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The sun coral as an ecosystem engineer

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Resumo

As invasões biológicas são uma das maiores ameaças à biodiversidade e aos ecossistemas marinhos nos dias de hoje. A introdução de espécies não-indígenas começou a ser comum no início do século XX devido ao grande aumento do tráfego marítimo decorrente da globalização. Regra-geral, a introdução de novas espécies não é propositada. Grande parte dos indivíduos pioneiros são transportados em águas de lastro ou viajam encrustados em navios transoceânicos. Os indivíduos transportados para fora da sua zona original de distribuição podem assumir um estatuto de espécie invasora se detiverem determinadas características: elevada resiliência a mudanças ambientais, grandes taxas de recrutamento e crescimento, grande variabilidade genética, curto período de gestação, maturidade sexual precoce, grande capacidade reprodutiva e/ou uma dieta muito diversificada.

A costa sudeste do Brasil, onde este estudo foi desenvolvido, não apresenta formações recifais de coral, contudo existem algumas espécies de coral na região, como é o caso do coral cérebro endémico *Mussismilia hispida* e do coral invasor *Tubastraea* spp.

Este trabalho tem como principal objetivo perceber de que forma o coral invasor, *Tubastraea* spp., influencia a estrutura da comunidade local e o seu impacto na teia trófica. Para tal, foram desenvolvidos dois estudos em paralelo, no verão de 2017. O primeiro visa compreender como a presença de coral-sol influencia a macrofauna associada ao substrato rochoso, tendo em conta três coberturas de coral diferentes (0%, 50%, 100%), em dois locais distintos na Ilha de Búzios, SP, Brasil (capítulo 2). Enquanto que o segundo trabalho pretende caracterizar a teia trófica facilitada pelo coral-sol e elucidar se o bivalve invasor *Leiosolenus aristatus* recebe alimento do seu anfitrião, *Tubastraea* spp (capítulo 3). Ambos os estudos focam questões em aberto sobre o efeito do coral-sol como engenheiro ecossistémico na região.

O género *Tubastraea* refere-se a um coral ahermatípico e azooxantelado, pertencente à ordem Scleractinia. É o único género de escleractíneos a invadir o Brasil atualmente, tendo uma alta taxa de invasão que o torna numa das maiores ameaças à biodiversidade marinha local. Coral-sol é a designação em português, devido à disposição dos seus pólipos e coloração amarela/alaranjada. As principais espécies a ocorrerem em águas brasileiras são *Tubastraea coccínea* e *Tubastraea tagusensis.* O coral-sol é nativo do Indo-Pacífico tendo uma vasta distribuição geográfica. O seu sucesso como espécie invasora advém da posse de algumas características, tais como o hermafroditismo, uma estratégia reprodutiva diversificada, uma elevada capacidade de fixação em substrato natural e artificial, altas taxas de recrutamento e crescimento, e uma preferência de assentamento em estruturas verticais. No oceano Atlântico, o início da sua invasão ocorreu no mar das Caraíbas (anos 1940) e o primeiro registo no Brasil foi nos anos 1980, numa plataforma petrolífera, na baía de Campos, a norte do estado do Rio de Janeiro.

O Capítulo 1 introduz o tema em estudo, apresentando os principais objetivos de trabalho da tese, o Capítulo 2, foca o impacto do coral-sol na fauna bentónica, o Capítulo 3 descreve a teia trófica em que se insere o coral-sol, com recurso a análise de isótopos estáveis, e o Capítulo 4 apresenta as conclusões gerais e perspetivas futuras sobre este tema.

O trabalho apresentado no Capítulo 2 contou com a recolha de amostras em dois locais distintos, separados por 3km, ao longo da Ilha de Búzios, São Paulo, Brasil, e duas áreas de amostragem em cada local, distanciadas por algumas dezenas de metros. O trabalho de campo consistiu na raspagem de três réplicas em cada área, em regiões saturadas pelo coral, parcialmente cobertas (aproximadamente 50% de cobertura) e sem presença do invasor. Todo o material recolhido foi lavado e peneirado em 9 crivos de malha com diâmetros decrescentes, onde ficou retida a macrofauna. Após separação, identificação e armazenamento da fauna encontrada, procedeu-se à análise de variáveis univariadas (abundância, biomassa e tamanho médio), à utilização do índice de diversidade e riqueza Shanon-Wiener e à análise multivariada da estrutura da comunidade. Todas as análises referidas seguiram o mesmo modelo, tendo "coral cover" como o principal fator ("no coral, half-coral e full coral"), examinados à escala espacial de dois locais e duas áreas. O coral-sol provou ser um elemento de exclusão de alguns macro-invertebrados (ex. tanaídeos, ostracodes e copépodes) e o responsável pelo declínio da abundância e riqueza na estrutura da comunidade local. É sugerida a existência de um cenário satisfatório, em termos de abundância, biomassa e riqueza, em regiões onde a presença do coral-sol é parcial ou inexistente. Perante os resultados obtidos, pode-se sugerir, também, que o limiar da resiliência do ecossistema estudado está iminente. Este estudo confirma o coral-sol como um importante engenheiro ecossistémico – organismo cuja presença ou atividade altera as características físicas circundantes, criando e modificando habitats e influenciando todas as espécies aí presentes. Medidas terão de ser tomadas rapidamente para evitar perdas permanentes de biodiversidade local.

