table 1).

Results of correlation for *L. crispatum* biomass had more significance with abiotic factors than the other species. *L. crispatum* biomass was negatively correlated with the velocity of wind from all directions and with the frequency of wind from south quadrants (SE, S and SW). However, positive correlated with winds from the north (N and NE).

Table 1. Summary of Spearman correlation results (r) between abiotic factors and biomass of rhodoliths. Bold numbers indicate significant values ($p<0.05$).

	L. crispatum	***M. erubescens***	***L. atlanticum***	***L. margaritae***
N%	**0.508569**	**–0.376957**	**–0.466979**	–0.146253
NE%	**0.416837**	–0.251020	**–0.358144**	0.075502
E%	–0.182531	0.085902	–0.172970	0.058079
SE%	**–0.375014**	–0.075640	–0.035682	0.193772
S%	**–0.618959**	**0.486569**	0.298285	0.146253
SW%	**–0.521163**	**0.581722**	**0.639093**	0.146253
W%	–0.092043	0.199401	**0.432463**	0.257130
NW%	**0.606365**	–0.281804	–0.126171	–0.146253
N (m/s)	**–0.315776**	–0.219458	–0.158355	0.060719
NE (m/s)	**–0.375014**	–0.075640	–0.035682	0.193772
E (m/s)	**–0.535934**	0.147782	0.170015	0.146253
SE (m/s)	**–0.333190**	–0.234694	**–0.417381**	–0.146253
S (m/s)	**–0.315776**	–0.219458	–0.158355	0.060719
SW (m/s)	**–0.315776**	–0.219458	–0.158355	0.060719
W (m/s)	**–0.476696**	0.003965	0.047343	0.013200
NW (m/s)	**–0.476696**	0.003965	0.047343	0.013200

In relation to associated organisms, epiphytic macroalgae occurred only in January 2015, with *Padina gymnospora* having the major cover, with 36.44 (±14.42) g/m^2, followed by *Amphiroa fragilissima* (Linnaeus) J.V.Lamourouxwith 3.90 (±1.54) g/m^2 and *Canistrocarpus cervicornis* (Kützing) De Paula & De Clerck, with1.57 (±0.83) g/m^2(Supplementary Table 2). Invertebrates increased from February 2015 to November 2016 (Fig. 8). However, only the biomass of Annelida ($H=10.22$; $p<0.01$) and Mollusca ($H=10.21$; $p<0.01$) presented significant differences.

Groupers (carnivores/piscivores) (Pauly *et al.*, 1998; Ferreira *et al.*, 2004; Anderson *et al.*, 2015), represented herein by *E. marginatus* and *M. acutirostris*, fisheries highly targeted species (Floeteret al., 2006; Andersonet al., 2014; Andersonet al., 2015), varied significantly in density according to the factor time (year). Densities seem to be increasing in time, especially from 2015 to 2016. Otherwise, the biomass of carnivores showed no significant differences, but seem also to be increasing in time (Fig. 9).

Grunts (macroinvertebrates feeders), positioned in the central region of the marine food web as mesoconsumers, (Paulyet al., 1998; Morales-Zárateet al., 2004), herein, are represented by *H. aurolineatum* and *A. virginicus*. Densities showed significant differences considering the factor time, on the other hand, biomass did not show significant differences. Considering both populational descriptors (density and biomass) populations of grunts show a modest decrease in time (from 2014 to 2016) (Fig. 9).

