Edson Faria Júnior

DISTRIBUIÇÃO ESPACIAL E ESTRUTURA DAS COMUNIDADES DE ANTOZOÁRIOS (CNIDARIA: ANTHOZOA) EM SUBSTRATOS CONSOLIDADOS NO LITORAL DE SANTA CATARINA, SUL DO BRASIL

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Orientador: Prof. Dr. Alberto Lindner

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"Distribuição espacial e estrutura das comunidades de antozoários (cnidaria: anthozoa) em substratos consolidados no litoral de Santa Catarina, Sul do Brasil"

por

Edson Faria Júnior

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Aos meus pais, por toda força e apoio nessa longa trajetória acadêmica.

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“Nós sabemos que quando protegemos nossos oceanos nós estamos protegendo nosso futuro”

(Bill Clinton)

RESUMO

Um padrão recorrente em comunidades bentônicas marinhas de água rasa é a transição entre comunidades com cnidários zooxantelados por outras dominadas por algas com o aumento da latitude. Pesquisas frequentemente usam fatores ambientais para explicar limites de distribuição e uso de habitat de espécies marinhas, entre eles a temperatura da água do mar ou outras variáveis influenciadas por ela estão geralmente relacionadas com esses limites. Compreender estes fatores nos limites de distribuição das espécies, e como comunidades bentônicas variam entre condições ambientais atuais, é um elemento chave para entendermos como estas comunidades serão afetadas com mudanças ambientais. No Brasil, muitas espécies marinhas associadas a substratos consolidados têm seu limite de distribuição no estado de Santa Catarina, com uma marcante transição entre 26°22’ S e 27°51’ S, o que confere uma grande importância biogeográfica a essa região. No presente trabalho avaliamos como mudanças em três variáveis ambientais, frequência de temperaturas baixas, inclinação do substrato e profundidade, influenciam a estrutura de comunidades de antozoários. Utilizamos um Modelo Linear Generalizado Misto (GLMM) para testar os efeitos dessas variáveis sobre as comunidades. As comunidades de antozoários foram influenciadas pela variação na frequência de temperatura (FT) abaixo de 16°C, profundidade e inclinação do substrato. Essas variáveis afetaram a comunidade alterando a composição de espécies, ou ainda, aumentando ou diminuindo a abundância de algumas espécies. O tempo de exposição a temperaturas frias teve a maior influência sobre as alterações da comunidade, com efeitos sinérgicos do estrato de profundidade e inclinação. Apesar de temperaturas mínimas serem largamente utilizadas para explicar mudanças em comunidades marinhas, nossos resultados indicam que o FT pode ser um melhor descritor para limites de tolerâncias termais, pois ele inclui a intensidade do stress termal e a frequência de exposição. No Atlântico Sul Ocidental, um FT em torno de 17% pode ser considerado como o limite da ocorrência de cnidários zooxantelados. Por fim, alterações nos valores de FT podem ser percebidos anteriormente a mudanças nas tradicionais variáveis de temperatura e por isso podem prever antecipadamente mudanças nas comunidades marinhas.

Palavras-chave: Zona de transição biogeográfica • recifes periféricos • mudanças climáticas • limites de temperatura • comunidade bentônica • limite de distribuição

ABSTRACT

A frequent pattern in marine benthic communities of shallow waters is the transition between communities with zooxanthellate cnidarians to communities dominated by algae in higher latitudes. Researches often use environmental factors to explain limits of distribution and habitat use of marine species, from which water temperature and environmental correlates are generally important factors. Understand limiting factors on the edges of distributions, and how benthic communities vary in the present environmental conditions, is key to understanding how these communities will respond to environmental changes. In Brazil, many marine epilithic species have their limit of distribution between 26°22'S and 27°51'S, which gives a significant biogeographical importance to this region. Here, we evaluate how changes in environmental variables such as frequency of low temperatures, bottom slope and depth affect the structure of anthozoan community. We performed a Generalized Linear Mixed Model to test the effects of the variables. The anthozoan community changed among the frequency of temperatures (FT) below 16°C, depth and bottom slope. These three variables affect the community by changing the abundance of some species or the species composition. Time of exposure to cold temperatures had the greatest influence in the anthozoan community, with synergistic influences of depth strata and bottom slope. Although minimum temperatures are widely used to explain changes in marine communities, our data indicate FT could be a better descriptor for the thermal tolerance limits, since it includes the intensity of the thermal stress as a frequency of exposition. In the southwestern Atlantic, FT around 17% can be considered the limit of zooxanthelate cnidarians. Finally, changes in FT values can be perceived before changes in traditional thermal variables and therefore can predict early shifts in marine communities.

Keywords: Marine biogeographic transition zone • Marginal Reefs • Climate change • Temperature limits • Benthic Community • Species distribution limits

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LISTA DE ABREVIATURAS E SIGLAS

FT	Frequência de temperaturas abaixo de 16°C
GLMM	Modelo Linear Generalizado Misto
DSInter	Estrato de profundidade intermediário
DSdeep	Estrato de profundidade fundo
Df	Graus de liberdade

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INTRODUÇÃO GERAL

A distribuição de espécies marinhas tem sido estudada em diferentes escalas e abordagens. Em escala global, muitos estudos tentam entender padrões global de distribuição e conectividade entre populações (e.g. Dinesen 1983, Floeter et al. 2004, Parravicini et al. 2013). Um clássico padrão em biologia e ecologia é a diminuição do número de espécies a partir dos trópicos para os polos, tanto em ambientes terrestres (e.g. Pianka 1966, Hillebrand 2004) quanto marinhos (e.g. Jablonski et al. 2006). Em ambientes marinhos, tanto táxons bentônicos quanto pelágicos são estudados em abordagens latitudinais (e.g. Fuhrman et al. 2008, Fautin et al. 2013). Em escala regional, estudos também abordam a influência de variáveis ambientais na distribuição de espécies ou na estruturação de comunidades marinhas (eg. Fishelson 1971, Kleypas et al. 1999). Em escala local, estudos frequentemente tentam entender a relação entre diferentes condições ambientais e o uso do habitat (e.g. Rule & Smith 2007, Martins et al. 2013, Mizrahi et al. 2014).

Entre alguns desses fatores ambientais estudados para explicar os limites de distribuição e uso do habitat por espécies marinhas, destacam-se a temperatura, a salinidade, os nutrientes, a penetração da luz e a sedimentação (e.g. Wilkinson & Evans 1989, Kleypas et al. 1999, Perry & Larcombe 2003). Em recifes de coral, um ambiente amplamente estudado, os limites de distribuição de espécies de corais estão geralmente relacionados com a temperatura da água ou variáveis ambientais relacionadas a ela (Kleypas et al. 1999, Harriott & Banks 2002). Outros cnidários que também possuem associação com zooxantelas, encontrados em recifes de coral, ambientes de recifes marginais ou recifes rochosos, também possuem os limites de suas distribuições relacionadas à temperatura da água (Reimer et al. 2008).

Essas variáveis, como a temperatura da água, influenciam a estrutura das comunidades marinhas. Um padrão frequentemente observado é a transição de comunidades bentônicas com grande abundância de zoantídeos zooxantelados em baixas latitudes, para comunidades dominadas por macroalgas em latitudes maiores (Harriott & Banks 2002). Por outro lado, alguns táxons possuem padrões distintos. Por exemplo, a riqueza de anêmonas do mar é maior entre 30° e 40° de latitude, e menor em baixas latitudes e regiões polares (Fautin et al. 2013). Na escala do habitat, espécies bentônicas podem ocupar um determinado ambiente de diferentes maneiras. Localmente, preferências de micro-habitat afetam a distribuição espacial dos indivíduos. Profundidade e outros processos operando na escala local possuem uma importante influência nas comunidades bentônicas (Martins et al. 2013). Por exemplo, a inclinação do substrato pode influenciar o uso do habitat por algumas espécies de corais (Segal & Castro 2000, Mizrahi et al. 2014).

No Atlântico Sul Ocidental, pesquisas consideram o estado de Santa Catarina, Brasil, como o limite sul de distribuição de diversas espécies de corais, peixes, e de outras espécies de invertebrados (e.g. Floeter et al. 2008, Capel et al. 2012). Ainda, trabalhos recentes registraram novas espécies de crustáceos tropicais, esponjas, cnidários e peixes para o estado (e.g. Bouzon & Freire 2007, Barneche et al. 2009, Teschima et al. 2012, Bouzon et al. 2012). Nessa região, a plataforma continental recebe influências das águas da pluma do Rio do Prata e de águas Sub-Antárticas no inverno, e das águas tropicais da Corrente do Brasil e da Água Central do Atlântico Sul (ACAS) no verão. As águas da costa do estado são resultado da influência dessas massas de água, juntamente com contribuições das água continentais (Piola et al. 2000, Piola 2005). As características das diferentes massas de água exercem grande influência na fauna marinha local (Amaral & Jablonski 2005).

Para muitas espécies bentônicas, Santa Catarina também o limite sul de distribuição, o que confere a região uma grande importância biogeográfica (e.g. Floeter & Soares-Gomes 1999, Floeter et al. 2005). Por exemplo, os corais e zoantídeos zooxantelados atingem seu limite sul de distribuição no estado de Santa Catarina (Capel et al. 2012, Bouzon et al. 2012), sendo que diversas observações não publicadas nos últimos cinco anos indicam uma marcante transição de comunidades bentônicas entre 27°16’S e 27°51’S ao largo da Ilha de Santa. Ainda, a região é considerada uma área de transição da fauna de corais azooxantelados antárticos e caribenhos (Kitahara 2006).

