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BÁRBARA RAMOS PINHEIRO

PERSPECTIVAS DOS EFEITOS DO AUMENTO DO CO_2 ATMOSFÉRICO SOBRE OS ORGANISMOS CONSTRUTORES DO ATOL DAS ROCAS- RN

RECIFE
2016

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Tese apresentada ao Programa de Pós-Graduação em Oceanografia da Universidade Federal de Pernambuco como parte dos requisitos para obtenção do título de doutor (a) em Oceanografia.
Orientador: Prof. Dr. Manuel de Jesus Flores Montes
Coorientadora: Dr. Rebecca Albright

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PERSPECTIVAS DOS EFEITOS DO AUMENTO DO CO_2 ATMOSFÉRICO SOBRE OS ORGANISMOS CONSTRUTORES DO ATOL DAS ROCAS- RN

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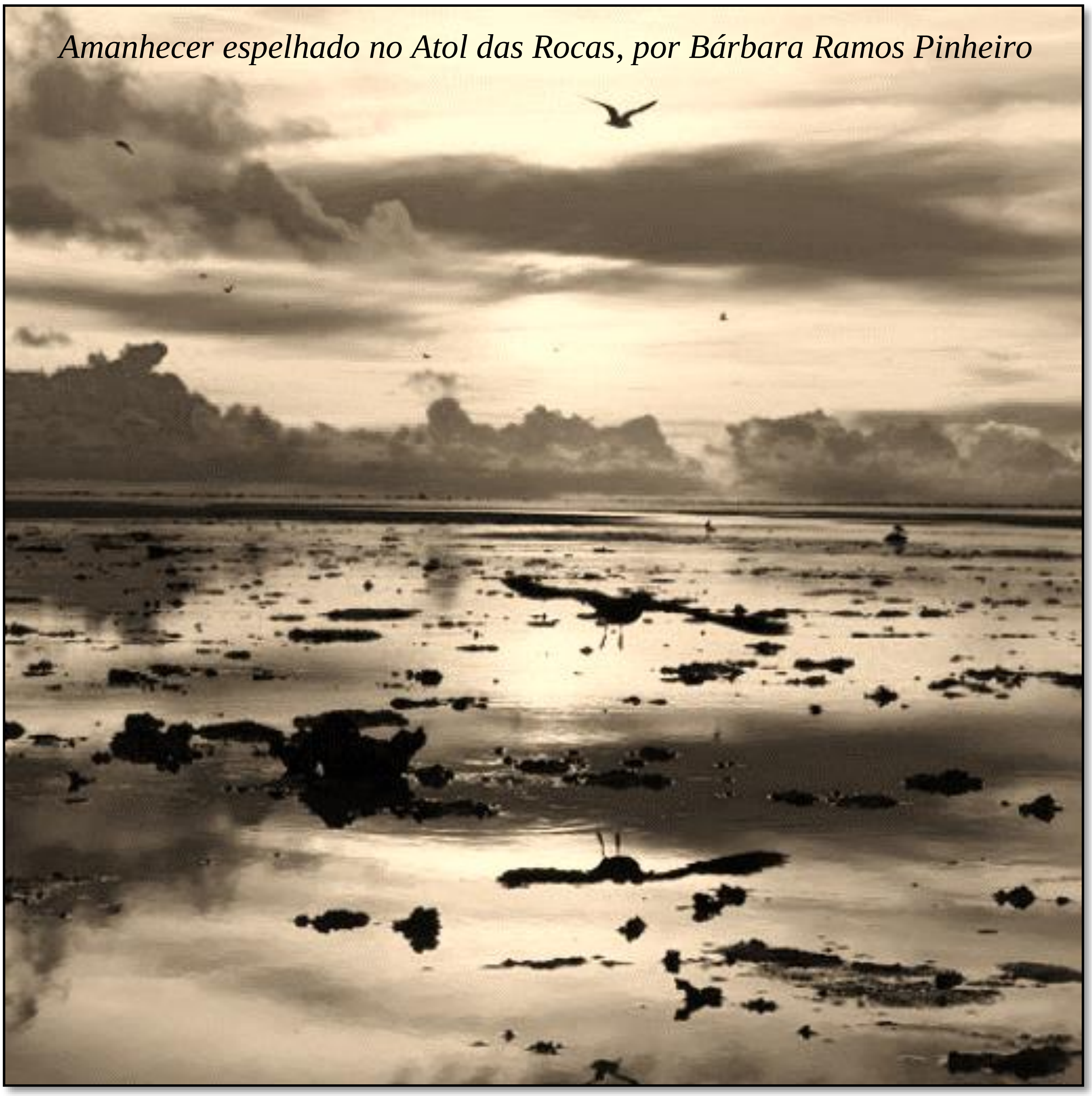


Amanhecer espelhado no Atol das Rocas, por Bárbara Ramos Pinheiro

> *“O Atol das Rocas é um lugar de contrastes. Ele exige daqueles que o visitam um comportamento extremamente pragmático, ao mesmo tempo em que os aproxima dos sonhos; ele liberta do mundo externo, mas aprisiona ao ritmo da natureza. Se o visitante resiste a entregar-se, Rocas revela toda a força de uma natureza indomável.”*
>
> ALICE GROSSMAN, 2012. **Atol das Rocas 3°51’S 33°48’W**.

RESUMO

O aumento da pressão parcial de dióxido de carbono (pCO_2) na atmosfera, que passou de uma média de 280ppm antes da revolução industrial para acima de 400ppm nos dias atuais, é um dos principais responsáveis por uma série de mudanças globais. Entre elas, a elevação da temperatura superficial da água do mar (TSM), a elevação do nível do mar, e a acidificação oceânica (AO). Os ambientes recifais têm sido apontados como os mais vulneráveis a estas mudanças. Efeitos da elevação da pCO_2 sob ambientes recifais no Atlântico Sul, são escassos e na sua maioria reportam apenas efeitos da elevação da TSM e eventos de branqueamento. O Atol das Rocas é a primeira Reserva Biológica marinha do Brasil e foi escolhido neste estudo por ser um exemplo de recife biogênico, oceânico e praticamente livre de impactos como sobrepesca, poluição, e turismo desordenado. Desta forma, o objetivo do presente estudo foi avaliar os efeitos da elevação da pCO_2 atmosférica sob os organismos construtores do atol para estabelecer um ponto de referência para futuras comparações, devido a sua vulnerabilidade a estes processos. A pesquisa foi dividida em três etapas, sendo essas a caracterização, a avaliação do estado e a experimentação dos prováveis efeitos da acidificação nos organismos calcários. Inicialmente são apresentados dados sobre a cobertura bentônica e a sua interação com os parâmetros abióticos (temperatura, salinidade, disponibilidade de nutrientes dissolvidos, pH e alcalinidade total). Foi observada dominância de macro e tufos de algas em locais com maior disponibilidade de nutrientes dissolvidos, indicando que maiores concentrações de nutrientes inorgânicos na água do mar contribuem para a distribuição dos organismos no atol. E, além disso, ambientes com alta frequência de organismos carbonáticos foram associados com uma diminuição da concentração de alcalinidade. Em seguida, dados foram obtidos sobre reprodução, crescimento e distribuição de frequência da população da espécie de coral dominante nas piscinas do atol (*Siderastrea stellata*). Foi observado um evento de planulação e o crescimento inicial dos pólipos primários, os quais, após 3 meses mostraram uma média de diâmetro de 1,49±0,45 mm, variando entre 0,9 e 2,28 mm e 14,70% de taxa de mortalidade. A média da taxa de extensão anual das colônias adultas foi de 6,8 ± 0,7 mm. ano^{-1}. Colônias com 4,1 a 10 cm de diâmetro também foram frequentes no atol (48,1±14,5%). A população de *S. stellata* no atol mostra-se com um alto potencial de manutenção e recuperação, embora tenha sido observado uma baixa taxa de recrutamento. Na outra etapa do estudo se fez uma caracterização do sistema carbonato no atol, avaliando a influência do metabolismo dos organismos sob as variações espaço-temporais observadas. Os resultados indicaram uma grande disponibilidade de carbonato dissolvido nas piscinas do atol. Os índices de saturação de aragonita não só suprem as necessidades metabólicas dos organismos, como estão acima dos observados para outros ambientes recifais. Desta forma, é possível que a intensa atividade biológica no atol das rocas possa servir como um tampão adicional para o equilíbrio do pH e mitigar alguns dos efeitos da acidificação oceânica localmente. Por fim, foi realizado um experimento com espécies que ocorrem no atol, o coral scleractíneo *Porites astreoides* e o zoantídeo *Palythoa caribaeorum*. Foram avaliadas as respostas fisiológicas (crescimento, respiração, fotossíntese, lipídios totais e clorofila *a*) desses organismos mediante condições de estresse térmico e acidificação. *P. astreoides* sofreu influência do aquecimento e da acidificação em todas as taxas metabólicas avaliadas, enquanto o *P. caribaeorum* teve um menor, ou nenhum impacto no seu metabolismo.

Palavras Chave: Ambientes recifais. Acidificação oceânica. Aquecimento global. Atol das Rocas. Brasil

ABSTRACT

The increase in carbon dioxide partial pressure (pCO_2) in the atmosphere, which rose from an average of 280 ppm before pre-industrial times to over 400 ppm today, it is one of the main responsible for a series of global changes. Among them, increasing sea surface temperature (SST), sea level rise and ocean acidification (OA). Coral reefs have been identified as the most vulnerable ecosystem to these changes. Investigations about the effects of elevated anthropogenic pCO_2 on coral reef environments in the South Atlantic are scarce and mostly only effects of the increase of SST and bleaching events were reported. Rocas Atoll is the first Marine Biological Reserve in Brazil and was chosen in this study because it is an example of a oceanic biogenic reef, and virtually free from impacts such as overfishing, pollution, and unregulated tourism. Thus, the aim of this study was to evaluate the effects of increased atmospheric pCO_2 on the atoll building organisms to establish a benchmark for future comparisons, because of their vulnerability to these processes. Initially are presented data on the benthic cover and its interaction with the abiotic parameters (temperature, salinity, availability of dissolved nutrients, pH and total alkalinity). It was observed a dominance of macro and tuff algae in places with higher availability of dissolved nutrients, indicating that higher concentrations of inorganic nutrients in seawater contribute to the spatial distribution of organisms on the atoll. And besides, environments with high frequency of carbonate organisms were associated with a decrease of alkalinity. Then, data were obtained on reproduction, growth and frequency distribution of the population of the dominant coral species in the atoll pools (*Siderastrea stellata*). A planulation event was observed and initial growth of primary polyps which, after 3 months showed 1.49 ± 0.45 mm average diameter ranging between 0.9 and 2.28 mm and 14.70% mortality rate. The average annual extension rate of adult colonies was 6.8 ± 0.7 mm. year^{-1}. Colonies with 4.1 to 10 cm diameter were also common in the atoll (48.1 ± 14.5%). The population of S. stellata in the atoll shows a high potential for maintenance and recovery, although it was observed a low recruitment rate. In another stage of the study, a characterization of the carbonate system of the atoll was made, in order to assess the influence of the metabolism of organisms under spatio-temporal variations. The results indicated a large availability of dissolved carbonate in the atoll pools. The aragonite saturation rates not only supply the metabolic demands of the corals, but are above those observed for other coral reef environments. Thus, it is possible that the intense biological activity of the Rocas Atoll can serve as an additional buffer for the pH equilibrium and locally mitigate some of the effects of ocean acidification. Finally, an experiment was conducted with species that occur in the atoll, the scleractinian coral *Porites astreoides* and the zoanthid *Palythoa caribaeorum*. The physiological responses of these organisms were evaluated (growth, respiration, photosynthesis, total lipids and chlorophyll *a*) under conditions of heat stress and acidification. *P. astreoides* was influenced by warmer temperatures and acidification in all measured metabolic rates while *P. caribaeorum* showed a minor or no impact on your metabolism.

Keywords: Brazil. Coral Reefs. Global warming. Ocean acidification. Rocas Atoll

LISTA DE FIGURAS

LISTA DE TABELAS

SUMÁRIO

1. INTRODUÇÃO

A concentração de dióxido de carbono (CO_2) na atmosfera vem sendo monitorada desde 1958 no observatório da Universidade da Califórnia San Diego (SCRIPS, UCSD) em Mauna Loa, Havaí (KEELING, 1998). Atualmente os níveis de CO_2 ultrapassaram 400ppm, e a média anual para 2015 (400,88ppm) bateu o recorde de mais elevada em alguns milhões de anos. Antes da revolução industrial esse valor não passava de 300ppm. Dentre as atividades humanas, a queima descontrolada de combustíveis fósseis e o desflorestamento são os principais fatores que contribuem para essa rápida elevação (CALDEIRA; WICKETT, 2003; SABINE et al., 2004). Esse aumento na concentração de CO_2 vem causando uma série de mudanças globais, alterando o clima, causando severas e mais constantes tempestades, furacões, enchentes, etc. Porém, dentre essas mudanças, três estão causando grande impacto nos ecossistemas marinhos: aumento da temperatura superficial do mar (TSM), elevação do nível do mar e acidificação oceânica. De acordo com o relatório do Painel Intergovernamental de Mudanças Climáticas (IPCC) o nível do mar subiu +0,19m, o pH diminuiu 0,1 unidades e a média de temperatura atmosférica global já aumentou 0,85°C, durante o século 20 (IPCC- AR5, 2014).

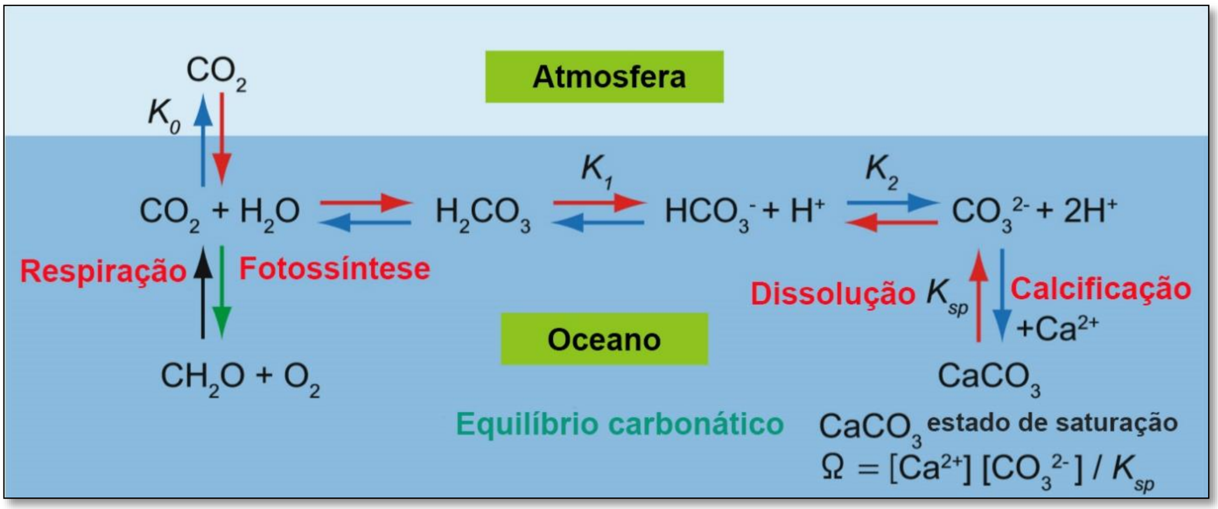
Aproximadamente 90% dessa energia térmica tem sido acumulada nos oceanos, o que causou uma elevação da temperatura superficial entre 0,09 e 0,13°C por década entre o período de 1971 e 2010 (IPCC-AR5, 2014). Nas décadas de 1980 e 1990, eventos de *El Niño* foram associados com alguns dos eventos mais expressivos de estresse térmico em ambientes recifais. Recentemente, no entanto, tem sido testemunhado eventos de estresse térmico independentemente do *El Niño*, devido ao aumento das médias de temperatura causadas pelo aquecimento global (MUMBY; VAN WOESIK, 2014).

Temperaturas elevadas causam impactos na simbiose cnidários-dinoflagelados. As microalgas simbiontes (zooxantelas) garantem reciclagem de nutrientes e fluxo de energia oriunda da atividade fotossintética para os organismos hospedeiros. Elas também são responsáveis pela coloração dos mesmos, e o estresse térmico leva a expulsão dos simbiontes e consequentemente o branqueamento dos corais (HOEGH-GULDBERG, 1999). Anomalias de 1 a 2°C acima do máximo registrado durante o verão pode causar branqueamento de corais em massa. Da mesma forma, pequenos aumentos na TSM (0-1,5°C) durante várias semanas ou uma grande elevação (3-4°C) durante poucos dias também causam branqueamento (HAYENNE, 2016). Elevadas temperaturas podem causar também efeitos prolongados nos corais quando eles experimentam condições que excedem a temperatura ideal para seus processos metabólicos. Já foram reportados redução na taxa de crescimento e calcificação, levando ao enfraquecimento do esqueleto dos corais uma vez excedido esse limite térmico (MUMBY; VAN WOESIK, 2014).

O CO_2 não fica concentrado apenas na atmosfera juto com outros gases responsáveis pelo efeito estufa. Assim como os oceanos absorvem a energia térmica, eles também absorvem o CO_2 em excesso na atmosfera. Desde a revolução industrial cerca de 30 a 40% do CO_2 antrópico é absorvido pelos oceanos a cada ano (BINDOFF et al., 2007). Esse CO_2 em excesso reage com a água do mar e por uma série de reações químicas causa um processo conhecido como acidificação oceânica (AO). Esse processo tem como consequências reduções no pH, nas concentrações do íon carbonato $[CO_3^{2-}]$, e nos índices de saturação dos minerais carbonáticos (Ω) (DONEY et al., 2009). De acordo com HOEGH-GULDEBERG et al. (2007) os ecossistemas recifais estão entre um dos mais ameaçados do ambiente marinho. Impactos da AO sob os organismos calcificadores são constantemente reportados. Processos fisiológicos como crescimento e calcificação são alguns dos mais estudados (DUPONT et al., 2010; ALBRIGHT; LANGDON, 2011; FABRICIOUS et al., 2011). Essas mudanças na fisiologia dos indivíduos podem alterar a dinâmica de suas populações e por fim afetar todo o ecossistema.

Organismos calcificadores, mobilizam o cálcio (Ca^{2+}) e o carbono inorgânico dissolvido (CID) presentes na água do mar para formação dos seus esqueletos e estruturas calcárias. A concentração desses elementos na água do mar é um fator crucial para o metabolismo e calcificação nos recifes. O CID é o somatório de todas as formas do carbono inorgânico: o CO_2 aquoso ou dissolvido, ácido carbônico (H_2CO_3), bicarbonatos (HCO_3^-) e carbonatos (CO_3^{2-}) (ZEEBE; WOLF-GLADROW, 2001). Em águas marinhas predominam os íons bicarbonatos (86,5%) e carbonatos (13%) e, em menor quantidade, o CO_2 aquoso (0,05%) (GATTUSO et al., 1999; ZEEBE; WOLF-GLADROW, 2001). Tanto o CO_2 como os carbonatos exercem uma grande influência na vida marinha, não só como fonte de carbono para a fotossíntese, como também para a formação de estruturas esqueléticas da grande quantidade de organismos que habitam os oceanos (MACÊDO et al., 2004). O ciclo do carbono num ambiente recifal é principalmente afetado por dois processos biogeoquímicos ilustrados na figura 1. O metabolismo do carbono orgânico através da fotossíntese e respiração são responsáveis pelas variações no CID, e o metabolismo do carbono inorgânico, com os processos de calcificação e dissolução alteram tanto o CID quanto a alcalinidade total (AT) numa proporção de aproximadamente 2:1 (ALBRIGHT et al., 2013).

Figura 1 – Diagrama esquemático do sistema carbonato oceânico. (Adaptado de KAYANNE, 2016)



Diversos estudos apontam que o crescimento e a reprodução de algumas espécies de organismos calcários e não calcários podem ser limitados pelas alterações químicas projetadas nos oceanos (ALBRIGHT et al., 2013; KROEKER et al., 2013). De todos os organismos marinhos, aqueles afetados mais intensamente são as espécies calcárias, como moluscos, crustáceos, equinodermas, corais, algas calcárias, foraminíferos e algumas espécies do plâncton. Essas mudanças provocam tanto uma redução da disponibilidade dos constituintes químicos necessários para a calcificação de conchas e placas, como afetam sua fisiologia (KLEYPAS et al., 1999a; 2006; MUNDAY et al., 2007). De acordo com MUNBY e VAN WOESIK (2014), que revisaram uma série de impactos no ecossistema recifal devido ao aquecimento e acidificação, as populações de corais, algas calcárias, ouriços e peixes recifais podem diminuir no futuro, enquanto que macroalgas e outros cnidários não calcificadores (coral mole, anêmona, zoantídeos) devem se beneficiar das elevadas concentrações do CID.

Previsões sobre o impacto das mudanças climáticas são feitos para a grande maioria dos ambientes recifais ao redor do mundo (FREEMAN et al. 2013; NAKAMURA et al., 2013). No entanto, não existem modelos ecológicos que indiquem o futuro desse ecossistema no Brasil. A escassez de banco de dados, e falta de padronização nas metodologias contribuem para essa ausência de modelos preditivos dos impactos das alterações físico-químicas dos oceanos sob os recifes brasileiros. Além disso, a maioria dos trabalhos que apresentam algum dado sobre a dinâmica das populações de organismos recifais, foram realizados em ambientes costeiros, sujeitos a impactos locais como elevadas taxas de sedimentação, eutrofização, pesca e turismo desordenado. E assim não é possível avaliar apenas o efeito causado pelos impactos do aquecimento e acidificação dos oceanos. Até o momento existe um trabalho publicado sobre o impacto da acidificação na comunidade meio-bentônica dos recifes (SARMENTO et al., 2015) e outro sobre taxas de calcificação, produtividade líquida e fluxos de CO_2, ambos em recifes do sul da Bahia (LONGHINI et al., 2015).

Reconhecido pela UNESCO como um patrimônio da humanidade e único atol do Oceano Atlântico Sul, o recife biogênico de Rocas pode ser considerado um atol, pois possui uma plataforma elíptica e circular, tem um anel recifal constituído com a predominância de algas calcárias e moluscos vermetídeos, além dos corais escleractínios (KIKUCHI; LEÃO, 1997; ECHEVERRIA et al., 1997). Transformado em uma unidade de conservação da categoria Reserva Biológica (REBIO) em 1979, cujo objetivo é proteger integralmente o Atol e águas circundantes de até 1.000 metros de profundidade, a REBIO não é aberta ao público, sendo permitido apenas o monitoramento ambiental, o patrulhamento e estudos científicos.

Desta forma, o recife biogênico do Atol das Rocas foi escolhido como laboratório natural, devido ao seu estado de conservação e isolamento de demais impactos antropogênicos, para a avaliação das condições atuais de seus organismos construtores, caracterização do sistema carbonato e a interação dos organismos com os parâmetros físico-químicos. Através destes dados, e de experimentos realizados com espécies de corais e zoantídeos que ocorrem no Atol das Rocas, foi possível analisar a susceptibilidade dos organismos aos efeitos causados pela elevação do CO_2 na atmosfera.

2. JUSTIFICATIVA

A biodiversidade dos ambientes recifais é uma das mais distintas e complexas entre os diferentes ecossistemas marinhos. Eles fornecem inúmeros benefícios, incluindo alimentos, proteção costeira, regulação climática, além de darem suporte e abrigo a uma variedade de comunidades marinhas de interesse econômico, como peixes, moluscos e crustáceos (MOBERG e FOLKE, 1999; ÖHMAN e CESAR, 2000). Os ambientes recifais têm sido apontados como os mais vulneráveis a elevação da temperatura superficial (TSM) da água do mar, a elevação do nível do mar, e a acidificação oceânica. Previsões sugerem que até cerca de 70% dos recifes de coral do mundo sejam perdidos durante as próximas quatro décadas, se as atuais ameaças e a intensidade e frequência dos impactos causados pelos efeitos combinados das mudanças climáticas e acidificação oceânica persistirem (HOUGH-GULDBERG et al., 2007).

O Atol das Rocas foi escolhido neste estudo por ser um exemplo de recife biogênico, oceânico e praticamente livre de impactos como sobre pesca, poluição, e turismo desordenado. Alguns estudos sobre cnidários foram realizados no atol e abordaram temas como distribuição das espécies (LABOREL, 1970; SCHLENZ; BELÉM, 1992; ECHEVERRIA et al., 1997), monitoramento da saúde recifal (FERREIRA; MAIDA, 2006) e branqueamento (MAŸAL et al., 2009 FERREIRA et al., 2012). Enquanto vários registros detalhados de parâmetros físicos e químicos têm sido coletados em amplas escalas espaço-temporais durante as últimas décadas em áreas oceânicas (FLORES MONTES et al., 2009; MACÊDO et al., 2009; MEDEIROS et al., 2009), há uma escassez de dados sobre como os parâmetros do sistema carbonato variam naturalmente em escalas espaço-temporais biologicamente relevantes em sistemas recifais.

Desta forma, a ausência de informações, falta de conhecimento da influência da acidificação na formação recifal e a identificação dos organismos que contribuem ativamente para o crescimento do recife biogênico do Atol das Rocas são as motivações principais para a elaboração desta pesquisa. Uma vez que o atol apresenta uma alta biodiversidade, e grande relevância para conservação e perpetuação de muitas espécies, sendo uma importante área de reprodução, dispersão, alimentação e abrigo para diversos animais. Além disso, apresenta grande importância estratégica e econômica devido a expansão da zona econômica exclusiva brasileira.

3. OBJETIVOS

3.1. Objetivo geral

Avaliar o estado de vulnerabilidade dos organismos construtores do Atol das Rocas diante de um cenário dos efeitos diretos e indiretos do aumento global de CO_2 atmosférico.

3.2. Objetivos específicos

- Caracterizar os parâmetros físicos e químicos em piscinas abertas e fechadas do atol;
- Caracterizar a cobertura bentônica em algumas das principais piscinas do atol;
- Avaliar a interação entre os parâmetros abióticos e a cobertura bentônica;
- Obter dados de reprodução, crescimento e frequência de tamanho da população da espécie de coral dominante (*S. stellata*) nas piscinas do atol;
- Investigar possíveis impactos das mudanças climáticas e acidificação oceânica sob a dinâmica populacional dessa espécie;
- Determinar variações espaço-temporais no sistema carbonato marinho do atol;
- Avaliar a interação entre os organismos e o sistema carbonato;
- Obter taxas de crescimento, fotossíntese, respiração e níveis de lipídio e concentração de clorofila$_a$ de espécies de cnidários que ocorrem no Atol das Rocas quando submetidos a condições de elevação de temperatura e níveis de pCO_2
- Investigar a susceptibilidade do Atol das Rocas mediante às mudanças biogeoquímicas dos oceanos.

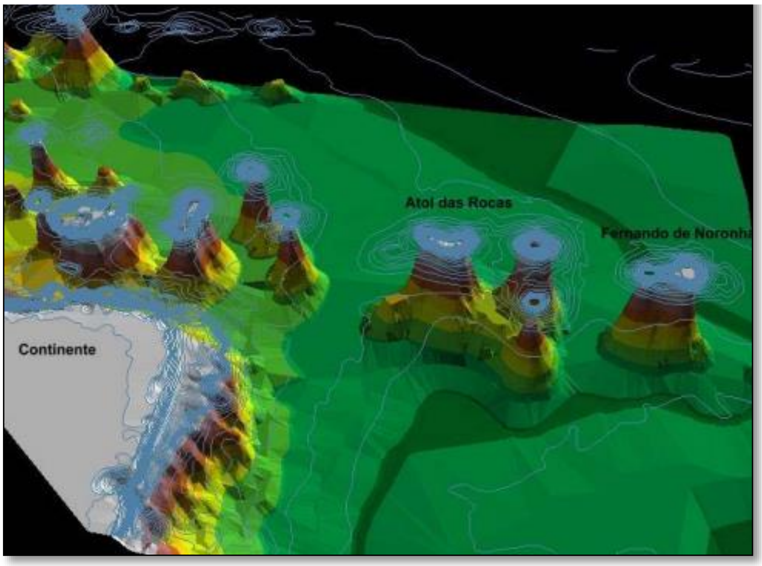
4. HIPÓTESE

O aumento das emissões de dióxido de carbono influencia na saúde ambiental do Atol das Rocas.