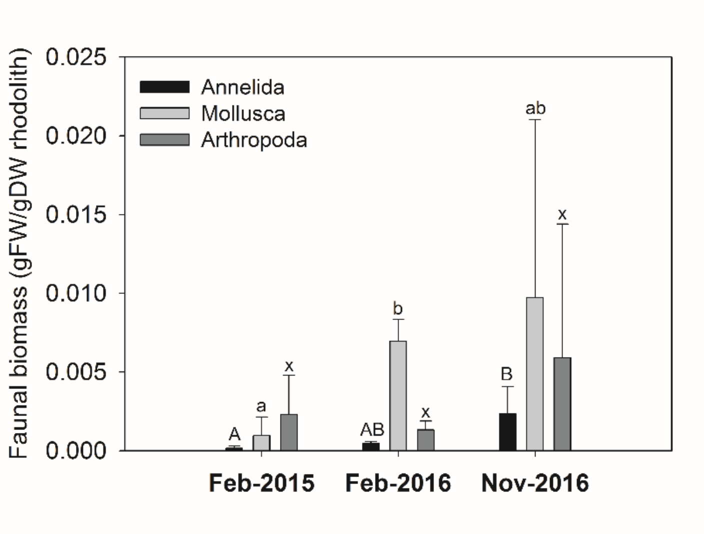


Fig.8. Biomass of Annelida, Mollusca and Arthropoda in gFW/gDW in January 2015 (n=9), February (n=3) and November 2016 (n=3) at Arvoredo MPA, Brazil. Letters indicate results of Kruskal-Wallis multiple comparisons ($p < 0.01$).

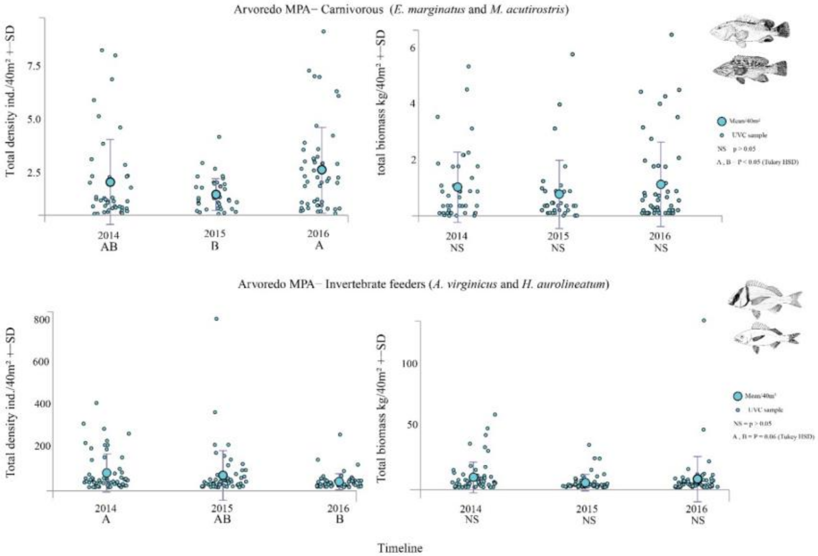


Fig. 9. Arvoredo MPA densities and biomass of Carnivores (A) and Invertebrate feeders (B), in time.

3.3.3. Productivity and respiration

The mean rates (mean ± 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) (Fig.10). Significant differences were detected in GP and respiration between species and times of incubation (Supplementary Table 1). *L. crispatum* alone GP and respiration had the highest values at all incubation moments. However, *L. crispatum* and *P. gymnospora* together (P + L) had the lowest values of GP, with a more pronounced effect at high intensities, reaching only 0.214 (±0.077) µmol O_2 cm^{-2} h^{-1}.

3.3.4. Calcification

All light calcification was positive and dark calcification was negative in all treatments (Fig.11). Significative differences were detected in light and dark calcification in all species and times of incubation (Supplementary Table 1). Light calcification of the rhodolith alone corresponded to the highest values at all times, reaching 0.293 (±0.014), while *P. gymnospora* reached only 0.063 (±0.014) µmol $CaCO_3$ cm^{-2} h^{-1}(Fig.11). The calcification of *L. crispatum* and *P. gymnospora* together was similar to the values for *P. gymnospora* alone. Decalcification in the dark was significantly higher in *L. crispatum*, reaching 0.071 (±0.005) µmol $CaCO_3$ cm^{-2} h^{-1}. The production of *L. crispatum* at the day of incubations corresponded to 8.7 ± 2.9 g $CaCO_3$ m^{-2} d^{-1}.