Especificamente, o Arquipélago do Arvoredo (27°16’S, 48°22’W), localizado 10km ao norte da Ilha de Santa Catarina, abriga as populações mais meridionais de corais recifais zooxantelados no Oceano Atlântico (*Madracis decactis*) (Capel et al. 2012). Ademais, algumas observações indicam que o arquipélago (27°16’S) também abriga uma considerável abundância do zoantídeo zooxantelado *Palythoa caribaeorum*, encontrado em pouca abundância em ilhas mais ao sul, como a ilha do Xavier (35km ao sul - 27°36’S, 48°23’W) e sem registro nas Ilhas dos Moleques do Sul (65 km ao sul - 27°51’S, 48°25’W), bem como em ilhas mais ao sul no Estado de Santa Catarina, onde se observa a presença de cnidários coralimorfários (Corynactis sp.) (Bouzon et al. 2012).

Apesar na grande importância biogeográfica para espécies marinhas, a fauna epilítica dessa área de transição continua pouco estudada. Um recente artigo apresentou 55 novos registros de espécies marinhas para Santa Catarina, entre esponjas, cnidários, briozoários e acídias (Bouzon et al. 2012), indicando que ainda podemos encontrar diversas novas espécies com o aumento do esforço. Os poucos estudos para a região englobam principalmente listas de espécies ou expansões de distribuição, e em contraste com outros grupos taxonômicos, como peixes, macroalgas e crustáceos (Ferreira et al. 2004, Horta et al. 2008, Faria Júnior 2010, Gaeta et al. 2011), há uma notável carência de estudos que se dedicam a investigar aspectos ecológicos de invertebrados bentônicos nessa importante área de transição. Dentre o que já foi estudado, a biodiversidade de antozoários (exceto Actiniaria) reportada para Santa Catarina se restringe a 4 espécies de octocorais (Castro et al. 1999, 2010), 15 escleractínios azooxantelados com registros na plataforma e talude (Kitahara 2006, Bouzon 2010), dois escleractínios zooxantelados (Castro & Pires 2001, Capel et al. 2012) três zoantídeos e um coralimorfário (Bouzon 2010).

Entender os fatores limitantes nas bordas das distribuições de espécies, e como comunidades bentônicas estão estruturadas na condições ambientais atuais, é imprescindível para compreender como essas comunidades irão responder a cenários de mudanças ambientais (Kleypas et al. 1999). Ainda, o conhecimento a respeito da estrutura dessas comunidades fornece patamares de referência essenciais para programas de monitoramento e gestão, o que é fundamental para se investigar alterações nas comunidades bentônicas no curto, médio e longo prazo. Estes patamares de referência são fundamentais em cenários de mudanças climáticas e bioinvasões marinhas, para que a verdadeira extensão das alterações nas comunidades locais possa ser mensurada.

Nesse contexto, o presente trabalho objetiva: 1) estabelecer patamares de referência sobre a estrutura das comunidades de antozoários na costa de Santa Catarina, sul do Brasil; 2) entender como temperatura, profundidade e inclinação do substrato afetam a estrutura dessas comunidades e os limites de distribuição de espécies de antozoários; 3) verificar uma possível transição de espécies nessa área. As hipóteses são: 1) temperaturas baixas limitam a distribuição de espécies tropicais de antozoários; 2) profundidade e inclinação do substrato influenciam secundariamente o uso do habitat; 3) em águas rasas (<8 metros) as mudanças na comunidade são mais acentuadas que em locais mais profundos.

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CAPÍTULO ÚNICO

(Formatado segundo padrões da Marine Ecology Progress Series)

Physical factors influencing the anthozoan community structure in marginal rocky reefs in the Southwestern Atlantic

ABSTRACT

A frequent pattern in marine benthic communities of shallow waters is the transition between communities with zooxanthellate cnidarians to communities dominated by algae in higher latitudes. Researches often use environmental factors to explain limits of distribution and habitat use of marine species, from which water temperature and environmental correlates are generally important factors. Understand limiting factors on the edges of distributions, and how benthic communities vary in the present environmental conditions, is key to understanding how these communities will respond to environmental changes. In Brazil, many marine epilithic species have their limit of distribution between 26°22’S and 27°51’S, which gives a significant biogeographical importance to this region. Here, we evaluate how changes in environmental variables such as frequency of low temperatures, bottom slope and depth affect the structure of anthozoan community. We performed a Generalized Linear Mixed Model to test the effects of the variables. The anthozoan community changed among the frequency of temperatures (FT) below 16°C, depth and bottom slope. These three variables affect the community by changing the abundance of some species or the species composition. Time of exposure to cold temperatures had the greatest influence in the anthozoan community, with synergistic influences of depth strata and bottom slope. Although minimum temperatures are widely used to explain changes in marine communities, our data indicate FT could be a better descriptor for the thermal tolerance limits, since it includes the intensity of the thermal stress as a frequency of exposition. In the southwestern Atlantic, FT around 17% can be considered the limit of zooxanthelate cnidarians. Finally, changes in FT values can be perceived before changes in traditional thermal variables and therefore can predict early shifts in marine communities.

KEY WORDS

Marine biogeographic transition zone • Marginal Reefs • Climate change • Temperature limits • Benthic Community • Species distribution limits

INTRODUCTION

Distribution of marine species has been studied in many different scales and approaches. In large-scales, several studies aim to understand global patterns of distribution and connectivity among populations, or the limits of a species' distribution (e.g. Dinesen 1983, Floeter et al. 2004, Parravicini et al. 2013). A classic large-scale pattern in biology and ecology is the decreasing number of species from the tropics to the poles, ih terrestrial (e.g. Pianka 1966, Hillebrand 2004) and marine environments (e.g. Jablonski et al. 2006). These latitudinal approaches often study different taxa, as benthic or pelagic fauna (e.g. Fuhrman et al. 2008, Fautin et al. 2013). In regional scales, studies also address issues related to environmental variables limiting species distribution or changes in marine communities (eg. Fishelson 1971, Kleypas et al. 1999). In local scales, studies often try to understand the relationship between environmental conditions and habitat use (e.g. Rule & Smith 2007, Martins et al. 2013, Mizrahi et al. 2014).

Among these environmental variables, temperature, salinity, nutrient levels, light penetration or suspended sediment concentrations are often used to explain limits of distribution and habitat use of marine species (e.g. Wilkinson & Evans 1989, Kleypas et al. 1999, Perry & Larcombe 2003). For example, in coral reefs, one of the most widely studied environments, the limits of distribution of coral species is generally related to water temperature and environmental correlates (Kleypas et al. 1999, Harriott & Banks 2002). Other zooxanthelate cnidarians, such as zooanthids, found in coral reefs, marginal reef environments or rocky reefs, also have their distribution limited by water temperature (Reimer et al. 2008).

These variables, as water temperature, change the structure of benthic communities. A frequent pattern found is the transition from benthic communities with high abundance of zooxanthelate cnidarians at low latitudes, to communities with higher cover of macroalgae at higher latitudes (Harriott & Banks 2002). On the other hand, some taxa show different patterns. For example, richness of sea anemones is higher between 30 to 40° latitude (North and South), and lower at lower latitudes and polar areas (Fautin et al. 2013). In the habitat scale, benthic species may use the habitat in different ways. Locally, microhabitat preferences affect spatial distribution, one important component of the community structure. Depth and processes operating in local scale have an important influence on benthic communities (Martins et al. 2013). For example, bottom slope may influence habitat use for some coral species (Segal & Castro 2000, Mizrahi et al. 2014).

In the southern Atlantic, studies consider the state of Santa Catarina, Brazil, as the southernmost limit of distribution for several tropical species of corals, fish, and many invertebrate species (e.g. Floeter et al. 2008, Capel et al. 2012). In addition, several recent studies revealed new records of tropical crustaceans, sponges, cnidarians, and fishes for Santa Catarina (e.g. Bouzon & Freire 2007, Barneche et al. 2009, Teschima et al. 2012, Bouzon et al. 2012). In this region, the continental shelf receives influence of the plume of the Plata River and Sub-Antarctic waters in the winter, an the tropical water of the Brazilian Current and the South Atlantic Central Water in the summer. The coastal water in state is the result of the influences of this water masses and continental inputs (Piola et al. 2000, Piola 2005). The characteristics of these waters have a great influence on the local marine fauna (Amaral & Jablonski 2005). For many marine benthic species, this region is also the southernmost limit of distribution, conferring a high biogeographic importance (e.g. Floeter & Soares-Gomes 1999, Floeter et al. 2005). For example, the southernmost occurrence of a reef coral species, Madracis decactis, in the Atlantic Ocean (Capel et al. 2012), and the southernmost records of zooxanthelate zoanthids in the Southwest Atlantic (Bouzon et al. 2012).

Despite the great biogeographic importance for marine species, the epilithic fauna of this transition area is still poorly investigated. For example, a recent article revealed 55 new records of epilithic species for Santa Catarina, among sponges, cnidarians, bryozoans and ascidian species (Bouzon et al. 2012). The few studies for the region address mainly species lists or distribution expansions, and ecological data for benthic communities is poorly known. Especially for anthozoan species, ecological data is almost absent in this important transition area.

Understanding limiting factors on the edges of a species distribution, and how benthic communities vary among current environmental conditions, is key to understanding how these communities will respond to a changing environment (Kleypas et al. 1999). In addition, knowledge of community structure patterns may provide essential background for monitoring and management programs. Considering this context, in this study I aim to: 1) establish a baseline about the anthozoan community structure in the southern Brazilian coast; 2) understand how temperature, depth and bottom slope affect the anthozoan community structure and the distribution limits of anthozoan species; 3) verify a possible anthozoan species replacement in this area. Hypothesis are: 1) low temperatures limit the distribution of tropical anthozoan species; 2) depth and bottom slope secondarily influence habitat use; and 3) in shallow water (<8 meters) community changes are more abrupt than in deeper sites.