Por outro lado, a análise isotópica do $\delta^{13}C$ e $\delta^{15}N$ apresentada no Capítulo 3 revelou que a teia trófica associada ao coral é maioritariamente composta por organismos filtradores e que as novas comunidades, após a invasão, são dominadas por seres heterotróficos, em vez de autotróficos (organismos dominantes antes da invasão). Para além da importante expansão do coral-sol, o mitilídeo *Leiosolenus aristatus,* nativo do mar das Caraíbas, mas com uma distribuição geográfica muito alargada, foi frequentemente encontrado no interior das bases rígidas do coral invasor. *Tubastraea* spp. e *Leiosolenus aristatus* são originários de localizações geográficas distintas, portanto a sua associação apenas ocorre em locais onde ambos são alóctones. Os resultados obtidos sugerem que tanto o coral-sol, como o bivalve, são organismos filtradores. Uma das hipóteses para a ocorrência desta associação, seria a de que o bivalve beneficiaria de alimento providenciado pelo coral, mas tal não se verificou. A invasão do mitilídeo é facilitada pelo coral, por este encontrar refúgio nas suas bases calcárias. É expectável que a continuação da invasão pelo coral-sol seja acompanhada pela expansão da distribuição deste bivalve invasor.

Conclui-se que a rápida invasão do coral-sol no litoral norte de São Paulo, é uma grave ameaça à biodiversidade local por estar iminente uma importante alteração do ecossistema, juntamente com a facilitação da introdução de um bivalve invasor, competidor com outras espécies nativas. A alteração de habitats, pode vir a ter consequências profundas nas comunidades locais. Ambos os estudos, são pontos de partida para o conhecimento do impacto negativo que o coral-sol pode ter na estrutura da comunidade associada aos fundos rochosos, como engenheiro ecossistémico. Sugere-se a continuação de estudos dentro desta temática, com o intuito de aumentar o conhecimento, contribuindo para a eventual gestão, minimização dos impactos ou erradicação desta espécie invasora.

***Palavras-chave*:** Espécie invasora, *Tubastraea* spp., engenheiro ecossistémico, teia trófica, estrutura da comunidade.

Abstract

Invasive species are a serious threat to biodiversity because they displace native species, change community structure and food webs and alter fundamental processes (such as nutrient cycling and sedimentation). Any organism that is outside of its native geographic range that may or has become injurious to animal or human health, the economy and/or natural environment is considered as invasive species. Globalization (i.e. increase of the international ship traffic) is the main driver of invasive species introduction. *Tubastraea* spp., commonly designated sun coral, is an ahermatypic and azooxanthellate scleractinian coral, the only scleractinian which has been introduced in Brazilian waters and one of the most widespread invaders in the world. The present work aimed to investigate the impact of *Tubastraea* spp. in the local biological community, examining the rocky shore associated macrofauna, in an area under rapid invasion, at Búzios Island, São Paulo, Brazil, under three different coral coverages (0%, 50% and 100%) (chapter 2) and characterizing the food web associated with *Tubastraea* spp., using stable isotopes (chapter 3), during the summer of 2017. Chapter 1 introduces the basis for this work and describes the main aims of this thesis. Chapter 2 investigates the impact of the sun coral on the benthic macrofauna, chapter 3 describes the food web where this coral is included, and chapter 4 presents the main conclusions and future perspectives.

The alteration of mobile invertebrate assemblages according to the degree of sun-coral space occupation was examined on vertical walls (with 3 different coral cover levels) and the differences found among two study sites and areas, within each study site were examined. It was observed that the sun coral may exclude major invertebrate groups (i.e. tanaids, ostracods and copepods). Abundance, biomass and richness of associated macrofaunal species declined in areas saturated by the sun coral, confirming that this coral is an ecosystem engineer.

The structure of the food web associated to the colonies of *Tubastraea* spp was previously unknwon. At the basis of this coral another invasive species is very often found, the bivalve *Leiosolenus aristatus,* a borer species that perforates the base of hard corals. Stable isotopic analysis was applied to all organisms occurring at the microhabitat built by *Tubastraea* spp. to 1) provide the first trophic characterization of the food web facilitated by *Tubastraea* spp., while also 2) elucidating if *L. aristatus* receives nutrition from its coral host *Tubastraea* spp. Stable isotopic analyses showed that the food web that accompanies this invasive coral seems to be mostly composed of suspension feeders, confirming that the new community established after *Tubastraea* spp. invasion is dominated by heterotrophs. It was also concluded that both *Tubastraea* spp. and *L. aristatus* are suspension feeders consuming similar resources. This way, *L. aristatus* seems to profit from the expansion of *Tubastraea* spp. because the coral provides it with a structure to live, but not a source of nutrition. As *Tubastraea* spp. progresses in its invasion of new areas, this borer bivalve should follow.

This work describes for the first-time the impact of *Tubastraea* spp. on the southeast Brazilian rocky bottoms' associated macrofauna and food webs. The rapid expansion of this ecosystem engineer is leading to the alteration of the native macrofaunal community. This work indicates that this invasion will result in a decline in local biodiversity and in profound alterations to the food web of subtidal rocky shores.

***Keywords*:** Invasive species, *Tubastraea* spp., ecosystem engineer, stable isotopes, community structure

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Chapter 1

1.1 General Introduction

1.1.1 Brazilian coastline characteristics and coral population distribution

Brazil is the fifth largest country in the world (Rosenberg, 2018) and includes an extensive coastline. The Brazilian coast has approximately 10800Km – from Cape Orange (4° N) to Chui (34°S) (Amaral et al., 2016). To define all the Brazilian coast, AB'SÁBER (2003) divided the Brazilian coast in six sectors: Equatorial Amazonian Coast, North Northeast, East Northeast, East, Southeast, and South. The Northern region (constituted by dunes, extensive sandy beaches with a considerable amount of rivers flowing down, being the Amazon River mouth one of the greatest and most complex in the world); the Northeast region (with more narrow beaches with sandstones reefs, which are often associated with calcareous algae and corals reefs); beaches with fine to very fine sand can be found in the Eastern region of the country; and the Southeast (where our study was carried out, at the north shore of São Paulo), which is the most diverse and rugged coastal sector in the country, having distinct morphological characteristics from the northern and southern regions (Amaral et al., 2016). Temperate shallow reefs are mainly covered by large browns macroalgae (Vermeij, 1978; Witman & Dayton, 2001), while tropical and subtropical reefs are dominated by a complex mosaic of very diverse assemblages of small macroalgae, mostly red and colonial fouling invertebrates (Witman & Dayton, 2001; Oigman-Pszczol et al., 2004; Porter et al., 2013).