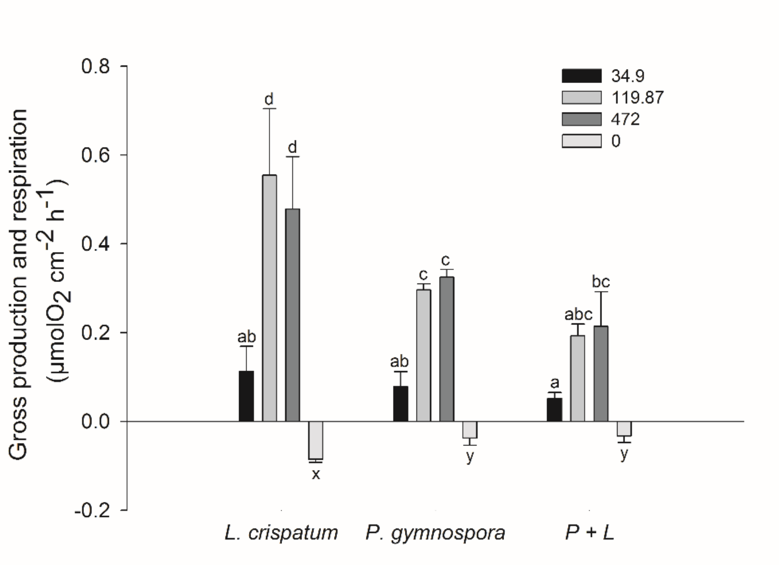


Fig.10. Gross Production (n=4) and respiration (n=3) in µmol O_2 cm^{-2} h^{-1}, in *L. crispatum* , *P. gymnospora* and *P. gymnospora* and *L. crispatum* together (P + L) in summer at Arvoredo MPA, Brazil. Shades of gray indicates mean PAR values (µmol photons m^{-2} s^{-1}). Letters indicates results of Newman-Keuls *post-hoc* test ($p < 0.01$).

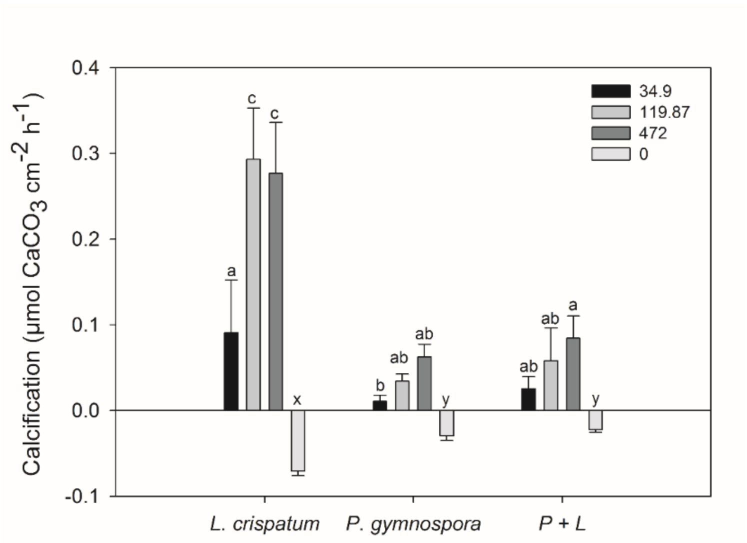


Fig.11. Calcification in light (n=5) and dark (n=3) expressed in µmol $CaCO_3$ cm^{-2} h^{-1} of *L. crispatum*, *P. gymnospora* and *P. gymnospora* and *L. crispatum* together (P + L) in summer at Arvoredo MPA, Brazil. Shades of gray indicates mean PAR values (µmol photons m^{-2} s^{-1}). Letters indicates results of Newman-Keuls *post-hoc* test ($p < 0.01$).