5. ÁREA DE ESTUDO

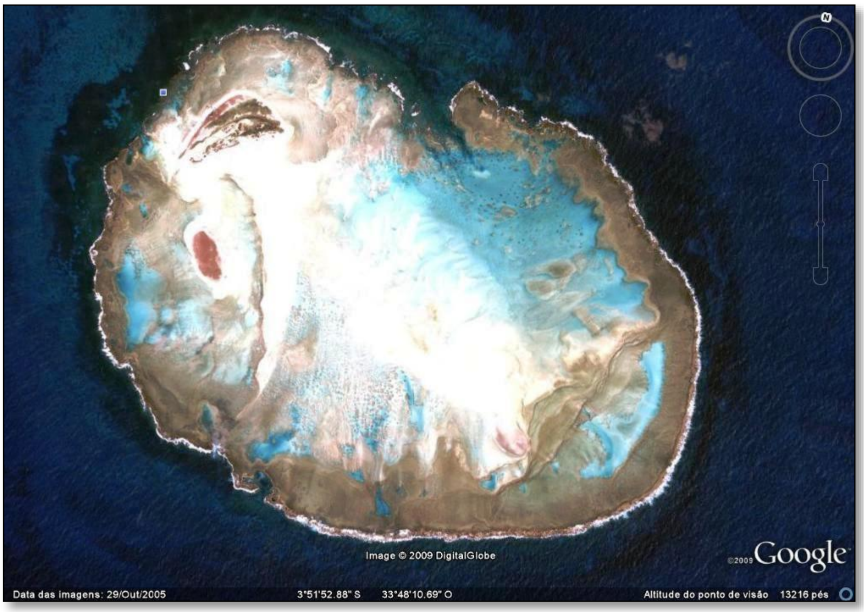
A Reserva Biológica do Atol das Rocas situa-se em um monte submarino pertencente à Cadeia de Montanhas Fernando de Noronha, que é de origem vulcânica e caracteriza-se por um conjunto de altos montes submarinos que se elevam acima do sopé continental, entre 2° S e 4° 30’ S, e estende-se da base do talude continental até a altura de 31° O (Fig. 2). O monte submarino do extremo leste emerge acima do nível do mar e forma o arquipélago de Fernando de Noronha. Os outros montes, alinhados na direção L – O até a costa brasileira (Ceará), ascendem até profundidades inferiores a 250 metros, sendo que alguns quase alcançam a superfície, como é o caso do Atol das Rocas (DAMUTH; PALMA, 1979).

Figura 2 - Cadeia de Montes Submarinos da Zona de fratura Fernando de Noronha. Fonte: Centro de Sensoriamento Remoto do IBAMA - MMA-ICMBio, 2007



O Atol das Rocas está situado em águas jurisdicionais brasileiras, a 144 milhas náuticas (267 km) a Leste-Nordeste da cidade de Natal, Estado do Rio Grande do Norte, e a 80 milhas náuticas (148 km) a oeste do Arquipélago de Fernando de Noronha, Estado de Pernambuco, na área definida pelas coordenadas 03°45’ e 03°56’ latitude sul e 33 37’ e 33 56’ longitude oeste. (Fig. 3).

Figura 3 - Imagem do Atol das Rocas. Fonte: Google Earth. SIO-NOAA, U.S. Navy, NGA, GEBCO Data: 29/10/2005. 3°51’52.88”S – 33°48’10.69”O.



O Atol das Rocas é a primeira unidade de conservação marinha brasileira da categoria Reserva Biológica (proteção integral), que se abrange o perímetro do atol até a isóbata de

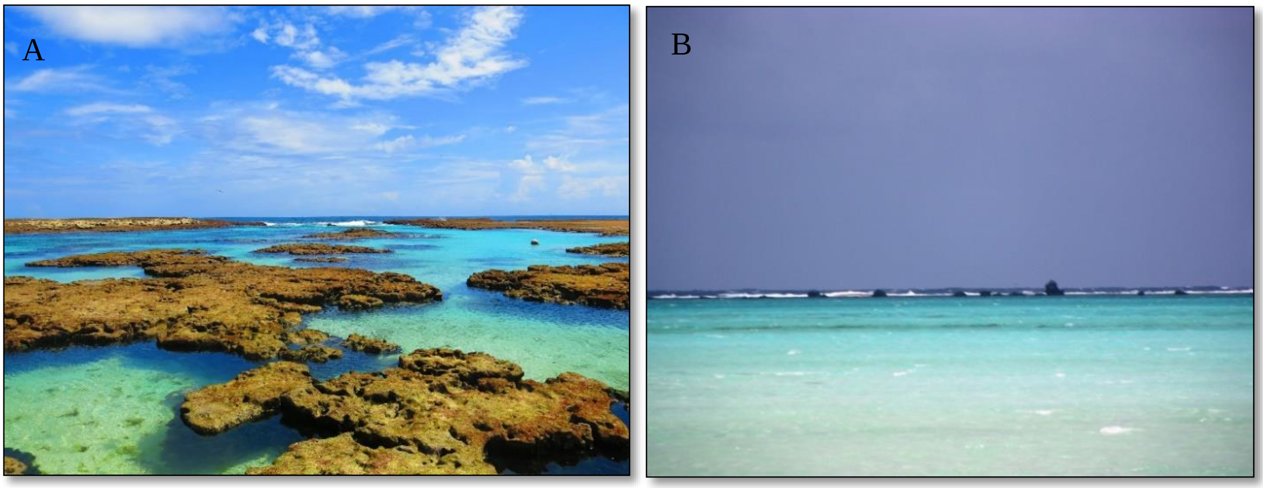
1000m. O Atol cresce sobre um monte submarino e sua extensão é de aproximadamente 7.200ha onde se encontram duas pequenas ilhas de origem biogênica: a ilha do Farol e a ilha do Cemitério (Fig. 4a) (KIKUCHI, 1994). No meio da ilha do Farol existe a baía da lama (Fig. 4 b)

Figura 4 - Ilhas biogênicas do Atol das Rocas (A). Detalhe da Baía da lama na ilha do Farol (B) Fotos cedidas por Maurizélia Brito, para fins educacionais.

O Atol fica praticamente exposto na maré baixa, apresentando suas diversas feições, especialmente o anel recifal com suas piscinas de águas extremamente límpidas, onde se encontram desde espécies de peixes ornamentais a tubarões, além de crustáceos, moluscos, corais, equinodermas, tartarugas, dentre outros (Fig. 5a). Já nos períodos de maré alta, todo o platô recifal é encoberto pelas águas, sendo avistado praticamente só o perímetro do atol (margem recifal, evidenciada por rochas que rolaram para cima do platô e que dão origem ao nome do atol, Fig. 5b) e as duas ilhas existentes.

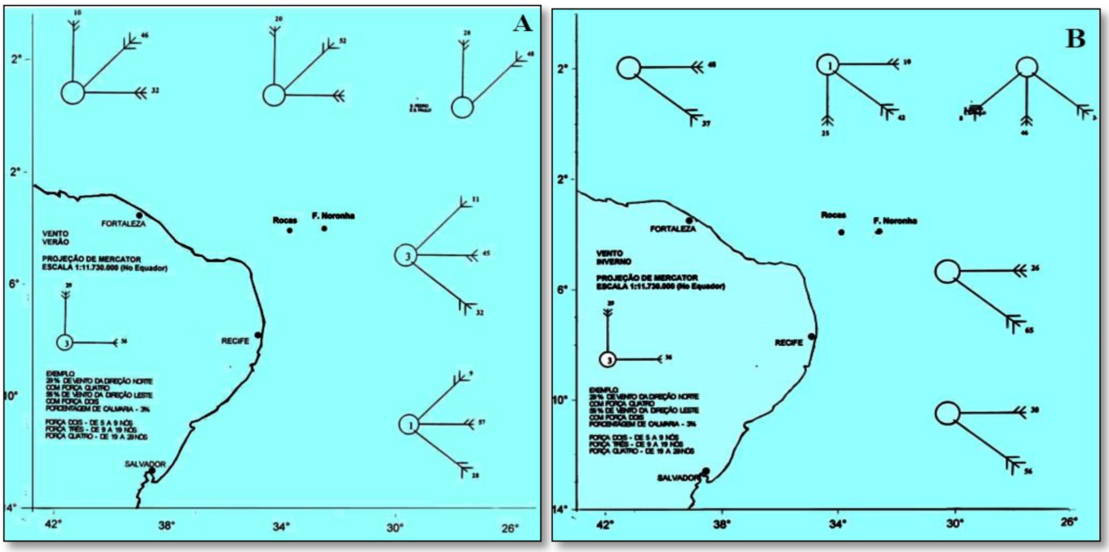
A REBIO do Atol das Rocas encontra-se na zona dos ventos alísios, o que justifica a constância dos ventos no quadrante SE, podendo oscilar ente L e S independentemente da época do ano. Segundo os dados da DHN, a predominância é dos ventos L, acima de 40%, seguidos pelos ventos de SE, com velocidades entre 4 a 6 nós. Nos meses de junho, novembro e dezembro, os ventos SE predominam. Estas informações são confirmadas por Silva e Alvarenga (1995) para a costa Nordeste brasileira (Fig. 6a, 6b). De acordo com KIKUCHI (1999), os dados de direção dos ventos indicam que os ventos dominantes de ESE sopram o ano todo, com uma frequência de 45% dos dias avaliados.

Figura 5 - A- Imagem do Platô Recifal, evidenciando as piscinas naturais durante a baixa-mar B- Perímetro do atol durante preamar sendo avistadas apenas as rochas que deram o nome ao atol, sendo a Pedra do Guarapirá, o ponto que não fica encoberto durante as marés altas de sizígia. Fotos: Bárbara Pinheiro. Setembro 2011.



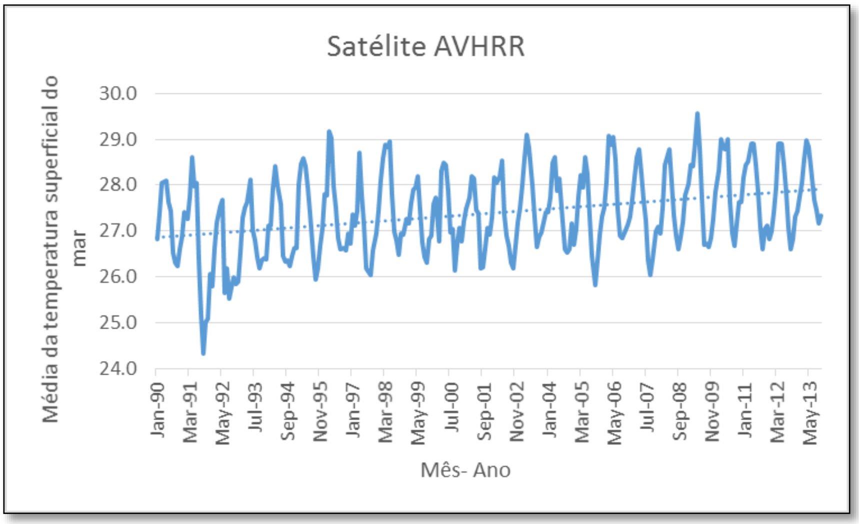
Entre junho e agosto (inverno), ventos de SE ocorrem em 35% dos dias e a frequência de ventos L é de 15% no mesmo período. Entre dezembro e abril (verão), ventos SE e L ocorrem em cerca de 20% dos dias com dados disponíveis. Ventos com velocidade variando de 6 a 10m/s dominam ao longo de todo o ano, mas, durante o inverno, velocidades entre 11 e 15m/s são comuns. Velocidades superiores a 20m/s foram registradas com mais frequência durante o verão.

Figura 6-Distribuição dos Ventos no Verão (a) e no Inverno (b). Fonte: Adaptado de SILVA e ALVARENGA, 1995.



A média da TSM na REBIO Atol das Rocas é 27,40±0,9°C com a mínima de 24,33 e a máxima de 29,56°C obtidas por dados do satélite NOAA/NASA Pathfinder *Advanced Very High Resolution Radiometer* (AVHRR) Version 5.2 entre 1990 e 2013 (Fig. 7).

Figura7- Média da temperatura superficial do mar na REBIO Atol das Rocas. Fonte: Satélite AVHRR entre 1990 e 2013, com linha de tendência



Na REBIO Atol das Rocas não existe estação meteorológica, e os dados de chuva apresentados aqui (Fig. 8) foram coletados na estação de Fernando de Noronha para os anos de 2012, 2013 e 2014 e publicados no site da Agência Pernambucana de Águas e Clima (APAC, 2016). Existem dois períodos bem definidos, um de agosto a janeiro, caracterizando o período chuvoso e 191±115mm para os anos 2012, 2013 e 2014 respectivamente. No período seco essas médias foram 19.6±25.3, 10.6±10.8 e 20.4±25.1mm.

As ondas que ocorrem no atol se concentram na porção SE (Barlavento), entretanto a refração de ondas no embasamento do atol pode gerar grandes arrebentações de ondas na porção O e SO (Sotavento) de Rocas (GHERARDI; BOSENCE, 2001). Para HOGBEN e LUMB (1967), 80% das ondas observadas na região de Rocas provêm de L e 15% de NE. São ondas com período curto, de 4 a 7s, e altura entre 1 e 2 m. MELO e ALVES (1993), contudo, ressaltam que entre dezembro e março esse comportamento pode mudar, com a ocorrência de ondas com período de 15s e 18s e alturas de até 2 m, provenientes do hemisfério norte (Fig. 9). O Atol das Rocas não possui tábua de maré própria, sendo adotada a tábua de maré de Fernando de Noronha, região mais próxima com os valores satisfatórios para a região. As marés do atol são classificas como mesomarés de regime semi-diurno, com amplitude máxima na sizígia de 2,7m (KIKUCHI, 1994).

Figura 8- Dados pluviométricos da estação meteorológica de Fernando de Noronha, evidenciando período seco e chuvoso para região. Fonte: APAC, 2016.

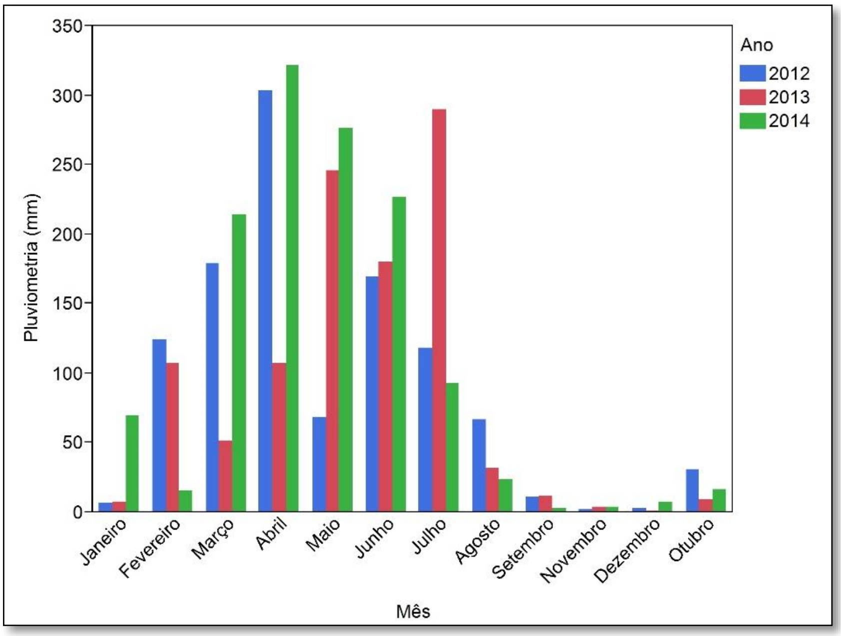
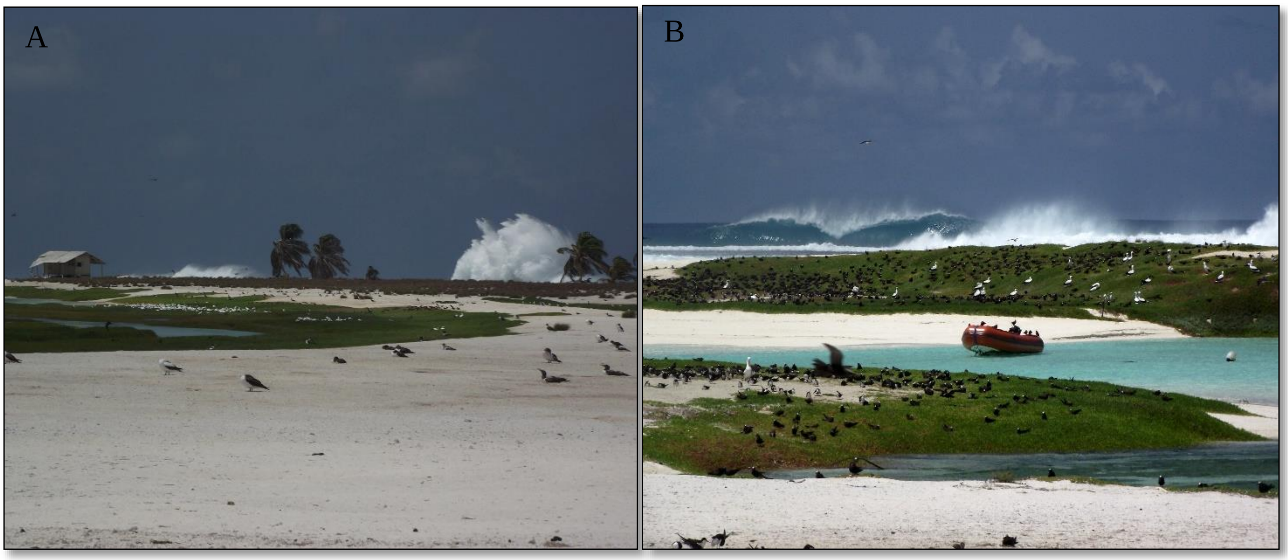


Figura 9 - Fotos de ondas na porção barlavento do Atol das Rocas, tiradas durante evento de Swell – Dezembro 2012 (a) e Dezembro 2013 (b) Fotos: Barbara Pinheiro



De acordo com PEREIRA et al. (2013) o sedimento no atol é 100% biogênico com 97,6% de fração arenosa (variando de areia fina a muito grossa) e 2,4% de fração grânulo. Os principais componentes bióticos deste sedimento descritos por PEREIRA et al. (2008) foram: algas calcárias, tubos de polychaetas, foraminíferos, gastrópodes, fragmentos de conchas de bivalves, fragmentos de crustáceos, esponjas, corais, espículas de esponjas e espinhos de equinodermos (Fig. 10)

Figura 10 - Sedimento do Atol. Foto: Bárbara Pinheiro, 2012.

6. CAPITULO I- ORGANISMOS CONSTRUTORES DO ATOL DAS ROCAS

Manuscrito 1- Population dynamics of *Siderastrea stellata* Verrill, 1868 from Rocas Atoll, RN: implications for predicted climate change impacts at the only South Atlantic atoll: aceito para publicação nos **Anais da Academia Brasileira de Ciências**;

Manuscrito 2- Interactions between Hydrology and Benthic Coverage at Rocas Atoll: aceito para publicação na **Tropical Oceanography**

Figura 11- Pedra do Guarapirá, Atol das Rocas. Foto: Bárbara Pinheiro.

6.1. Population dynamics of *Siderastrea stellata* Verrill, 1868 from Rocas Atoll, RN: implications for predicted climate change impacts at the only South Atlantic atoll.

6.1.1. Abstract

Coral reefs are one of the most vulnerable ecosystems to ocean warming and acidification, and it is important to determine the role of reef building species in this environment in order to obtain insight into their susceptibility to expected impacts of global changes. Aspects of the life history of a coral population, such as reproduction, growth and size-frequency can contribute to the production of models that are used to estimate impacts and potential recovery of the population, acting as a powerful tool for the conservation and management of those ecosystems. Here, we present the first evidence of *Siderastrea stellata* planulation, its early growth, population size-frequency distribution and growth rate of adult colonies in Rocas Atoll. Our results, together with the environmental protection policies and the absence of anthropogenic pressures, suggest that *S. stellata* population may have a good potential in the maintenance and recovery in the atoll. However, our results also indicate an impact on corals' recruitment, probably as a consequence of the positive temperature anomaly that occurred in 2010. Thus, despite the pristine status of Rocas Atoll, the preservation of its coral community seems to be threatened by current global changes, such as more frequent thermal stress events.

6.1.2. Resumo

Os recifes de coral são um dos ecossistemas mais vulneráveis ao aquecimento e acidificação dos oceanos, e é importante compreender o papel das espécies construtores de recifes neste ambiente, a fim de se obter uma visão sobre a sua susceptibilidade aos impactos das mudanças globais esperados. Aspectos da história de vida de uma população de corais, tais como reprodução, crescimento e frequência de tamanho podem contribuir para a produção de modelos que são usados para estimar os impactos e o potencial de recuperação da população, agindo como uma poderosa ferramenta para a conservação e gestão desses ecossistemas. Aqui, nós apresentamos a primeira evidência de planulação de *Siderastrea stellata*, seu crescimento inicial, distribuição de tamanho de frequência da população e taxa de crescimento de colônias adultas no Atol das Rocas. Nossos resultados, em conjunto com as políticas de proteção ambiental e a ausência de pressões antrópicas, sugerem que a população de *S. stellata* pode ter um bom potencial de manutenção e recuperação no atol. No entanto, nossos resultados também indicam um impacto sobre o recrutamento dos corais, provavelmente em decorrência da

anomalia de temperatura positiva que ocorreu em 2010. Assim, apesar do estado de conservação do Atol das Rocas, a preservação de sua comunidade coralínea parece estar ameaçada pelas atuais mudanças globais, como eventos de estresse térmico mais frequentes.

6.1.3. INTRODUCTION

Increasing carbon dioxide (CO_2) concentration in the atmosphere has been changing physical and chemical aspects of the planet, causing global warming, sea level rise, more frequent and intense storms, and ocean acidification (SABINE et al. 2004; ANTHONY et al. 2011; ZEEBE, 2012). Coral reefs are directly impacted by those changes; a rise in sea surface temperature causes severe bleaching (HOEGH-GULDBERG, 2011), ocean acidification suppresses growth and calcification (ALBRIGHT et al., 2016) and sea level rise causes submergence of coral reefs and atoll islands (KAYANNE, 2016). Consequently, they are the one of the most threatened ecosystems (KLEYPAS et al. 1999 a, b; KROEKER et al., 2013) and it is important to estimate their recovery potential from natural physiological disturbances and from anthropogenic perturbation. According to EDMUNDS (2007) aspects of the life history of a coral population, such as reproduction, or growth and size- frequency are crucial to understand their role in the marine ecosystem and to obtain insight into their susceptibility to changes in the external physical and chemical environment. This information can be used in coral models and function as excellent tools to study demography, physiology/growth, and ecology, helping the conservation and management of this important ecosystem (PINIAK et al., 2006).

In the South Atlantic Ocean there is only one atoll, Rocas Atoll, the first Brazilian marine protected area, created in 1979 and considered a pristine reef ecosystem (LONGO et al., 2015). Due to its isolation and conservational status, Rocas Atoll can act as an excellent opportunity to study the mechanism and impacts of global changes on reef systems. However, there is a gap of knowledge about corals population dynamics in this area. Its reef structure is constructed mainly by encrusting coralline red algae (70%) with the secondary framework builders composed by vermetid gastropods, encrusting foraminifera, polychaetes worm tubes, and corals (less than 10%) (KIKUCHI; LEÃO, 1997; GHERARDI; BOSENCE, 2001). The dominant reef building coral species is *Siderastrea stellata* Verrill, 1868 occurring in all tidal pools of the atoll (ECHEVERRIA et al., 1997). New information about its early growth, size frequency distribution and growth rate of adult colonies will contribute to model this population and predict effects of possible impacts such as ocean acidification or global warming.

S. stellata belongs to the genus *Siderastrea* de Blainville, 1830 and to the family Siderastreidae Vaughan and Wells, 1943. According to WELLS (1956), this genus has existed since the Cretaceous and is represented by five extant species which has spread mainly in the Atlantic ocean, although two of them (*Siderastrea savignyana* and *Siderastrea glynni*) can be found in the Pacific and Indian Oceans (BUDD; GUZMAN, 1994). *S. stellata* together with the species from the Caribbean Sea (*Siderastrea siderea* and *Siderastrea radians*) compose the "Atlantic *Siderastrea* complex" (VERON, 1995). The taxonomy of this group has been debated and previously *S. stellata* was considered the only siderastreid in Brazil (LABOREL 1974, MAIDA; FERREIRA, 1997). Recently, the presence of *S. radians* and *S. siderea* was confirmed on the Brazilian coast (NEVES et al., 2008, 2010, NUNES et al., 2011), however, neither of those investigations included specimens collected at Rocas Atoll and up to now, only the occurrence of *S. stellata* is confirmed in this atoll.

S. stellata is a colonial, zooxanthellated and massive coral species with high resistance to environmental stress, such as sedimentation, wave action, temperature and salinity variations (LEÃO et al. 2003). Until recently, it was accepted that its spatial distribution in the South Atlantic was from Parcel do Manuel Luiz, Maranhão (00°53'S, 044°16'W) to Cabo Frio, Rio de Janeiro – (23°S, 042°W, Lins-de-Barros and Pires, 2007), but CORDEIRO et al. (2015) shows that this species can also be found in reef communities adjacent to the Amazon River Month in the coast of the Para state (00°21'14"S 46°53'56"W). According to LINS DE BARROS et al. (2003) *S. stellata* is a gonochoric brooder species, with a high female to male sex ratio and an annual reproductive cycle. Planulation occurs preferably during the austral summer, concomitant with the seasonal sea surface temperature (SST) rise. *S. stellata* planula larvae were also observed in laboratory experiments to be released in January and April. The larvae contain zooxanthellae, with varied size from 500 µm to 1.4 mm in diameter and they start settlement between 72 hours to 15 days in close contact with parental polyps (NEVES; SILVEIRA, 2003).

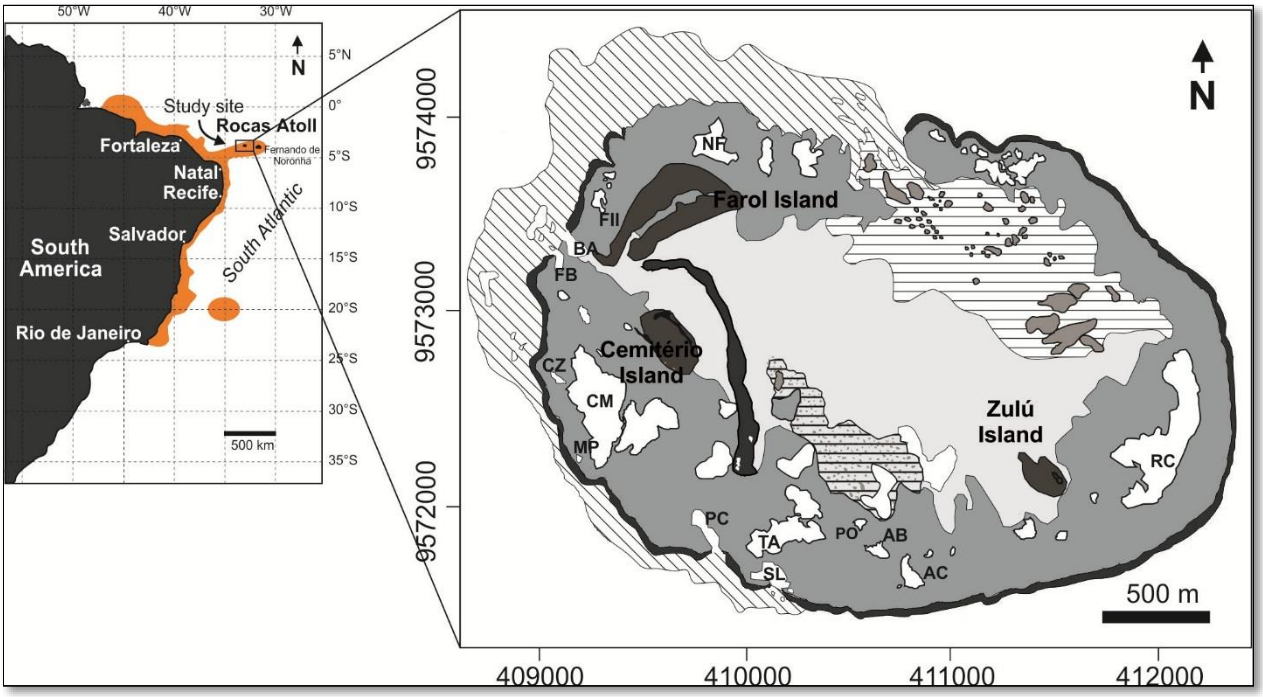
LINS DE BARROS and PIRES (2006 a, b, 2007) studied some aspects of the life history of this species such as reproduction, growth and size frequency for other sites on the coast of Brazil. Nevertheless, at Rocas Atoll, despite the existence of information on *S. stellata* abundance (ECHEVERRIA et al., 1997; FONSECA et al., 2012), percent coverage (LONGO et al., 2015), and its importance as a natural archive for paleoclimate studies (MAŸAL et al., 2009; OLIVEIRA, 2012; PEREIRA et al., 2016), there is no record of other aspects of its population dynamics. Part of the reason of the absence of population models for Brazilian coral species are due to this lack of information to produce them. In this study we present the first evidence of *S. stellata* planulation, its early growth, size frequency distribution and growth rate of adult colonies. In addition, we discuss the implications of our results under a scenario of predicted impacts due to warming and acidification for the conservation of *S. stellata* population at Rocas Atoll.