Leão & Dominguez (2000) described the tropical Brazilian Coral Reefs as "one of the most prominent marine ecosystems, particularly because of the unique character of its low-diversity coral fauna which is rich in endemic species". This statement indicates the great importance of Brazilian Coral Reefs. They are distributed from 0°50'S to 18°00'S (Leão et al., 2016). In the Southeastern and Southern regions, from the mouth of the Doce River (19° 30' S) to the coast of the state of São Paulo, no coral reef is known, although corals are present, including the endemic brain coral species *Mussismilia hispida* (Migotto, 1995; Migotto et al., 1999; Creed, 2006, Leão et al., 2016).

Despite the heterogeneous distribution of corals along the Brazilian coast, corals can be found almost all over the coastline. The great latitudinal variance of the Brazilian coastline is under the influence of a diverse set of oceanographic and ecological conditions. Locally, areas may be under the continuous influence of the oligotrophic tropical waters of the Brazilian Current, or seasonally affected by upwelling of cold, nutrient-rich waters (Ekau & Knoppers, 1999). The nature of the substrate varies from rocky, to considerable coral cover, conferring the Brazilian coast a great diversity of ecosystems and associated species (Floeter et al., 2001).

1.1.2 Invasive species

The term "invasive species" is commonly used in the field of "invasion ecology theory", but can be subjectively interpreted (Colautti & Macisaac, 2004). Non-indigenous species are those which can be found outside off their native range, usually introduced by human activity (Colautti & Macisaac, 2004). Alien, exotic, non-native and allochthonous species are all synonyms of non-indigenous species (NIS), according to (Olenin et al., 2010). NIS can have four main stages: "localized and numerically rare", "widespread but rare", "localized but dominant" or "widespread and dominant" (Olenin et al., 2010). Invasive species are included in the "widespread and dominant" stage of NIS because they are able to fix, to develop, to reproduce and to compete actively outside of their native range (Colautti & Macisaac 2004; Olenin et al., 2010). That means that invasive species are NIS, which are locally dominant and widespread (Colautti & Macisaac, 2004).

Invasive species are a serious threat to the local biodiversity community because they "displace native species, change community structure and food webs and alter fundamental processes (such as nutrient cycling and sedimentation)" (Molnar et al., 2008). Hereupon, it is acceptable to define invasive species as "any organism that is outside of its native geographic range that may or has become injurious to animal or human health, the economy and/or natural environment" (Ziska et al., 2011).

Due to the increase in human population in the last decades, "many species have invaded and continue to invade new regions at an unprecedented rate, exerting strong impacts on ecosystems and human welfare" (Kleunen et al., 2010). Globalization is the main driver of invasive species introduction, the major vector being the international ship traffic (Murray et al., 2011; Chainho et al., 2015). Invasive species have some general characteristics in common, such as environmental tolerance, high genetic variability, short generation time, early sexual maturity, high reproductive capacity, and a broad diet (Essink & Dekker, 2002; Parker et al., 2013). All these attributes, together with proliferation in ecosystems without natural enemies, provide the ideal conditions for the highly successful establishment of the species in new regions and, consequently, for the invasion in those areas (Torchin et al., 2003).

Typically, invasive species have a rapid establishment rate on non-invaded areas because of their great capacity for rapid dispersal and colonization. This phenomenon is accelerated in marine environments, due to the lack of natural barriers, leading to a risk of native biological heritage loss (Ruiz et al., 2000; Secord, 2003; Sammarco et al., 2010). On the other hand, there are some studies that support that NIS cannot be harmful to the native species, and invasional meltdowns can occur (Simberloff & Holle, 1999; Parker et al., 2013).

1.1.3 The sun coral (genus *Tubastraea* Lesson, 1829) and the beginning of its invasion

The present study focuses on the ahermatypic/azooxanthellate scleractinian coral, of the genus *Tubastraea* Lesson, 1829 (Order: Scleractinia Bourne, 1900; Suborder: Dendrophylliina Vaughan and Wells, 1943; Familly: Dendrophylliidae Gray, 1847), commonly called "sun coral" or "orange cup coral" because of its orange/yellow pigmentation (De Paula & Creed, 2004; Sammarco et al., 2010).

The natural range of the sun coral *Tubastraea* spp. is the Indo-Pacific region and it has two main species (*T. coccinea* and *T. tagusensis*), which are at the epicentre of the invasion (Creed et al., 2016), even though *T. coccinea* had a greater research effort by the scientific community. In general terms, both are hermaphrodites with a vast reproductive strategy, with sexual and asexual reproduction, both have a great planulae release, a great fixing capacity in natural (cave ceilings and undersides of big rocks) or artificial (dock pilings and buoys) substract, high recruitment and growth rates and settlement preference in vertical surfaces (Cairns, 2000; Creed & De Paula, 2007; De Paula et al., 2014; Mizrahi et al., 2014 (b)). However, there are some differences between both species, such as that *T. tagusensis* seems to be more sensitive to environmental changes (e.g. water temperature variation), the depths at which they can occur (*T. coccinea* from 1 to 110 m in its native range and until 16m at Ilhabela, Brazil; *T. tagusensis* from 3 to 43 m in Galapagos region and until 15m in Ilhabela, Brazil), the growth rate (*T. coccinea* with 1.01 cm/year against 0.92 cm/year in Brazil), as well as it being documented that *T. coccinea* has a longer reproductive period than *T. tagusensis* (Wells, 1982; Glynn & De Weerdt, 1991; Creed & De Paula, 2007; De Paula et al., 2014; Mizrahi, 2014; Creed et al., 2016). Sun coral (a direct translation of coral-sol in Portuguese) is the term that has been used, by researchers in Brazil, when referring to the two *Tubastraea* species (Mangelli & Creed, 2012; De Paula et al., 2014; Creed et al., 2017) invading Brazilian shores. Independently of the species, all of the previously mentioned features make the sun coral the most rapidly invading species of the Brazilian rocky shore, negatively affecting the native biodiversity, as evidenced by the decreasing population of the endemic Brazilian brain coral *Mussismilia hispida.* (Creed, 2006).