3.4. Discussion

Environmental drivers that define patterns and produce shift baselines are variables and dependent of complex combinations involving natural and anthropogenic factors (Steller et al., 2003; Nelson et al., 2012; Horta et al., 2016). While meteo-oceanographic conditions seem to cause the change in seasonal abundance and composition of rhodoliths in Arvoredo Rhodolith bed, genesis of associated benthic community variability seem to be more complex. Integrated analysis signalizes that observed shifts were a consequence of the alteration of trophic interactions. A trophic cascade effects caused a top-down control structuring a benthic community with a reduced abundance of fleshy macroalgae, as observed in different reef systems (Littler et al., 1995; Stachowicz and Hay, 1996; Scherner et al., 2010). Suppression of fleshy algae canopy cover seems to increase potential primary production, which, however, contradicts the common sense supported by the functional group theory (Steneck and Dethier, 1994).

3.4.1. **Community structure**

Rhodolith bed of Arvoredo represents the tropical South Atlantic limit of beds distribution. *L. crispatum*, the most abundant species of rhodolith in summer, is frequently referred for Brazilian beds (Amado-Filho et al., 2012b; Pascelli et al., 2013; Cavalcanti et al., 2014; Amado-Filho et al., 2017) and the associated flora had lower abundance comparing with other tropical formation (ie. Amado-Filho et al., 2007; Riul et al., 2009; Bahia et al., 2010) that was reduced to almost zero after 2015. The annual production of the Arvoredo bed (105.97 [±49.26] g m^{-2} yr^{-1}) is lower than registered values in tropical beds, such as in Abrolhos (1000± 700 g m^{-2} yr^{-1}: Amado-Filho et al. 2012a). However, is similar to the neighbor bed, in Deserta Island, for *Lithophyllum* sp. (55 - 136.3 g m^{-2} yr^{-1}) (Gherardhi, 2004), and close to reported values for temperate beds (490 g m^{-2} yr^{-1} in Martin et al., 2007; 200.3 g m^{-2} yr^{-1} in Teichert and Freiwald, 2014).

3.4.2. **Rhodolith composition**

Total biomass of rhodoliths was higher in winter months. However, rhodoliths have slow growth and do not respond to environmental factors quickly as faster growth macroalgae (Wilson et al. 2004, Francini-Filho et al. 2013). Besides their slow growth (Basso, 2012), there is no evidence showing they lose a significant amount of biomass annually. Therefore, major changes in their abundance should be related to local dynamic and rhodolith displacement. To analyze the influence of environmental factors on its development, is necessary to consider previous data of the season. Thus, the mean values of wind direction and velocity in a six-month window prior to each collection were used. The correlation analyzes between these data and total rhodolith biomass indicates a negative correlation with wind velocity, which suggests that stronger currents generated by winds could cause scattering in most rhodoliths. Similar results were found for a fragile, lighter and more branched morphotype *L. crispatum*, which was not observed for the other species. Pascelli et al. (2013) performed one sample in 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 historicity of wind course before the period of collections revealed that wind changes are not restricted to seasons and even so, the rhodolith biomass responds to them.

In relation to wind direction, while *L. crispatum* had the positive correlation with north quadrants and negative with south quadrants, *L. atlanticum* had the opposite response. When the frequency of winds from north quadrant is higher, lighter, more fragile and branched rhodoliths (i.e.: *L. crispatum*) tends to accumulate at the sampling site, placed in the north portion of the Arvoredo Island. Together with this, the months prior to February 2015, when *L. crispatum* had the highest biomass, had the lower velocity of wind in all quadrants. Either plausible displacement of lighter rhodoliths for the north portion of the Island or the selective buried of *L. atlanticum* and *M. erubescens*, heavier and sleeker morphotypes, should be considered mechanisms of seasonal rhodolith abundance changes. When the south wind return, lighter rhodolith was scattered and heavier rhodolith, unearthed. Even if rhodolith composition is correlated to wind direction and velocity, another environment factors can influence the waves and the bottom currents. Due to this, we suggest future monitoring of other environmental changes together with community composition observation.