6.1.4. MATERIALS AND METHODS

Study site

The Rocas Atoll is situated 266 km northeast of the coastal city of Natal, northeastern Brazil (Fig. 12). It is one of the smallest atolls in the world, with an axis of 3.35 km by 2.49 km, a reef area of 6.56 km^2 and a perimeter of 11 km (PEREIRA et al., 2010) and is the only atoll located in the western part of the South Atlantic (3°51´S, 33°49´W).

Figure 12- Location of the Rocas Atoll and the geographical distribution of the species *S. stellata* in the South America (orange area). The geomorphological map of the Rocas Atoll shows the intertidal reef- flat pools where colonies of *S. stellata* were collected and investigated - Abrolhos (AB), Âncoras (AC), Cemitério (CM), Cemitériozinho (CZ), Falsa Barreta (FB), Mapas (MP), Porites (PO), Podes Crer (PC), Tartarugas (TA) and Salão (SL)



Rocas is dominated by the South Equatorial Current (SEC), with consistent westerly flow (GOES, 2005) and a mean velocity of 30 cm per second in the 4°S parallel (RICHARDSON; WALSH, 1986). The tidal regime is semi-diurnal and meso-tidal (GHERARDI; BOSENCE, 2001). No tidal range records exist in Rocas Atoll. In Fernando de Noronha's harbor (144 km east from Rocas) the maximum tidal range is 2.8 m (DHN, 2014). The equatorial location of the Rocas Atoll leads to minimal seasonal SST variability, with an annual range of 3°C for monthly mean temperatures (FERREIRA et al., 2012). Salinity in the surrounding sea waters varies from 36 to 37 (GHERARDI; BOSENCE, 1999). There is a wet season from approximately March through July and a dry season from approximately August through February (APAC, 2016).

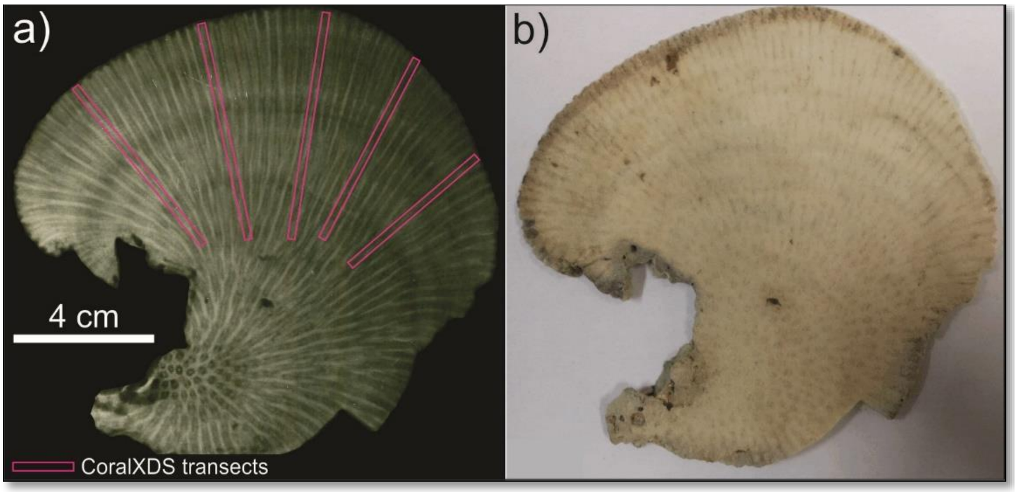
Determination of early growth of *S. stellata* primary polyps

Five colonies of *S. stellata* (diameters between 10 and 20 cm) were collected during the last week of December 2012 at Cemitério pool and kept in 30 L seawater tanks with circulation and air pumps, covered with preconditioned ceramic tiles. The tanks were kept at the scientific base at Rocas Atoll in a shade dock that allows natural luminosity, but protects from direct solar incidence. Seawater in the tanks was renewed daily and temperature and salinity subsequently determined. During this process, the presence of planula larvae in the water column and the settlement of the primary polyps on the tiles was checked. From January until March 2013 the growth of the recruit was evaluated. The ceramic tiles were analyzed using a stereomicroscope and photographed. The size of the recruits was determined by measuring the maximum diameter at the base of the living tissue and the total area of the primary polyp using the Image J software. Polyp mortality was identified by the absence of living tissue on the skeleton, or when recruits were covered by epibenthic algae. At the end of the expedition in March 2013, the ceramic tiles and coral colonies were fixed back on the pool.

Growth rate of adult colonies

The growth rate pattern for *S. stellata* was analyzed in seven colonies of this species collected during June of 2012 from the following tidal pools: Abrolhos (1), Cemitério (1), Cemitériozinho (1), Falsa Barreta (1), Mapas (1), and Tartarugas (2). Colonies were cut into halves, and one half was cut into 5-mm thick slices parallel to the vertical growth axis of the whole colony. After cutting, these slices were air-dried and X-ray images were taken and digitalized for analysis of the extension rate by using the CoralXDS 3.0 Software (HELMLE et al., 2002). Afterwards, several transects were analyzed in the digital image of the coral X-radiography in order to totally cover the lateral extension of the coral slab (Fig. 13).

Figure 13 - a) Radiography of a 5 mm-slabs of one *S. stellata* colony collected at the Rocas Atoll showing the transect locations along the growth axis and through the lateral extension of the colony slab where CoralXDS analysis were carried out; (b) image of the 5 mm-slab of the same colony.



<u>*S. stellata* population size structure</u>

During January and May 2014, the *S. Stellata* population data were collected by scuba divers along eight belt transects in each tidal pool. All *S. stellata* colonies within a 1 m belt transect, along 20-m transect, were counted and their size were categorized in four different classes according their maximum diameter size: < 2 cm, 2.1 – 4.0 cm, 4.1 – 10 cm and above 10 cm. Colonies in the transect edge were only considered in the count if they were more than 50% inside the delimited belt transect area.

6.1.5. RESULTS

<u>Early growth of S. stellata primary polyps</u>

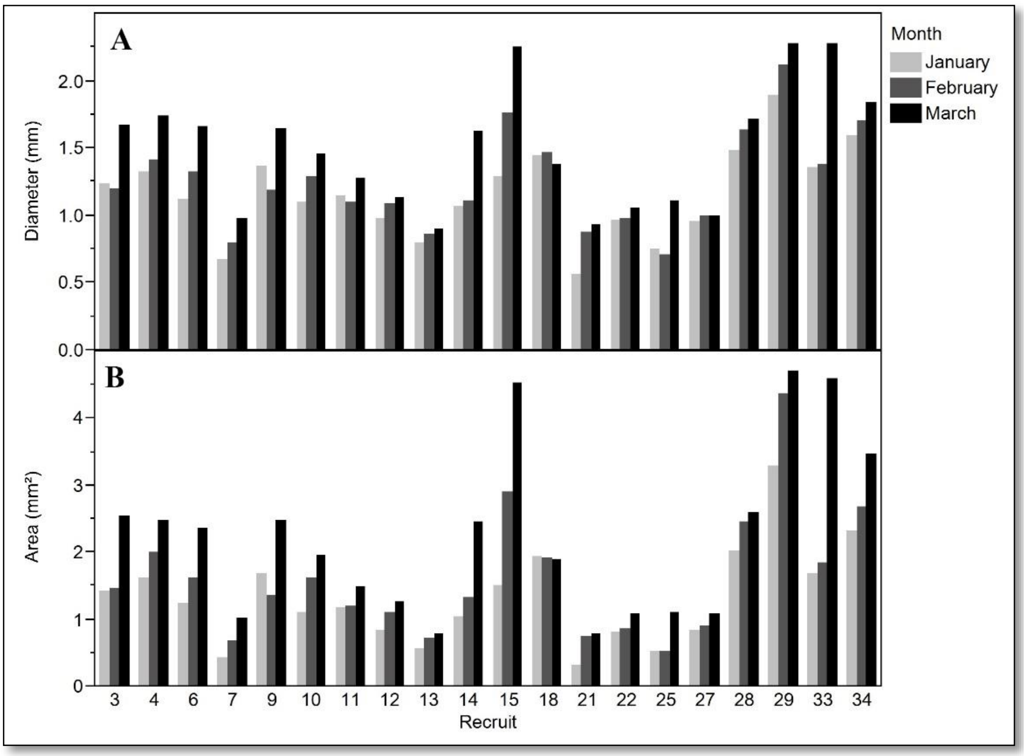
During the period of the experiment (late December 2012 to early March 2013), the mean (± standard deviation) temperature and salinity in the tanks with the colonies and ceramic tiles were 29.01±2.03 °C and 35.24±0.8 ppt, respectively. Five to seven days after the sampling period of the colonies, planula larvae was observed searching for suitable places in the ceramic tiles to settle (Fig 14b, c). In total, 34 *S. stellata* recruits were observed. Five of them died during the study, corresponding to a mortality rate of 14.70%. Fusion of three primary polyps was observed (Fig 14f), therefore those records were not used in the calculation of the growth rate due to the difficulty in identifying the base of the recruits. In addition, six other recruits were excluded from the evaluation due to the fact that their tentacles were always extended and the base of the polyps was partially covered by algae. From the 34 recruits observed, only 20 had their growth evaluated during the entire experimental period. In January (about 17 days old), the mean diameter of the recruits (± SD) was 1.15±0.33 mm, ranging from 0.56 to 1.90 mm. In February (about one month), the recruits had a mean diameter of 1.25± 0.36, ranging from 0.71 to 2.12 mm. In March (aging around 45 to 50 days old), the recruits had mean values of diameters of 1.49±0.45 mm, ranging from 0.9 to 2.28 mm (Fig 15.a)

The mean area of the recruits (± SD) was 1.32±0.73 mm² in January, ranging from 0.32 to 3.28 mm². In

February, the recruits presented a mean area of 1.61± 0.94 mm², with a minimum of 0.51 and maximum of 4.38 mm². Average area of the recruits measured in March was 2.23±1.26 mm² ranging from 0.78 to 4.7 mm² (Fig 15.b).

Figure 64 - Parental colonies (a), planula larvae (b, c) and recruits nearly 50 days old (d, e, f) of *S. stellata* from Rocas Atoll.

Figure 75- Size of the *S. stellata* recruits according to a- diameter and b- area, measured between January and March 2013 at Rocas Atoll.



Growth rate of adult colonies

Table I presents the annual extension rate of the seven colonies of *S. stellata* studied, obtained from the analysis of their radiographies using CoralXDS. Mean coral extension rates varied from 6.0 to 8.1 mm/year with an average of 6.8 ± 0.7 mm/year (±SD, n=35).

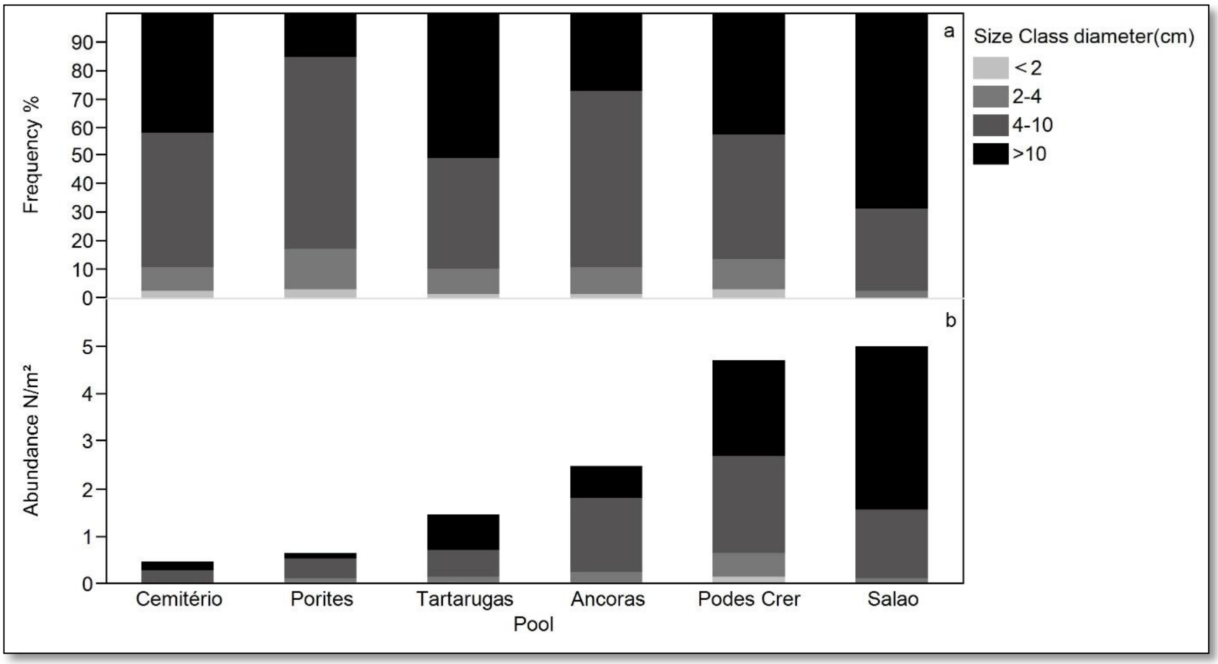
Table 1. Extension rate results for the seven analyzed colonies of *S. stellata* colleted at the Rocas Atoll. Extension rates are expressed by millimeter per year (mm/year).

Location/Transect nº	**T1**	**T2**	**T3**	**T4**	**T5**	**Mean (mm/year)**
Abrolhos	11.7	7.5	6.8	7.2	7.2	8.1±2.0
Cemitério	5.6	6.5	6.9	8.1	6.5	6.7±0.9
Cemitériozinho	7.4	6.0	5.1	6.1	5.4	6.0±0.8
Falsa Barreta	8.5	6.3	5.9	5.2	6.7	6.5±1.2
Mapas	6.9	5.5	7.0	7.9	7.5	7.0±0.9
Tartarugas 1	6.0	7.3	6.3	6.1	6.3	6.4±0.5
Tartarugas 2	7.7	11.0	6.3	5.5	5.7	7.2±2.3
Mean growth rate						**6.8±0.7**

Population Size structure

The pools connected to the open ocean, Salão and Podes Crer, presented the highest *S. stellata* abundance, with 4.995 and 4.705 colonies m^{-2}, followed by Âncoras and Tartarugas with 2.495 and 1.44 colonies m^{-2}, respectively. The lowest abundance was recorded at Porites and Cemitério, with 0.645 and 0.465 colonies m^{-2}, respectively (Fig 16. a). The frequency of the smallest size classes (recruits: diameters up to 2 cm and young colonies: 2.1 to 4 cm) were the lowest, representing less than 20% in all pools. Podes Crer was the pool were we observed more recruits: 26 in an eight belt transect (20 m² each) survey. The most frequent size class consisted of diameters between 4.01 and 10 cm. This was the dominant size frequency at Porites and Âncoras with 67.4 and 62.3%, respectively, at Cemitério and Podes Crer the size class 4.01-10cm was as frequent as the largest size class (>10cm). Half of the colonies observed at Tartarugas had a diameter higher than 10 cm. This class size was the dominant one at the Salão pool, with 68.9% of the colonies belonging to this size class (> 10 cm) (Fig. 15. b)

Figure 86 - *S. stellata* colony size- frequency distribution at the pools of Rocas Atoll (a) and abundance (m^2) (b).



6.1.6. DISCUSSION

The results presented here begin to fill a gap in the knowledge about the dynamics of the dominant coral species at Rocas Atoll, and will contribute to the construction of models that would provide assistance for conservation and management of this population, and insight into their vulnerability to global change impacts. This study showed for the first time a *Siderastrea stellata* reproduction event at Rocas Atoll, with planula larvae being observed during the first week of January. According to LINS DE BARROS et al. (2003), it was observed latitudinal differences in the *S. stellata* period of planulation, e.g. December- early January in Buzios, and February to mid-March in Abrolhos-BA, and this difference was attributed to a punctual upwelling phenomenon that occurs in Buzios-RJ, which lowers the SST by many degrees. Planulation as consequence of the stress and handling during collection was detected by NEVES and SILVEIRA (2003), where they inferred immaturity due to a high mortality rate of extruded larvae within 24–48 h of a free-swimming existence.

Our colonies were handled carefully and kept in tanks, within less than 1 km of distance from the sampling pool, with natural light and daily water change. During our experiment, larval swimming behavior or mortality was not observed. Out of all the recruits obtained in the experiment, only 14.70% died by the end of the third month. In the LINS DE BARROS and PIRES (2007) study on the reproduction of *S. stellata* in Fernando de Noronha, they observed in colonies collected in late January that even though the planulation season had already started, oocytes were present in all of the examined polyps. They also observed that there was high polyp fecundity *versus* low number of larvae (37%), which suggested that most of the oocytes produced had not been fertilized. Therefore, although we have had observed larvae release, metamorphose and settlement of the *S. stellata* at Rocas Atoll, further studies are necessary to clarify the reproductive peak period of this specie and fertilization rate of its population.

Juvenile life stages play critical roles in the population dynamics of virtually all organisms, and therefore precise estimates of juvenile growth and survival are important for accurate demographic analyses (EDMUNDS, 2007). In our study the mean diameter of the recruits as measured in March (aging around 45 to 50 days old) was 1.49±0.45 mm, ranging from 0.9 to 2.28 mm. According to PINHEIRO (2006), which monitored the growth of *S. stellata* recruits at the no take zone from the Coral's Coast Marine Protected Area (Tamandaré, PE) during one year, recruits with about the same age (50 days old) had an average diameter of 2.11± 0.69 mm (n= 16), and by the end of the monitoring year they measured 7.19± 4.5 mm, with a maximum observed diameter of 12.7 mm. Those recruits were kept on the natural reef, providing more stability and nutrients for the corals to grow. Although caution was taken to maintain good conditions in the tanks (water flow, oxygenation, and daily seawater change), it is likely that our results could reflect this experimental condition. CASTRO (2008) observed *S. stellata* recruits with 1.5 years and diameters of 2.9 and 3.35 mm and juvenile corals with 7.29 mm (2.16 years) and 6.41mm (2.66 years) in a study in the south of Bahia state (Eastern Brazil), but it is not clear if those results represent recruits kept in an aquarium setup or on a natural reef. Either way, those diameter sizes and growth are very small compared to a rough estimation done with linear regression of the results observed during the three months of this study, which indicate a diameter range of 4.46 to 7.78 mm for one-year age recruits.

Some variations in growth rates of coral recruit have been attributed to different intensities of competition caused by the growth of algae and other organisms (HARRISON; WALLACE, 1990; VERMEIJ, 2006), differences at the family taxonomic level, related to the spawning modes (BABCOCK, 1985), and changes in the microhabitats conditions such as luminosity differences (ANTHONY; HOEGH-GULDBERG, 2003). Even though it is common to observe variations in the growth rates, it is important to have precise estimates. Discrepancies have important implications, because it suggests that the recruitment dynamics of coral populations may function over time scales longer than those usually considered (EDMUNDS, 2007). This study is the first to show the initial growth of S. *stellata* recruits in Rocas Atoll, although longer studies are needed to draw conclusions about the earlier growth rates of this species.

Concerning the annual extension rate for adult colonies, a growth rate of 6.8 ±0.7 mm. yr^{-1} (min. 5.1 and max.11.7 mm.y^{-1}) was observed. This is in accordance with the study by OLIVEIRA (2012) who applyied a combined technic of radiometric U/Th dating and density banding counting to find a growth rate of 6.01±1.08 mm.yr^{-1}, ranging from 3.76 to 8.53 mm. yr^{-1} for *S. stellata* from Rocas Atoll.

In reefs off the coast of Bahia state, linear extension rates of 2.73 ±035 mm yr^{-1} were found by LINS DE BARROS and PIRES (2006b), which measured in colonies stained with alizarin red S, following the method of LAMBERT (1978). Additionally, REIS and LEÃO (2000) reported a linear growth rate of 2.38±0.20 mm yr^{-1} by counting the density banding revealed in X-radiographies. Although the methodology used by LINS DE BARROS and PIRES (2006b) could cause handling stress during coral staining, and thus lead to a lower growth rate, the results presented by REIS and LEÃO (2000) pointed to the same value, indicating that the observed growth rate might be site dependent.

Differences in the mean annual linear extension were also observed for *Siderastrea siderea*, in Panama. There, GUZMAN and TUDHOPE (1998) observed a 7.6 ± 0.7 mm mean annual linear extension during the period from April 1991 to March 1992. In a previous study, GUZMAN and CORTES (1989), reported a decadal mean annual linear extension of 5.2 mm (ranging from 2 to 6.3 mm; 1976 to 1986), about 2.4 mm lower than the rate recorded in the 90's. Variations of the annual extension rate were also observed for *S. siderea* in the Caribbean Sea, from 3.5 to 4.3 mm. yr^{-1} in Puerto Rico (TORRES; MORELOCK, 2002).

The lower linear growth rates observed for *S. stellata* at the reefs from Bahia coast compared to Rocas Atoll (this study and OLIVEIRA, 2012), may be due to the differences in the environmental conditions from the two localities. Although, there is an agreement in the scientific community that coral extension rates are species specific (MUSLIC et al., 2013), studies measuring linear extension rates within individual species indicated that a variety of factors such as season, rainfall, the El Niño Southern Oscillation (ENSO) cycle, light levels and location within the reef, correlate with (and may influence) coral linear extension rates (ANTHONY; HOEGH-GULDBERG, 2003; DE'ATH et al., 2009). There are important differences between Rocas Atoll and reefs from the south of Bahia, especially regarding aspects such as sedimentation rates. Rocas is an oceanic island, isolated from the influence of river discharges and it is probably the most effective marine reserve and the closest to a pristine reef in the Tropical Southwestern Atlantic (LONGO et al., 2015). Reefs from the Coast of Bahia are experiencing increasing degradation due to a combination of large-scale natural threats (e.g. sea level oscillations and ENSO events). Local scale anthropogenic stressors, such as accelerated coastal development, reef eutrophication, marine pollution, tourism pressure, over-exploitation of reef resources, overfishing and destructive fisheries and, more recently, the introduction of non-indigenous invasive species are also related to this degradation (LEÃO; KIKUCHI, 2011). There is a record of the impact of ENSO events in the coral community at the atoll (FERREIRA et al., 2012) but overall, the differences in the linear extension rates for *S. stellata* we observed in this study may reflect the higher environmental quality of the reef system in Rocas compared to those from Bahia.

Size-frequency distributions have been used to assess the ecological status of different populations in a variety of ecosystems. In coral reef systems, size reflects many life-history processes such as maturation, fecundity, survival and the response of corals to time-varying influences of the environment, including the intensity and frequency of disturbances and the degree of environmental degradation (ZVULONI et al. 2008).

As a dominant coral specie at Rocas, the abundance of *S. stellata* we found in this study (Fig. 16) is in accordance with the hard coral coverage evaluated by FERREIRA et al. (2012). They reported a higher percentage in the open pools compared to the isolated ones: 50.6 ±6.0 % at Salão; 34.0 ±14.2% at Podes Crer; followed by 22.5 ±7.8% in Tartarugas and the lowest coverage, 5.6 ±6.1% at Cemitério. Besides great abundance, the open pools have a high frequency of larger colonies. In the Salão pool, for instance, 68.87% of the colonies have diameters greater than 10 cm. Coral colony size might be considered important for maturation and fecundity. According to LINS DE BARROS and PIRES (2006a), the number of oocytes produced per polyp in *S. stellata* populations is highly variable, although it was always greater in larger colonies, averaging eight oocytes per polyp, and nonetheless colonies larger than 5 cm in diameter had at least one oocyte. Thereby, the size frequency distribution of *S. stellata* population at Rocas Atoll presented here can be considered to be representative of a mature community, with overall high frequency of colonies with diameters higher than 10 cm (41.2± 18.5%).

Another factor that may contribute to the potential of maintenance and recovery of *S. stellata* population in the atoll is the tidal dynamics that results in strong currents when the atoll is either filling or draining and during high tides (LONGO et al., 2015). *S. stellata* larvae started to settle between 72 hours and 15 days in close contact with parental polyps (NEVES; SILVEIRA, 2003), and even though it is still necessary to elucidate dispersion and larval recruitment in the atoll, it is likely that the larvae produced by the colonies in the open pools can be dispersed around the atoll. This would explain the higher frequency of juvenile colonies in the closed pools, where we observed frequencies of 67.4% at Porites and 62.3% at Âncoras in colonies with 4.1 to 10 cm diameters. FERREIRA et al. (2012) indicate that the occurrence of two sequential positive SST anomalies (2009 and 2010), which triggered up to 50 % coral bleaching in the Rocas Atoll and Fernando de Noronha reefs, reduced post-bleaching coral recovery and intensified the outbreak of diseases, specifically black-band, plague and dark-spot diseases affecting primarily *Siderastrea* spp. at the atoll. Thus, the low frequency of young colonies with diameters up to 2 cm (1.8±1.12%) and from 2.1 to 4 cm (8.9±3.87%) that we found in our study may be a consequence of a reduced recruitment event.

Several authors have investigated negative effects of increasing SST on coral reefs. EDMUNDS (2007) highlights a gradual decline in the growth rates of juvenile corals in St. John, US Virgin Islands and links this decline with rising seawater temperature and depressed aragonite saturation state. The author further suggests that the effects of global climate change may have already reduced the growth of juvenile corals. DE’ATH et al. (2009) show that linear extension rates in corals decrease as a result of SST increase. ANLAUF et al. (2011) points out that in future scenarios of increased temperature and oceanic acidification, coral planulae will be able to disperse and settle successfully, but primary polyp growth may be hampered. According to ALBRIGHT (2011), available information indicates that ocean acidification (enhanced by warming) may negatively affect sperm motility and fertilization success, larval metabolism, larval settlement, and post settlement growth and calcification.

Our results suggest that the population of *S. stellata* at Rocas Atoll has a high potential of maintenance and recovery, especially because the atoll is one of the most effective marine protected areas in the South Atlantic, and an oceanic island. Rocas is practically free of anthropogenic impacts such as declining water quality, over-exploitation of key marine species, destructive fishing and pollution but still, its location and local police cannot protect it from global- scale risks making it highly vulnerable to warming and acidification of the oceans waters.

6.2. Interactions between Hydrology and Benthic Coverage at Rocas Atoll

6.2.1. Abstract

Abiotic parameters and benthic coverage were determined in shallow habitats at Rocas Atoll. It was found daily and seasonal variations on seawater characteristics related to tides, pluviometry, daily solar cycle, and organisms' metabolism. Habitats with high coverage of carbonatic organisms were associated with the alkalinity of seawater, whereas habitats with elevated abundance of turf and macro algae were correlated to dissolved inorganic nutrients. Therefore, it is suggested that the availability of nutrients and carbonates in seawater are important for the organism's distribution in the atoll. Only seven corals settled on the plates during the experiment (*Porites* spp. and *Siderastrea* spp.). In order to better constrain the causes of the low coral recruitment in the atoll and predicted the effects of climate changes and ocean acidification over this important reef ecosystem, it is necessary to assess, in high resolution (i.e. week to monthly), the environmental variables that overlaps a short-term period.

6.2.2. Resumo

Parâmetros abióticos e a cobertura bentônica foram determinados em habitats rasos no Atol das Rocas. Verificou-se variações diárias e sazonais nas características da água do mar relacionadas com marés, pluviometria, ciclo solar diário, e metabolismo dos organismos. Habitats com alta cobertura de organismos carbonáticos foram associados com a alcalinidade da água do mar, enquanto habitats com elevada abundância de tufos de algas e macroalgas foram correlacionados com a concentração de nutrientes inorgânicos dissolvidos. Portanto, sugere-se que a disponibilidade de nutrientes e de carbonatos em água do mar são importantes para a distribuição do organismo no atol. Apenas sete corais assentaram nas placas durante o experimento (*Porites* spp. e *Siderastrea* spp). A fim de melhor identificar as causas do baixo recrutamento de coral do atol e prever os efeitos das mudanças climáticas e acidificação dos oceanos sobre este importante ecossistema recifal, é necessário avaliar, em alta resolução (ou seja, semanal a mensal), as variáveis ambientais que se sobrepõe a um curto período de tempo.