The sun coral invasion started in the Caribbean Sea (first recorded in 1943 by Vaughan & Wells) and began its descent towards Southwestern Atlantic (late 1980s), passing by the Gulf of Mexico and Florida (1977) (Cairns, 2000; Castro et al., 1999; Fenner & Banks, 2004; De Paula & Creed, 2004). De Paula & Creed (2004), reported that the orange cup coral invasion in Brazil started in the late 1980s, when some specimens were found at offshore oil platforms in the northern region of Rio de Janeiro State, at the Campos oil basin. After that, colonies were identified in Ilha Grande bay (1990s) and Itajaí, Santa Catarina State (2000). Joel Creed (2016) and his colleagues concluded that *T. coccinea* is native in the Indo-Pacific, cryptogenic in the North Pacific and North-eastern Atlantic, and invasive in the Caribbean Sea, Gulf of Mexico and Southwestern Atlantic. On the other hand, it is possible to assume that *T. tagusensis* has a significantly smaller distribution around the world, being native to the Galapagos, cryptogenic in Indo-Pacific and Persian Gulf, and invasive in Southwestern Atlantic. It is important to mention that the sampling region for the present study was São Paulo’s north shore where the first sun coral colonies were recorded in Ilhabela, between 2008 and 2010. (Mantelatto et al., 2011).

1.1.4 The sun coral as an ecosystem engineer

“Ecosystem engineer” can be defined as “an organism whose presence or activity alters the physical surroundings or changes the flow of resources, creating or modifying habitats and influencing all associated species” and that “modulates the availability of resources to other species, by causing physical state changes in biotic or abiotic materials, so, they modify, maintain and create habitats” (Jones et al., 1994; Jones et al., 1997). The “ecosystem engineering” concept proposed by Jones et al., (1994, 1997) was accepted by some authors (Dangerfield et al., 1998; Casas-Crivillé & Valera, 2005; Wild et al., 2011), trivialized by others (Holdsworth et al., 2007; Menge et al., 2008), criticized (Reichman & Seabloom, 2002) and updated by Andrew Wilby (2002). This concept caught the attention of many ecologists, for the most varied reasons.

The present study will use the concept given by Jones (1994, 1997), exploring the idea that an ecosystem engineer is responsible for changing the ecosystem, being a biodiversity mechanism of exclusion or facilitation. Ferreira (2003) and Lages et al. (2011) reported the important impact of *Tubastraea* spp. on native local biodiversity of Brazilian rocky shores. Creed (2006) showed how the sun coral can cause tissue necrosis on the endemic Brazilian brain coral *Mussismilia hispida* and highlighted the possibility of sponges, coralline algae and even sun coral recruits overgrowing in the invaded regions (Creed, 2006).

1.1.5 Aims and scopes of the dissertation

Given that the sun coral is an important invasive species in the Southwestern Atlantic, and that its proliferation in non-native regions is a serious threat to the local biodiversity maintenance (Lages et al., 2011; Silva et al., 2011; Mizrahi et al., 2014 (a)), it is important to understand the impact of this invasion and its trophic role in the rocky shore ecosystem.

The present work aimed to investigate the impact of *Tubastraea* spp. in the local biological community, examining the rocky shore associated macrofauna under three different levels of coral coverage (100%, 50% and 0%), (chapter 2) and to characterize the food web associated with *Tubastraea* spp., using stable isotopes (chapter 3), in an area under rapid invasion, southeast Brazil.

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Chapter 2

Impacts of the sun coral invasion on the structure of mobile invertebrate assemblages in a tropical rocky reef

2.1 Abstract

Invasive species are a serious threat to the local biodiversity community because they displace native species, change community structure and food webs and alter fundamental processes (such as nutrient cycling and sedimentation). *Tubastraea* spp., commonly designed as sun coral, is an ahermatypic and azooxanthellate scleractinian coral, being the only scleractinian which has been introduced in Brazilian waters, one of the most widespread invaders and it is becoming a serious threat to the local biodiversity. The present work aimed to investigate the impact of *Tubastraea* spp. in the local biological community, examining 1) the associated macrofauna on vertical rocky reef substrates with 3 different coral cover (0%, 50% and 100%) and 2) understand the differences found among study sites (PEL and POL) and areas (PEL1 and PEL 2; POL1 and POL 2), during the Summer of 2017 in an area under rapid invasion, at Búzios Island, SP, Brazil. It was observed that sun coral may exclude (i.e. tanaids, ostracods and copepods) major invertebrate groups. Abundance, biomass and richness declined in areas saturated by the sun coral. The potential role of sun coral as an ecosystem engineer for the local community structure was confirmed.

Keywords: Invasive species, *Tubastraea* spp., ecosystem engineer, exclusion, community structure.

2.2 Introduction

In general, corals are considered extremely sensitive to environmental change and have low survival rates during transport (Lages et al., 2011). The sun coral, *Tubastraea* spp., belongs to the group of organisms that seems to have a great resilience to environmental exchanges, high recruitment and growth rates – the invasive species main features that allow them to invade (Bax et al., 2003). The sun-coral is the only scleractinian that is invasive in Brazilian waters (De Paula & Creed, 2005).

The Brazilian southeast coast has a great ecosystem complexity, with a wide range of habitats and reefs mainly covered by small macroalgal beds and associated macrofauna, which are the primary production and primary consumers, respectively. Lubchenko (1978) demonstrate that the abundance and algae species are controlled by marine herbivorous. Moderate grazing allows inferior algal species to persist and intense grazing eliminates most individuals and species. The effect of this consumers on plant species diversity depends on the relationship between herbivore food preference and competitive abilities of the plants. Space has been shown to be a primary limiting resource in many rocky intertidal communities (Paine, 1966; Lubchenco & Menge, 1978).