MATERIAL AND METHODS

Study Area

The study area comprised 14 sampling sites off the state of Santa Catarina, Brazil, in the Southwestern Atlantic, located in seven islands and seven submerged rocky reefs between 26°22’ S and 28°44’ S (Figure 1). The study sites comprise approximately 280km of coastline and encompasses the southernmost Brazilian rocky reefs, characterized by the influence of warm waters from the north and cold waters from the south. The continental shelf is strongly influenced by the proximity of the South Atlantic subtropical convergence zone. In summer the region is influenced by the tropical water of the Brazilian Current and the South Atlantic Central Water. In winter, the region receives influences of the plume of the Plata River and Sub-Antarctic waters (Seeliger et al. 1998, Piola et al. 2000, Piola 2005)

Two depth strata were sampled on study sites in the islands, referred to herein as “shallow” (2 to 5 m depth) and “intermediate” depths (8 to 12 m depth), while study sites in the submerged rocky reefs were sampled between 20 and 30 m deep, herein referred to as the “deep” stratum.

Benthic Sampling

To sample the benthic community, we obtained 30 cm X 30 cm photoquadrats from the benthic community for each site, swimming parallel to the rocky reef, using SCUBA diving. Photoquadrats were taken at intervals of three seconds, for 30 to 40 min, totaling 87 to 167 quadrats per depth per stratum per site. From all the photos taken at each site, we randomly selected 60 photos for each depth stratum. Exceptionally for the submerged rocky reef called “Laje da Jagua”, we had 27 instead of 30 photoquadrats.

We use the software photoQuad v1.0 to analyze the anthozoan coverage in the selected photoquadrats (Trygonis & Sini 2012). We used the absolute area of coverage (cm²) for each species of Anthozoa found. To obtain the absolute area, each species was carefully contoured freehand using a pen tablet. This method has the highest precision among other traditional methods, as random points, including for species of small size (Trygonis & Sini 2012).

Environmental data

To characterize the environmental conditions to which anthozoan assemblages occured in each investigated site, we obtained in situ data of winter temperature, depth and bottom slope. Temperature data were obtained through data loggers (HOBO® Data Logger UA-002) installed underwater during SCUBA diving sessions. Each data logger was fixed in a depth stratum with epoxi resin and an anchoring weight that together prevented loss of the equipments through hydrodynamics. A total of 14 data loggers were installed: 12 at the islands (six on the “shallow” stratum and 6 on the “intermediate”) and two at the submerged rocky reefs (“deep”) (Figure 1). The devices recorded water temperature (°C) at an interval of 20 min. To standardize the temperature data for all sites, we used only data collected in the winter, between June and September. This was due to the occurrence during this season, of the lowest temperatures, that are hypothesized to limit the distribution of anthozoans.

In five sampled sites was not possible to install the data loggers. Temperature for these sites was estimated by a linear model based on the data obtained for the other 14 devices, considering latitude and depth as predictors.

Based on the time series of temperatures recorded by data loggers, we obtained the average and minimum temperatures and the frequency of temperatures lower than 16°C (FT) to represent local thermal variation. This cutline was chosen because water temperatures below 16° C limit the occurrence of zooxanthellate cnidarians in other parts of the world (e.g. Reimer et al. 2008) and it was assumed that it could be the case on Southwestern Atlantic reefs as well. With temperature data, we built an interpolation map showing the average, minimum and frequency of temperatures lower than 16°C using the Inverse Distance Weighting method.

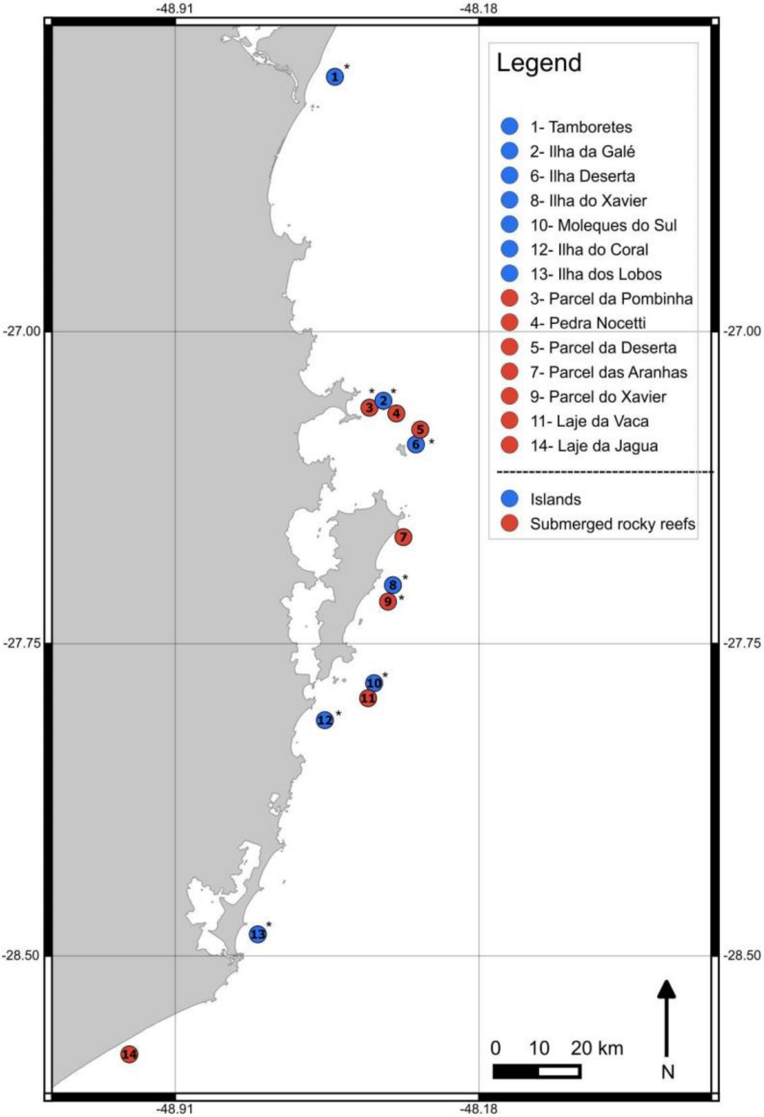

Figure 1 Study area in Southern Brazil. Blue dots represents the Islands, sampled at two depth ranges (between 2 and 5 m deep and 8 to 12 m deep), Red dots represent the submerged rocky reefs, sampled between 20 m to 30 m deep. * Sites where temperature data loggers were installed. In the islands, twelve data loggers were installed at 5 m and 12 m depth, in the submerged rocky reefs two were installed at 25 m depth, totaling 14 devices.

To assess the slope of each photoquadrat, we used a simple analog inclinometer, made with a protractor tied to a float and a weight. Measured angles ranged from 0° to 180°. The inclinometer with a float attached measured the angle of substrates where the epilithic fauna faced up (from 0° to 90°), while the inclinometer with the attached weight measured the angle of substrates facing down (Figure 2). This device was attached to the photoquadrat´s frame, so that all photos taken contained their respective slope measure visible (Supplementary Figure 1).

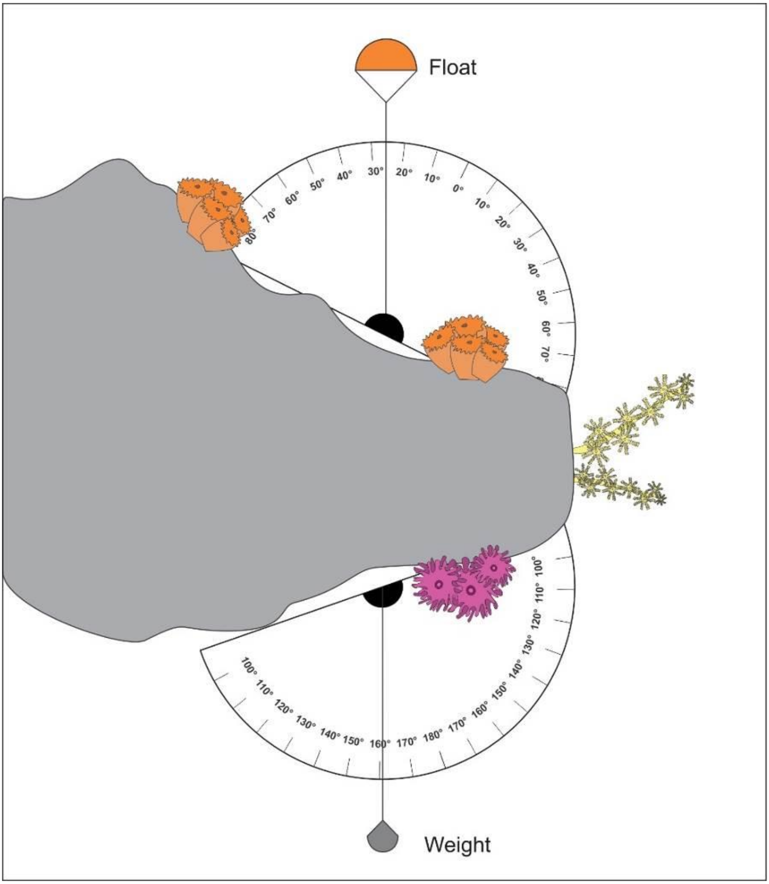

Figure 2 Method used to measure the bottom slope. The protractor with a float attached measures the slope of substrates facing up (from 0° to 90°), while the protractor with a weight attached measures the slope of substrates facing down (90° to 180°).

Data Analysis

Absolute cover area (in cm²) for each anthozoan species was measured in all quadrats as an abundance proxy (n=1227 photoquadrats). We considered as community structure the species composition and their respective abundances for each sampled site. In order to reduce the dimensionality of the community based on a Bray-Curtis dissimilarity matrix we used a Non-metric Multidimensional Scaling (nMDS) ordination performed using one dimension. The resulting ordination axis was used as the response variable to test the effects of the environmental variables [depth strata (categorical with three levels), frequency of low temperatures (FT) and bottom slope] on the anthozoan community structure. To test this, we performed a Generalized Linear Mixed Model (GLMM) using an inverse -gaussian distribution. Environmental variables were included as fixed effects and site as a random effect, since assemblages on different depth strata of the same island would tend to be more similar to each other than random. We also included in the model an interaction term between FT and depth strata, because we expected the effect of FT could have different intensity regarding the strata sampled. We checked for the existence of correlation between the explanatory environmental variables. The GLMM was fitted using the “glmer” function of the “lme4” package in the software R (R Development Core Team 2012). Finally, we also used a direct ordination to describe the general distributions of the anthozoan species throughout the environmental gradients tested above. The direct ordination procedure organizes directly the samples against the environmental gradient to verify how each species is distributed against it.