6.2.3. INTRODUCTION

Rocas Atoll is the unique oceanic reef formation at the South Atlantic and offers an ideal system to study natural variations of benthic community assemblages. Its reef framework is well described by KIKUCHI and LEÃO (1997) and GHERARDI and BOSENCE (1999, 2001). One of Roca’s characteristics that distinguishes it from other atolls concerns its composition. Encrusting coralline red algae, shells of vermetid gastropods, encrusting foraminifera and polychaetes worm tubes are the main carbonatic organisms responsible for the structure of Rocas Atoll. This is in contrast to the structure of atolls from the Indo-pacific and Caribbean waters, which are mainly constructed by hermatypic corals (KIKUCHI and LEÃO, 1997; GHERARDI and BOSENCE, 2001).

FONSECA et al. (2012) studyied reef flat community structure at Rocas, and found a great scarcity of hermatypic corals species and cover, stating that the reef flat is near solely dominated by turf forming and crustose macroalgae species. According to these authors, local, small-scale variability of physical and biotic factors in a well-defined reef geomorphic zone may harbor microcosms, each supporting unique benthic communities. In fact, LONGO et al. (2015) observed variations in benthic and reef fish communities, and feeding pressure on the benthos between open and closed pools at the atoll. They suggest that the dynamic in open pools is mostly driven by physical factors and the tolerance of organisms to harsh conditions, while in closed pools direct and indirect effects of species interaction play an important role.

The increasing demand for progress, since the industrial revolution, the concentration of carbon dioxide (CO_2) in the atmosphere has raised from 280 ppm to over 400 ppm in the present days (ALBRIGHT et al., 2016). This elevation is mainly caused by the fossil fuel burn and deforestation and has been causing a series of problems to the Earth equilibrium, such as climate changes, sea level rise and most recently a process known as ocean acidification (OA) (ANTHONY et al., 2011; ZEEBE, 2012). OA can be summarized as the process by which the rising atmospheric CO2 is absorbed by the ocean surface waters, increases the partial pressure of CO2 (pCO2), leading to a number of chemical changes including increased hydrogen ion concentrations (lower pH, more acidic) and reduced carbonate ion concentrations. (IGLESIAS-RODRIGUEZ et al., 2016).

Impacts of OA on marine calcifiers (organisms that depend on carbonate ions available on the seawater to build their skeletons, shells, etc.) are constantly been reported around the world, affecting physiological processes such as calcification, photosynthesis, and neurophysiological pathways. (DUPONT et al., 2010; ALBRIGHT and LANGDON, 2011; FABRICIUS et al., 2011; MELZNER et al., 2011). According to HOEGH-GULDBERG et al. (2007), reef ecosystems are among one of the most threatened environments. Nevertheless, OA can cause positive effects in other marine organisms, especially algae and seagrass, which use the CO2 in excess on the water to increase their photosynthetic activities elevating their primary production and growth (KROEKER et al., 2013). Those changes in the physiology of individuals can alter the dynamics of their populations and ultimately affect entire ecosystems (IGLESIAS-RODRIGUEZ et al., 2016).

As an isolated, near-pristine system, where natural mechanisms can still be studied under limited human impact, the comprehension of processes influencing biological communities and how they promote ecosystem functions is particularly important to Rocas Atoll (LONGO et al., 2015). In this context, the goal of this study was to improve the understanding of physical-biological interactions at benthic communities in Rocas Atoll. Therefore providing data to support future investigations of the climate change and OA impacts at one of the most effective marine protected area in Brazil.

6.2.4. STUDY AREA

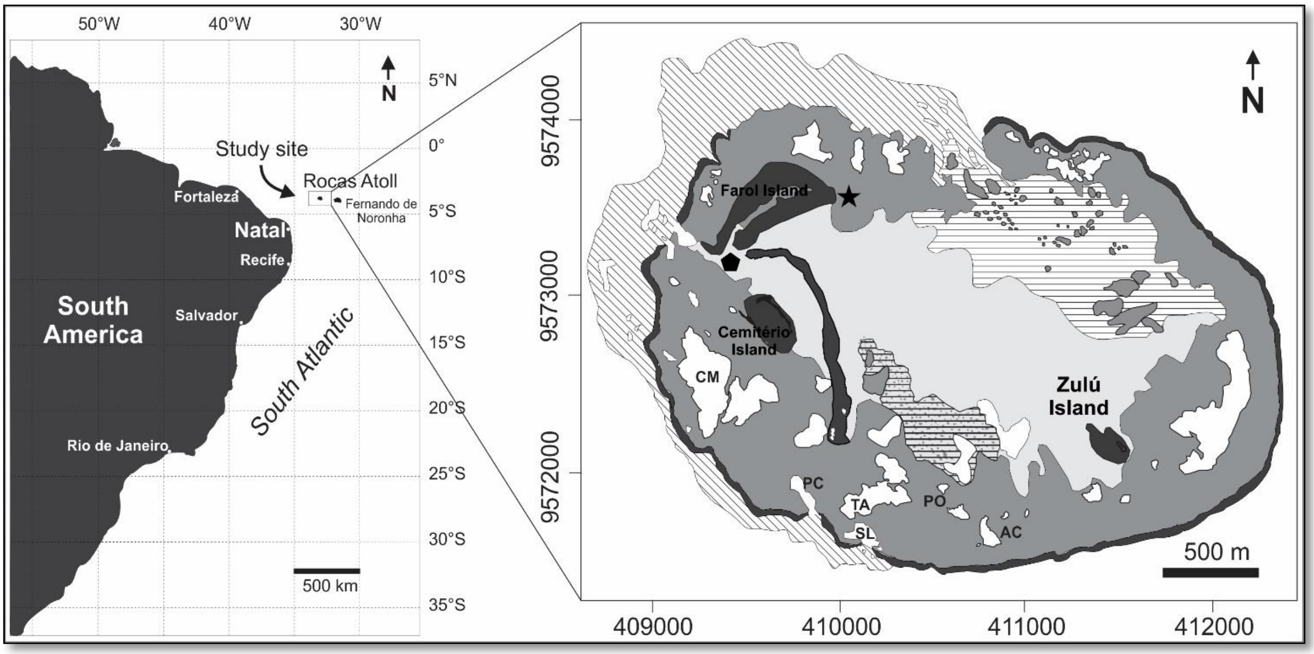
Rocas Atoll is situated at latitude 3°51’S and longitude 33° 49’W, 266 km from the city of Natal, Rio Grande do Norte, and 145 km from Fernando de Noronha Archipelago, Pernambuco, Northeastern Brazil (Fig. 17). Rocas is the only atoll formation in the South Atlantic and is placed on the Fernando de Noronha Seamount Chain (KIKUCHI; LEÃO, 1997). With an axis of 3.35 km by 2.49 km, a reef area of 6.56 km^2 and a perimeter of 11 km, Rocas is one of the smallest atolls in the world (PEREIRA et al., 2010).

According to VILLAS-BOAS et al. (2005), the variation in shape and growth of framework building coralline algae and their role in reef structure is directly related to hydrodynamic energy. The reef rim perimeter can be as wide as 600m, and presents a number of intertidal pools, from narrow fissures to large pools with sandy bottoms (KIKUCHI and LEÃO, 1997; GHERARDI and BOSENCE, 2001).

There are two sand islands, Farol and Cemitério. The research base was constructed at the Farol Island, and it is surrounded by low-standing vegetation that is used as nesting sites for thousands of marine birds. In the middle of this cay there is the Lama Bay, whose fauna depends on the tide dynamics, and it is usually a refugee area for juvenile lemon sharks. Rocas' sedimentary environment is composed entirely of carbonate skeleton derived from its own reef structure, which goes through continuous degradation by physical processes such as wave action (PEREIRA et al., 2013).

The climate is equatorial, and the prevailing wind directions is from southeasterly with maximum wind speed of 11 m s-1 (HOFLICH, 1984). There is a rainy season from approximately March through July and a dry season from approximately August through February (APAC, 2016). The tides range from 0–3.8 m in a semi-diurnal and mesotidal regime, resulting in a half-daily cycle of almost complete submersion during high tide (only the sandy islands remain emerged) and almost complete emersion during low tide. This tidal dynamics results in strong currents when the atoll is either filling or draining and during high tides (GHERARDI and BOSENCE, 2001). The available reef area in its internal portion during the low tide, when tidal currents have ceased, can be distinguished in three main habitats: the shallow permanent lagoon, and the open and closed pools. Open pools communicate with the exterior of the atoll even during low tides, and are more exposed to wave action than closed pools, which remain completely isolated from the exterior area of the atoll during low tide (LONGO et al. 2015).

Figure 17 - Studied areas at Rocas Atoll, indicating the sampling sites. Stations near the channels: pentagon (Station I) and star (Station II); Closed pools: CM (Cemitério); TA (Tartarugas); AC (Âncoras); PO (Porites) and Open pools: PC (Podes Crer) and SL (Salão). Adapted from PEREIRA et al., 2013.



The available reef area in its internal portion during the low tide, when tidal currents have ceased, can be distinguished in three main habitats: the shallow permanent lagoon, and the open and closed pools. Open pools communicate with the exterior of the atoll even during low tides, and are more exposed to wave action than closed pools, which remain completely isolated from the exterior area of the atoll during low tide (LONGO et al. 2015).

6.2.5. MATERIAL AND METHODS

The data was sampled during December 2012 through December 2014. In total, were six research expeditions to Rocas Atoll, lasting between 3 to 4 weeks, four during the dry and two during the rainy season. Two open pools (Salão and Podes Crer), four closed ones (Cemitério, Tartarugas, Âncoras and Porites) and two fixed stations, one in each extremity of Farol's island were chosen as sampling sites. Station I is a shallow pond, that during the slack water period (about 3 hours between the end of the ebb tide trough the low tide and the begging of the flood tide) reaches around 0.7 m deep. This station receives influence from the Lama Bay discharge during the ebb tide and during the flood and spring tides from the Barretinha Channel (Northwest). The station II is the shallowest, with average 0.4 m water depth during the slack water period and receives influence from the Barretão Channel (North).

Hydrology

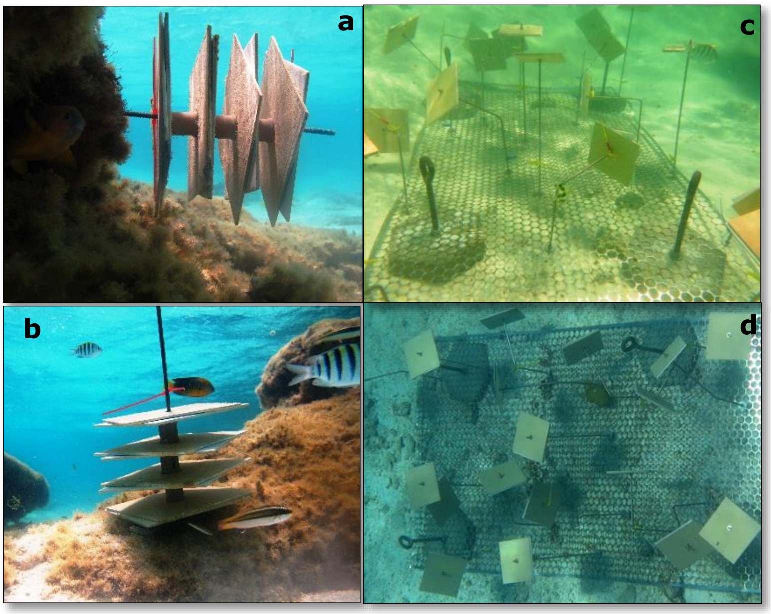
Seawater samples were collected using Niskin bottle during the low tide at the sub-surface and near the bottom of the pools and at the fixed stations, the water samples were collected only at sub surface in intervals of 2 hours for 12 hours. Abiotic parameters such as water temperature (C) and pH (total) were determined in situ, using a HANNA electrode with 0.01 precision. Dissolved oxygen (DO) analysis were carried out at the Rocas Atoll research station within 24 hours (with an accuracy of ± 0.03 mL. L^{-1}) according to the modified methodology of Winkler, described at STRICKLAND and PARSONS (1972). Other parameters such as salinity (S), total alkalinity (TA) and dissolved inorganic nutrients were analyzed in the laboratory of chemical oceanography at Universidade Federal de Pernambuco (UFPE). Seawater samples were poisoned with saturated mercuric chloride (DICKSON et al., 2007) and TA was measured by open cell titration as described in ROUNDS (2012). The quality of the measurements was confirmed by analyzing certified reference materials (Batch 132) provided by Andrew Dickson, from Scripps Institution of Oceanography before and after a round of samples. Measurements were corrected based on the mean difference between the measured and the certified values of the CRMs (accuracy 4.94%). Replicates of seawater samples (50 mL) were kept protected from temperature and light variations, and used to measure the salinity according to the Mohr-Knudsen method described by STRICKLAND and PARSONS (1972). Other seawater replicates (500 mL) were immediately frozen in Rocas and transported to the laboratory were levels of phosphate, nitrate, nitrite (STRICKLAND and PARSONS, 1972) and silica (GRASSHOFF et al., 1983) were determined.

Benthic coverage

Ceramic tiles (225cm^2), conditioned for three months, were arranged into settlement units and deployed at Âncoras, Cemitério, Porites and Podes Crer pools. From December 2012 through December 2013, 10 unites were distributed per pool. Each unit consisted of four pairs of tiles separated by a PVC ring of three cm. The units were fixed at the reef on the horizontal and vertical positions (Fig. 18 a, b). From December 2013 to December 2014, we changed the deployment of the tiles. Throughout this period, the settlement units consisted in 18 pairs of tiles, divided in three different orientations (vertical, horizontal and inclined 45°), randomly arranged into a stainless steel mesh and anchored at the sand bottoms of the pools. In each pool, we installed three settlement unit (Fig. 18 c, d).

At the end of each year the settlement plates were collected from the pools and transported to the scientific station were they were analyzed under stereomicroscope and photographed. The density of organisms from different categories was then determined: bryozoans (Bry), vermetidis (Verm), serpulids (Serp) and corals (Coral). When present, coral recruits were identified and measured. To estimate the benthic coverage of macroalgae (MAL) and crustose coralline algae (CCA), the area (cm^2) occupied by those organisms was measured with the software ImageJ using the photography of the plates. During the expedition of November 2014, the benthic coverage on the pools was also evaluated with point intercept transect surveys. Salão pool was the only one where transect observations were not carried out due to unsafe dive conditions. In total, four transects of 20 m, with 40 points at 0.5 m intervals, and 5m apart from one another were evaluated in each pool by scuba diver. The identification of the organisms were grouped in categories as follow: macroalgae (MAL), turf algae (TUR) – layer of tightly, crustose coralline algae (CCA), sponge (ESP), sand (SAND*), Zoanthus sociatus* (ZSO), and the corals *Mussismilia hispida* (MHI), *Porites astreoides* (PAS) and *Siderastrea stellata* (SST).

Figure 18 - Settlement units displayed in 2013 (a, b) and 2014 (c, d) at tidal pools in Rocas atoll.



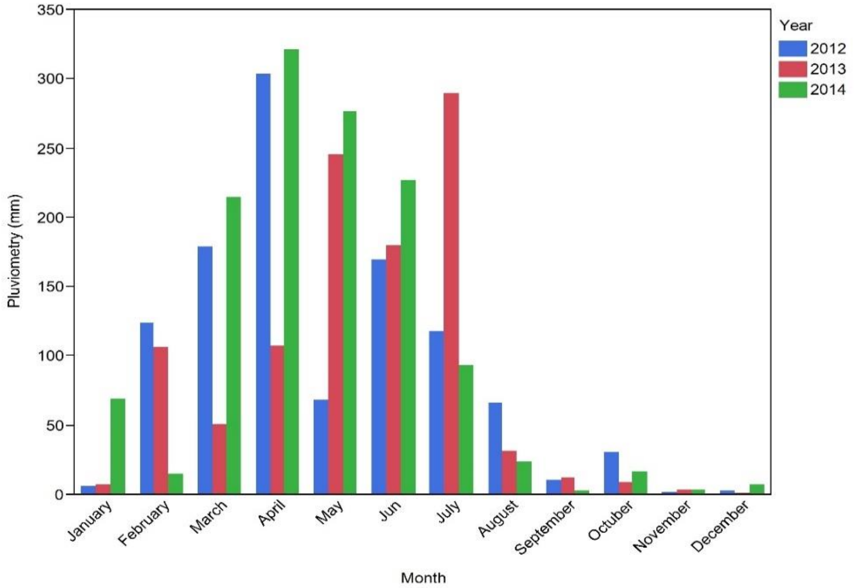
Data analysis

The environmental variables were tested for significance by comparing the different sampling sites (Âncoras, Cemitério, Porites, Tartarugas, Podes Crer, Salão, and Fixed station I and II), grouped sites (open pools, closed pools and channels), climate periods (dry and rainy season) and sampling years (2012-2014), with Wilcoxon/Kruskall-Wallis tests. The benthic coverage categories of the settlement plates were compared by sampling sites and sampling years also with Wilcoxon/Kruskall-Wallis tests. To explore potential relationships between the abiotic parameters and the structure of the benthic community we conducted a Principal Component Analysis (PCA). Statistical analyses were performed using the software JMP®10.0.2 (SAS Institute Inc., 2012) and the level of significance adopted was 0.05.

6.2.6. RESULTS

The annual average precipitation (Fig. 19) for the years 2012, 2013 and 2014 were 89.9±92.9mm, 87±101mm and 106±120mm, respectively. During the present study, the main pluviometry was 172±92.2mm for the rainy season (February until July) and 16.9±20.7mm for the dry season (August until January).

Figure 99 - Monthly precipitation (mm) of the region throughout the years of study. Source: APAC, 2016 for Fernando de Noronha station.



At the fixed stations it was observed diurnal variations for some of the environment parameters analyzed, such as temperature, pH, and DO that presented lower values from 5 pm until 8 am and high values around 10 am and 4 pm. Total alkalinity did not show a significant variation along the day, but indicate a tendency of high values during nighttime and lower values along the day (Fig. 20 a). Unlike the variables described before, the nutrient salts and silica did not show diurnal variations (Fig. 20 b).

Figure 20 - Daily and seasonal variations of the environmental parameters collected at the fixed stations at Rocas atoll. Diamont: station I, Asterisk: station II. In red data collected during the rainy season and blue the dry one. T- Temperature (°C), pH (total scale), DO- Dissolved oxygen (mL. L^{-1}), TA- Total alkalinity (µmol. Kg_{sw}^{-1}), NO_2 – Nitrite (µM), NO_3- nitrate (µM), PO_4- phosphate (µM), SiO_2 – Silica (µM).

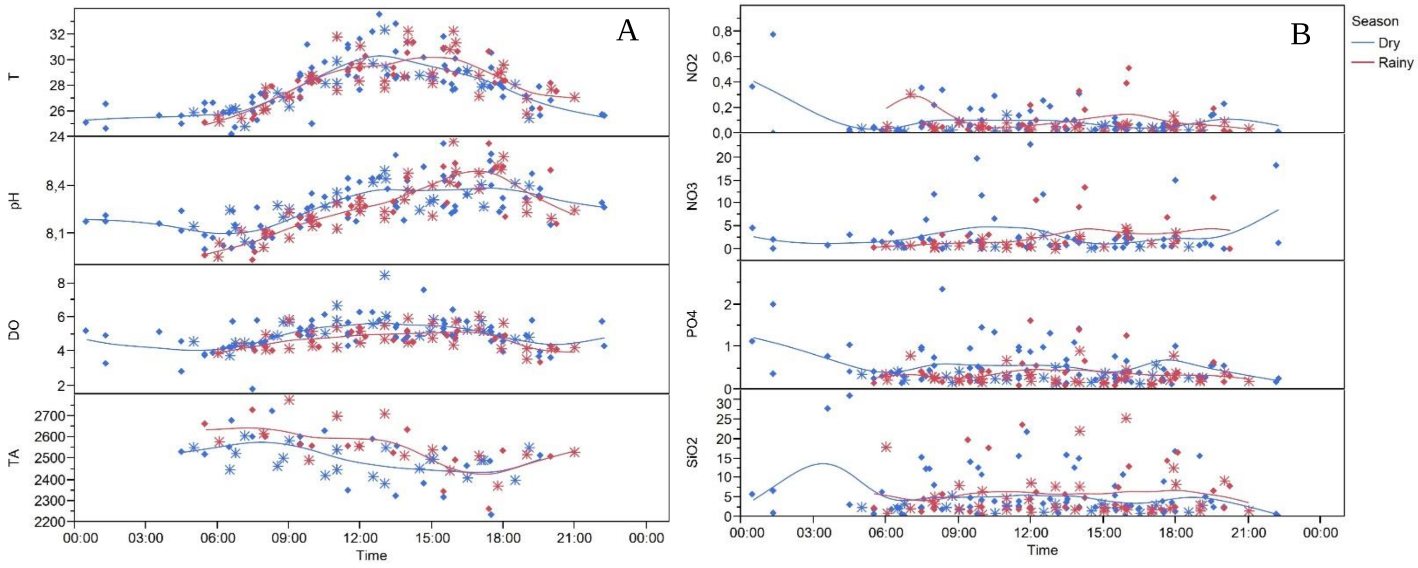


Table 2 summarizes all the results obtained for the environment variable analyzed. The fixed stations near the channels showed the largest values (2520±107 µmol. Kg_{sw}^{-1}) of TA and of PO_4 (0.47± 0.51 µM) when compared to open and closed pools. At the open pools, it was observed high average values for DO (5.77±1.04 mL.L^{-1}) and pH (8.38±0.18). Analyzes of variations among the sampling points, indicates the influence of the pH values measured at Podes Crer pool in this difference mentioned above. This open pool, in particular, also stood out for lower mean TA (2339±122 µmol. Kg_{sw}^{-1})

Table 2. Spatial and seasonal variation of hydrological parameters (mean±SD) measured at Rocas Atoll. (*) Significant different mean values ($p<0.05$, Wilcoxon test). T- Temperature (°C), pH (total scale), DO- Dissolved oxygen (mL. L^{-1}), TA- Total alkalinity (µmol. Kg_{sw}^{-1}), NO_2 – Nitrite (µM), NO_3- nitrate (µM), PO_4- phosphate (µM), SiO_2 – Silica (µM).

		T (C)	**pH**	**S**	**DO**	**SiO_2**	**PO_4**	**NO_2**	**NO_3**	**TA**
Site	Channel	28.2± 1.96	8.28± 0.16	35.4± 1.14	4.92± 0.83	5.37± 5.92	0.47± 0.51*	0.1± 0.18	2.84± 4.18	2520± 107*
	Close	28.3± 1.04	8.26± 0.09	35.5± 1	5.34± 0.86	7.08± 8.08	0.38± 0.66	0.06± 0.04	1.48± 1.46	2445± 56.6
	Open	28.9± 1.61	8.38± 0.18*	35.6± 1.05	5.77± 1.04*	8.51± 10.3	0.35± 0.25	0.06± 0.05	1.66± 1.23	2388± 101
Sampling points	Âncoras	27.9± 0.96	8.25± 0.09	35.1± 1.05	5.27± 0.9	6.63± 6.7	0.38± 0.4	0.08± 0.05	1.83± 1.35	2458± 47.5
	Cemitério	28.4± 0.95	8.26± 0.09	35.6± 0.93	5.34± 0.81	7.46± 9.34	0.3± 0.4	0.05± 0.03	1.5±2	2442± 25.8
	Fixed Station I	28.2± 2	8.27± 0.16	35.6± 1.16	4.85± 0.81	5.94± 6.33	0.57± 0.61	0.13± 0.22*	3.38± 4.7	2522± 122
	Fixed Station II	28.3± 1.9	8.28± 0.15	35.2± 1.08	5.05± 0.87	4.31± 4.95	0.3± 0.17	0.05± 0.05	1.34± 1.22	2518± 91.9
	Podes Crer	29.4± 1.6	8.49± 0.17*	35.5± 0.95	6.35± 0.93	10.9± 12.2*	0.34± 0.2	0.05± 0.07	1.41± 1.21	2339± 122*
	Porites	28.3± 1.08	8.27± 0.09	35.5± 0.97	5.6± 0.94	6.25± 6.92	0.27± 0.11	0.05± 0.03	1.53± 1.14	2438± 101
	Salão	28.2± 1.36	8.23± 0.07	35.8± 1.2	4.94± 0.5	5.03± 5.27	0.37± 0.31	0.06± 0.03	2.22± 1.15	2437± 34.9
	Tartarugas	28.4± 1.17	8.26± 0.08	35.7± 1.02	5.16± 0.81	7.85± 9.25	0.54± 1.14	0.06± 0.03	1.17± 1.11	2444± 26.9
Season	Dry	28± 1.72	8.28± 0.14	36± 0.65*	5.14± 0.91	5.52± 5.88	0.5± 0.66*	0.07± 0.1	2.55± 4.01	2469± 91.9
	Rainy	28.7± 1.61*	8.29± 0.16	34.8± 1.22	5.18± 0.94	7.27± 8.83	0.34± 0.28	0.09± 0.18	2.13± 2.61	2488± 123

There was significant differences on the nutrient values when comparing Fixed station I and Fixed Station II separately, Station I had the highest values for PO_4 (0.57± 0.61 µM),

NO_2(0.13±0.22 µM), NO_3 (3.38± 4.7 µM). DO, phosphate and salinity showed seasonal variation with higher values generally observed in the dry season and temperature more often displayed larger values during the rainy season (Table 2).

The benthic coverage at Rocas pools was evaluated with two different methodologies. The results obtained for algal cover was similar in both methodologies, the open pool showed high coverage of CCA, while the close pools where dominated by macro and turf algae. However, it was observed only seven coral recruits on the settlement experiment, and the coral cover was better estimated with transects.

Overall, the macroalgae (MAL) was the most abundant benthic coverage in the settlement plates, ranging from 74.7± 23.9% at Cemitério and 35.8± 20.4 % at Podes Crer. It was observed significant difference between the pools, Cemitério and Âncoras presented the highest MAL percentage and Tartarugas and Podes Crer the lowest. Podes Crer was the pool with higher crustose carbonate algae coverage (CCA%). For this open pool it was possible to recover the ceramic tiles on both years studied, therefore, annual differences in the recruitment could be tested. In 2013, the surface area coverage by CCA was 61.3± 41.2 cm^2 while in 2014 was 115± 69.8 cm^2. The percentage of area with no recruitment was significantly different for Tartarugas settlement plates, were about half of the surface area was not colonized (nude) (Table 3).

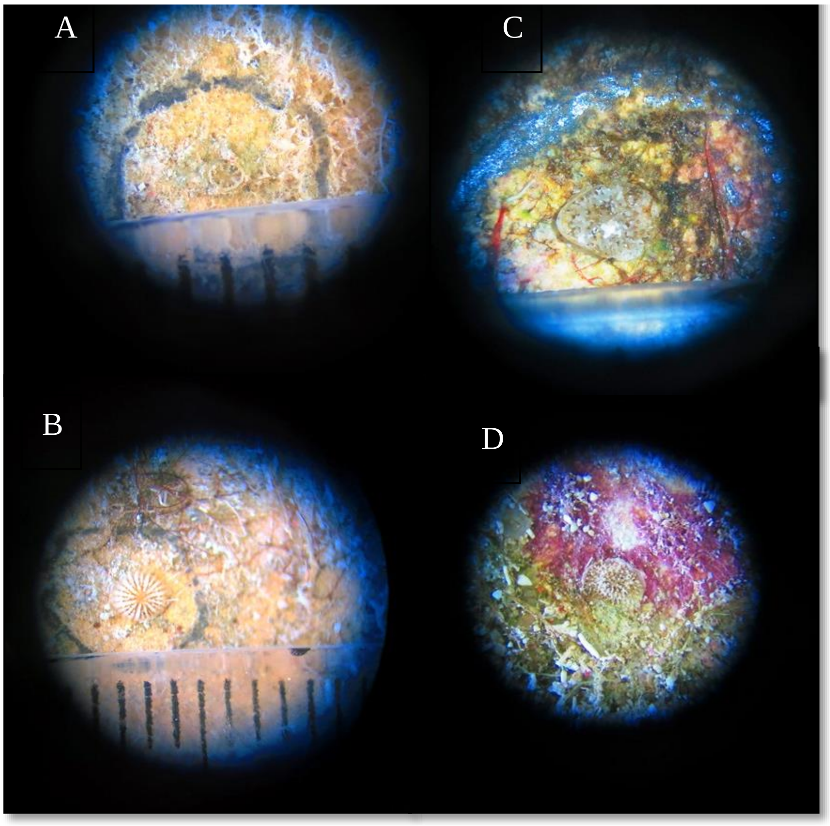
The density of bryozoans (BRY) was similar at Âncoras and Tartarugas with 41.7± 62.7 individuals per 225 cm^2 and 21.1± 36.1 individuals per 225 cm^2 respectively. There was no difference between the densities of serpulids polichaetes (mainly *Spirobis* sp.) among the pools in 2013, but the density observed at Podes Crer in 2014 was significantly lower than the one for the previous year. The density of vermetids represented by two different species identified on the plates (*Pentaloconchus* sp. e *Dendropoma* sp.) was significantly lower than the ones observed for bryozoans and serpulids. However, they show the same pattern of distribution as bryozoans among the pools. Âncoras and Tartarugas formed the group of pools with higher density while Cemitério and Podes crer showed the lowest (Table 3).