3.4.3. **Associated fauna**

The faunal biomass, contrary to what the expected, had lower values for Annelida, Mollusca and Arthropoda in February 2015, when the mean velocity of wind of previous months was lower, with consequent decrease of local currents. Generally, higher current velocity disturbs the settlement of mobile animals (Maughan and 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 influencing directly and indirectly the dynamic balance of marine food webs (Dunne et al., 2004; Bellwood et al., 2017). Their biology (e.g., feeding behaviors, functional roles/trophic affinities) can influence variations in levels of densities and biomass of populations in the trophic web of rocky and coral reef systems (Dunne et al., 2004; Bellwood et al., 2017). The significant invertebrate communities' biomass increase detected herein, raised two hypotheses regarding reef fish probable influences. 1) Top-down control (Worm and Myers, 2003; Begon et al., 2006; Baum and Worm, 2009): mediated by predator populational increase in the studied area, over time. 2) Top-down control associated to "fear effect" (Worm and Myers, 2003; Côté et al., 2014; Heupel et al., 2014), both mediated by the presence of an alien predator recently detected inhabiting the rhodolith beds of in the studied area.

Considering the first hypothesis the modest increase in predator's populations in 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 macro-invertebrates (e.g., annelids, mollusks and crustaceans) and their populational decrease may have caused the opposite effect on their prey's densities and biomass ("prey release effect") (Friedlander and DeMartini, 2002; Heithaus et al., 2008). Otherwise, populations of grunts in 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 increment in populations of invertebrates. Moreover, considering biogeographic aspects, fish populations inhabiting thresholds of distribution, such as 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 Austral winters) (Almada and Faria, 2004; Anderson, 2017).

Considering the second hypothesis, the presence of an alien species may cause a dramatic effect in local populations in a short period of time (Anderson et al., 2017; Andradi-Brown et al., 2017). In the Austral summer of 2015, the black-spotted snake eel *Quassiremus ascensionis* (Studer, 1889), was first detected 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 Arvoredo MPA (Arvoredo Is., Deserta Is. and Galé Is.). The species is a cryptic predator (e.g., preys with the body buried in the substrate, with only the head showing), preying mainly in small fish and invertebrates (Froese and

Pauly, 2018). 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 subsequent increase in densities and biomass of their preys (annelids, mollusks and crustaceans).

Further investigations and long-term monitoring are necessary to understand the mechanism involved in populations dynamics of organisms inhabiting the rhodolith beds of Southern Brazil.Beyond the aspects of trophic web, temperature changes can also influence faunal abundance. In summer 2015, the mean temperature registered in seawater at Rebio Arvoredo was the highest of three years (Fig. 3), while the coolest was in winter 2016. This could be related to El Niño occurred in2015/2016, reflecting substantial environmental changes. This event could cause altered rain regimes, winds and marine currents, with consequent influence at the temperature (Freire et al., 2017). Climate changes and temperature increase can cause a reduction in survivorship of invertebrates and fishes (Vinagre et al., 2018). However, at the Rozegat maerl bed, the faunal biomass increased when seawater temperature rose from 10°C to 18°C (Grall et al., 2006). Temperature can also cause an increase in fauna respiration (Martin et al., 2006). The survival of the polychaeta *Streblospio benedicti* Webster, as well as its body size and larval production are higher under winter-spring than summer-fall conditions (Levin and Creed, 1986). In relation to large gastropods, marine heatwaves caused a decrease in abundance in *Lunella* (Smale et al., 2017). McConnico et al (2017) reported an increase in mollusks in summer, following the growth in macroalgal biomass. Here, the opposite occurred. The variable response of faunal behavior to temperature and wind indicates that experiments involving the faunal community and larger replication are necessary to improve the knowledge of which environmental condition can influence the local faunal biomass and explain the observed temporal changes.

3.4.4. Associated macroalgae

At the first moment, the occurrence of epiphytes only in February 2015 indicates that the highest temperature and lower wind velocity favored fleshy algal growth, mainly *Padina gymnospora*. This species can grow in tropical temperatures, similar to the recorded here in summer (Guillou et al., 2002; Martin et al., 2007; Scherner et al., 2016) and lower wind speeds have been associated to increase of abundance and richness of fleshy algae on a rhodolith bed (Hily et al., 1992; Hinojosa-Arango et al., 2009). However, previous data of total epiphytes biomass of February 2002 (11.41 [±9.16], Horta, 2002, unpublished data), February and July 2008 (0.9 [±1.12] and 0.16 [±0.22], Pascelli, 2009), althoughin smaller quantity, shows that the occurrence of epiphytes before February 2015 was not so rare (Supplementary Fig. 2).