RESULTS

Benthic coverage

We found 21 species of Anthozoa in total (considering all studied sites): three species of Zoantharia, one Corallimorpharia, three Scleractinia, two Actiniaria and 12 Octocorallia (Supplementary Table 1, Supplementary Figure 2 to 5). The other groups that comprised the sessile epilithic community, which were not analyzed in this study, included mainly hydrozoans, sponges, bryozoans, ascidians and algae (Horta et al. 2008, Bouzon et al. 2012).

Average anthozoan cover across all sites considering all species was 5.78%, ranging from 0.58% at Coral Island to 18.86% at Tamboretes Islands (Figure 3). Contribution of each species in total anthozoan cover differed in each sampled site. *Palythoa caribaeorum* had the greatest cover, with maximum coverage of 23.39% in the shallow of Tamboretes Islands and 1.82% of average cover in all sites. *Carijoa riisei* was the second most abundant species, with 1.27% of average cover in all sites, and a maximum coverage of 6.06% at Pedra Nocetti. This species and *Corynactis viridis* were particularly abundant in deep sites (Figure 4).

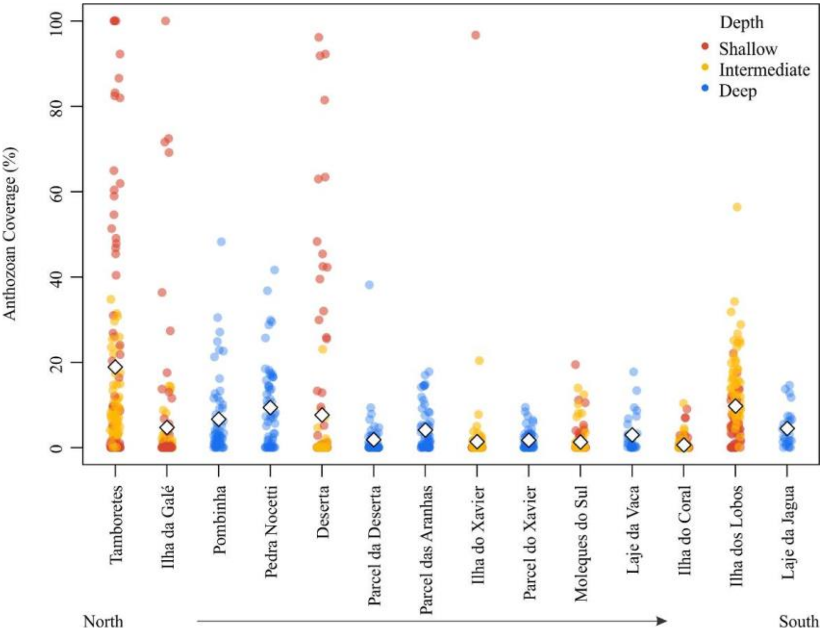

Figure 3 Anthozoan coverage (%) in sampled sites of Santa Catarina State, Southern Atlantic (26°22’ S to 28°44’ S). Sites are ordered from the northernmost (left) to the southernmost (right). Dots represent total anthozoan cover in one sample (30 x 30 cm quadrat). White rhombuses represent average anthozoan cover in each site. Dots color represents sampling depths: red (2 -5 m), yellow (8 -12 m) and blue (20 -30 m).

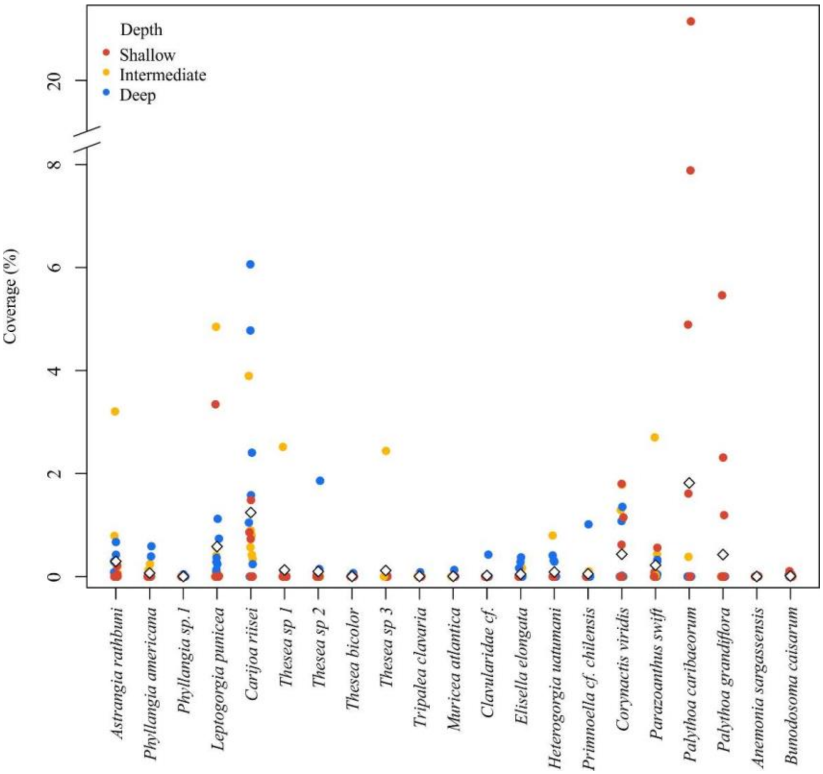

Figure 4 Coverage (%) of each species recorded in sampled sites at Santa Catarina state, Southern Atlantic (26°22’ S to 28°44’ S). Dots represent average cover of each species in a given site. White rhombuses represent average cover of each species in all sampled sites. Dots color represents sampling depths: red (2 -5 m), yellow (8 -12 m) and blue (20 -30 m).

Time series of temperature

Average winter temperature (June to September 2013) was similar among all the studied sites, ranging from 17.1°C in Laje da Jagua, the southernmost site, to 17.6°C in Tamboretes Islands, the northernmost site. Minimum temperatures ranged from 13.7°C in Laje da Jagua (southernmost site) to 15.8°C in Tamboretes Islands (northernmost site). Frequency of temperatures below 16°C showed greater variation among sites, ranging from 0.02 in Tamboretes Island to 0.34 in Ilha dos Lobos (Figure 5), which means that in the southernmost sampled Island, in 34% of the winter, water temperature was below 16°C. Temperature variables between the "shallow" and the "intermediate" strata was similar within a same site. FT values has less variation among sites in the "deep" stratum than other depth strata (Supplementary Table 2).

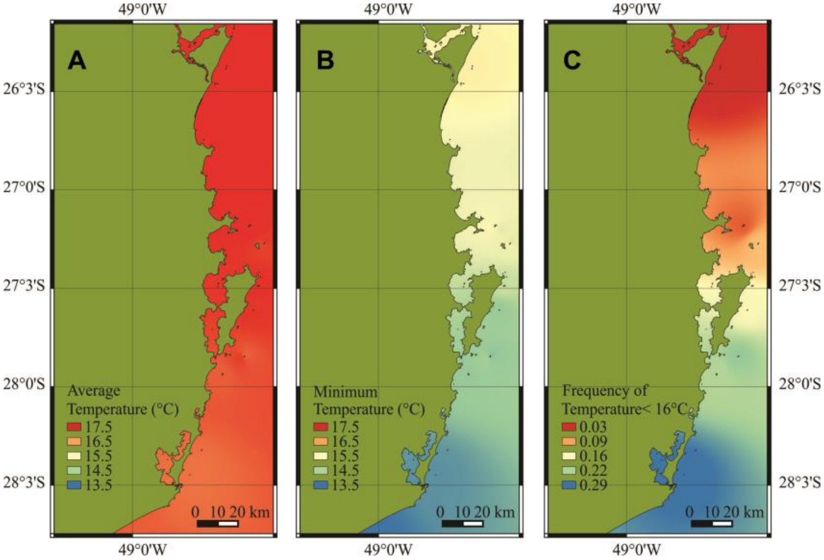

Figure 5 Interpolation map showing water temperature in the coast of Santa Catarina state, southern Brazil. (A) Average water temperature (°C), modeled based on in situ temperature measurements between 5 m to 25 m deep; (B) Minimum temperatures (°C) and (C) frequency of temperatures below 16 °C (FT). The time series of temperature was obtained in the winter months, between June and September 2013 for all sites [see asterisks (*) in Figure 1 for location of temperature sensors].

Community structure

The three environmental variables used in the model (FT, depth strata and bottom slope) were important to explain the observed changes in the community across the sites (Supplementary Table 3). FT had the greatest influence ($\chi^2=13.98$, Df=1, $p<0.001$) depending on the depth strata (Supplementary Table 4). For the shallow stratum, we observed a strong community change along the gradient of FT values. Reductions on the abundance of *Palythoa caribaeorum* and *Palythoa grandiflora* towards the south, until their complete disappearance further south from Xavier Island, is the most characteristic change. This means that sites exposed to temperatures below 16 °C for more than 17% of the time during winter months did not present *Palythoa* species.

Community also changed, although less with FT in intermediate and deep strata. In addition, in the highest FT values the community shows a big change, mainly caused for increasing abundance of *Leptogorgia punicea*, *Thesea* spp. and *Heterogorgia uatumani*. In the deep stratum, we observed a fainter change. The community did not show great changes with increasing FT values. However, when the FT value is greater than 0.25, we observe a more significant change in the community, caused mainly by the increase in the abundance of *Primnoella* cf. *chilensis*, Clavularidae sp1 and *Thesea* spp (Figure 6).