It was not observed variations on coral recruitment. In 2013, four recruits were recognized, one *Siderastrea* sp. and two *Porites* sp. at Podes Crer and one at *Porites* sp Âncoras (Fig. 21). In 2014, two recruits of Siderastrea sp. and one Porites sp. were observed at Podes Crer.

Table 3. Benthic coverage and density of organisms (N/225 cm^2) recruited at the settlement plates displayed at tide pools at Rocas Atoll during 2013 and 2014. Legend: Crustose carbonatic algae (CCA), Macroalgae (MAL), bryozoans (Bry), vermetidis (Verm), serpulids (Serp) and corals (Coral).

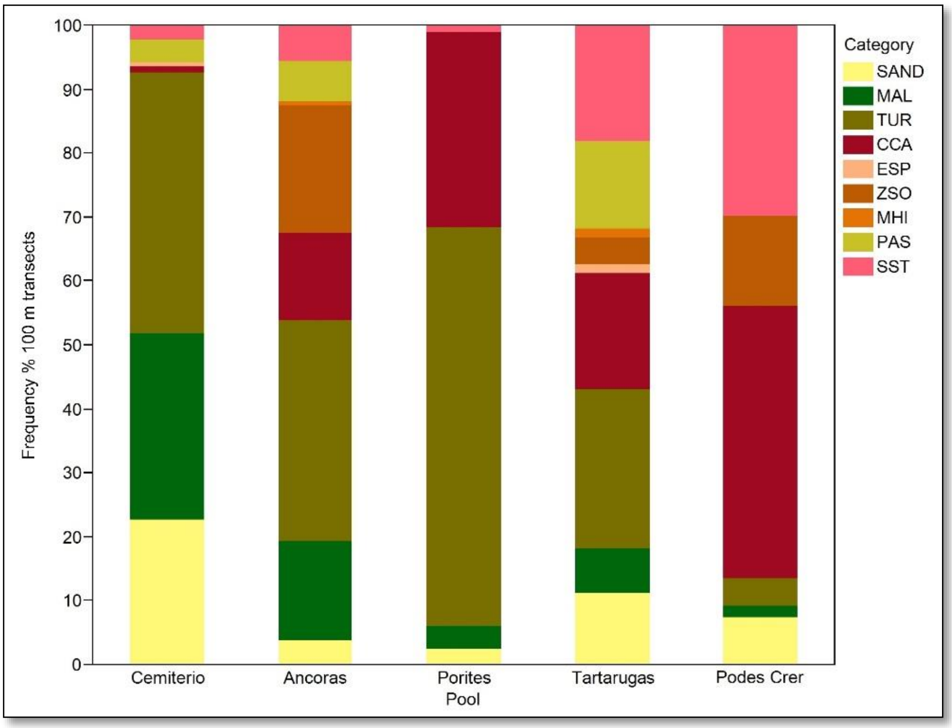
Year	**2013**				**2014**	
Pool (n)	**Âncoras (29)**	**Tartarugas (16)**	**Cemitério (23)**	**Podes crer (37)**	**Cemitério (38)**	**Podes crer (28)**
CCA (cm²)	31.7± 30.9	32.1± 33.1	23± 33.8	61.3± 41.2	9.1± 13.5	115± 69.8
CCA (%)	13.3± 13	13.5± 14	9.69± 14.2	25.9± 17.4	3.91± 5.76	49.1± 29.2
MAL (cm²)	148± 66	88.1± 62.8	177± 56.7	84.9± 48.5	179± 57.8	102± 68.8
MAL (%)	62.3± 27.8	37.1± 26.5	74.7± 23.9	35.8± 20.4	77.8± 23.3	45.1± 30.5
NUDE (%)	24.4± 23.4	49.3± 31.2	15.6± 14.4	38.4± 23.8	18.3± 24	5.78± 12.5
BRY	41.7± 62.7	21.1± 36.1	12.8± 14.1	21.7± 32.3	19.3± 18.3	9.93± 9.57
SERP	55.1± 69.9	19.2± 17.8	25.2± 33.5	61.9± 56.9	23.7± 24.2	5.07± 5.62
VERM	1.55± 3	1.13± 1.81	0.22± 0.52	0.51± 1.12	0.49± 0.99	0.67± 1.14
CORAL	0.03± 0.19	0	0	0.08± 0.36	0	0.11± 0.42

Figure 21 - Coral recruits observed at the settlement plates displayed at Podes Crer (A, B, C) and Âncoras (D) pool during 2013. The recruit B is *Siderastrea* sp. The others (A, C, D) are *Porites* sp. Size of Recruits: A- 0.405 mm^2; B- 3.667 mm^2; C- 3.592 mm^2; D- 3.248 mm^2



The results for the benthic coverage evaluated by point intercept transects are shown at Figure 22. The most abundant category at the only open pool surveyed (Podes Crer) was CCA, which represents 42.7% of the coverage, followed by the percentage of Siderastrea stellata coverage (29.9%). While for all closed pools, the non calcified algal turfs (TUR) was the dominant category, with 62.2% at Porites, 40.7% at Cemitério, 34.4% at Âncoras and 25% at Tartarugas.

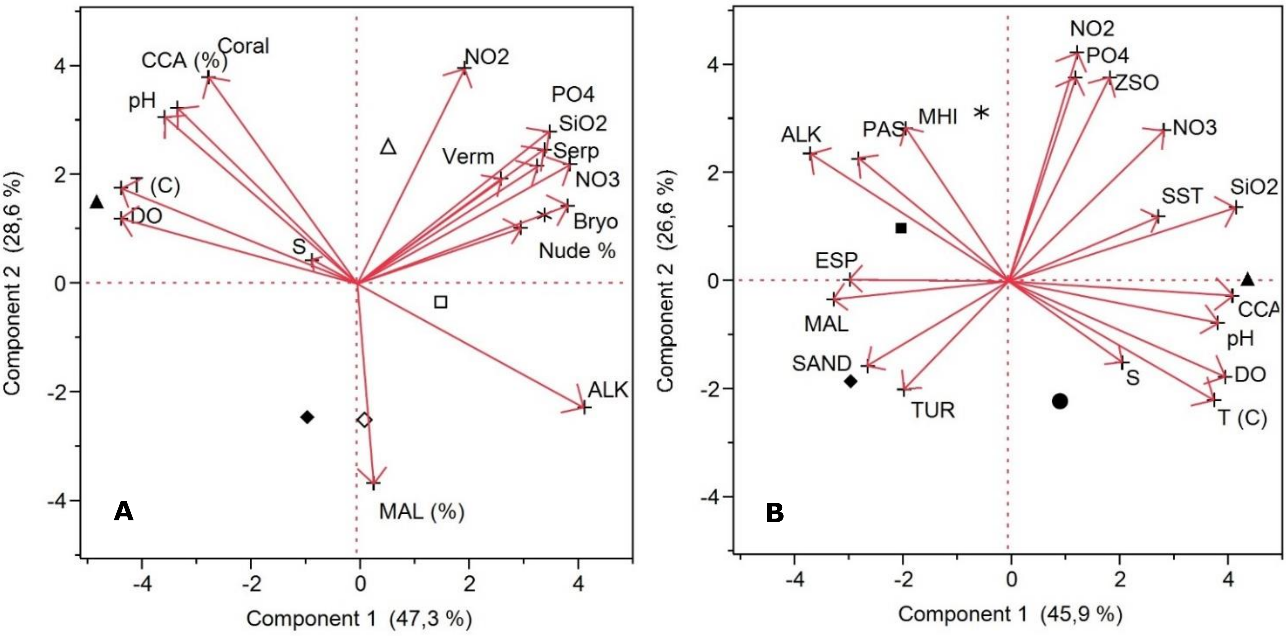
Figure 22 - Percent coverage of the main benthic categories observed at Rocas atoll tidal pools. macroalgae (MAL), turf algae (TUR), crustose coralline algae (CCA), sponge (ESP), sand (SAND), *Zoanthus sociatus* (ZSO), *Mussismilia hispida* (MHI), *Porites astreoides* (PAS) and *Siderastrea stellata* (SST).



The interaction between the abiotic parameters and benthic community at Rocas pools was investigated with PCA. The PCA revels that two sets of components explained 75.9% (Fig 23. A) and 72.5% (Fig 23. B) of the variances included in those environmental parameters. While samples from the open pool (Podes Crer) were grouped by direct association between temperature, pH, DO, salinity, CCA and corals, samples from closed pools (Cemitério) were separated by the positive correlation from MAL, TUR, SAND and opposite to the availability of nutrient.

Therefore, results from this analyses suggests the tendency of habitats with high coverage of carbonatic organisms consume the alkalinity of seawater, and habitats with elevated abundance of algae (MAL and TUR) are direct related to the assimilation of dissolved inorganic nutrients.

Figure 23 - Principal Component Analyzes of hydrological data and benthic coverage obtained at the settlement plates (A) and point intercept transects (B). Pools: diamond – Cemiterio; asterisk – Ancoras; square- Tartarugas; circle- Porites; triangle- Podes Crer. 2013 -open symbols; 2014-closed ones. Benthic coverage: macroalgae (MAL), turf algae (TUR), crustose coralline algae (CCA), sponge (ESP), sand (SAND), *Zoanthus sociatus* (ZSO), *Mussismilia hispida* (MHI), *Porites astreoides* (PAS) and *Siderastrea stellata* (SST). Recruitment categories: bryozoans (Bryo), serpulids (Serp); vermetidis (Verm), corals (Coral) Hydrology: T (C)- temperature (°C); S– salinity; DO– Dissolved oxygen; SiO_2- Silicate, NO_3– nitrate, NO_2– nitrite, PO_4– phosphate, ALK-total alkalinity.



6.2.7. DISCUSSION

The results presented here reveal diurnal variations for some abiotic parameters such as temperature, DO, pH and TA, while others were relatively constant (dissolved inorganic nutrients) at the fixed stations. These diurnal changes suggest a link with tides, daily solar cycle, and the volume exchange with semi-enclosed pools. Nonetheless, they also demonstrate the ability of Rocas Atoll organisms' metabolism to alter open superficial seawater characteristics. One evidence that the biology may influence these abiotic parameters is the similar daily variation between pH and DO. These parameters showed values increasing along the day, when photosynthesis is taking place and an inverted pattern at night, due to the dominance of respiratory processes (ANTHONY et al. 2011; SHAW et al. 2012). Accordingly, processes of calcification and dissolution may be responsible for the variation on TA values (ALBRIGHT et al., 2016).

The present study also observed seasonal variations in temperature, salinity and phosphate. JALES (2015), studying phytoplankton seasonal and spatial variations at Rocas, also observed higher temperatures during the rainy season, however, the salinity reported was also high (36.2). In the present study the salinity recorded was 34.8±1.22 for the rainy and 36±0.65 for the dry season. It is more likely that the difference in the methodologies to obtain these values are responsible for the variation among the studies, since JALES (2015) used a manual Atago refractometer, model S/Mill-E with a scale range of 0 to 100 and an interval of 1, and we adopted the Mohr-Knudsen method. The results of this study are in accordance with FEITOSA and PASSAVANTE (2004) that obtained a salinity of 35.29 (Mohr- Knudsen method) for the dry season (January 1999).

Amongst the fixed stations, it was clear the impact of the Lama Bay over the nutrients concentration in station I. The results indicate an influence of the excrement of seabirds that can be washed away during the tide dynamics. The phosphate concentration was higher at station I, and those values contributed to the seasonal variation reported here. Swell events occurred during the dry season increased the hydrodynamics at the atoll, causing relatively longer periods of water residence time at Lama Bay (PINHEIRO, Pers. Comm), suggesting more dilution of the seabirds' guano. The influence of the seabirds' excrement on the concentration of nutrients was also discussed by FEITOSA and PASSAVANTE (2004).

Among the sampling sites, it was chosen two open pools, and in between them, the Salão presented more constant values for the abiotic parameters studied, similar to the observed for oceanic waters surrounding the atoll (JALES, et al., in press). Unfortunately, due to persistent strong waves and currents, it was not possible to realize the transects and the settlement units we deployed were completely destroyed. In contrast, Podes Crer showed significant variations compared to all the other pools: lowest TA (2339±122 µmol.Kg_{sw}^{-1}) and highest pH (8.49±0.17), and SiO_2 (10.9± 12.2 µM), and those results seem to influence its benthic cover.

The number of coral recruits observed during the study was extremely low compared to recruitment rates observed at others reef ecosystems in northeastern Brazil (MAIDA; FERREIRA, 1995; CASTRO et al., 2006). Variations in recruitment rates are generally attributed to factors such as fluctuations in larvae production (SAMMARCO; ANDREWS, 1988), planktonic phase survival (BAK; ENGLE, 1979), and post-settlement mortality processes, which occurs by predation, competition with other organisms on the substrate and premature death of individuals settled on inappropriate substrate (FABRICIUS; METZNER, 2004). Abiotic factors such as light, temperature, salinity and sedimentation have also been observed to influence the recruitment process and may induce or inhibit settlement (SAMMARCO 1983; RUIZ-ZÁRATE; ARIAS-GONZALEZ, 2004).

PINHEIRO et al. (in press), studying some aspects of the dominant coral specie (Siderastrea stellata) life history at Rocas, point out that 41.2± 18.5% of its population is considered mature (diameters higher than 10 cm) and has a high potential of maintenance and recovery. However, they observed a low frequency of young colonies with diameters ranging from 0 to 2 (1.8±1.12%) and 2.1- 4 cm (8.9±3.87%) that may be a consequence of a reduced recruitment event caused by two sequential positive sea surface temperature anomalies (2009 and 2010) (FERREIRA et al. 2012). It is possible that the results observed here indicate this impact of warming waters on coral reproduction, but further studies about larval dispersal, tidal dynamics, and polyp fecundity rates are necessary in order to draw solid conclusions about the recruitment failure event.

Although only *S. stellata*, *P. asteroides* and *M. hispida* were shown in the present study, *Montastrea cavernosa*, *Favia gravida*, *Porites branneri* and *Madracis decactis*, were also observed during the fieldwork, but not recorded as results due to the methodology and low abundance (PINHEIRO, per comm.) The total coral coverage we found was 33.15% at Tartarugas, 29.9 at Podes Crer, 12.51% at Âncoras, 5.93% at Cemitério and 1.22% at Porites. Those results are in accordance with a previous study by FERREIRA et al (2012) that observed 50.6 ±6.0 % at Salão; 34.0 ±14.2% at Podes Crer; followed by 22.5 ±7.8% in Tartarugas and the lowest coverage, 5.6 ±6.1% at Cemitério.

Turf algae and macroalgae were the most representative categories of benthic cover respectively at transects and settlement plates methodologies. In a study conducted by LONGO et al. (2015), the algal turfs were also the dominant group in tidal pools inside the atoll.

However, they classified the turf in two categories; articulated calcareous algae largely dominated algal turfs of open pools, whereas turfs from closed pools presented a greater contribution of non-calcified algae. In their research, it was considered comparative analysis of the reef fish assemblage, benthic cover, the composition, nutritional traits and associated cryptofauna of algal turfs, and fish feeding pressure on benthos. They found differences in patterns of community structure and feeding pressure on benthos between the open and closed pools, and attributed those differences also to the distinct hydrodynamic conditions and related amount of sediment in open and closed pools.

In the present study, the PCA showed a clear correlation between the benthic coverage and abiotic parameters that corroborated the findings of LONGO et al (2015). Habitats with high coverage of carbonatic organisms were direct correlated with temperature, pH, and DO, and indirect correlated with the alkalinity of seawater, whereas habitats with elevated abundance of macro and turf algae were indirect associated with the concentration of dissolved inorganic nutrients.

6.2.8. CONCLUSION

Here we presented an integrated approach describing environment variables and its associations at shallow reef habitats at Rocas atoll. Our main results suggest that:

(1) Abiotic parameters variations might be related with tides, daily solar cycle, and volume exchange from semi-enclosed pools as well as organisms' metabolisms (photosynthesis, respiration, calcification and dissolution) and seabirds' excrements.

(2) The availability of dissolved inorganic nutrients on the seawater may contribute for the distribution of the organisms in the atoll, since sites with dominance of macro and turf algae were indirectly associated with the concentration of nutrients.

(3) Habitats with high frequency of carbonatic organisms might be associated with decreased concentration of alkalinity.

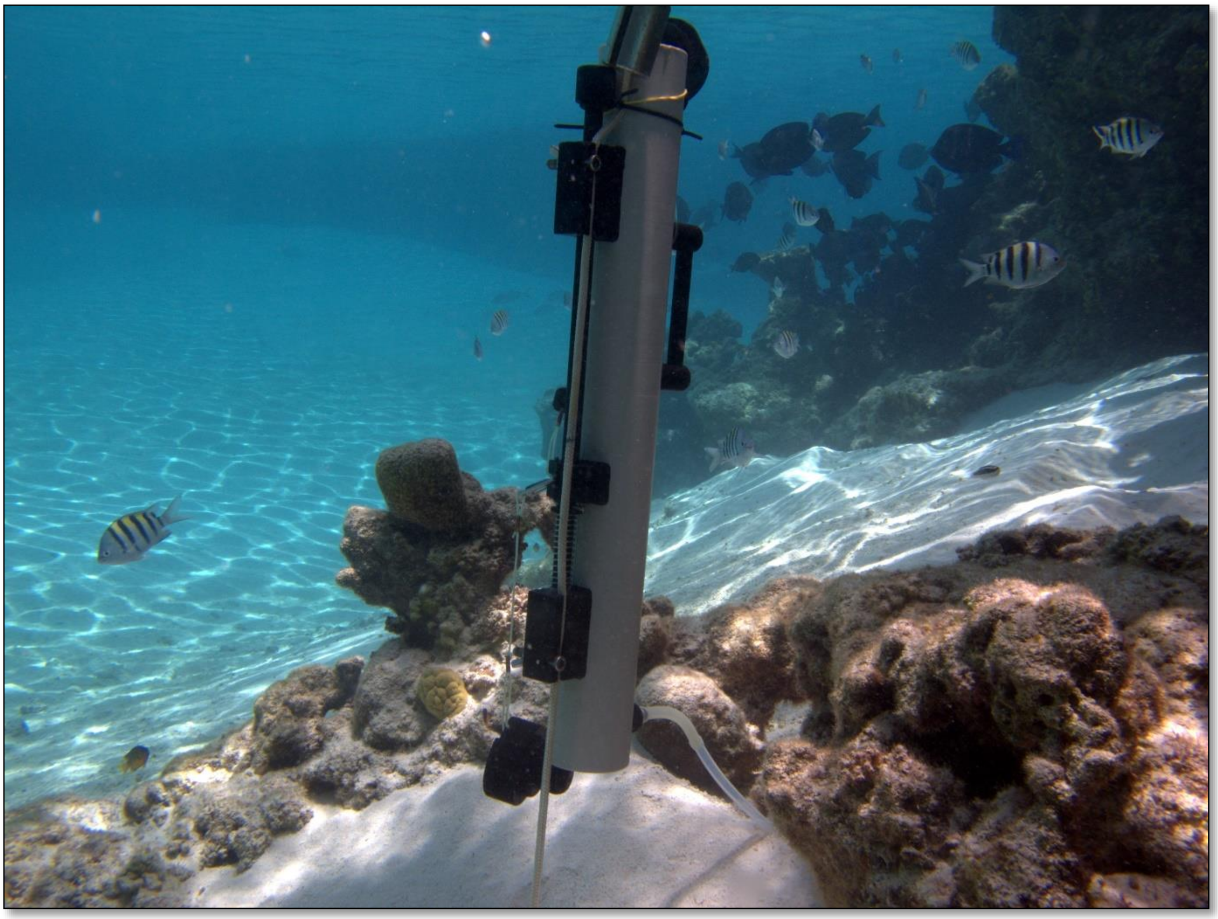
(4) The number of corals settled on the ceramic tiles was low when compared to recruitment rates of others studies in Brazil and may indicate an impact of warming waters on coral reproduction, however, further studies about larval dispersal, and polyp fecundity rates are necessary to draw solid conclusions about the recruitment failure event.

Nevertheless, especially due to the predicted effects of increasing CO_2 in the atmosphere (ocean warming and acidification), that can bring negatives impacts on carbonatic organisms and positive ones on macroalgae, it is recommended to closely monitor such interaction. Rocas, as the only atoll in the South Atlantic and the first and more effective marine reserve in Brazil, needs to be alert to the consequences of potential phase shifts processes there are happening in other reefs around the world.

7. CAPITULO II- CARACTERIZAÇÃO DO SISTEMA CARBONATO NO ATOL DAS ROCAS

Manuscrito 3- Rocas Atoll, an example of how a reef ecosystem modulates and interferes with the seawater carbonate chemistry: submetido para publicação na **Marine and Freshwater Research.**

Figure 24 – Garrafa de Niskin utilizada na coleta de amostras de água para análises químicas. Foto: Thiago Albuquerque



7.1. Rocas Atoll, an example of how a reef ecosystem modulates and interferes with the seawater carbonate chemistry

7.1.1. Abstract

Increasing concentration of atmospheric carbon dioxide (CO_2) is affecting the marine carbonate chemistry and several studies indicate that coral reefs are one of the most threatened ecosystems. The Rocas Atoll, in the tropical South Atlantic Ocean is a marine reserve since 1979 and a great laboratory to study the dynamics of the carbonate system, once the reef environment is in equilibrium and isolated of any coastal and anthropic influences. We aimed to evaluate the diurnal and seasonal variation as well the hydrodynamic influence over the carbonate parameters at the atoll. These parameters were calculated using the total alkalinity (TA), pH, temperature and salinity values, collected at two fixed stations inside the Rocas Atoll and at six pools of the atoll ring. By the metabolic rates analysis (net ecosystem calcification – NEC and net community production – NCP) we observed that the organic production (via photosynthesis) relative to calcification indicates that NCP is the primary controlling influence on carbonate chemistry in the pools inside the Rocas Atoll. The elevated concentration of carbonate ions, and therefore also values of aragonite saturation state, suggest that the intense biological activity happening inside the atoll could mitigate some of the effects of ocean acidification and also function as a small additional sink for anthropogenic CO_2 during the wet season.

7.1.2. Resumo

O aumento na concentração atmosférica do dióxido de carbono (CO_2) tem afetado a química do sistema carbonato marinho, e vários estudos indicam que os ecossistemas de recifes de coral são os mais ameaçados por essas mudanças. O Atol das Rocas é uma reserva marinha desde 1979, localizada na região tropical do oceano atlântico sul. Seu ambiente recifal encontra-se em equilíbrio devido ao seu isolamento com relação à influência costeira e impactos antrópicos diretos, tornando-o um excelente laboratório natural para o estudo da dinâmica do sistema carbonato. Nosso objetivo foi o de avaliar as variações diurnas, sazonais e hidrodinâmicas sobre os parâmetros do sistema carbonato no atol. Esses parâmetros foram calculados a partir dos valores de alcalinidade total (AT), pH, temperatura e salinidade coletados em duas estações fixas dentro do Atol sob influência do mar de fora e em seis piscinas de maré. Através das análises das taxas metabólicas (taxa líquida de calcificação - TLC e produtividade líquida- PL)

nós observamos que a produção orgânica (via fotossíntese) relativa a calcificação indica que a PL é o principal fator que influencia a química do sistema carbonato nas piscinas de maré. A elevada concentração de íons carbonato e, portanto, os valores de saturação de aragonita (Ω_{Ar}) sugerem que a intensa atividade biológica que acontece dentro do Atol possa mitigar alguns dos efeitos da acidificação oceânica, além de funcionar como um pequeno sumidouro para o CO_2 antropogênico durante o período chuvoso.

7.1.3. INTRODUCTION

The effects of rapid rise of carbon dioxide (CO_2) in the atmosphere due to growing rates of burning fossil fuels, deforestation, cement production and other human activities, has been Calling the attention the scientific and public community for a while, bringing issues like global warming and climate change to focus (HOEGH-GULDBERG 1999, WILKINSON, 2000, SABINE; TANHUA, 2009). Nonetheless, the CO_2 do not only stay in the atmosphere with another gases and water vapor causing the greenhouse effect, it is also absorbed by the ocean's surface. Since the beginning of the industrial revolution, around 30-40% of the anthropogenic CO_2 has been absorbed by the world's surface oceans each year (BINDOFF et al., 2007). The CO_2 that dissolves into the oceans reacts with the water to form carbonic acid (H_2CO_3) and its dissociation products, bicarbonate ($\mathrm{HCO_3^-}$) and carbonate ($\mathrm{CO_3^{-2}}$) (MILLERO, 2007).

The rising concentration of $CO_{2\,(atms)}$ is changing the carbonate chemistry of the oceans, concentrations of $CO_{2\,(aq)}$ and HCO_3^- are increasing, while the concentrations of CO_3^{2-} and the pH of seawater decreases; with these changes collectively referred to as ocean acidification (KLEYPAS et al., 1999a; CALDEIRA; WICKETT, 2003; ORR et al., 2005). Serious concerns about the potential effects of ocean acidification (OA) on marine organisms and ecosystems, especially those organisms producing shells, tests or skeletons of calcium carbonate are growing (ANDERSSON et al., 2007). The fate of tropical coral reefs and scleractinian corals, in particular, have received most of the attention in the ongoing OA discussion (KLEYPAS et al., 1999 a, b; HOEGH-GULDBERG et al., 2007; KROEKER et al., 2013). The most probable consequences of OA and warming for reef ecosystems are usually considered as reduction on calcification/ reef accretion and increased frequency and severity of coral bleaching respectively (ALBRIGHT; MASON, 2013).

According to ANDERSSON et al. (2013), projections of future seawater CO_2 chemistry have been focused simply on changes in the pH and aragonite saturation state (Ω_{ar}) of open-ocean surface seawater conditions surrounding coral reefs, rather than the reef systems themselves (FEELY et al., 2009; SILVERMAN et al., 2009; ZEEBE, 2012). Only recently, *in situ* natural variability in the carbonate chemistry has been utilized to investigate coral reef community calcification, to understand the carbon cycle on reefs and to predict and monitor the effects of OA (SHAW et al., 2012; SILVERMAN et al., 2012; ALBRIGHT et al., 2013; ANDERSSON et al., 2013; CYRONAK et al., 2014; MURILLO et al., 2014).

The coral reef carbon cycle is mainly driven by two biogeochemical processes, organic carbon metabolism (photosynthesis and its opposite effect, respiration) causing variations in dissolved inorganic carbon (DIC) concentrations, and inorganic carbon metabolism (calcification and its opposite effect, dissolution) which alters both, the total alkalinity (TA) and DIC concentrations in a proportion of ~2:1 (ALBRIGHT et al., 2013). On reef systems, several environmental factors including benthic community composition, biological activity (which can vary with temperature, light and nutrient availability), salinity, tidal regime, water depth and residence time can dictate the variation of the carbonate chemistry. As a result, it is observed large fluctuations in both diurnal and seasonal timescales that can vary from reef to reef, and often differ from open ocean conditions (ALBRIGHT et al., 2013).

In the tropical South Atlantic Ocean coral reef communities were recorded from the Parcel do Manuel Luis' State Marine Park (00°53'S) to Cabo Frio (23°S), and in the Fernando de Noronha archipelago and Rocas Atoll, but the southernmost true reefs are in Abrolhos area (18°S) (CASTRO; PIRES, 2001). According to KERR et al. (2015), the Western South Atlantic Ocean lacks appropriate observations for determining regional OA effects, including the effects of OA on key sensitive Brazilian ecosystem, such as coral reefs. Following the trend of the rest of the world, most of the available CO_2 system data for the South Atlantic was collected from research cruises or moored buoys on the open ocean, aiming the evaluation of air-sea CO_2 fluxes (LEFRÈVE et al., 2008) and climatological distribution of the carbonate chemistry parameters (TAKAHASHI et al., 2014). Some studies were conducted on the coastal area, with the vast majority on rivers and estuarine ecosystem, evaluating their importance to the global carbon budget (ABRIL et al., 2013). In situ measurements of carbonate system parameters for a coastal coral reef system was only reported by LONGHINI et al., (2015). Some projects investigating the effects of rising CO_{2atm} in the ocean and in coastal ecosystems are ongoing (e.g. PIRATA, CARECOS, CORAL VIVO, INCT Amb-Trop) (KERR et al., 2015).