Coralline algae can adopt strategies to controls fleshy macroalgal such as reduce growth rate and recruitment success (Vermeij et al., 2011) and production of allelopathic substances (Gross, 2003; Kim et al., 2004). Suzuki et al. (1998) suggested that an allelopathic nonpolar 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 reduction after 2015 indicates a combination of climate events referred at section 4.1.2 and an increase of invertebrate's biomass that possibly act in control of epiphytes.

The association with macroinvertebrates can benefit the rhodolith 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, preventing the overgrowth by *Ulva* sp. and other grazers (McQuaid and 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 can be potentially deleterious to the host (Underwood et al., 1992; Stachowicz and Whitlatch, 2005). Some animals can even feed on rhodoliths, without causing mortality. The chiton *Choneplax lata*Guildinggrazes on the coralline alga *Porolithon pachydermum*(Foslie) Foslie and stimulates new meristematic activity, removing sporelings of competitive epiphytes (Littler et al., 1995).

3.4.5. Community production/consumption balance

In this work, the association with herbivorous invertebrates probably benefit the rhodoliths, since the experiment results showed that the interaction between *Padina gymnospora* and *L. crispatum* caused a decrease in photosynthetic and calcification rates, if compared to treatments of these organisms alone. However, photosynthesis of *L. crispatum* alone had the highest value. This can be related to the fact that red coralline algae are found in a wide range of depth and irradiance, from shallow tropical coral reefs (PAR >1500 µmol photons m^{-2} s^{-1}) (Burdett et al., 2013) to high depths (>200 m PAR=0.0015 µmol photons m^{-2} s^{-1}) (Littler et al., 1986). Light and dark calcification results correspond to the similar pattern as observed in gross photosynthesis and respiration.

Epibiosis is usually considered harmful to the host alga because of the competition for light and nutrients, resulting in a decrease in growth and reproduction (Amsler et al., 2008). Competition among algae for one or more limiting resources may be direct (interference competition) or indirect, through the depletion of a resource (exploitative competition) and can occur within or between algal species (Reiskind, 1989). *Padina gymnospora* might 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). 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 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 *Fucus* thallus surface, creating a barrier for nutrient uptake and gas exchange.

The presence of *P. gymnospora* caused not only a decrease in photosynthesis, but also in calcification. This suggests that the calcification is connected with photosynthesis and shade caused by *P. gymnospora* demaged rhodolith calcification. The decalcification 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 and Larkum, 1987). Calcification requires light and sufficient Ca^{2+} and HCO_3^- ions. Photosynthetic CO_2 assimilation results in a pH increase and CO_3^{2-} around the cells (Borowitzka and Larkum, 1987). Although calcification is correlated to photosynthesis, active H^+, CO_2, and HCO_3^- uptake and respiration releases CO_2 and H^+, 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 experiment showed the negative effect of overgrowth of *P. gymnospora* on the rhodoliths surface, which coincided with invertebrates decrease. In the following years, an opposite pattern was observed. Epiphytes disappeared, the biomass of invertebrates increased, while invertebrates feeders, slightly decrease. These effects on bed community are probably the results of environmental changes occurred at study years. Changes in temperature and wind regimes ware detected, which can cause not only altered food websbut displacement in rhodolith composition and biomass. The variation in characteristics of the community along these two years and the environmental changes make us aware of how climate change events can affect the ecosystems.

3.5. Conclusion

In this paper, we conclude that environmental factors, like winds and temperature, as well as biological factors, can cause differences in community structure in the course of time. The consequences of these changes, benthic organisms can respond with respects to the occurrence or increase/decrease at biomass. The overgrowth of *P. gymnospora* on *L. crispatum* can cause a decrease in photosynthetic and calcification rates of the rhodolith. It is necessary more long-term experiments in other to improve the knowledge about the role of environmental changes on rhodolith bed community and the response of sessile and mobile organisms associated. Finally, can be proposed that a healthy trophic structure, with abundant top predators, has as an indirect consequence increase in rhodolith fitness and potentially in their resilience considering climate change and local stressors threats.