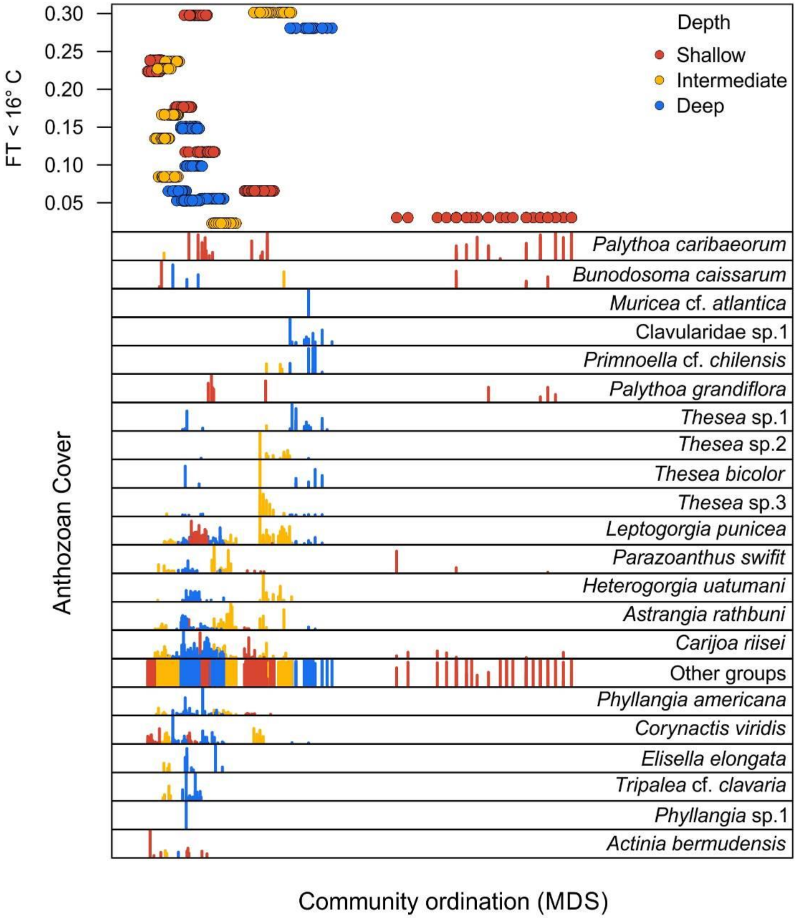

Figure 6 Community ordination using a Nonmetric Multidimensional Scaling (nMDS) and respective species composition. Top diagram shows the community ordination performed using one dimension. The second diagram shows the species composition of the community, with their respective coverage of each species. The cover bars are not proportional among species. FT < 16°C represents the frequency of temperatures below 16°C. Dots color represents sampling depths: red (2 -5 m), yellow (8 -12 m) and blue (20 -30 m). "Other groups" represents the remaining epilithic community except Anthozoa.

Community composition also changed among depth strata (χ^2=182.34, Df=2, p<0.001). More anthozoan species were found in the deep and intermediate strata (19 and 17 species respectively) in comparison with the shallow stratum (10 species). Some species were exclusively found in deeper sites, such as *Heterogorgia uatumani* and *Muricea atlantica*. In addition, species composition tended to vary less from site to site in deeper places than in shallower ones. At greater depths, some species were widely distributed. For example, in the shallow stratum, *Leptogorgia punicea* shows an increase in abundance towards higher FT values, while in the deep it is widely distributed (Figure 7). The same pattern could be observed for the corallimorpharia *Corynactis viridis*. On the contrary, the zoanthid *Parazoanthus swifti*, tended to concentrate on smaller FT values in the shallow and intermediate strata, but was also widely distributed in the deep stratum (Figure 7).

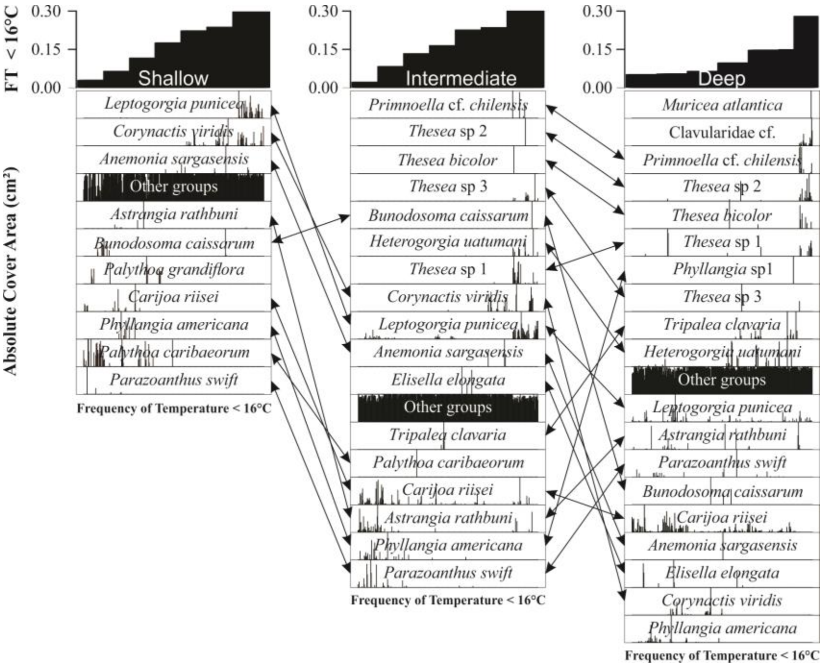

Figure 7 Direct ordination describing general distributions of anthozoan species along the gradient of FT (Frequency of Temperatures) below 16°C and depth. Each column shows the species composition for each depth strata, shallow (2 -5 m), intermediate (8 -12 m) and deep (20 -30 m). The black bars represents the absolute cover area (cm²) for each species, and are not

proportional among species. The arrows guide the species with occurrence in more than one depth strata.

Finally, bottom slope had the lowest influence in the community changes, when compared to the other environmental variables (χ^2=9.19, Df=1, p=0.002). This variable is more important for changes in the abundance of some species individually, and its effect decreases when looking for the entire community. When looking for the six more abundant species we observe different patterns to use the habitat, according to the bottom slope. For example, Palythoa caribaeorum do not occur in face down substratum, limiting their habitat use at a slope of 90° (Figure 8a). The other zoanthid Parazoanthus swiftii is more abundant on near vertical substrates, and in shallower waters mainly occur in vertical or faced down rocks (Figure 8b). The azooxanthelate coral Astrangia rathbuni had a similar pattern, in shallow waters mainly occurring in vertical or faced down rocks, however it can be found in others slopes below 8 m deep (Figure 8c). Corynactis viridis and the “snowflake” coral Carijoa riisei, when found in the shallows mainly occur near vertical or facing down substrates too, in deeper places these species cover all slopes (Fiugre 8d, e). Finally, the octocoral Leptogorgia punicea cover mainly positive substrates in all depth strata (Figure 8f).

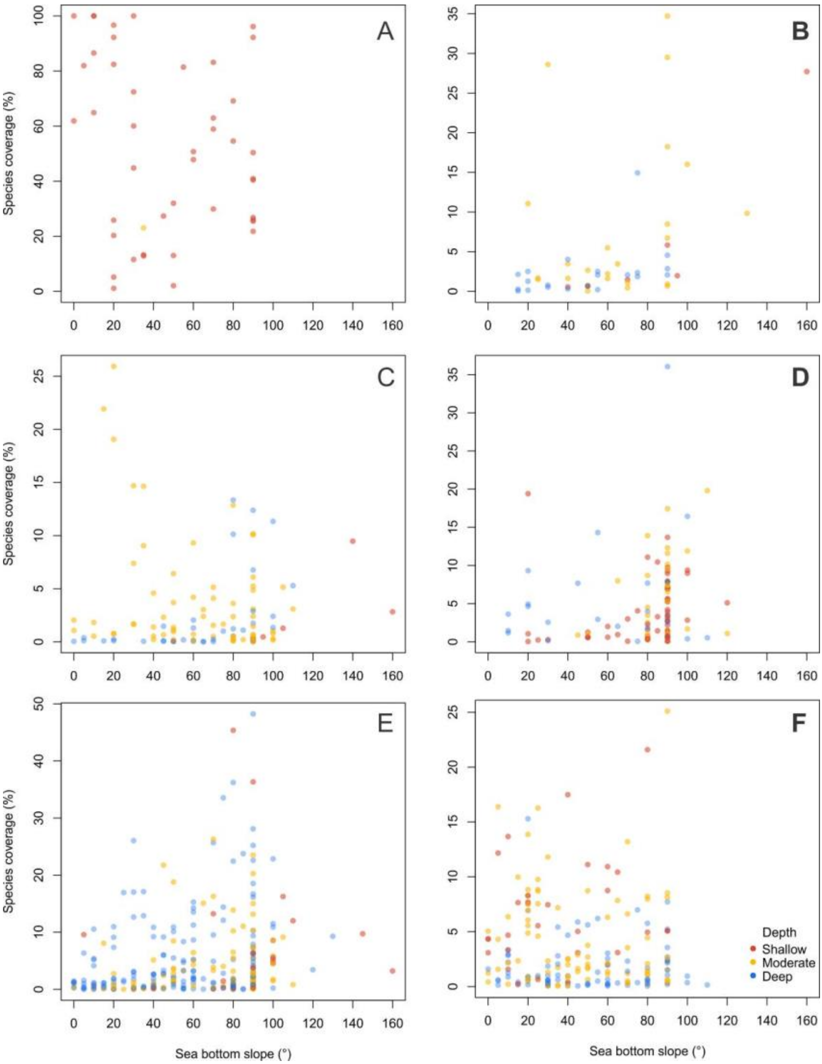

Figure 8 Relation between species coverage (in percentage %) and the sea bottom slope (°). Each dot represents the percentage cover of the following species in a given sample: (A) *Palythoa caribaeorum*, (B) *Parazoanthus swifitii*, (C) *Astrangia rathbuni*, (D) *Corynactis viridis*, (E) *Carijoa riisei*, (F) *Leptogorgia punicea*. Dots color represents sampling depths: red (2 -5 m), yellow (8 -12 m) and blue (20 -30 m).