The lack of knowledge concerning natural variability of carbonate chemistry on reef ecosystem in the Tropical South Atlantic ocean, and how those ecosystem modulate and interfere on the surrounding seawater, were the main drivers for this study. Rocas Atoll, a pristine reef environment, and Brazilian Federal Marine Biological Reserve since 1979, was chosen due to its isolation from different anthropogenic effects as fishing, tourism and other direct human impacts. Its architecture relies on carbonate-secreting organisms, and therefore, as other reef ecosystem, ocean warming and acidification seriously threaten it. In addition to collaborate with new *in situ* data to enable better accuracy on the prediction of ocean acidification effects on coral reefs ecosystem, we aimed to evaluate the Rocas Atoll susceptibility to projected changes in ocean biogeochemistry.

7.1.4. METHODS

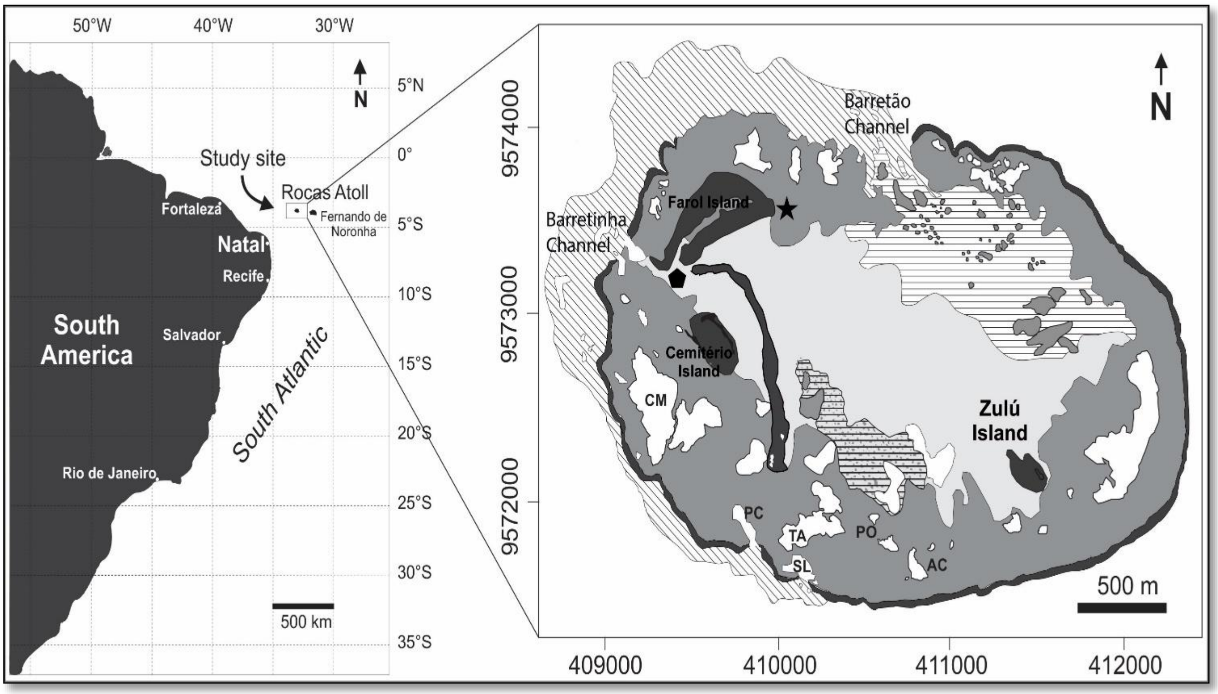
Study site

The Rocas Atoll (3°51'S; 33° 49'W) lays at 266 km offshore from the closest point in mainland Brazil and 145 km from the Fernando de Noronha Archipelago (Brazil) (Fig. 25). It is one of the smallest atolls in the world, with an axis of 3.35 km by 2.49 km, a reef area of 6.56 km^2 and a perimeter of 11 km (PEREIRA et al., 2010).

The climate in the region is equatorial, and the prevailing wind direction is southeasterly with maximum wind speeds of 11 $m\ s^{-1}$ (HOFLICH, 1984). The tidal regime is semi-diurnal, mesotidal, and hence can cause very strong tidal currents over the reef (GHERARDI; BOSENCE, 2001). However, there is no available data of tidal range from Rocas Atoll, the data available is from Fernando de Noronha's Harbor which shows a maximum height of 2.8 m

(DHN, 2014). Rainfall is mainly concentrated from March through July (wet season) (APAC, 2016).

Figure 25 - Location of the Rocas Atoll and location of the pools and fixed stations where the water samples were collected. Stations near the channels: pentagon (Station I) and star (Station II); Closed pools: CM (Cemitério); TA (Tartarugas); AC (Âncoras); PO (Porites) and Open pools: PC (Podes Crer) and SL (Salão). Adapted from PEREIRA et al., 2013



The reef is constructed almost exclusively by encrusting coralline red algae and the secondary framework builders is composed by vermetid gastropods, encrusting foraminifera, Polychaeta worm tubes, and corals (KIKUCHI; LEÃO, 1997; GHERARDI; BOSENCE, 2001). There are two sandy islands, Farol and Cemitério. The research base was constructed at the Farol Island, and is surrounded by low-standing vegetation that is used as nesting sites for thousands of marine birds. In the middle of this cay there is the Lama Bay. The Rocas' sedimentary environment is composed entirely of carbonate skeleton derived from its own reef structure, which goes through continuous degradation by physical processes such as wave action (PEREIRA et al., 2013)

Water sampling and analysis

Four expeditions to the atoll were realized, two during the dry season (October 2013 and December 2013-January 2014) and two during the wet season (February-March and May 2014). Discrete water samples were collected at two fixed stations placed in two shallow tide pools, (maximum depth at high tide 2.3 m) at the extremities of Farol Island, and near the channels that connect the lagoon with the open ocean (Fig. 25). These remain without direct hydraulic connection with the sea during low tide. The station I is a shallow pond that during the slack water period (about 3 hours between the end of the ebb tide trough the low tide and the begging of the flood tide) reaches around 0.7 m deep, receives influence from the Lama Bay discharge during the ebb tide and during the flood tide from the Barretinha Channel. The station II is shallower, with average 0.4 m water deep during the slack water period and receives influence from the Barretão Channel. At the two fixed stations, water samples were collected every ~2 hours during one full tidal period (12 hours).

Additionally, six selected pools (depth between 3 and 10 m) on the reef crest (atoll ring) were sampled during the low tide at the sub-surface (between 10 and 30 cm bellow surface). Four of the selected pools remain without direct hydraulic connection with the sea during low tide (*Cemitério*, *Tartarugas*, *Âncoras* and *Porites*, Fig. 25). The other two are permanently connected with the open ocean (*Salão* and *Podes Crer*). The hard coral coverage is higher in the pools permanently connected with the open ocean. Reef Check surveys made in 2007 and 2010 reported 34%± 14.2 and 50.6%± 6.0 to *Podes Crer* and *Salão,* respectively. At the closed pools they observed coverage of 22.5± 7.8% at *Tartarugas* and 5.6± 6.1% at Cemitério (FERREIRA et al., 2012).

Water samples were collected from Niskin bottle into 125 mL and 300 mL amber glass bottles with screw cap lid, preventing the formation of air bubbles in the drawing tube and sample bottles. The 125 mL sample was fixed on site for dissolved oxygen (DO) analysis and the 300 mL sample was poisoned with 200µl of saturated mercuric chloride for total alkalinity (TA) determinations. Plastic bottles of 100 mL were used to collect samples to salinity. Abiotic parameters such as water temperature (°C) and pH were determined in situ, using a HANNA electrode with 0.01 precision. DO analysis were carried out at the Rocas Atoll research station within 24 hours after collection (with an accuracy of ± 1.3 µmol L^{-1}) according to the methodology of Winkler modified, described at STRICKLAND and PARSONS (1972).

Salinity was measured according to the Mohr-Knudsen method described by STRICKLAND and PARSONS (1972), and TA was measured by titrating 50 ml of seawater in an open cell with sulfuric acid 18 mN as described in ROUNDS (2012). The quality of the measurements was confirmed by analyzing certified reference materials (Batch 132) provided by Andrew Dickson, from Scripps Institution of Oceanography before and after a round of samples. Measurements were corrected based on the mean difference between the measured and the certified values of the CRMs (accuracy 4.94%).

Carbonate chemistry

DIC, $p\mathrm{CO_2}$, Ω_{Ar} and concentrations of the bicarbonate [$\mathrm{HCO_3}$] and carbonate [$\mathrm{CO_3}$] ions were calculated from the TA, pH, temperature and salinity data using the Excel macro- $\mathrm{CO_2}$SYS (PIERROT et al., 2006), with the carbonic acid dissociation constants of MEHRBACK et al. (1973) as refit by DICKSON and MILLERO (1987) and the K_{SO4} for the bisulfate ion from DICKSON (1990).

Net ecosystem calcification (NEC) and Net community production (NCP) calculations

The metabolic rates (NEC, mmol $\mathrm{CaCO_3}$ $\mathrm{m^{-2}}$ $\mathrm{h^{-1}}$ and NCP, mmol C $\mathrm{m^{-2}}$ $\mathrm{h^{-1}}$) for each day where calculated according to LANGDON et al. (2010), during the slack water period at low tide, using the equations bellow:

$$nec = -0.5\rho h \frac{\Delta \mathrm{TA}}{\Delta t}, \qquad (1)$$

where $\Delta\mathrm{TA}$ is the change in total alkalinity (mmol $\mathrm{kg^{-1}}$), ρ is the density of the seawater (kg $\mathrm{m^{-3}}$), h is the mean water depth (m) and Δt is the time interval between observations (h).

$$ncp = -h\rho \frac{\Delta \mathrm{DIC} - 0.5\Delta \mathrm{TA}}{\Delta t} - kS(pCO_{2\,w} - pCO_{2\,a}), \qquad (2)$$

where $\Delta\mathrm{DIC}$ is the change in dissolved inorganic carbon (mmol $\mathrm{kg^{-1}}$), and the term $kS(pCO_{2\,w} - pCO_{2\,a})$, approximates gas transfer flux, calculated using the difference between the average $p\mathrm{CO_2}$ of two consecutive measurements in seawater and atmospheric $p\mathrm{CO_2}$. The values of $p\mathrm{CO_2}$ were obtained at Earth system Research laboratory from NOAA, at Maxaranguape-RN station, and the average for the dry and wet season were the same, 396 µatm. k is the gas transfer velocity and S is the solubility of $\mathrm{CO_2}$ calculated as a function of salinity and temperature. All other parameters are defined above. The wind speed parameterization of

HO et al. (2006) was used to calculate k, and the mean wind speed for each day was obtained from Fernando de Noronha station at the National Institute for Space research – Integrated System of Environmental Data (INPE/ SINDA, 2014).

Hydrodynamics influence

To further exam the influence of the hydrodynamics at Rocas, we grouped the data in three categories: open pools (Salão and Podes Crer, connected to the open ocean); closed pools (Cemitério, Tartarugas, Âncoras and Porites, isolated from the open ocean during the low tide) and the data collected at the fixed stations near the channels. The values of TA and DIC were salinity- normalized (by multiplying their values by the ratio of 36 to the measured in situ salinity), allowing a simple comparison between them. It was assumed that for every mol of organic carbon produced (via photosynthesis), one mol of DIC is consumed, and TA remains unchanged, and that for every mol of $CaCO_3$ produced (during calcification), TA decreases by 2 mol and DIC decreases by 1 mol. Therefore, it was considered the NEC: NCP ratio as $\frac{1}{\left(\frac{2}{m}\right)-1}$, where m is the slope of the TA- DIC line for each group of data (ALBRIGHT et al., 2013).

Statistical treatment

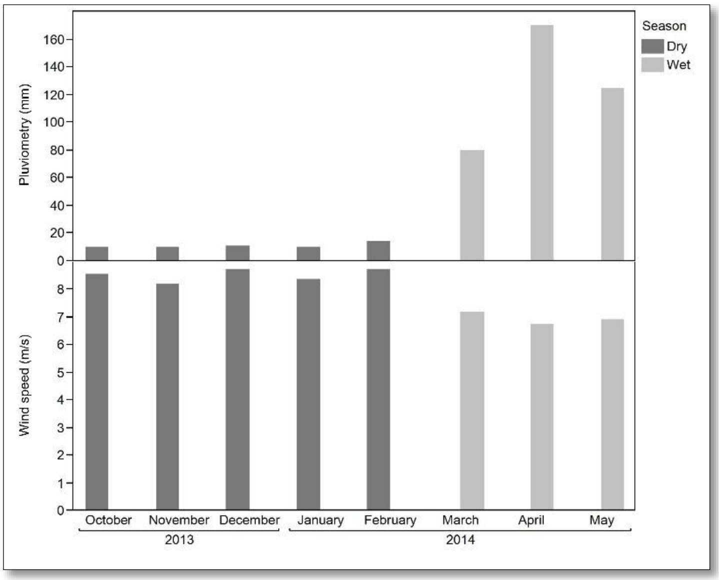
We used analysis of variance, ANOVA to examine the seasonal and spatial variation in the carbonate chemistry parameters. A *Kolmogorov-Smirnov* test was performed to check the normality of the data and the *Levene*'s test the homoscedasticity of the variances. It was assumed a significance level of 0.05.

7.1.5. RESULTS

In general, the Rainfall regime at Rocas Atoll present a clear seasonality, the dry period occurs from September to February and the wet one from March to August. Data collected from the meteorological station at Fernando de Noronha (APAC, 2016) was used to characterized the Dry – Wet seasons for the period of this study (Fig. 26). The average precipitation on the dry season, from October 2013 to February 2014, was 10.9± 17.2 mm and the wet season from

March to May 2014 was 124± 95.8 mm. The average wind speed was 8.52± 1.47 m s^{-1} at the dry season and 6.97± 1.66 m s^{-1} at the wet one.

Figure 26 - Pluviometry (mm) and wind speed (m s^{-1}) at 10m collected from the Fernando de Noronha's meteorological station, characterizing the dry and wet season during the period of the study.



Daytime and Seasonal variations

The diurnal and seasonal variations of the physical and chemical parameters of the seawater collected at the fixed station near the channels, and the closed and pools are presented at Figure 27 and Table 4. The average seawater temperature measured inside Rocas Atoll was 28.3± 1.61 °C and it varies in diurnal and seasonal scales (ANOVA, p<0.001). Early in the mornings the temperature were colder (min. 24.8°C), warming along the day between noon and early afternoon (max. 32.4 °C) and getting colder again by the end of the day (Fig 27.A). The temperature was colder during the dry season and warmer at the wet one, averaging 27.98± 1.5 and 28.85± 1.5°C respectively. The values of pH_{sw}, Ω_{Ar} and CO_3^{2-} also presented this pattern (Fig. 27 D, H and J), varying along the day and season (ANOVA, p<0.001). In the beginning and the end of the day, the values were lower than during noon and early afternoon. The average values observed during the study were 8.35± 0.17 pH, 6.29± 1.47 Ω_{Ar} and 392± 89 µmol kg_{sw}^{-1} for CO_3^{2-}. During the wet season the average values were higher (pH 8.42± 0.18; Ω_{Ar} 6.87± 1.5; 427± 93 µmol kg_{sw}^{-1} for CO_3^{2-}) than the dry one (pH 8.35± 0.18; Ω_{Ar} 5.96± 1.3; 372± 80 µmol kg_{sw}^{-1} for CO_3^{2-}). Although it was not found significant difference among the sampling sites grouped, the extreme values of those parameters were always observed on the shallow fixed stations near the channels.

The daytime distribution pattern of DIC, pCO_2 and HCO_3^- mirrored the ones of temperature, pH_{sw}, Ω_{Ar} and CO_3^{2-}, with the higher values found early in the morning and late at night and lowering throughout the day, with minimum values usually around noon (Fig. 27 F, G and I). Those parameters also presented significant difference between season and hydrodynamics of the sampling groups (Table 4). The higher average values were found during the dry period: DIC= 1806± 161 µmol kg_{sw}^{-1}, pCO_2= 189± 90 µatm and HCO_3^- = 1430± 232 µmol kg_{sw}^{-1}. The averages for the wet season were DIC= 1685± 202 µmol kg_{sw}^{-1}, pCO_2= 141± 96 µatm and HCO_3^- = 1255± 287 µmol kg_{sw}^{-1}. The pools connected with the open ocean (Salão and Podes Crer) presented the lowest average values for DIC and HCO_3^-. For pCO_2, these pools also presented the lowest values, but it was not significantly different from the values found at the closed pools, only differing from the ones collected at the fixed station near the channels.

Figure 27 - Diurnal and seasonal variation of the physical and chemical parameters of the seawater collected at the fixed station near the channels (crosses), closed pools (filled circles) and open pools (open circles). The blue ones were collected during the dry season and the red ones at the wet season at Rocas Atoll, and theirs smooth lines represent the main values collected at the respective station.

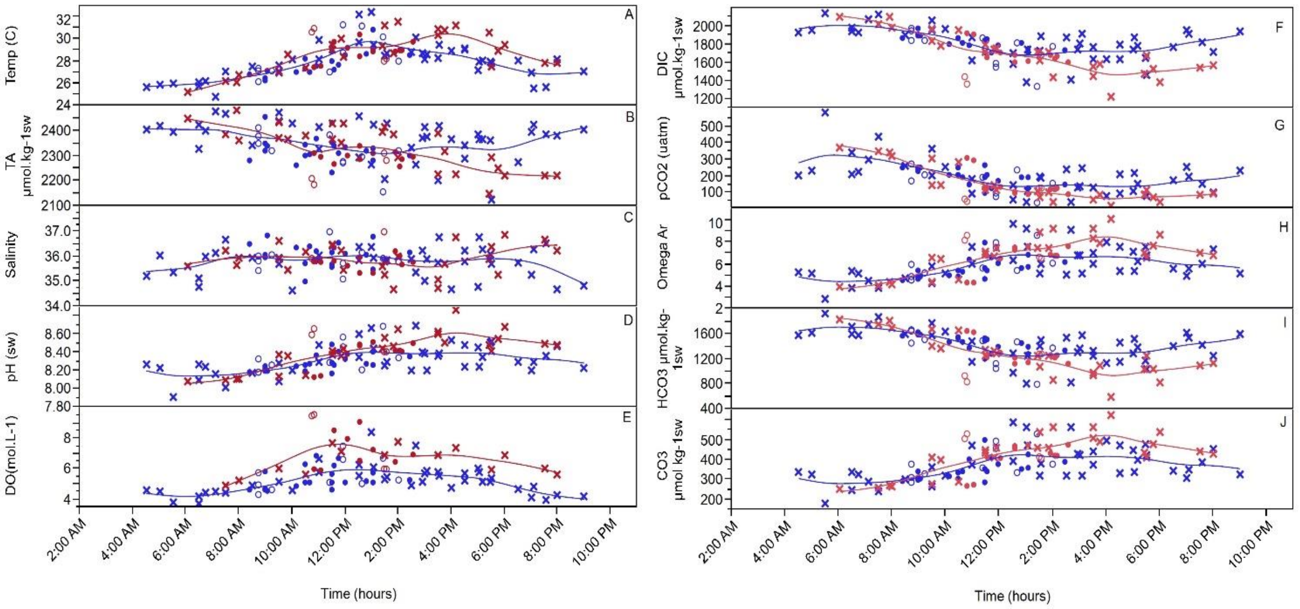
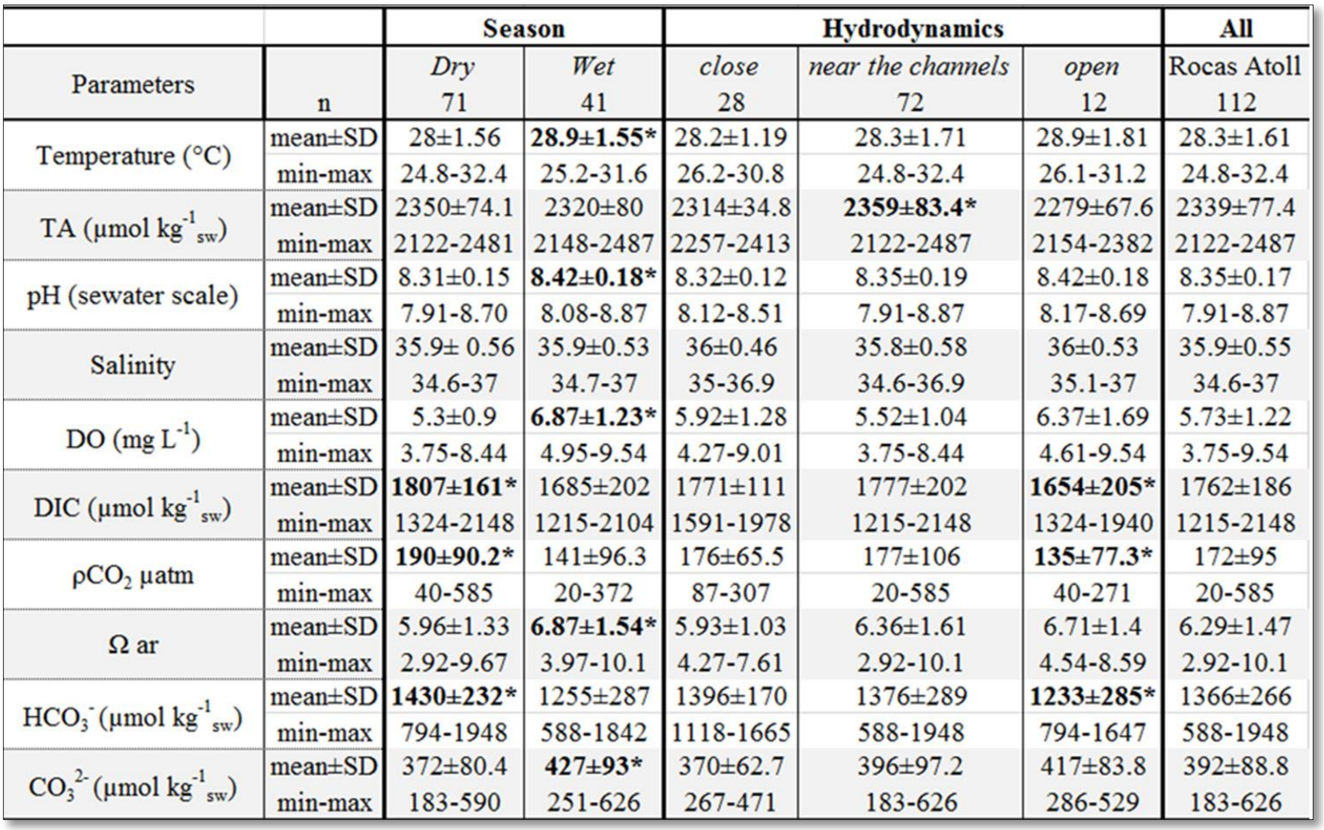


Table 4. Mean ±SD and range values from all the physical and chemical parameters sampled at fixed stations and pools inside the ring of Rocas Atoll showing the seasonal and hydrodynamics variations. (*) highlight significant difference of the means (ANOVA, $p<0.05$)



		Season		**Hydrodynamics**			**All**
Parameters	n	*Dry* 71	*Wet* 41	*close* 28	*near the channels* 72	*open* 12	Rocas Atoll 112
Temperature (°C)	mean±SD	28±1.56	**28.9±1.55***	28.2±1.19	28.3±1.71	28.9±1.81	28.3±1.61
	min-max	24.8-32.4	25.2-31.6	26.2-30.8	24.8-32.4	26.1-31.2	24.8-32.4
TA (μmol kg^{-1}_{sw})	mean±SD	2350±74.1	2320±80	2314±34.8	**2359±83.4***	2279±67.6	2339±77.4
	min-max	2122-2481	2148-2487	2257-2413	2122-2487	2154-2382	2122-2487
pH (sewater scale)	mean±SD	8.31±0.15	**8.42±0.18***	8.32±0.12	8.35±0.19	8.42±0.18	8.35±0.17
	min-max	7.91-8.70	8.08-8.87	8.12-8.51	7.91-8.87	8.17-8.69	7.91-8.87
Salinity	mean±SD	35.9± 0.56	35.9±0.53	36±0.46	35.8±0.58	36±0.53	35.9±0.55
	min-max	34.6-37	34.7-37	35-36.9	34.6-36.9	35.1-37	34.6-37
DO (mg L^{-1})	mean±SD	5.3±0.9	**6.87±1.23***	5.92±1.28	5.52±1.04	6.37±1.69	5.73±1.22
	min-max	3.75-8.44	4.95-9.54	4.27-9.01	3.75-8.44	4.61-9.54	3.75-9.54
DIC (μmol kg^{-1}_{sw})	mean±SD	**1807±161***	1685±202	1771±111	1777±202	**1654±205***	1762±186
	min-max	1324-2148	1215-2104	1591-1978	1215-2148	1324-1940	1215-2148
ρCO_2 μatm	mean±SD	**190±90.2***	141±96.3	176±65.5	177±106	**135±77.3***	172±95
	min-max	40-585	20-372	87-307	20-585	40-271	20-585
Ω ar	mean±SD	5.96±1.33	**6.87±1.54***	5.93±1.03	6.36±1.61	6.71±1.4	6.29±1.47
	min-max	2.92-9.67	3.97-10.1	4.27-7.61	2.92-10.1	4.54-8.59	2.92-10.1
HCO_3^- (μmol kg^{-1}_{sw})	mean±SD	**1430±232***	1255±287	1396±170	1376±289	**1233±285***	1366±266
	min-max	794-1948	588-1842	1118-1665	588-1948	794-1647	588-1948
CO_3^{2-} (μmol kg^{-1}_{sw})	mean±SD	372±80.4	**427±93***	370±62.7	396±97.2	417±83.8	392±88.8
	min-max	183-590	251-626	267-471	183-626	286-529	183-626

It was only observed a significant difference of DO values among the seasons (ANOVA, $p<0.0001$), the average during the dry period was 5.3± 0.9 mol L^{-1} and during the wet one was 6.87± 1.2 mol L^{-1}. Although it is possible to observe a tendency of variation throughout the day (Fig. 27 E), with the lower values found at the fixed stations during the begging and in the end of the day, while the highest values were recorded around noon.

TA values (Fig. 27B) vary according the daytime and site, with average of 2339± 77 μmol kg_{sw}^{-1} for the study. Early in the mornings, the values were higher and decreased along the day and the samples collected on the fixed stations near the channels were on average higher than the ones collected on the closed and open pools, mean values of 2359± 88, 2314± 35 and 2278± 68 μmol kg_{sw}^{-1} respectively. Salinity was the only parameter constant throughout the study (Table 4), did not vary along the day, nor seasonally or among the sampling groups, and presented a mean value of 35.9± 0.55 (Fig. 27 C).

Metabolic rates

Rates of NEC and NCP calculated using equations (1) and (2), during the slack water period at the fixed stations are presented in Figure 28. Negative and positive values of NEC indicate net dissolution and precipitation of $CaCO_3$ respectively and of NCP indicate net respiration and net photosynthesis respectively. Due to logistical difficulties at the atoll, this analysis could only be done for the shallow tide pools at the extremities of the Farol Island.

The NEC values range was from -18.76 to 39.7 mmol $CaCO_3$ m^{-2} h^{-1} during the dry season and from -10.84 to 16.6 mmol $CaCO_3$ m^{-2} h^{-1} during the wet season. Net dissolution was observed early in the morning during both season, and by the end of the afternoon only during the dry one. The NCP values range was from -49 to 100 mmol C m^{-2} h^{-1} during the dry season and -39.81 to 39.5 mmol C m^{-2} h^{-1} during the wet season. Net respiration was only observed early in the morning during the wet season, and at the end of the day for both seasons.

Hydrodynamics influence

Since it was not possible to calculate the metabolic rates for all the sampling sites applying the slack water equations, it was used the correlation of the salinity-normalized TA (nTA) and DIC (nDIC) values to obtain the NEC:NCP ratios for the different group of sampling sites by season (Fig. 29). Overall from the ratios calculated in this study it was identified that the high organic production relative to the calcification indicates that the primary production exert a great control over the carbonate chemistry in the pools inside Rocas Atoll.