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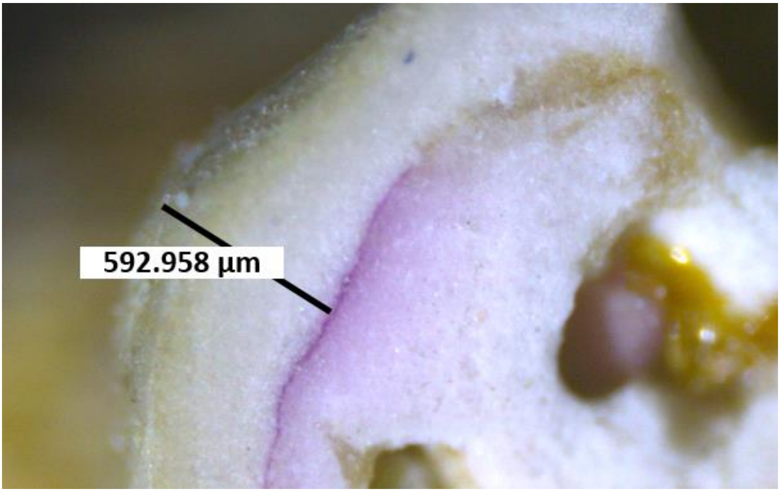
Supplementary material



Supplementary Fig 1. Rhodolith protuberance longitudinal section. View under microscopy, 1.5 year after alizarin red staining (lines indicate the growth).

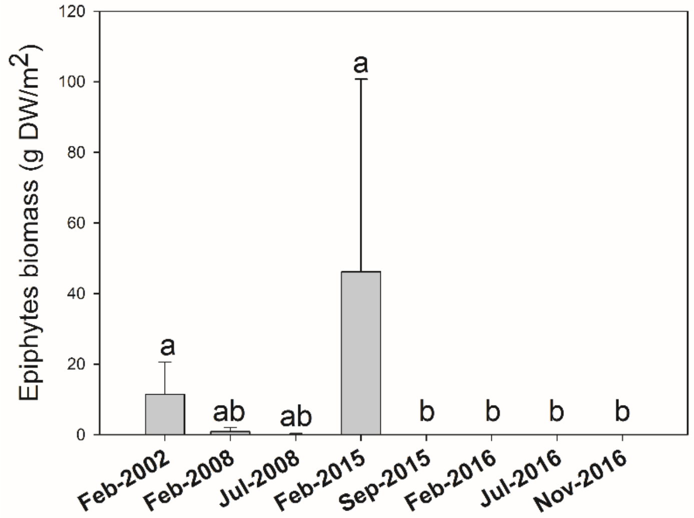
Supplementary Table 1. Summary of F and p values of two-way ANOVAs for Gross Production (GP) and Light Calcification and one-way ANOVAs for Respiration (R) and Dark Calcification. H and p values of Kruskal-Wallis test for biomass of fauna biomass, weight of individual rhodoliths and total rhodolith biomass.

	df	MS	F/H	p
GP				
Species	2	0.647	F=28.58	<0.01
Time of incubation	2	1.104	F=48.78	<0.01
Species * Time of incubation	4	0.101	F=4.49	<0.01
R				
Species	2	0.010	F=14.49	<0.01
Light Calcification				
Species	2	0.153	F=113.68	<0.01
Time of incubation	2	0.045	F=33.38	<0.01

Species *Time of incubation	4	0.012	F=9.57	<0.01
Dark Calcification				
Species	2	0.002	F=98.68	<0.01
Mollusca biomass				
Collections			H=10.21	<0.01
Arthropoda biomass				
Collections			H=0.08	0.95
Annelida biomass				
Collections			H=10.22	<0.01
Weight of individual rhodoliths				
Species			H=14.21	<0.01
Total rhodolith biomass				
Collections			H=14.21	<0.01

Supplementary Table 2. Mean (± SE) macroalgal species biomass (g/m^2) at the Arvoredo MPA (Brazil) rhodolith bed (southeastern Brazil) in summer 2015.