On rocky bottoms ecosystems it is possible to find communities of sessile benthic invertebrates and macroalgae matrix, both with different associated macrofauna and algae species, which will attract diverse species of consumers with diversified food habits. The precise consumer effect, probably, depends on the relationship between its preferences and food's competitive abilities and on the intensity of the grazing or predation pressure (Lubchenko, 1978). Mobile invertebrates such as small crustaceans (copepods, tanaids, ostracods, amphipods and isopods), bivalves, gastropods and polychaetas are, mainly, detritivores and suspension feeders, fundamental organisms for primary predators such as juvenile fishes, included fishes with high economic value (Floeter et al., 2007). Coasts invaded by the sun coral in Brazil have changed from being dominated by macroalgae and zooxanthellate cnidarians to being dominated by this azooxanthellate hard coral, thus changing from autotrophic to heterotrophic communities (Lages et al., 2011).

Scleractinian corals are ecosystem engineers that create microhabitats and modify nearby physical and chemical processes because they are principle architects (Lages et al., 2011). *Tubastraea* spp, once established, tends to dominate altering community structure and function (De Paula, 2007, Miranda et al., 2016). An ecosystem engineer can be considered as an organism responsible for creating or modifying habitats, influencing all associated species around (Jones et al., 1994; Jones et al., 1997). Autogenic and allogenic engineers are the two main groups of ecosystem engineers (Jones et al., 1994). Corals, in general, are considered autogenic engineers whose alter the surrounding environment via their own physical structures (i.e. their living and dead tissues) (Jones et al., 1994).

Given that the sun coral is an important invasive species in the Southwestern Atlantic, and its proliferation in non-native regions is a serious threat to the local biodiversity maintenance (Lages et al., 2011; Silva et al., 2011; Mizrahi et al., 2014 (a)), it is important to understand the impact of this invasion and its trophic role in the rocky shore ecosystem.

The present work aimed to investigate the impact of *Tubastraea* spp. in the local biological community, examining 1) the associated macrofauna on vertical rocky reef substrates with 3 different coral cover (0%, 50% and 100%) and 2) understand the differences found among study sites (PEL and POL) and areas (PEL1 and PEL 2; POL1 and POL 2), in an area under rapid invasion, at Búzios Island, SP, Brazil.

2.3 Materials and Methods

2.3.1 Study area

This study was undertaken at Ilha de Búzios (Búzios Island: 23 48’ 11” S; 45 08’ 21” W), which belongs to the Ilhabela Archipelago off-shore São Sebastião, Southeastern Brazil (Fig.2.1). Búzios Island is 755 ha large and is inhabited by nearly 200 people. Artisanal fisheries is the main economic activity in the area. The island is located 8 km northwest off Ilhabela and 25 km southeast from the nearest mainland. A tropical climate prevails in the region, with hot and humid summers, when tropical storms are frequent, and a drier winter. Coastal waters are often oligotrophic to mesotrophic, with eventual pulses of primary production during summer, owing to episodical upwelling after prolonged periods of northwesterly winds, and winter, after the passage of cold fronts (Stech & Lorenzzetti, 1992, Calado et al., 2006; Ciotti et al., 2010). Coastal plumes containing large inputs of terrestrial organic matter are frequent after heavy rainfall, but their contribution to benthic food webs is largely unknown. The relative abundance of benthic macroalgae and sessile or encrusting invertebrates that dominate the shallow rocky reefs in the study area is given in Mizrahi et al. (2017).

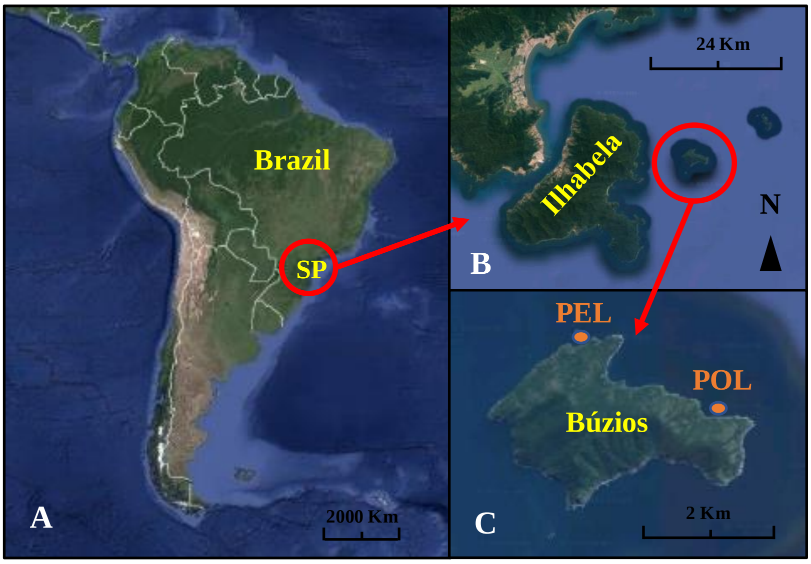

Fig.2.1 Representative map of (A) Brazil and São Paulo location in South America, (B) Búzios Island location at Northeast of Ilhabela and (C) Samplig sites region in Búzios Island: Pedra Lisa (PEL) and Ponta Leste (POL).

2.3.2 Sampling

We aimed to investigate how mobile invertebrate assemblages change according to the degree of sun coral space occupation. During the summer of 2017, we surveyed vertical rocky reef substrates, at a depth ranging from 3 to 15m, at two areas several tens of meters apart (PEL1 and PEL2; POL1 and POL2), within two sites nearly 3 km from each other (Pedra Lisa - PEL; S 23°47’54.2”; W 45°09’24.6”; and Ponta Leste - POL; S 23°48’6.79”; W 45° 7’21.65”; Fig.2.1). At each area, three replicate plots (0.5 m^2 quadrats) were haphazardly sampled at each of three habitat types; no coral, half coral cover (around 50%), and full coral cover. Sun coral colonies were removed with chisels and encrusting invertebrates or turf / canopy-forming algae were scrapped off the substrates and suctioned using an air-lifting device coupled to SCUBA tanks (Munro, 2013).