During the dry season, it was observed significant correlations between nTA and nDIC for all the sampling groups of pools. The seawater samples collected at the close pools presented the higher ratio NEC:NCP, 0.30, followed by the shallow tide pools (fixed stations) near the main channels that connect the open ocean water to the lagoon inside Rocas Atoll, 0.18, and the pools connected to the open ocean, 0.15. During the wet season, the ratio NEC:NCP was not significant for the samples collected at the closed pools (0.03). For the samples from the fixed stations, the ratio was slightly bigger, 0.20 and for the open pools remained the same value of 0.15.

Figure 108 - Net ecosystem calcification (NEC, mmol $CaCO_3$ m^2 h^{-1}) and net community production (NCP, mmol C m^2 h^{-1}) of the fixed stations by time of the day and season (dry in blue; wet in red, and theirs smooth lines represent the mean values during the respective season. Positive and negative values are separated by the reference line.

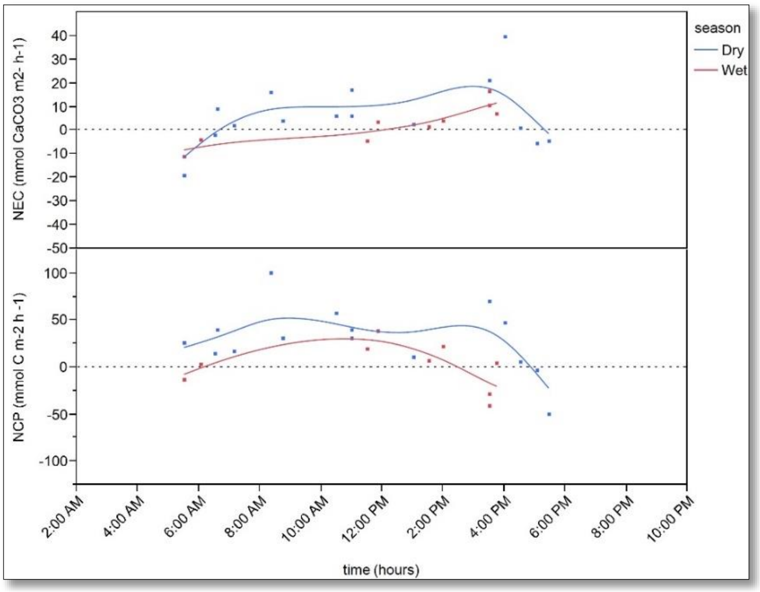
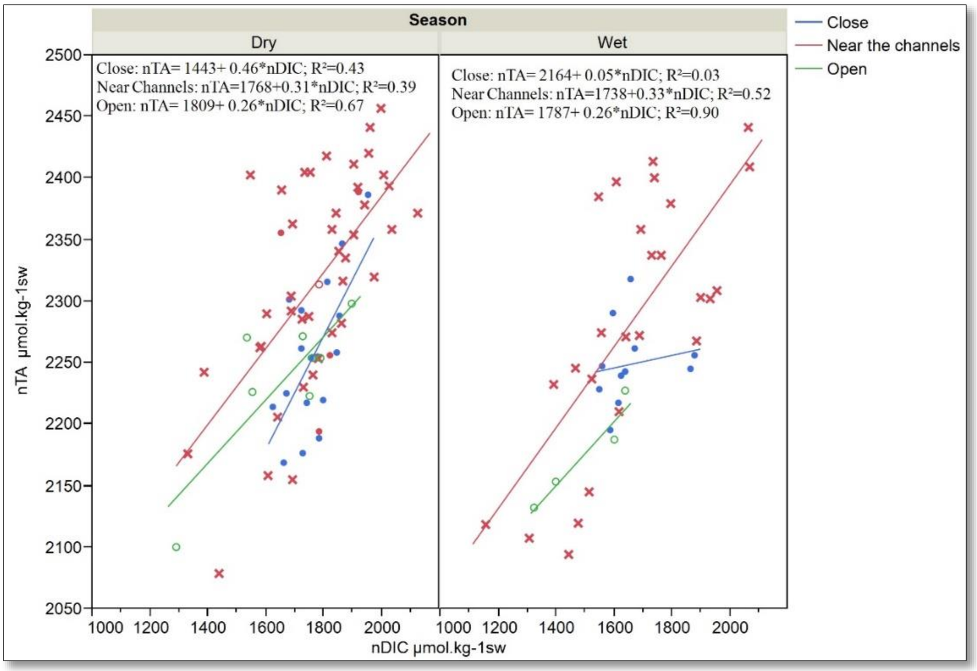


Figure 29 - Total alkalinity versus dissolved inorganic carbon diagram by groups of sampling sites and season. TA and DIC data where normalized to a salinity 36 (nTA and nDIC, respectively) by multiplying the TA and DIC data by the ratio of 36 to the measured in situ salinity. Symbols and regression line in blue represent the samples from the closed pools, in red the ones from the fixed station near the channels and in green, the ones from the pools connected to the open ocean.



7.1.6. DISCUSSION

Dynamics of seawater carbonate chemistry

The huge variability of the physical and chemical parameters collected inside the tidal pools at Rocas Atoll demonstrate the ability of their organisms' metabolism to radically alter open superficial seawater characteristics. Data collected at an oceanographic campaign in 2012, in the surface open ocean around Rocas Atoll, obtained values of 8.13 to 8.21 pH, 2380 µmol kg_{sw}^{-1} TA, 2059 µmol kg_{sw}^{-1} DIC, 3.63 Ω_{ar} and 422 µatm $p$$CO_2$., with are in accordance with the expected values for this region following the models of TAKAHASHI *et al.*, (2014). The mean values obtained for the pools inside the atoll on this study were 8.35 ± 0.17 pH, 2339 ± 77 µmol kg_{sw}^{-1} TA, 1762 ± 186 µmol kg_{sw}^{-1} DIC, 6.29 ± 1.47 Ω_{Ar} and 172± 95 µatm $p$$CO_2$, showing that the biogeochemical variations may arise from its organisms' metabolism, as also related for Indo-Pacific Atolls (SUSUKI; KAWAHATA, 2003; SILVERMAN et al., 2012). One evidence of the biological influence on the seawater carbonate chemistry of Rocas Atoll is due to the similar daily variation between pH and DO mirrored with the variations of pCO_2 and DIC (Fig. 26). Diel cycles in coral reef CO_2 system are largely driven by rates of primary production (ALBRIGHT et al., 2015). It is observed DIC decreasing and pH increasing along the day, while photosynthesis are taking place, and at night, these patterns inverts due to the dominance of respiratory processes (ANTHONY et al. 2011; KLEYPAS et al. 2011; SHAW et al. 2012). Our results showed large variations on some of those parameters along the day, among seasons and sampling sites. The higher ranges were observed at fixed stations in the extremities of Farol Islands, near the main channels that transport the open ocean waters to the lagoon inside the atoll and vice-versa, followed by the pools connected with the open ocean. The closed pools presented the more stable results.

The interactions involving tides, daily solar cycle, and the water volume at the shallow tide pools were the cause for the large temperature variation found at the fixed stations. The Ω_{Ar} values we calculated for these shallow tide pools ranged from 2.92 to 10.13, which are larger than the variability found in previous studies of CO_2 system for a reef environment (SHAW et al., 2012, SILVERMAN et al., 2012). Rocas Atoll differs from other reefs situated in the Caribbean Sea and Indo-Pacific Ocean because it is mainly composed of crustose coralline algae (CCA) and does not present evidence of the joint activity of coralline algae and corals as constructors of the reef (KIKUCHI; LEÃO, 1997; GHERARDI; BOSENCE, 2001). On this reef, the coralline alga *Porolithon* cf. *pachydermum* is a dominant organism and the primary reef constructor, being the basis for the development of secondary constructors such as vermetid gastropods and encrusting foraminifera, mainly *Homotrema rubrum* (VILLAS BÔAS et al., 2005). According to ALBRIGHT et al. (2013), dissolution in supersaturated waters has been reported previously in other reef systems and is believed to be the result of under saturation in pore waters, bio erosion of sediments by endolithic microbes and boring forams, and/or dissolution of more soluble forms of calcium carbonate (e.g., high –Mg calcite). Since approximately 70% of the reef framework at Rocas are constructed by CCA (KIKUCHI; LEÃO, 1997), that are rich in high Mg- calcite, the most soluble form of calcium carbonate, we believe that the dissolution of fragments of CCA and particles of sediment could be one of the causes for this huge availability of carbonate in the water column and therefore in the values of Ω_{Ar} we observed.

Besides the large diurnal variation, our results also show a seasonal variation of the parameters. According to SHAW and MCNEIL (2014), lower latitude regions with depleted nutrient levels have seasonal pCO_2 variability driven by temperature effects where the pCO_2 maximum occurs in summer. When summertime pCO_2 are above the concentration of the atmosphere, the water act as a source of CO_2 to the atmosphere, whereas during the winter the low concentration on the water may cause them to act as a sink. For the Rocas Atoll we observed the higher pCO_2 average and the lowest temperatures during the dry season (Table 4), but in both seasons, the pCO_2 average was lower than the concentration at the atmosphere resulting in a local characteristic of sink of CO_2 all year around.

Calcification and photosynthesis in Rocas Atoll

Concerning the metabolic rates we calculated for the fixed stations, we found a huge variation along the day. The NEC averaged 6.5±13 mmol $CaCO_3$ m^{-2} h^{-1} during the dry season and 2.9 ± 8 mmol $CaCO_3$ m^{-2} h^{-1} during the wet one. However, when transformed those averages to daily rates, the production was 156 mmol (15.6g) $CaCO_3$ m^{-2} d^{-1} in dry season and 69.6 mmol (6.96g) $CaCO_3$ m^{-2} d^{-1} during the wet one, with an annual calcification rate of 4.1kg $CaCO_3$ m^{-2} y^{-1} (assuming 0.5yr for each net rate). This rate is similar to the ones reported for coral reef flat environments in Indo-Pacific (ALBRIGHT et al., 2013).

In our study, NEC was significant correlated with pH and concentration of CO_3^{2-} at both seasons, with highlights the potential impact of ocean acidification over the calcification rates on reefs ecosystems as point out in several studies (KLEYPAS et al., 1999 a, b; HOEGH-GULDBERG et al., 2007; ANDERSSON et al., 2013; KROEKER et al., 2013). Nonetheless, as observed by CHALLENER et al. (2015) for a shallow seagrass- dominated ecosystem in Florida, it is important to point out that the wide variation on the seawater carbonate are essential aspects to consider in the design of OA experiments concerning reef environments. Those authors argue that maintaining static pH and pCO_2 values over the course of an experiment will not reflect natural conditions, once the usual fluctuation may serve as critical periods of organismal recovery from hypercapnic conditions. Therefore, it is recommended special attention to the pH and pCO_2 natural variation when choosing the experimental design of studies addressing the question of the OA influence over the building organisms of Rocas Atoll. The calculated NCP was higher during the dry season at the fixed stations, and showed a huge range along the day. The mean values for this period was 29.7 ± 34 mmol C m^2 h^{-1} and 2 ±25 mmol C m^{-2} h^{-1} for the wet one. However, when we evaluate the ratio NCP:NEC according to the sampling groups and season it wasn't found significant difference between the seasons for the fixed station and open pools. Nonetheless, it is important to point out that for the closed pools the productivity was higher during the wet season with is in agreement with the higher mean DO values we found for this period.

Based on the ratios of NEC:NCP we observed that the organic production (via photosynthesis) relative to calcification indicates that NCP is the primary controlling influence on carbonate chemistry in the pools inside the Rocas Atoll. Studies realized in reef ecosystems at the Great Barrier Reef in Australia also shown this pattern (ALBRIGHT et al. 2013; 2015). It is suggested that the biogeochemical processes happening there play an important role, modulating and interfering on the CO_2 system, as described by THOMPSON et al. (2014), possible due to the potential pH buffering effect of elevated TA and $[CO_3^{2-}]$, which could mitigate some of the effects of OA. In addition, our pCO_2 estimations and our high NCP indicate that Rocas Atoll might serve as a sink, not a source, for atmospheric CO_2, as also observed for reefs in Japan (KAYANNE et al., 1995).

7.1.7. CONCLUSION

This study was the first to characterize the carbonate system for the biological reserve of Rocas Atoll, constituting an initial database to evaluate the effects of increased pCO_2 in the atmosphere, on the chemical characteristics that influence the metabolism of calcifying organisms found at the atoll. The variation of the evaluated parameters is influenced by two biogeochemical processes, the organic and inorganic carbon metabolism. Photosynthesis and respiration were the primary controlling influence for the seawater carbonate chemistry variations of the pools inside the atoll. Our results also indicate a large availability of $CaCO_3$ for calcifying organisms, which are currently undergoing aragonite saturation state values within the range consistent with their metabolic needs. And not only that, the values that we found in this study where elevated compered to others found in reef ecosystems, and suggest that the intense biological activity could mitigate some of the effects of OA and also function as a small local additional sink for anthropogenic CO_2.

8. Capitulo III - EFEITOS DO AQUECIMENTO E ACIDIFICAÇÃO OCEÂNICA SOB OS ORGANISMOS RECIFAIS

Manuscrito 4- Different physiological responses to warming and acidification may increase the potential of phase shifts between hard corals and zoanthids (Cnidaria: Anthozoa). A ser submetido para **Coral Reefs**

Figure 28 – *Palythoa caribaeorum* competindo por espaço com *Porites astreoides* num recife do sul da Flórida- EUA Foto: Barbara Pinheiro, Julho 2015

8.1. Different physiological responses to warming and acidification may increase the potential of phase shifts between hard corals and zoanthids (Cnidaria: Anthozoa).

8.1.1. Abstract

One knows that increasing anthropogenic CO_2 concentrations cause global warming and ocean acidification (OA), and those processes have particularly negative consequences on coral reef ecosystems. The majority of the investigations have been focused on effects of reef- building corals and the transition from hard corals to non-calcifying macroalgae communities. Here we report the effects of OA and thermal stress over physiological characteristics of a hard coral and a zoanthid. *Porites astreoides* showed impacts on the growth rate, photosynthesis, respiration, chlorophyll a concentration and total lipid content, while little or no effect was observed for *Palythoa caribaeorum*. These results suggest that reef communities in the Tropical Atlantic regions may shift from calcifying to a non- calcifying cnidarians under predicted changes on the oceanographic conditions.

8.1.2. Resumo

Sabe-se que o aumento das concentrações do CO_2 antropogênico tem contribuído para problemas atuais como o aquecimento global e a acidificação oceânica. Esses processos apresentam efeitos negativos particularmente sobre os ecossistemas coralíneos. A maioria dos estudos tem focado nos efeitos sobre os corais construtores de recifes e na transição de comunidades de corais duros para comunidades de macroalgas não calcificantes. No presente trabalho nós reportamos os efeitos da acidificação oceânica e do stress térmico sobre as características fisiológicas de um coral duro (*Porites astreoides*) e um zoantídeo (*Palythoa caribaeorum*). Foram observados impactos sobre a taxa de crescimento, fotossíntese, respiração, concentração de clorofila-a e conteúdo lipídico total, sobre o *P. astreoides*, enquanto pouco ou nenhum efeito foi observado sobre o *P. caribaeorum*. Esses resultados sugerem que as comunidades coralíneas na região do atlântico tropical podem sofrer uma substituição passando de organismos calcários para comunidades de cnidários não calcificantes sob as mudanças previstas das condições oceanográficas.

8.1.3. INTRODUCTION

Anthropogenic activities such as burning of fossil fuel and deforestation are increasing carbon dioxide (CO_2) concentrations in the atmosphere. Nowadays, records monitored by the SCRIPS/ UCSD observatory in Mauna Loa, Hawaii are above 400 μatm, and the year 2015 hit record high average, 400.88μatm. One of the most alarming effects of this CO_2 elevation in the atmosphere is the increase of global average temperature, that over the last thirty years has being raised by 0.2°C per decade (HANSEN et al., 2006). The oceans have been absorbing much of that heat such that the frequency and intensity of extreme thermal stress events have increased dramatically. According to MUMBY and VAN WOESIK (2014), in the 1980s and 1990s, El Niño events were associated with some of the most detrimental thermal stress events on coral reefs. Most recently, however, thermal stress events independent of El Nino have been witnessed, due to elevated background temperatures being forced higher by global warming.

The "other CO_2 problem" rises from the fact that approximately one-quarter of the anthropogenic CO_2 released into the atmosphere each year is absorbed by the global oceans. This excess CO_2, throughout a series of chemical reactions, causes a process known as ocean acidification (OA), that represents measurable declines in surface ocean pH, carbonate ion concentration ($[CO_3^{2-}]$) and saturation state of carbonate minerals (Ω) (DONEY et al., 2009). OA represents a threat to marine species worldwide, and predicting the ecological impacts of acidification is a high priority for science, management, and policy (KROEKER et al., 2013). According to HOEGH-GULDBERG et al. (2007), reef ecosystems are among one of the most threatened environments. Impacts of OA on the marine calcifiers (organisms that depend on the carbonate ions available on the seawater to build their skeletons, shells, etc.) are constantly being reported around the world, affecting physiological processes such as growth, calcification and photosynthesis (DUPONT et al., 2010; ALBRIGHT; LANGDON, 2011; FABRICIUS et al., 2011; MELZNER et al., 2011). Those changes in the physiology of individuals can alter the dynamics of their populations and ultimately affect entire ecosystems (IGLESIAS-RODRIGUEZ et al., 2016).

As climate change alters oceanographic conditions, the geographic range of ocean habitat suitable for the growth of coral reef ecosystems is shifting. Corals of the order Scleractinia provide the foundation of shallow-water coral reef ecosystems. Scleractinian corals secrete calcium carbonate skeletons, which accumulate as reef structures that in turn support highly biodiverse communities (FREEMAN et al., 2013). According to MUMBY and VAN WOESIK (2014), who review a series of impacts on coral reef systems with the warming and acidification of the oceans corals, calcified algae, urchins and reef fish may decline in the future, whereas algal turfs, non-calcifying macrophytas and non-calcifying zooxanthellate cnidarians should benefit from elevated dissolved inorganic carbon. ALBRIGHT et al. (2016) run an *in-situ* experiment, manipulating the carbonate chemistry of a reef in Australia and concluded that the present day conditions may already be impairing coral growth.

Phase shifts on coral reefs are characterized by a decrease in abundance or coverage of corals, followed by a persistent increase in non-reef builders such as algae and soft corals. The consequence of this phenomenon is the loss of reef-building capacity, which is responsible for maintaining the structure of the reef and its structural complexity, therefore, the reef loses the capacity to maintain its local diversity (CRUZ et al. 2015a, and references therein). Nonetheless, predictions about the ecological consequences of oceanic uptake of CO_2 are particularly focused on calcifying organisms that play critical roles in the formation of habitats or their maintenance (CONNELL; RUSSELL, 2010). According to CRUZ et al. (2015a), most of the studies predicting phase shift scenarios on reefs due to the impacts of climate change and other anthropogenic effects address the change from a coral-dominated community to an algal-dominated community. This focus overlooks the direct effects of ocean warming and acidification on non-calcareous taxa, particularly those that play critical roles in ecosystem shifts.

Understanding how CO_2-enhanced productivity of non- and less- calcifying anthozoans applies more widely to tropical ecosystems is a priority where such organisms can dominate benthic ecosystems, in particular following localized anthropogenic stress (SUGGETT et al., 2012). In fact, a phase shift from a coral dominated to a zoanthid (*Palythoa* cf. *variabilis*, initially identified as *Epizoanthus gabrieli*) dominated reef have been reported (CRUZ et al., 2015a, 2016) and this also effects the reef fish communities (CRUZ et al., 2015b). *Palythoa caribaeorum* Duchassaing and Michelotti, 1860 is considered a strong competitor when interacting with other organisms for space on the reef (BASTIDAS; BONE, 1996, RABELO et al., 2013). Brazilian coastal reefs, for instance, are covered mainly by zoanthids, and the dominant species is *P. caribaeorum*, which is common in the western Atlantic (ACOSTA; GONZALES, 2007; SILVA et al., 2015). Therefore, investigation of physiological impacts of

OA and warming on this organism, would contribute to the predictions of phase-shift scenarios from hard to soft-bodies cnidarians in the reefs of the future.

The present study measured the growth, photosynthesis, respiration, total lipid content and chlorophyll *a* concentration of a calcifying and a non- calcifying cnidarian over thermal and acidification stresses. We compared these physiological responses among the organisms that were pre-conditioned to high and low pCO_2 treatments on ambient temperature (27°C) during the first phase with the effects of the pCO_2 treatments and warming (31.5°C) at the second part of the research. The aim of this study was to evaluate the cnidarians metabolic differences when submitted to the same stress condition, shedding light on the important question in the field of eco-physiology and conservational science, of which will be the “winner” and “loser” organisms on the reefs of the future.

8.1.4. MATERIALS AND METHODS

Collection and experimental design

Colonies of the scleractinian coral *Porites astreoides* Lamarck, 1816 (3) and the zoanthid *Palythoa caribaeorum* (4) were collected off Miami Beach (25.84716°N; 80.10425°W), by Scuba divers with hammer and chisel, from aproximately 5m depth and transported in coolers back to the University of Miami (UM). Cores were removed from the parental coral colonies using a handheld drill fitted with a 7.85 cm^2 round diamond tipped coring bit. Zoanthid colonies were cut in pieces of 17.1 ±3.21 $cm^2$with sterilized razors, and placed in tanks under control conditions (27 °C, pCO_2 400µatm) to recover for two weeks prior to the beginning of the experiment. During this process, some zoanthid pieces showed tissue necrosis and were subsequently removed from the tanks, treated with lugol, and allowed to recover in separete tanks with the same conditions. The pieces that showed more of 50% necrosis were replaced by new pieces. The research was realized in the summer of 2015, at the South Florida Corals and Climate Change laboratory at the UM Rosenstiel School’s Experimental Hatchery. For detail description of the aquaria set-up, see TOWLE et al. (2015a).

The study consisted of two phases: the first one (P1) with high (~900 µatm) and low (~400 µatm) pCO_2 treatments at 27°C, (from July 15th to August 14th) and the second phase (P2, from August 14th to September 11th) also with high and low pCO_2 treatments but the temperature was set at 31.5°C, to evaluate the impact of warming on pre-aclimated CO_2

conditions. Each treatment was replicated twice. In total, 72 cores/pieces of each organism were analyzed. All pieces were distributed among the tanks in the beginning of the first phase (18 cores/pieces per tank). By the end of this phase half of them were collected and frozen (-80°C) for posterior analyses. For the second phase only 9 cores/pieces of organisms were kept in the treatment tanks until the end of the experiment, then also frozen for analyzes. The organisms were fed twice a week with powdered zooplankton.

Seawater chemistry

Two to three times a week, around 12pm, temperature and salinity were measured by a handheld salinity, condutivity and temperature system (YSI model 30) and discrete water samples were taken from each tank and poisoned with mercuric chloride to be analyzed for dissolved inorganic carbon (DIC) and total alkalinity (TA). DIC was measured using a DIC Analyzer (Apollo Sci-Tech Inc.) and TA mesured on an automated Gran titrator (developed by C. Langdon) and standardized using certified reference material from Dr. A. Dickson (Scripps IO). The mean temperature, salinity, TA and DIC were used to calculate pCO_2, pH and aragonite saturation state (Ωar) for each treatment using the CO_2Sys Excel Macro (PIERROT et al., 2006). The carbonic acid dissociation constants from MEHRBACK et al. (1973) refitted by DICKSON and MILLERO (1987) were adopted , as well as the bisulfate ion dissociation constant described by DICKSON (1990).

Physiological measurments

Four days prior to the end of each phase photosynthesis and respiration were measured on 9 cores/pieces of each organism taken randomly from all the tanks. Corals were incubated in 225 mL chambers, and zoanhids in 485 mL chambers at the Hatchery and transported to Dr. Chris Langdon’s Lab across the street where a temperature controlled water bath was set-up. The incubation was continuously stirred with a magnetic coupled stirring bar for about one hour and the artificial light provided by a lamp was about 300 µmol photons m^{-2} s^{-1}. The difference between the photosynthesis (P) batch and the respiration (R) was that the chambers were carefully wrapped in aluminum foil during the tests. Therefore the respiration rate was obtained from the measurement of net photosynthesis in the dark. Duplicate samples from seawater were taken from the tanks just prior the organisms being trapped in the chambers and fixed for posterior analyzis. Duplicate chambers containing only seawater were used as blanks and recieved the same procedure as the chambers containing organisms. After the incubation period, seawater samples were collected and fixed for dissolved oxygen (DO) analyzis. DO (µM) was measured using an automated titrator following the Winkler methodology as described in STRICKLAND and PARSONS (1972). P and R rates were estimated by the production or consumption of oxygen and normalized by the volume of the chamber, organisms' surface area and time of incubation. The gross photosynthesis (GP, total oxygen production) rates represent the photosynthetic activity of the endo-symbiotic algae, and are achieved independently of the host respiration measurements (GP=P+R). Initial O_2 concentrations in each experiment and treatment were close to 200mmol.kg^{-1} (the expected saturation concentration at 26°C and 35ppt), and absolute O_2 concentrations never fell below 160 mmol.kg^{-1}, 80% of saturation (2mg.L^{-1} or ~60 mmol.kg^{-1} is typically identified as physiologically stressful by the EPA and NOAA).

For the analysis of lipid content and chlorophyll *a* (chl.*a*) concentrations, the organisms collected by the end of each phase were unfrozen and the coral tissue was completely removed from the skeleton using an air- pick and filtered seawater (0.45µm), then homogenized. For the zoanthids, an area of 2.25cm² was cut in the center of each piece, ground with filtered seawater, then homogenized. The volume of the total blastate was recorded for each core or piece of organism. An aliquot of 5 mL (for lipids) and another of 2 mL (for chlorophyll *a*) were filtered onto GF/A filters and frozen at -80°C until further analysis. Total lipid mass was analyzed according TEECE et al. (2011) and chl. *a* following HOLM-HANSEN and RIERMANN (1978), both briefly described in TOWLE et al. (2015b). Those data were normalized by the organisms' surface area. For corals the surface area was estimated by the aluminum foil density method (MARSH, 1970 described in VEAL et al., 2010), and the pieces of zoanthids were photographed to have their surface area measured using the ImageJ software. The growth rate (cm². d^{-1}) was estimated by the difference between the surface area at the beginning and at the end of each phase divided by the correspondent number of days.

Data Analysis

The response of the following physiological variables was tested with a oneway ANOVA: growth, photosyntesis, respiration, lipids and chlorophyll *a*, with the phase as fixed factor and by CO_2 treatment (high and low) and organism (coral and zoanthid). A significance level of 0.05 was adopted. Prior to running any analysis, the data were checked for normality and homoscedasticity with Kolmogorov-Smirnov and Bartlett's tests, respectively. To explore potential relationships between the physiological measurements and the carbonate chemistry of the seawater during the study we conducted a Principal Component Analysis (PCA). All statistical analyses were performed in the program JMP®10.0.2.

8.1.5. RESULTS

A significant difference ($p>0.05$) was observed in the carbonate chemistry parameters among the study phases (Table 5). However, high and low treatments were considered independently at each phase, where during P1, the pCO_2 treatment was characterized by high= 985± 211 µatm and low= 438± 42.8 µatm; and during P2: high= 1096± 208 and low= 517± 82.3 µatm. Therefore, during the first phase, the impact of the high and low pCO_2 treatment at 27°C on the physiological parameters was evaluated, while during the second phase, the effect of warming (31.5°C) and more acidified waters was investigated.

Table 5. Summary of the mean (±SD) water chemistry parameters throughout the study period.