DISCUSSION

The present study represents the first effort to assess the anthozoan community at marginal rocky reefs in the state of Santa Catarina, western South Atlantic, which is a vital step to understand the ecological significance of these reefs (Harriott et al. 1999). Abundance values found for the different recorded species can also be considered a baseline for future assessments. On rocky reefs further north in the Brazilian coast, benthic communities with high abundance of zoanthids also had Palythoa caribaeorum as the most abundant anthozoan species (Rogers et al. 2014), as shown herein for the northernmost sites of Santa Catarina. This pattern highlights the importance of Palythoa caribaeorum in the structure of rocky reef benthic communities, mainly in shallow waters. Other species found in the community, such as octocorals and corallimorpharians, still uninvestigated and have no ecological data in other similar sites, which prevents comparisons with our results.

Considering the anthozoan community differed among the analyzed environmental variables (frequency of temperatures below 16°C, depth and bottom slope), these variables may affect the community in two main ways: by changing the abundance of some species or the species composition within the community. Increasing values of FT influenced differences in the community structure, indicating that the time of exposure to cold temperatures influences the anthozoan community. Additionally, the depth strata and bottom slope also affected the community, showing the synergistic influences of different environmental variables to structure the benthic community.

Traditionally, environmental variables are used to explain patterns in distribution or structure of marine communities (e.g. Wilkinson & Evans 1989, Kleypas et al. 1999, Harriott & Banks 2002, Nozawa et al. 2008). These approaches often explain the patterns in different scales: evolutionary, biogeographic, regional or local scale (e.g. Johannesl et al. 1983, Paula & Creed 2005, Jablonski et al. 2006). One of the most used variables to explain changes in marine communities is sea temperature (e.g. Horta e Costa et al. 2014). Despite being a variable related with distribution of marine species, temperature responds best to large-scale variations. However, temperature data with high accuracy, which could be used to explain small-scale patterns, are rare. Our results indicate that temperature is an important environmental variable to explain local and regional differences in anthozoan community. On the other hand, average temperatures or minimum temperatures could not be the best predictors for the observed differences in anthozoan community. Studies show minimum temperatures as an important factor to determine distributions of benthic species, as zoanthids or scleractinian corals (Kleypas et al. 1999, Reimer et al. 2008). Our results indicate that the time frequency of exposure to low temperatures may be a better predictor to understanding changes in anthozoan community, mainly in the edge of the distributions of some species.

In large scale, benthic communities change from a high abundance of cnidarians to increasing abundance of algae and reducing abundance of zooxanthelate cnidarians in higher latitudes (Harriott & Banks 2002). In our study, we observed a similar pattern, decreasing abundance of zooxanthelate zoanthids not only with increasing latitude, but also specially with increasing FT values. Areas with sea temperatures below 16°C can limit the distribution of zooxanthelate zoanthids, as shown by Reimer et al. (2008) for the NW Pacific Ocean. Here we show, that in addition to minimum temperature, time of exposition of temperatures below 16°C can be an important limiting factor for zooxanthellate zoanthids in the SW Atlantic. The evidence for this is the absence of Palythoa caribaeorum in samples at sites with FT < 16°C greater than 17%, suggesting that this value can limit of zooxanthelate cnidarians in marginal rocky reefs in the SW Atlantic. The thermal tolerance of one species is determined by the intensity and the duration of a thermal stress, thus a single temperature can not accurately describe a tolerance limit (Rezende et al. 2014). Consequently, the FT could be a better descriptor for the thermal tolerance limits, since it includes the intensity of the thermal stress as a frequency of exposition. Observing this thermal limit for zoanthids in the Santa Catarina State reinforces the region as an important biogeographic transition area.

Other anthozoan species present in the studied communities, such as corallimorpharians and octocorals, show an opposite pattern, increasing their abundance in higher FT. This shows that FT values may influence the anthozoan community in both ways, limiting species distributions to the south (those that may not tolerate cold waters), and limiting species distributions to the north (those that may not tolerate warmer waters). The community changes observed in the different depth strata can be related to other physical factors that vary with the depth, as luminosity (Rule & Smith 2007). The lowest light penetration can be a limiting factor for algal growth, which are important competitors and may limit the growth of cnidarians (McCook et al. 2001, Bonaldo & Hay 2014). Thereby, a lowest algal growth in higher depths may favor a greater abundance of some species of anthozoans. Vertical variations in benthic communities are recorded for different reefs (e.g. Eston et al. 1986, Rule & Smith 2007).

In the submerged rocky reefs, with higher depth, we observed a fainter change in the community from North to South (see Figure 6). This pattern may be related to more homogenous FT values along this depth stratum. So, latitudinal changes in the community may depend on depth, since deeper waters may be colder, and thus can serve as a corridor for species that prefer habitats with these characteristics.

The last environmental factor that influenced the community, bottom slope, had the smallest influence in all the communities. Bottom slope is recorded as a variable that can influence different benthic species, which can have a different use of the substratum depending of their declivity (e.g. Paula & Creed 2005). Bottom slope is related to factors as sedimentation and light incidence on the substrate, and it may influence the habitat use for different species. As the tolerance for these physical factors is different for different species (Dinesen 1983), the bottom slope may have more influence specifically for species than the entire anthozoan community.

Considering the differences observed herein in the anthozoan community off Santa Catarina, SW Atlantic, it is possible to extract some general patterns. First, anthozoan species richness increases with depth, considering the depth range studied (2-30 m). Second, the intensity of the changes caused by FT values interacted with depth. Therefore, the species replacement gradient in shallower waters is stronger, and decreases with increasing depth, possibly related to stronger influence of exposure to lower temperatures for species that are found only in shallow waters (e.g., zooxanthellated zoanthids). These changes, indeed, are mainly caused by limiting the distribution of zooxanthelate cnidarians. Finally, as FT had the strongest influence on the community, variations in FT values may be considered as an important factor to assess reef communities in long term monitoring programs. Understanding how benthic communities vary over present ranges of exposure to low temperatures in limits of distributions is key to understanding how these communities will adapt to the environmental conditions in climate changes scenarios. Changes in FT values can be perceived before changes in traditional thermal variables as temperature average or minimum temperatures, and can predict early shifts in marine communities.

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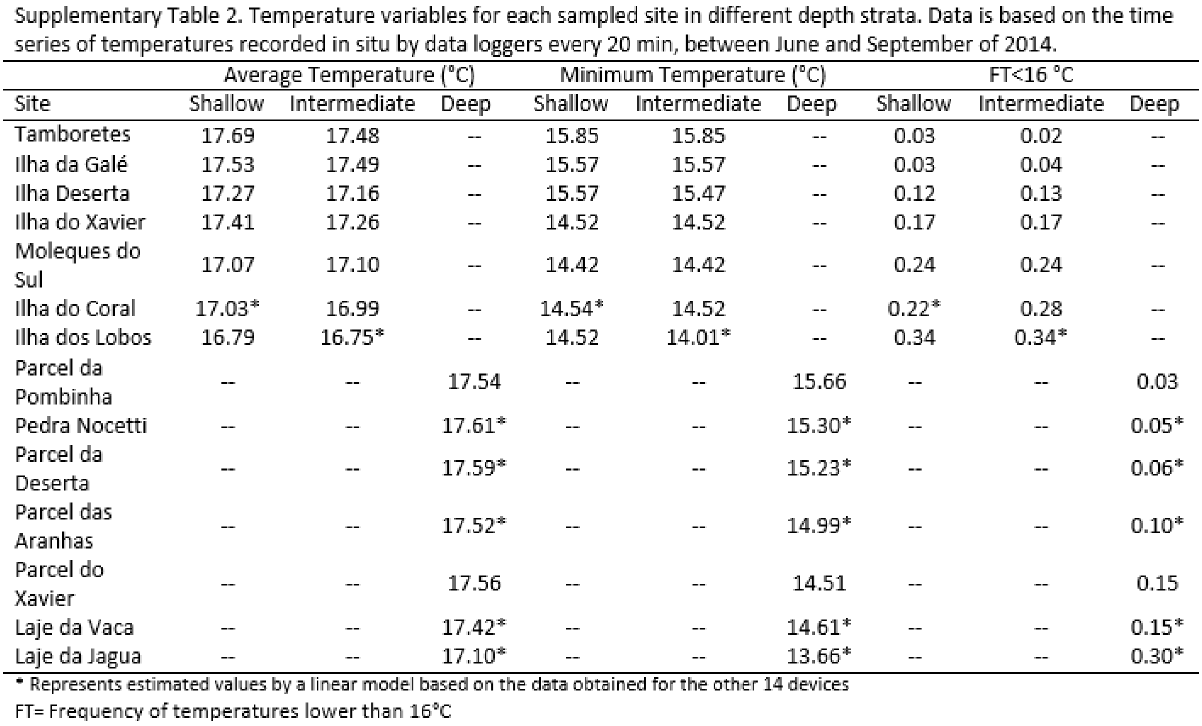
SUPPLEMENTARY MATERIALS

Supplementary Table 1. List of anthozoan species recorded in the sampling sites ordered from the northern to the southern site

Species	Tam	Gal	Pom	Noc	Pde	Des	Par	Xav	Pxa	Mol	Lav	Cor	Lob	Jag
Palythoa caribaeorum	x	x				x		x						
Palythoa variabilis	x	x				x								
Parazoanthus swiftii	x	x	x	x	x	x	x	x	x			x		
Corynactis viridis				x	x			x		x		x	x	x
Astrangia rathbuni	x	x	x	x	x	x	x	x	x		x	x	x	x
Phyllangia americana	x	x	x	x	x	x						x		
Phyllangia sp1.											x			
Carijoa riisei	x	x	x	x	x	x	x	x	x		x	x	x	
Clavularidae sp1.														x
Ellisella elongata			x	x			x					x		
Heterogorgia uatumani			x	x			x		x		x	x	x	
Leptogorgia punicea	x	x	x	x	x	x	x	x	x		x		x	x
Muricea atlantica														x
Primnoella cf. *chilensis*													x	x
Thesea bicolor							x		x				x	x
Thesea sp1.			x	x			x		x	x			x	x
Thesea sp2.					x		x		x				x	x
Thesea sp3.													x	x
Tripalea clavaria							x	x	x		x			
Anemonia sp								x		x			x	
Bunodosoma caissarum	x				x		x			x			x	

Tam: Tamboretes, Gal: Ilha da Galé, Pom: Parcel da Pombinha, Noc: Pedra Nocetti, Pde: Parcel da Deserta, Des: Deserta, Par: Parcel das Aranhas, Xav: Ilha do Xavier, Pxa: Parcel do Xavier, Mol: Moleques do Sul, Lav: Laje da Vaca, Cor: Ilha do Coral, Lob: Ilha dos Lobos, Jag: Laje da Jágua



Supplementary Table 2. Temperature variables for each sampled site in different depth strata. Data is based on the time series of temperatures recorded in situ by data loggers every 20 min, between June and September of 2014.