2.3.3 Laboratory procedures

All samples were vigorously washed to release mobile invertebrates from any surfaces, and then sieved in different size classes (mm) to obtain estimates of average individual size (i.e. 0.5-1.2, 1.2-1.7, 1.7-2.8, 2.8-4.0, 4.0-6.3, 6.3-8.0, 8.0-12.5, 12.5-25.0). All organisms were preserved in a saline formaldehyde (4%) solution. Identification to main taxonomic groups and counting were carried out on white trays, with the naked eye, for individuals retained in the six coarser sieves (i.e. with a body size larger than 1.7mm), or under a dissecting microscope, for smaller individuals. Subsamples were obtained for size fractions retaining an exceedingly high number of individuals ($n \geq 150$ indivuduals). A Folsom plankton splitter was used for this purpose because very large numbers were only observed for very small organisms, in the smallest fractions, that could be easily suspended in the rotating drum. All organisms were stored in containers with ethanol 70%.

2.3.4 Data analyses

Univariate variables abundance, biomass, average size, Shannon-Wiener diversity and richness, and the multivariate variable community structure, were all analysed using the same mixed linear model, with the fixed main factor ‘coral cover’ (no coral, half-coral cover, full coral cover), examined at both the ‘site’ (POL, PEL) and ‘area’ (nested in ‘site’; 1, 2) spatial scales (both random factors). For univariate variables, variance heterogeneity was first tested using the Cochran’s C test, appropriate data transformations were undertaken when needed to meet homoscedasticity, and *F*-ratios were obtained through analyses of variance. The SNK procedure was used for *post-hoc* comparisons to further explore signficant sources of variation. Community structure was examined using permutational analyses of variance to generate pseudo–*F* statistics. Data were first fourth-root transformed and the resemblance matrix was calculated using Bray-Curtis distances. Significant sources of variation were further investigated using pairwise comparisons, based on 9,999 unrestricted permutations of raw data. Non-metric multidimensional scaling (NMDs) plots were used to visualize sample clustering.

2.4 Results

Analyses of univariate metrics of the sampled invertebrate assemblages indicate that effects of sun-coral are complex. There were no pervasive changes across the spatial scales tested, with differences among assemblages holding only at sites, separated by a few km, or only even at areas within sites, just tens of meters apart (Table 2.1). Abundance followed the former trend (Table 2.1; Fig. 2.2A). There was a clear decreasing tendency in invertebrate overall abundance from no-coral to full-coral cover habitats in Pedra Lisa, with statistical support for higher abundance at no-coral compared to the remainder habitats, while at Ponta Leste abundance was higher at the half-coral habitat compared to the others (SNK; $p < 0.05$). Biomass contrasts were consistent in Pedra Lisa, higher on no-coral and half-coral compared to full-coral plots, but not in Ponta Leste, where biomass was higher on half-coral compared to the rest at Area 2, but no differences were observed at Area 1 (Table 2.1; Fig. 2.2B). Decreasing overall trends of richness, especially no-coral and half-coral compared to full-coral cover, were observed across areas (Fig. 2.2C) and backed by a marginal, although not significant, p-value (0.067; Table 2.1). Processes not addressing here and operating at the 'area' spatial scale (Table 2.1), were important and probably masked any effects of the sun-coral cover. No effects on average individual size or diversity were detected (Table 2.1).

Table 2.1 Summary results of analyses of variance testing the effects of sun-coral cover on univariate metrics of mobile invertebrate assemblages at two spatial scales; between sites (3 km apart) and between areas within sites (several tens of meters apart). Significant p-values are marked in bold.

		Abundance		Biomass		Average size		Diversity		Richness	
	d.f.	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Coral cover: Co	2	1.44	0.409	2.18	0.314	1.76	0.362	3.53	0.221	14.01	0.067
Site: Si	1	1.77	0.315	1.02	0.418	2.91	0.230	0.01	0.940	0.18	0.713
Area: Ar (Si)	2	3.28	0.055	1.21	0.314	1.82	0.183	2.35	0.117	8.42	**0.002**
CoXSi	2	45.54	**0.002**	2.13	0.235	0.67	0.563	1.21	0.389	0.42	0.684
CoXAr(Si)	4	0.14	0.967	3.47	**0.023**	1.03	0.411	2.05	0.120	1.88	0.146
Res.	24										
		$C = 0.386$; $p > 0.05$ Raw data		$C = 0.268$; $p > 0.05$ Raw data		$C = 0.620$; $p < 0.01$ √x transformed		$C = 0.139$; $p > 0.05$ Raw data		$C = 0.378$; $p > 0.05$ Raw data	

Sixteen major taxonomic groups were found in this study (Fig. 2.3). Amphipods, polychaetes and tanaids clearly dominated target assemblages, followed by copepods, ostracods, isopods, gastropods and bivalves which were common, and brachyuran crabs and ophiuroids which were only occasional. Other five groups, i.e. nemerteans, nematodes, hermit crabs, caridean shrimps and sea urchins, accounted separately for less than 1% of the whole sample and were considered rare.