Parameters	**Phase 1**		**Phase 2**	
	Low	**High**	**Low**	**High**
Temperature (°C)	27± 0.14	27± 0.27	31.4± 0.13	31.5± 0.3
Salinity	37.5± 0.9	37.6± 0.9	34.9± 1.13	35± 1.17
DIC µmol.kg^{-1}	1950± 43.8	2109± 61.8	2020± 59.1	2165± 57.1
TA µmol.kg^{-1}	2252± 48.2	2266± 55.8	2320± 43.7	2329± 52.6
pH (total scale)	8.00± 0.04	7.71± 0.09	7.95± 0.05	7.68± 0.08
pCO_2 µatm	438± 42.8	985± 211	517± 82.3	1096± 208
ΩAr	3.32± 0.28	1.96± 0.35	3.59± 0.33	2.18± 0.35

Significant differences in the growth rate among the organisms was observed (ANOVA, F= 40.085, $p<0.0001$). For *P. astreoides* the average growth during P1 was 0.187 ±0.088 and 0.093 ±0.059 cm². d^{-1} during P2. The coral cores showed a faster growth rate on the low pCO_2 treatment during the second phase (ANOVA, F= 6.79, p=0.0131). *P. caribaeorum* showed a reduction in the mean surface area during P1, while the second phase mean growth rate was 0.1±0.06 cm². d^{-1} (Fig. 29-I). The organisms show different intensity of their metabolic rates (ANOVA, F= 98.781, $p<0.0001$ for GP and F= 302.655, $p<0.0001$ for R and F= 6.438, p= 0.0125 for GP: R ratio). Coral cores revealed higher metabolic rates then zoanthid pieces in the course of the incubations (Fig. 29, II-IV). *P. astreoides* GP rates were higher in P2 (33±10 nmol

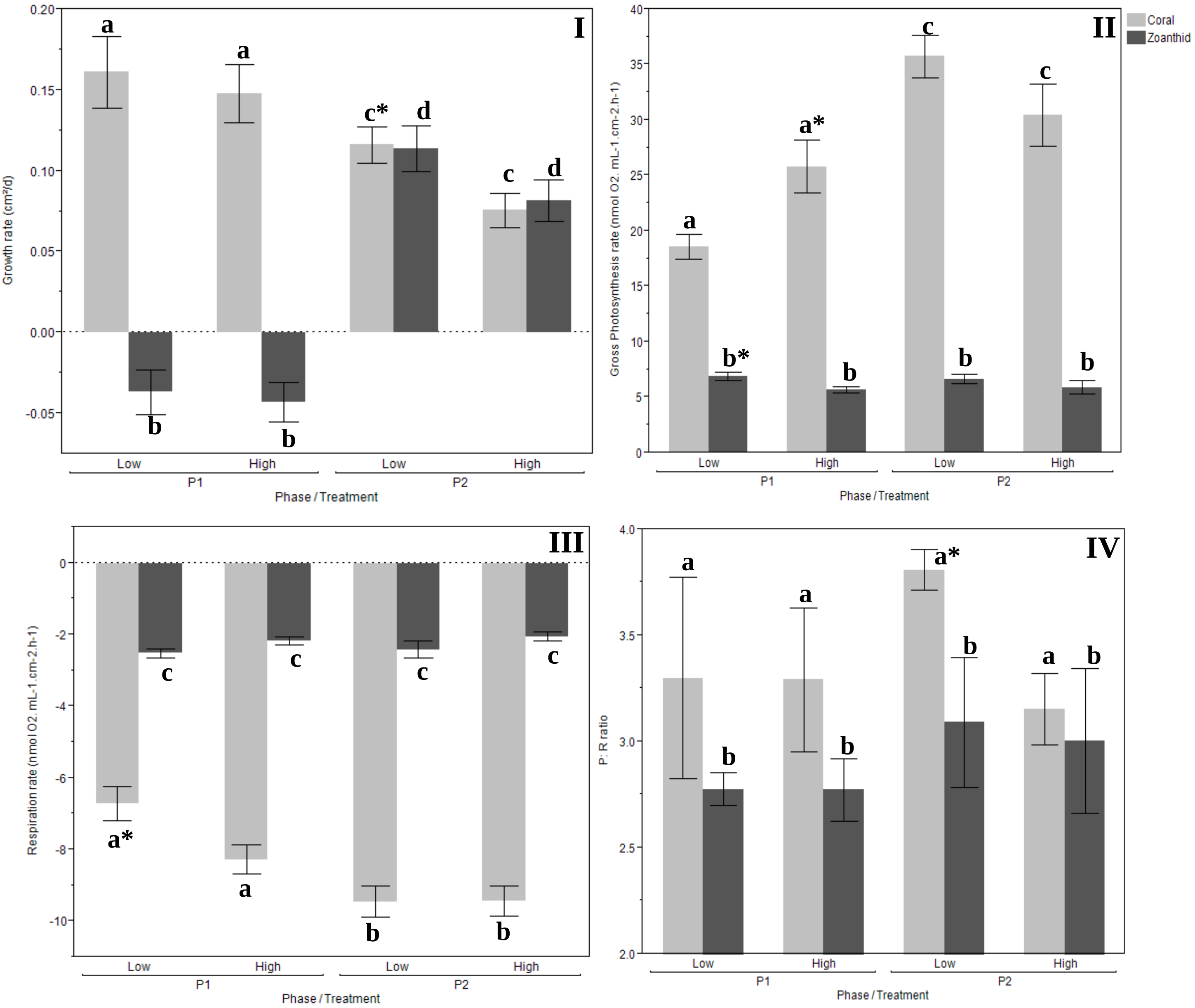
O_2. mL^{-1}. cm². h^{-1}) than during P1 (22.7±7.41nmol O_2. mL^{-1}. cm². h^{-1}). Over the first phase *P. astreoides* showed higher GP rates at the low pCO_2 treatment (ANOVA, F= 6.218, p=0.0220), while *P. caribaeorum* at the high treatment (ANOVA, F= 6.239, p=0.0195, Fig. 29, II). The mean oxygen consumption was also higher throughout the second phase for *P. astreoides*. However, higher rate of oxygen consumption in the high pCO_2 treatment during P1 was observed (ANOVA, F= 5.99, p=0.0191).

The average respiration rates were -7.5±2.12 and -9.87 ±1.73 nmol O_2. mL^{-1}. cm². h^{-1} during P1 and P2, respectively, for the coral cores, while the zoanthid pieces were -2.3±0.54 and -2.2±0.81 nmol O_2. mL^{-1}. cm². h^{-1} in P1 and P2, respectively (Fig. 29, III). The mean GP: R ratio for P. astreoides was 3.4±0.92 while for *P. caribaeorum* was 2.9±1.07. A significant difference in the GP:R ratio of *P. astreoides* in the low pCO_2 treatment (3.81±0.38) during the second phase was observed (Fig 29. IV).

Chlorophyll *a* concentration and total lipid content also vary among the organism (ANOVA, F= 381.001, p<0.0001 for Chl. *a* and F= 302.655, p<0.0001 for lipids), however, for those parameters, *P. caribaeorum* presented the higher means. The only significant variation on the Chl. *a* concentration was among phases (ANOVA, F= 4.468, p=0.0363). *P. astreoides* showed an elevated concentration during the second phase (1.03±0.57 µg. cm-²) compared to 0.73±0.23 µg. cm^{-2} recorded during P1 (Fig. 30, I). However, an inverse behavior was observed for the total lipid content. The mean *P. astreoides'* content was higher in P1 (5.67±2.06 $mg.cm^{-2}$), and decreased to 3.9±0.72 $mg.cm^{-2}$, during P2 (Fig. 30, II). *P. caribaeorum* showed elevated lipid content during the second phase at the low pCO_2 treatment (ANOVA, F= 15.37, p=0.0007).

The interactions between seawater physical and chemical parameters and physiological factors were further investigated with PCA. Those analyzes revealed that two sets of components explained 61.9% for *P. astreoides* (Fig. 31a) and 58.4% for *P. caribaeorum* (Fig. 31b) of the variances observed during this study. When submitted to different temperature and pCO_2 conditions the results for the coral species showed that total growth and respiration rates increased with low temperature and low pCO_2 concentrations. Both, total lipid and Chl. *a* concentration were influenced by of the temperature, Chl. *a* had a positive correlation, and lipids decreased at high temperatures. Gross photosynthesis rates were positively correlated with temperature and negatively with salinity.

Figure 11 - *P. astreoides* (light gray) and *P. caribaeorum* (dark gray) physiological responses over the different phases (P1- 27°C; P2 -31.5°C) and pCO_2 treatments (High and Low). I - growth rate (cm^2. d-1), II - gross photosynthesis rate (nmol O_2. mL^{-1}. cm^2. h^{-1}), III- respiration rate (nmol O_2. mL^{-1}. cm^2. h^{-1}, negative values represent consumption of oxygen during the incubation) and IV- GP: R ratios. Error bars represent the standard deviation. Different letters represent significant variation of the means between the organisms and phase, while asterisk indicate difference among the pCO_2 treatments within each phase (ANOVA, $p<0.05$).



It was also observed that a small, but positive influence of the CO_2 treatment on the GP rates had occurred (Fig. 29 II). *P. caribaeorum* results reveal that chlorophyll *a* and GP rates had little or almost no correlation with abiotic parameters. Respiration rates and total lipid contents were more influenced by the CO_2 treatments such that, respiration showed a small but positive correlation with pCO_2 and DIC, while lipids showed positive correlation with pH and salinity. The growth rate seems to be only influenced by temperature.

Figure 30 - *P. astreoides* (light gray) and *P. caribaeorum* (dark gray) chlorophyll a concentration (I- µg. cm^{-2}) and total lipid content (II- mg. cm^{-2}) over the different phases (P1- 27°C; P2 -31.5°C) and pCO_2 treatments (High and Low). Error bars represent the standard deviation Different letters represent significant variation of the means between the organisms and phase, while asterisk indicate difference among the pCO_2 treatments within each phase (ANOVA, $p<0.05$).

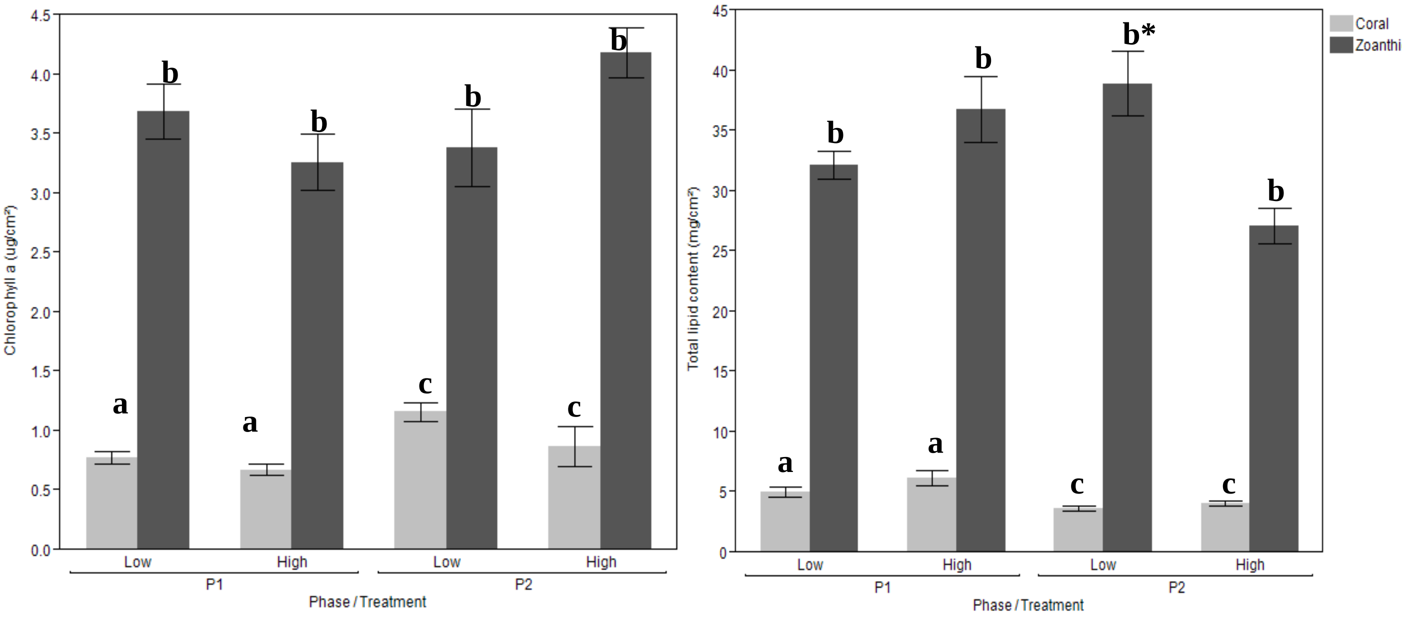
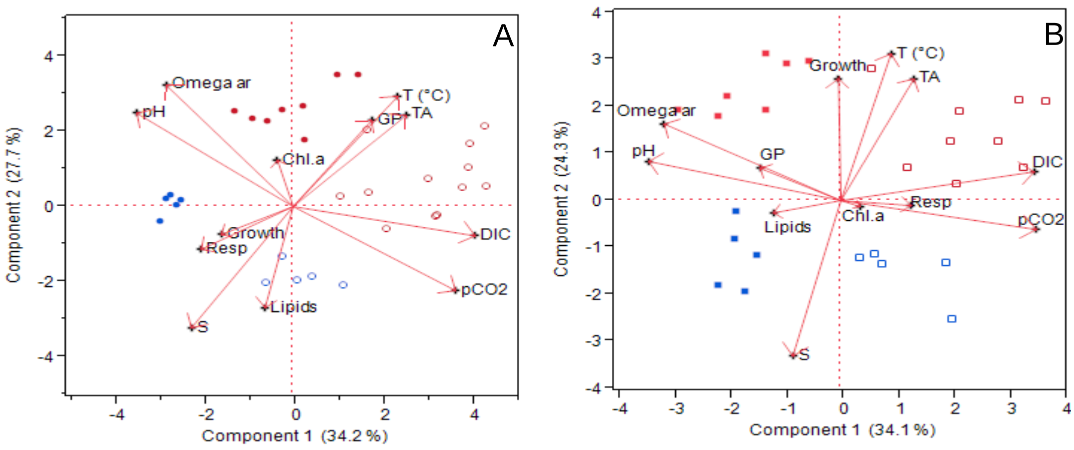


Figure 121 - Principal component analysis between the seawater parameters and physiological factors for *P. astreoides* (A) and *P. caribaeorum* (B). Blue represent data from the first phase (27°C) and red from the second (31.5°C). Open symbols represent data from the high CO_2 treatment and closed symbols from the low CO_2 treatment. Corals are represented by circles and zoanthids are indicated by squares.



8.1.6. DISCUSSION

The present study examined the physiological responses of two common cnidarians species of the Caribbean/Tropical Atlantic regions. *P. astreoides*, a calcifying scleractinian coral showed clear impact of warming and acidification on its metabolism, while little effect was observed in *P. caribaeorum*, a non-calcifying zoanthid. The influence of increase temperature and/or pCO_2 on *P. astreoides* is well documented. Impacts on multiple early life history processes were reported, such as larval availability (gamete production, fertilization, etc.), larval settlement, post settlement growth, metabolism and survival (ALBRIGHT et al., 2008, ALBRIGHT; LANGDON, 2011). Also impacts on, respiration and photo-physiology (EDMUNDS, 2012) calcification and extension rates (COOK et al., 2013, VENTI et al., 2014, MANZELLO et al., 2015) on adult colonies, concluded that this species can be or already is affected by global change impacts in the oceans. Nevertheless, for *P. caribaeorum* only one study reported impacts of OA and warming on the association zoanthid/symbiont, providing evidence that *P. caribaeorum* -*Symbiodinium* spp. are more likely to prevail in warm and acidified oceans (GRAHAM and SANDERS, 2016). In fact, there is only a few studies reporting those effects on non-calcifying cnidarians. SUGGETT et al., (2012) examined an increased growth of sea anemone population along a natural CO_2 gradient at Vulcano, Italy; TOWANDA and THUESEN (2012) observed growth of the algal symbionts in intertidal sea anemones under elevated CO_2 conditions and INOUE et al. (2013) reported a dominance of a soft coral in acidified zones in natural CO_2 seep in Japan.

The *P. astreoides* growth reported here was influenced by temperature, with a decrease of 50.3% on the growth rate from the first (27°C) to the second phase (31,5°C), which is in accordance with the findings by MANZELLO et al., (2015) that showed heat stress negatively correlates with calcification of *P. astreoides*. Elevated pCO_2 conditions also affected the *P. astreoides* growth. The influence of acidified conditions on the coral growth was observed during the second phase, higher growth rates on the low pCO_2 treatment were observed. Moreover, a trend toward lower growth rate for the *P. astreoides* under high CO_2 conditions in the first phase was witnessed. Although this different was not significant, it is believed that if we had evaluated the calcification rate, we could also find the effect of the pCO_2 treatment on the first phase. CROOK et al., (2013) also did not find significant differences on the linear extension rates ($cm.y^{-1}$) for the *P. astreoides* in undersaturated waters ($\Omega_{arag} < 1$) compared to ambient conditions ($\Omega_{arag} > 3.5$), but they reported a significant decline in the annual calcification rates. They predicted a decline of 30% in calcification from ambient conditions by the time Ω_{arag}=2 and up to 66% comparing ambient to $\Omega_{arag} < 1$. They attributed this decrease in calcification to a decrease in skeletal density with decreasing Ω_{arag}. Therefore, it is likely that CO_2 conditions would be also influence the calcification of *P. asteroides* in the first phase of the study if we had measured this parameter.

As for *P. caribaeorum*, the decrease in the growth rate observed during the first phase of the study seems to have been more influenced by the slower healing process of the fragmentation two weeks prior the beginning of the experimental phase, than the impact of the stress conditions. During the second phase, the zoanthids started to grow even though, the mean rate observed for low CO_2 conditions on this phase (0.132 ±0.79 $cm^2. d^{-1}$), was slower than reported for natural conditions (0.36 $cm^2. d^{-1}$, RABELO et al., 2013). We observed a small tendency of impact on the growth on the high CO_2 treatment; however, further studies are necessary to draw conclusions about the effect of increased CO_2 conditions on the growth rate of *P. caribaeorum*.

It was determined that there were significantly higher means of gross photosynthesis, respiration and chl. *a* for the *P. astreoides* cores with the increase of temperature during the second phase. Those metabolic results are related to the zooxanthellae production and it is well known that the host-symbiont association is affected by temperature and may cause expulsion of the symbionts causing bleaching (NAKAMURA et al., 2004). It has been shown that corals undergo vast physiological changes before bleaching occurs. The loss of zooxanthellae at high temperatures was suggested to be a final strategy to defend corals from oxidative stress, once the heat stress leads to production of active O_2 by the photosynthesis, which subsequently causes cellular damage and expulsion of the symbiont (AL HORANI, 2005). Therefore, the increase in those metabolic rates has a maximum temperature tolerance. If the heat stress is too intense, or lasts for long periods, the corals lose their symbionts, and there is a decrease in their metabolism (HOEGH-GULDBERG, 1999). FUJIMURA et al. (2008) and HENNIGE et al., (2010), also reported similar results of the rising temperature effects on the coral metabolic rates. According to MANZELLO et al., (2007) the bleaching threshold for corals on the Florida Keys is 30.4°C. During the present study, the temperature in the second phase was setup at 31.5°C, however, only few coral cores were observed became pail (4) or bleached (2) (PINHEIRO, pers. obs).

It would be expected that, as a zooxanthellate anthozoan like *P. astreoides*, respecting the degree of inter and intra specific variation, *P. caribaeorum* presented the same variations, however GRAHAM and SANDER (2016), demonstrated that the response of symbiotic cnidarians to thermal stress and OA must be considered on a host-specific and symbiont-specific basis. It was shown that warming did not affect carbon fixation or fixed carbon translocation in the *Zoanthus* sp./A4 association, and high pCO_2 increased carbon fixation. In contrast, both thermal stress and high pCO_2 inhibited carbon fixation in the *Palythoa* sp./C1 association. However, carbon fixation increased in C1 symbionts when maintained at combined high temperature (31 °C) and pH 7.65 (GRAHAM; SANDER, 2016). According to KEMP et al. (2006) *P. caribaeorum* from south Florida reefs harbored two genetic types of zooxanthellae, C1 and D1a and individual colonies may contain populations of only C1 or D1a, or combinations of C1 and D1a. In the present study *P. caribaeorum* did not show significant effect on respiration and chl.*a* concentrations, but during the first phase an increase of 17.37% in the GP ratios on low pCO_2 treatment was detected (Fig. 32, II). However, when evaluating the GP:R ratios the impact of acidified conditions on this species association was not detected. It is suggested that *P. caribaeorum* could have a high tolerance for internal hypercapnic conditions, as observed for other non-calcifying alga- invertebrate symbioses (HALL-SPENCER et al., 2008; TOWANDA; THUESEN, 2012), but further investigation is needed in order to test this hypothesis.

An influence of pCO_2 levels on the total lipid contents of *P. astreoides* was not detected however, with the increase of temperature in the second phase, a mean reduction of 31.22% was observed. This result is in accordance with TOWLE et al. (2015b), which studied *in-situ* metabolic rates of *P. astreoides* in the Florida Reef Tract, and reported that lipid content was significantly affected by season; with a decrease on the *P. astreoides* lipid content and elevated mean sea surface temperatures during summer. Moreover, partial or complete loss of zooxanthellae by the coral host is accompanied by significant variations in total lipid content and lipid class proportions in coral colonies (IMBS, 2014). TEECE et al. (2011) showed that zooxanthellae are the dominant source of fatty acids for corals, however, *P. astreoides* could exhibit great plasticity in their ability to switch from autotrophic to heterotrophic nutritional inputs. Here, both, coral and zoanthid, received the same food regime, being feed twice weekly with powdered zooplankton. It has been shown that vulnerability of corals to disturbance can be influenced by their energetic status, and lipid reserved stored by corals may allow them to increase their resilience and resistance to stress (TEECE at al., 2011; TOWLE, et al., 2015a). In the present study the total lipid content for *P. astreoides* ranged from 3.68 to 6.21 mg. cm^{-2} while the *in situ* values reported in TOWLE et al. (2015b) were 2.3 to 3.5 mg. cm^{-2}. Although those concentrations could be indicative of enough energy stored to keep up with the OA effects, still, temperature showed to have influence in the total lipid content in *P. astreoides*.

An influence of the pCO_2 treatment on total lipid contents for *P. caribaeorum* was not detected during the first phase. However, the combined effect of elevated temperature and the prolonged pCO_2 conditions caused a reduction in the total lipid contents on the zoanthids submitted to a higher acidified stress. Based on current knowledge, this is the first study to investigate the impact of warming and OA on total lipid contents on zoanthids. There are three studies on the lipid and fatty acid (FA) composition of *Palythoa* spp. The first, by MIRALLES et al. (1989), reported the FA composition of five Senegalese *Palythoa* spp.; followed by a study of FA composition of total lipids and major phospholipids of *P. caribaeorum* from Puerto Rico (CARBALLEIRA; REYES, 1995) and most recently a study about lipid class and FA composition of *Palythoa caesia* from the South China Sea (IMBS, 2014). Investigations of *P. caesia* uncovered the peculiarities of lipid classes and FA composition that distinguish zoanthids from reef-building and soft corals. According to IMBS (2014), *P. caesia* contained significantly more structural lipids (polar lipids and steroids) and less reserve lipids (triglycerides) than reef building corals. Many answers remains unknown, partly because the total lipid content can come either from the host itself or from other associated organisms. Therefore, additional studies are necessary to determine the actual impact of warming and OA on *P. caribaeorum* lipid content.

However, results of the principal component analyses for both organisms studied here indicated that the physiological aspects of the zoanthid had less or no impact to warming and OA when compared to the reef building coral. Therefore, if raising atmospheric CO_2 and its consequences do not have a negative effect on its metabolism, it would be expected that *P. caribaeorum* could enhance its abilities as a voracious competitor on the reef. Future studies should aim to determine the impact of thermal and acidification stress on different zoanthid genotype metabolisms or on the production of *P. caribaeorum* mucus (that protects the organism from desiccation and has powerful toxins against predators). Additional future studies should aim to identify how (or if) those organisms will adapt (or not) to upcoming oceanographic conditions predicted for the end of the century. So far, there have been reported phase- shifts from corals to soft- corals in high CO_2 zones in Japan (INOUE et al., 2013) and an increased growth of sea anemone papulation along a natural CO_2 gradient in Italy (SUGGETT et al., 2012). CRUZ et al. (2015a) reported a shift from a coral to a zoanthid dominant reef in Brazil, but they argue that the loss of coral cover may be a result of local anthropogenic disturbances. However, given the large number of human impacts, the specific causes of this shift was not conclusive. This study suggests that warming and ocean acidification could induce shifts from hard coral- to zoanthid-dominated communities in the Tropical Atlantic regions.

9. CONSIDERAÇÕES FINAIS

Os organismos construtores do atol estão sob influência dos efeitos da crescente concentração de CO_2 atmosférico. Essas mudanças podem causar alterações nos padrões de distribuição, dinâmica populacional e equilíbrio do ecossistema recifal do Atol das Rocas. Os parâmetros abióticos estão relacionados com ciclo diurnos de maré, insolação e volume de troca de água nas piscinas. O metabolismo dos organismos (fotossíntese, respiração, calcificação, dissolução, excreção e decomposição) também influenciaram a disponibilidade espaço-temporal dos nutrientes em um ambiente oligotrófico. Foi observado que a disponibilidade de nutrientes inorgânicos na água do mar pode contribuir para a distribuição dos organismos no atol, uma vez que locais com dominância de macro e tufos de algas estiveram associadas com maiores concentrações de nutrientes dissolvidos. E além disso, ambientes com alta frequência de organismos carbonáticos podem estar associados com uma diminuição da concentração de alcalinidade.

Baseado nos dados de reprodução, crescimento e distribuição de frequência da população da espécie *Siderastrea stellata*, coral dominante nas piscinas do atol, foi observado que a população dessa espécie se mostra com um alto potencial de manutenção e recuperação. Uma vez que essa apresenta elevada taxa de crescimento e boa representatividade de colônias adultas e jovens. Os dados apresentados devem contribuir com a construção de modelos que poderão auxiliar na conservação e manejo dessa população, além de uma melhor compreensão sobre sua vulnerabilidade aos impactos das mudanças globais. Os dados obtidos foram importantes para indicar que o ecossistema ainda se encontra em equilíbrio, sendo de extrema importância a continuação de estudos de longo prazo para identificar se o aumento do CO_2 trará mudanças individuais ou estruturais, sendo esta última a mais provável em consequência do desequilíbrio ecológico que poderá se instalar. Falhas no recrutamento e na reprodução como observamos, precisam ser melhor avaliadas para se obter melhores conclusões sobre os impactos na estrutura dessa comunidade. Estudos sobre dispersão larval e taxas de fecundidade dos pólipos podem elucidar questões sobre um possível efeito das mudanças globais.

Esse estudo foi o primeiro a caracterizar o sistema carbonato marinho para o Atol das Rocas. Os dados obtidos poderão servir de base para avaliar os efeitos da elevação do CO_2

atmosférico sob as mudanças previstas das características físico-químicas do oceano e as consequências na fisiologia dos organismos encontrados no atol. As variações dos parâmetros analisados foram relacionadas com os metabolismos orgânico e inorgânico do carbono como a fotossíntese e respiração que foram os principais fatores que interferiram na variação do sistema carbonato. Além disso, os nossos resultados indicam uma grande disponibilidade de carbonato dissolvido nas piscinas do atol. A calcificação e a dissolução influenciaram os índices de saturação de aragonita que não só suprem as necessidades metabólicas dos organismos, como estão acima dos observados para outros ambientes recifais. Desta forma, é possível que a intensa atividade biológica no atol das rocas possa mitigar alguns dos efeitos da acidificação oceânica.

Os resultados dos experimentos com espécies de coral e zoantídeo que ocorrem no atol (*Porites astreoides* e *Palythoa caribaeorum*), coletadas no Sul da Florida, mostraram que a espécie de coral duro construtor de recife, sofreu influência do aquecimento e da acidificação em suas taxas metabólicas, enquanto o zoantídeo teve um menor, ou nenhum impacto no seu metabolismo causado pela acidificação ou aquecimento. Portanto, se o aumento de CO_2 na atmosfera e suas consequências não tem um efeito negativo sobre o seu metabolismo, seria de esperar que o *P. caribaeorum* poderia aumentar suas habilidades como um competidor voraz no recife. Estudos futuros devem determinar o impacto do estresse térmico e acidificação sobre o metabolismo de outros genótipos de zoantídeo, principalmente *Zoanthus sociatus*, que é a espécie em maior abundancia no platô recifal do Atol. Pois, os resultados apresentados aqui indicam que o aquecimento e a acidificação dos oceanos poderiam induzir mudanças nas comunidades bentônicas, de dominadas por coral duro para dominadas por zoantídeo nas regiões do Atlântico Tropical.

A Reserva Biológica do Atol das Rocas é praticamente livre de impactos antrópicos tais como sobre-explotação de espécies marinhas, pesca destrutiva e poluição orgânica, mas, ainda assim, a sua localização e sua conservação regida por rigorosa lei, não pode protegê-la de impactos em escala global. Rocas está altamente vulnerável aos impactos oriundos do aumento da concentração do CO_2 atmosférico, uma vez que o aquecimento e acidificação dos oceanos podem causar danos em espécies que utilizam o carbonato para construir seus esqueletos. Embora no atol ainda seja encontrada uma grande disponibilidade desse mineral, já existem estudos mostrando impacto devido ao estresse térmico. Além disso, o prognóstico da elevação do nível do mar é outra ameaça que poderá provocar fortes mudanças no atol, desde o afogamento da área como a reestruturação da mesma e é preciso avaliar se o recife poderia crescer na mesma velocidade do afogamento.

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