Species	**Feb/2015**
Padina gymnospora	36.44 (±14.42)
Amphiroa fragilissima (Linnaeus) J.V.Lamouroux	3.90 (±1.54)
Canistrocarpus cervicornis (Kützing) De Paula & De Clerck	1.57 (±0.83)
Dictyopteris delicatula J.V.Lamouroux	1.09 (±0.83)
Gelidium crinale (Hare ex Turner) Gaillon	0.45 (±0.39)
Filamentous red algae	0.36 (±0.11)
Hypnea spinella (C.Agardh) Kützing	0.24 (±0.17)
Jania adhaerens J.V.Lamouroux	0.18 (±0.16)
Hypnea musciformis (Wulfen) J.V.Lamouroux	0.12 (±0.10)
Gelidiopsis intricata (C.Agardh) Vickers	0.10 (±0.08)
Ernodesmis verticillata (Kützing) Børgesen	0.064 (±0.049)
Cladophora vagabunda (Linnaeus) Hoek	0.061 (±0.025)
Champia parvula (C.Agardh) Harvey	0.052 (±0.038)
Rosenvingea intricata (J.Agardh) Børgesen	0.021 (±0.021)
Dictyopteris plagiogramma (Montagne) Vickers	0.018 (±0.018)
Total	**46.22 (±54.56)**



Supplementary Fig. 2. Biomass of total epiphytes in gDW/m^2 in February 2002, 2008, 2015 (n=9) and 2016 (n=15), July 2008 (n=3) and 2016 (n=5), September 2015 (n=6) and November 2016 (n=9) at Arvoredo MPA, Brazil. Letters indicate results of Kruskal-Wallis multiple comparisons ($p < 0.01$).

4. CONCLUSÃO GERAL

Neste trabalho, foi visto que o equilíbrio das relações entre os membros da comunidade dos bancos de rodolitos é influenciado tanto pelas variações ambientais em escala macroecológica quanto pelas mudanças sazonais.

O Capítulo 1 mostra temperatura, nutrientes, velocidade de corrente e transparência da água são os maiores condutores ambientais da abundância e ocorrência dos bancos de rodolitos. A maior abundância de rodolitos entre os bancos a dez metros está localizada na região tropical, quanto as áreas mais favoráveis foram mais abundantes na zona de transição e na região temperada quente. Os modelos preditivos indicaram alta biomassa a 60 km de distância da costa entre o Paraná e São Paulo, áreas ainda não bem exploradas. Com relação às epífitas, apesar de não haver um padrão latitudinal claro quanto a biomassa total, há diferenças na composição de algas epífitas entre as regiões estudadas. Os maiores condutores dessas diferenças parecem ser temperatura e nitrato, com as espécies mais adaptadas a temperaturas mais quentes em regiões tropicais e as mais adaptadas águas mais frias e maior aporte de nutrientes na região temperada quente. Embora em menor abundância, espécies tropicais que surgiram no verão de 2015 não referidas anteriormente para bancos da região temperada quente pode indicar um evento de tropicalização.

No Capítulo 2, conclui-se que enquanto as condições de vento parecem causar alterações na composição e abundância sazonal no banco de rodolitos, mudanças na comunidade bêntica associada parecem ser uma consequência de mudanças nas interações tróficas. Um controle *top down* parece ter estruturado a comunidade bêntica, com a redução de macroalgas carnosas. O eventual sobrecrescimento de algas epífitas parece diminuir a produção primária do banco de rodolitos. Os resultados mostram caminhos para experimentos a longo prazo, com o objetivo de esclarecer o papel das mudanças ambientais na comunidade dos bancos de rodolitos e a resposta de organismos associados sésseis e móveis. Finalmente, pode-se propor que uma estrutura trófica saudável, com predadores de topo abundantes, tenha como consequência indireta o aumento da aptidão dos rodolitos e, potencialmente, na sua resiliência, considerando as alterações climáticas e as ameaças dos estressores locais.

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