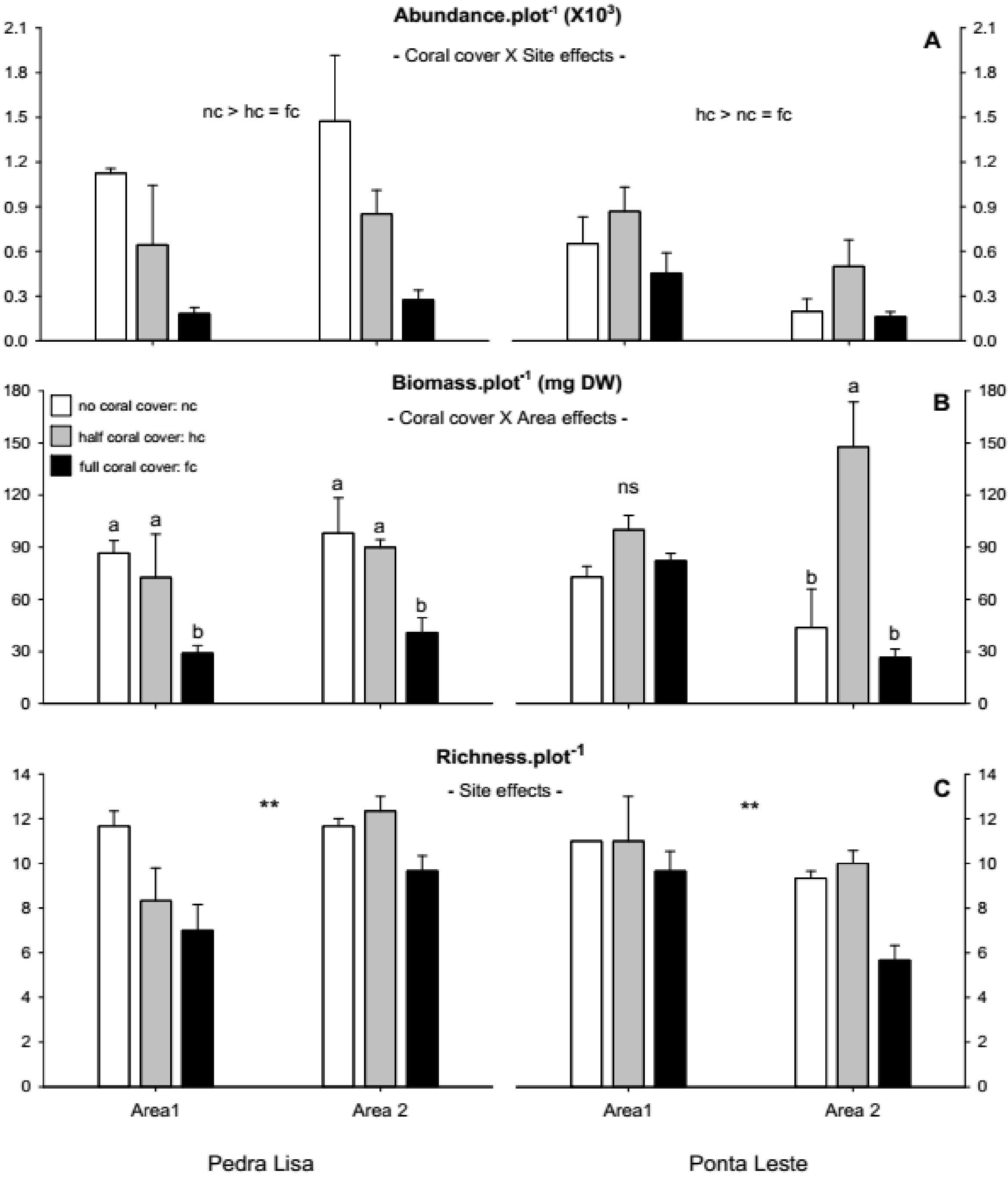

Fig. 2.2 Univariate variables (A) abundance, (B) biomass and (C) richness of mobile assemblages associated to reef habitats with contrasting sun-coral cover at different sites, and areas within sites, in Búzios Island. Bars and whiskers stand for average values and respective standard errors. In panel B, different letters indicate statistical differences ($p < 0.05$) among groups within areas, and 'ns' stands for non-significance ($p > 0.05$). In panel C, ** indicates $p < 0.01$.

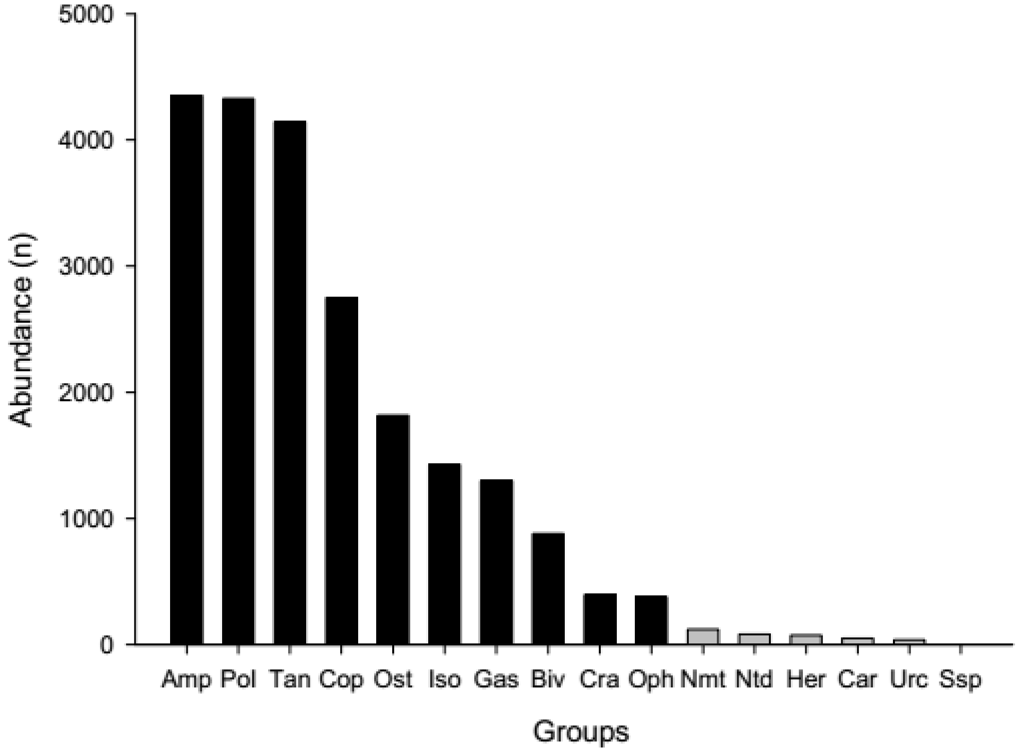

Fig. 2.3 Overall distribution of frequencies of the main taxonomic groups found at the sampled reef sites. Groups with frequencies lower than 1% of the whole sample were considered rare and removed from multivariate analyses (see text for details). Amp: Amphipods; Pol: Polychaetes; Tan: Tanaids; Cop: Copepods; Ost: Ostracods; Iso: Isopods; Gas: Gastropods; Biv: Bivalves; Cra: Brachyuran crabs; Oph: Ophiuroids; Nmt: Nemerteans; Ntd: Nematods; Her: Hermit crabs; Car: Caridean shrimps; Urc: Sea urchins; Ssp: Unidentified