	Average Temperature (°C)			Minimum Temperature (°C)			FT<16 °C		
Site	Shallow	Intermediate	Deep	Shallow	Intermediate	Deep	Shallow	Intermediate	Deep
Tamboretes	17.69	17.48	--	15.85	15.85	--	0.03	0.02	--
Ilha da Galé	17.53	17.49	--	15.57	15.57	--	0.03	0.04	--
Ilha Deserta	17.27	17.16	--	15.57	15.47	--	0.12	0.13	--
Ilha do Xavier	17.41	17.26	--	14.52	14.52	--	0.17	0.17	--
Moleques do Sul	17.07	17.10	--	14.42	14.42	--	0.24	0.24	--
Ilha do Coral	17.03*	16.99	--	14.54*	14.52	--	0.22*	0.28	--
Ilha dos Lobos	16.79	16.75*	--	14.52	14.01*	--	0.34	0.34*	--
Parcel da Pombinha	--	--	17.54	--	--	15.66	--	--	0.03
Pedra Nocetti	--	--	17.61*	--	--	15.30*	--	--	0.05*
Parcel da Deserta	--	--	17.59*	--	--	15.23*	--	--	0.06*
Parcel das Aranhas	--	--	17.52*	--	--	14.99*	--	--	0.10*
Parcel do Xavier	--	--	17.56	--	--	14.51	--	--	0.15
Laje da Vaca	--	--	17.42*	--	--	14.61*	--	--	0.15*
Laje da Jagua	--	--	17.10*	--	--	13.66*	--	--	0.30*

* Represents estimated values by a linear model based on the data obtained for the other 14 devices

FT= Frequency of temperatures lower than 16°C

Supplementary Table 3: Analysis of Deviance Table (Type III Wald tests)

	χ^2	Df	P
Intercept	7.44	1	p=0.006
FT	13.98	1	p<0.001
Bottom Slope	9.19	1	p=0.002
Factor(Depth)	182.34	2	p<0.001
FT:Depth	146.20	2	p<0.001

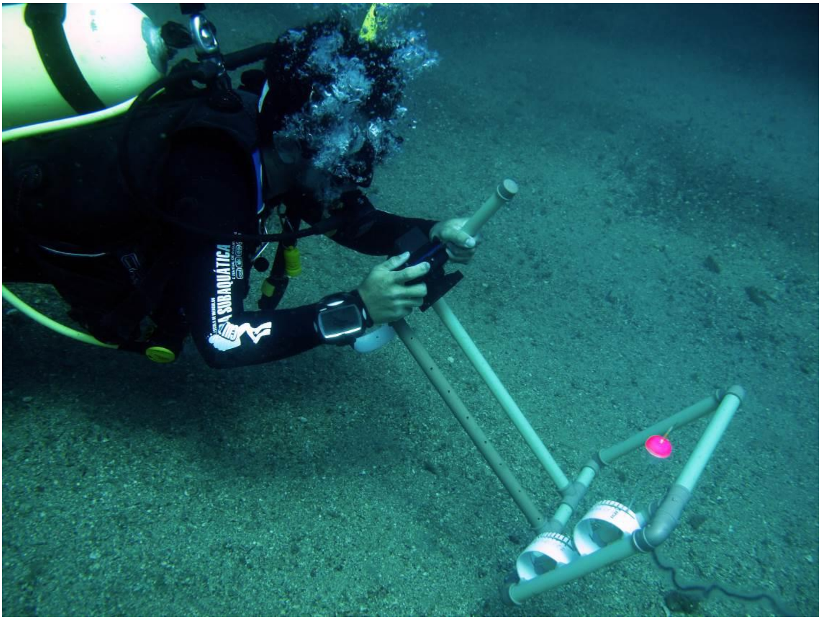
FT= Frequency of temperatures lower than 16°C

Supplementary Table 4: Model averaged estimated coefficients of explanatory variables of a generalized linear mixed model with anthozoan community from Southwestern Atlantic rocky reefs. All coefficients are from standardized variables.

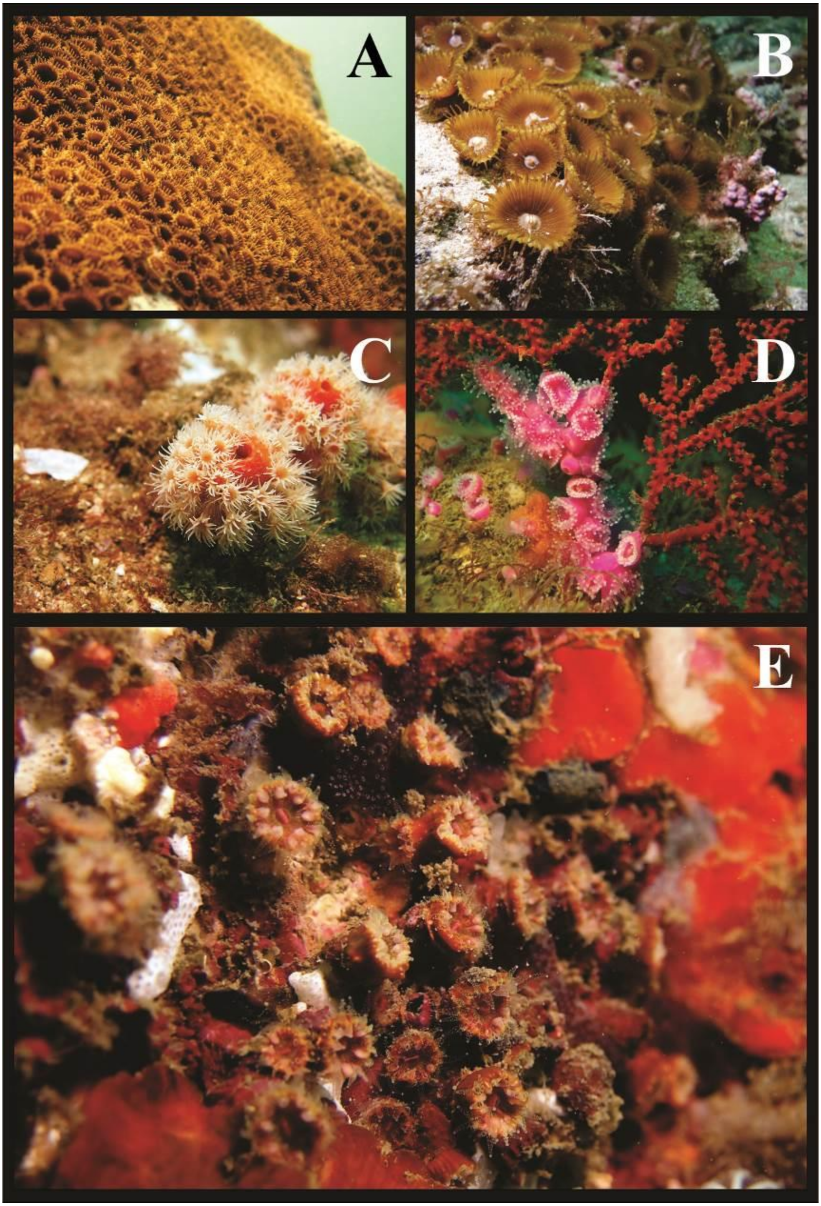
Random effects	Variance	Std. Dev.
Site	0.04	0.20
Residual	0.20	0.45

Fixed effects	Estimate	Std. Error.	t value	Pr(>|z|)
(Intercept)	1.00	0.09	11.69	<0.001
FT	0.29	0.08	3.74	<0.001
Bottom Slope	0.04	0.01	3.03	0.002
DSInter	0.20	0.03	6.11	<0.001
DSdeep	0.06	0.05	1.13	0.257
FT: DSInter	-0.31	0.03	-11.52	<0.001
FT: DSdeep	-0.30	0.04	-7.79	<0.001

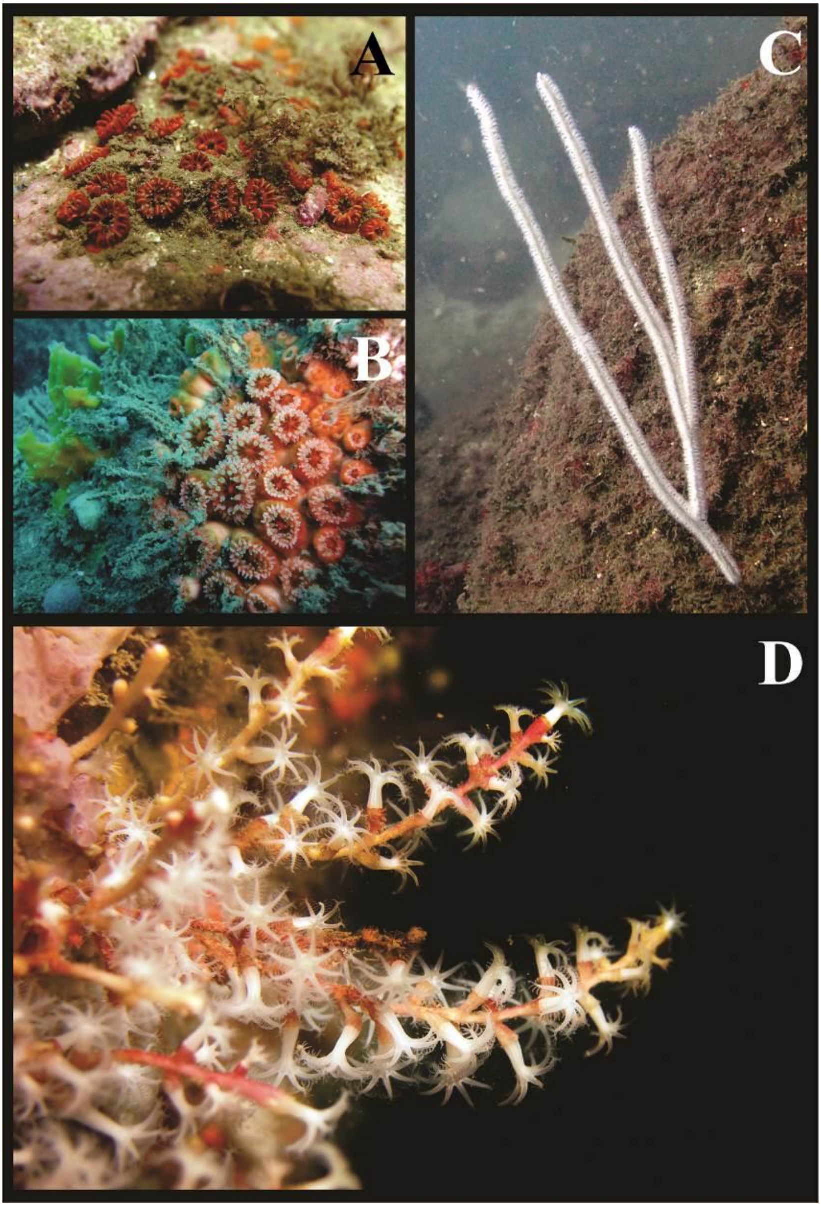
FT= Frequency of temperatures lower than 16°C; DSInter= Intermediate Depth Stratum; DSdeep= Deep Depth Stratum



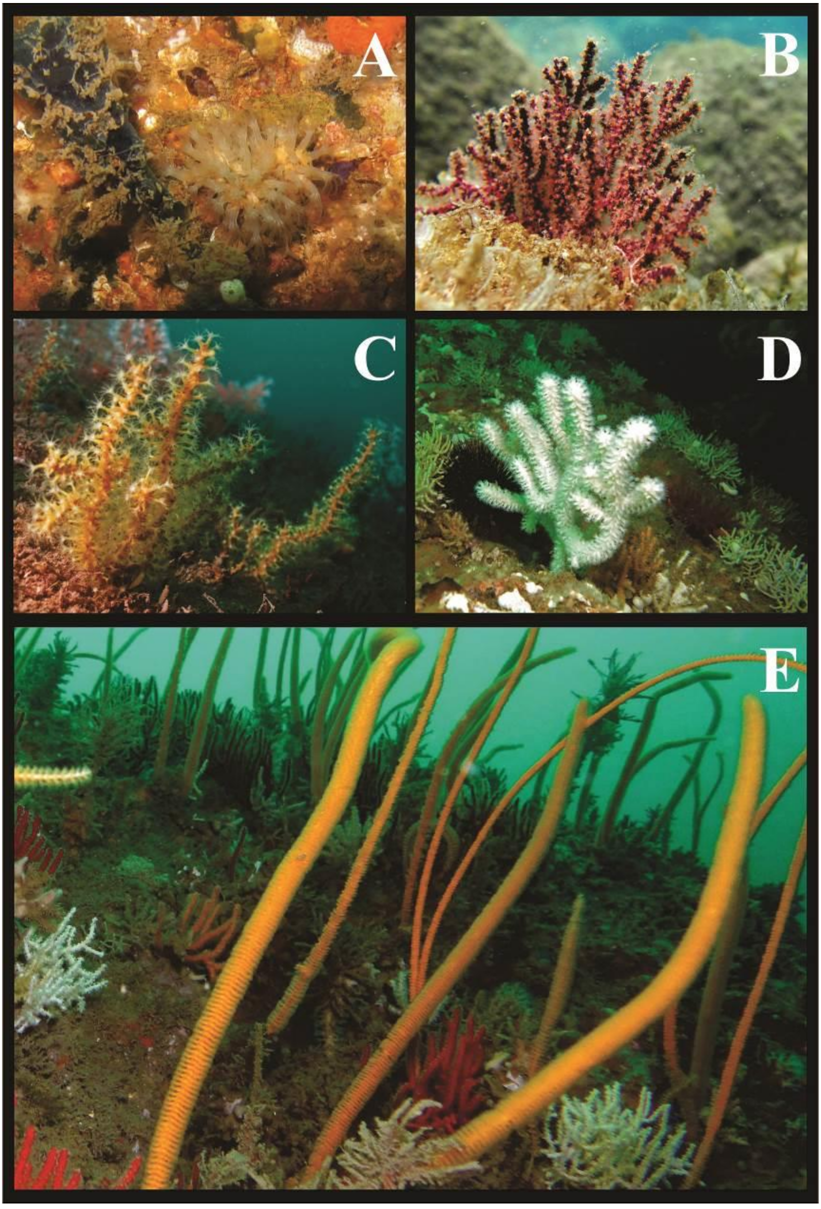
Supplementary Figure 1 Underwater samplings using SCUBA diving and photoquadrats with inclinometer attached.



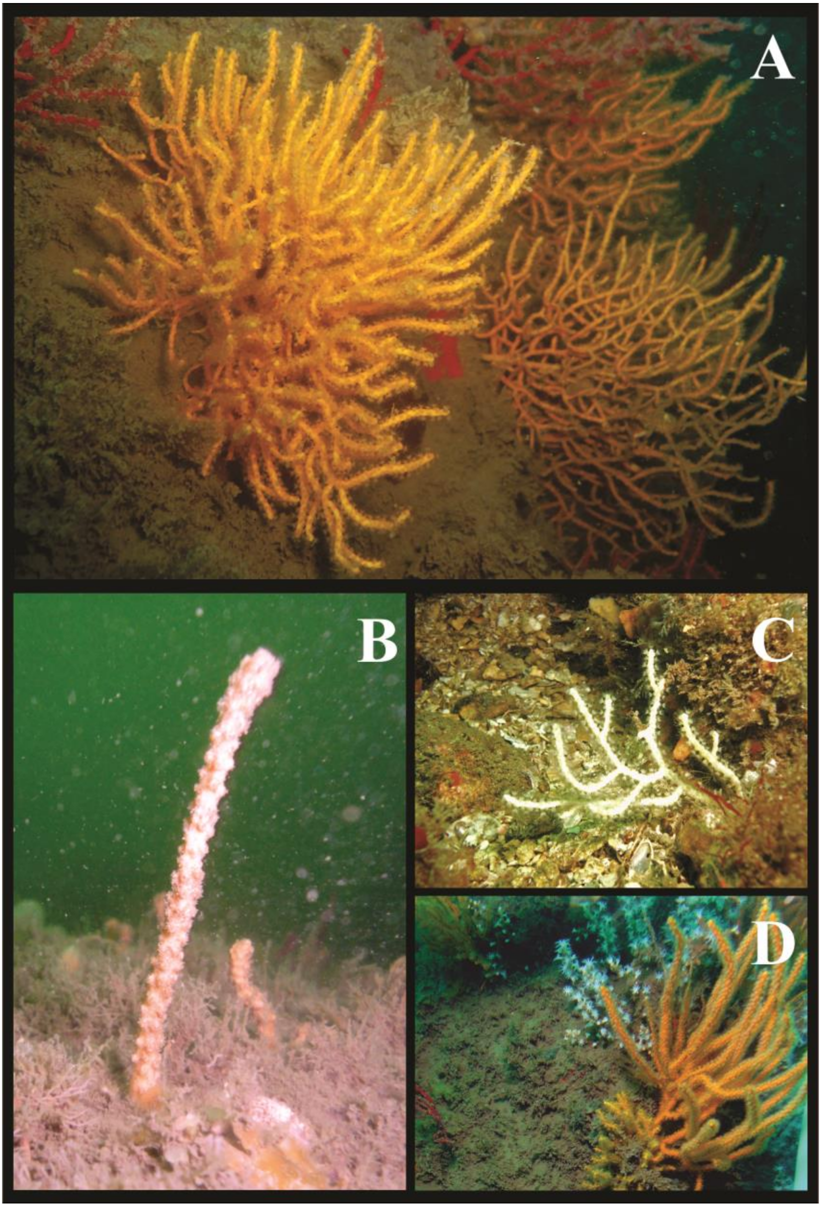
Supplementary Figure 2 Some species recorded in the samplings: (A) *Palythoa caribaeorum*, (B) *Palythoa grandiflora*, (C) *Parazoanthus swifti*, (D) *Corynactis viridis*, (E) *Astrangia rathbuni*



Supplementary Figure 3 Some species recorded in the samplings: (A) *Phyllangia americana*, (B) *Phyllangia* sp., (C) *Ellisella elongata*, (D) *Carijoa riisei*



Supplementary Figure 4 Some species recorded in the samplings: (A) Clavularidae sp1., (B) *Leptogorgia punicea*, (C) *Heterogorgia uatumani*, (D) *Muricea atlantica*, (E) *Primnoella* cf. *chilensis*



Supplementary Figure 5. Some species recorded in the samplings: (A) *Thesea* sp1, (B) *Tripalea* cf. *clavaria*, (C) *Thesea* sp2, (D) *Thesea* sp3.