Changes in community structure were also intricate and 'area' specific (Table 2.2). Again, samples obtained from plots with no or only half-coral cover tend to cluster together, aside from samples from full-coral cover plots (Fig. 2.4). The exception is Area 1 at Pedra Lisa (Fig. 2.4A). Pairwise comparisons did not however fully support visual trends. Marginal *p*-values, between 0.093 and 0.104, were obtained for contrasts of no coral vs. half-coral cover (PEL1; Fig. 2.4A), no coral vs. full-coral cover (PEL1, PEL2, POL1, POL2; Fig. 2.4A-D), and half-coral vs. full-coral cover (PEL2, POL2; Fig. 2.4B,D). Seven taxonomic groups contributed substantially (above 10%) to at least one pairwise comparison, and 2 to 3 groups were typically responsible for cumulative 50% dissimilarity across comparisons (SIMPER; Table 2.3). The abundance of taxonomic groups contributing the most to dissimilarities in each area is shown in Figure 2.5. Abundance patterns of tanaids (Fig. 2.5A-C), ostracods (Fig. 2.5A-B) copepods (Fig. 2.5B-C) and, to a lesser extent, gastropods (Fig. 2.5D) apparently underlie the clustering of no-coral and half-coral cover plots, apart from full-coral cover plots. The distribution of polychaetes follows a similar pattern, except for PEL1 (Fig. 2.5C). Exceedingly high variance to average ratios precluded a clear interpretation of the patterns observed for amphipods and isopods (Fig. 2.5 C-D).

Table 2.2 Summary results of permutational analyses of variance testing the effects of sun-coral cover on the community structure of mobile invertebrate assemblages at two spatial scales; between sites (3 km apart) and between areas within sites (several tens of meters apart). Significant *p*-

	Community structure		
	d.f.	pseudo-*F*	*p*
Coral cover: Co	2	3.81	0.087
Site: Si	1	0.77	0.659
Area: Ar (Si)	2	5.34	**<0.001**
CoXSi	2	1.27	0.329
CoXAr(Si)	4	2.37	**0.011**
Res	24		

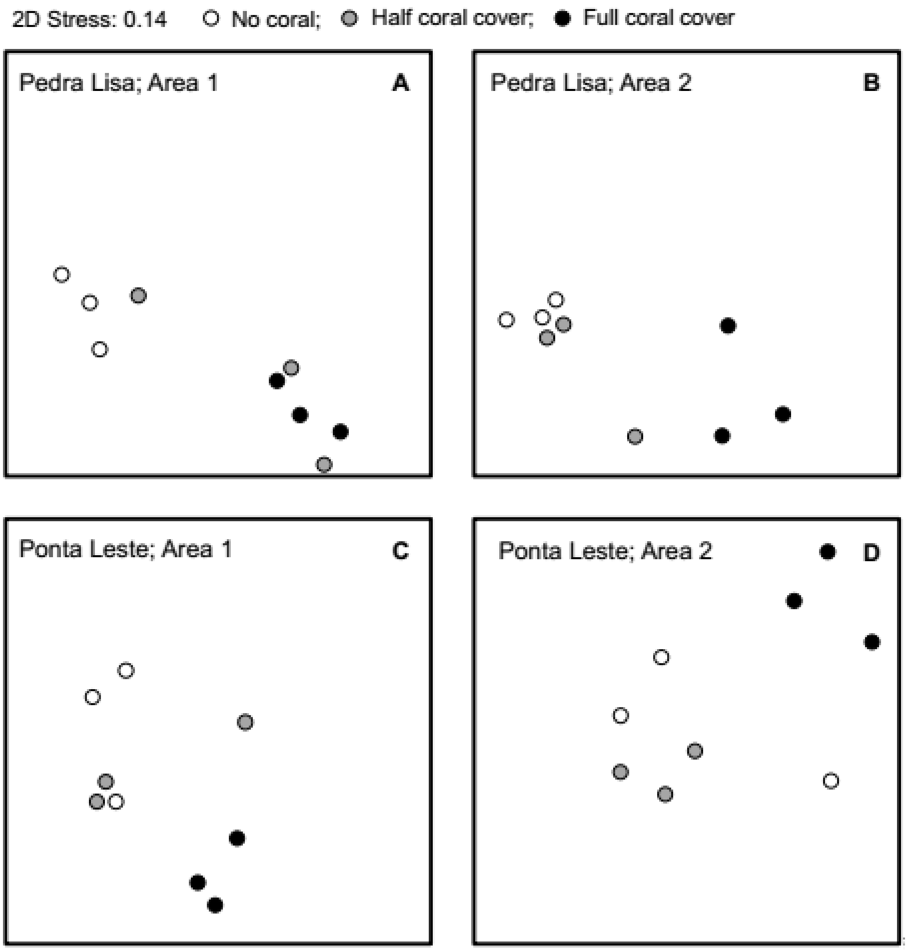

Fig. 2.4 Non-metric multidimensional scaling (NMDs) plots showing the variation of the structure of mobile invertebrate assemblages at reef habitats with varying sun-coral cover. The original plot was split into four separate plots for a clearer visualization of specific dissimilarities among reef habitats for each sampled area.

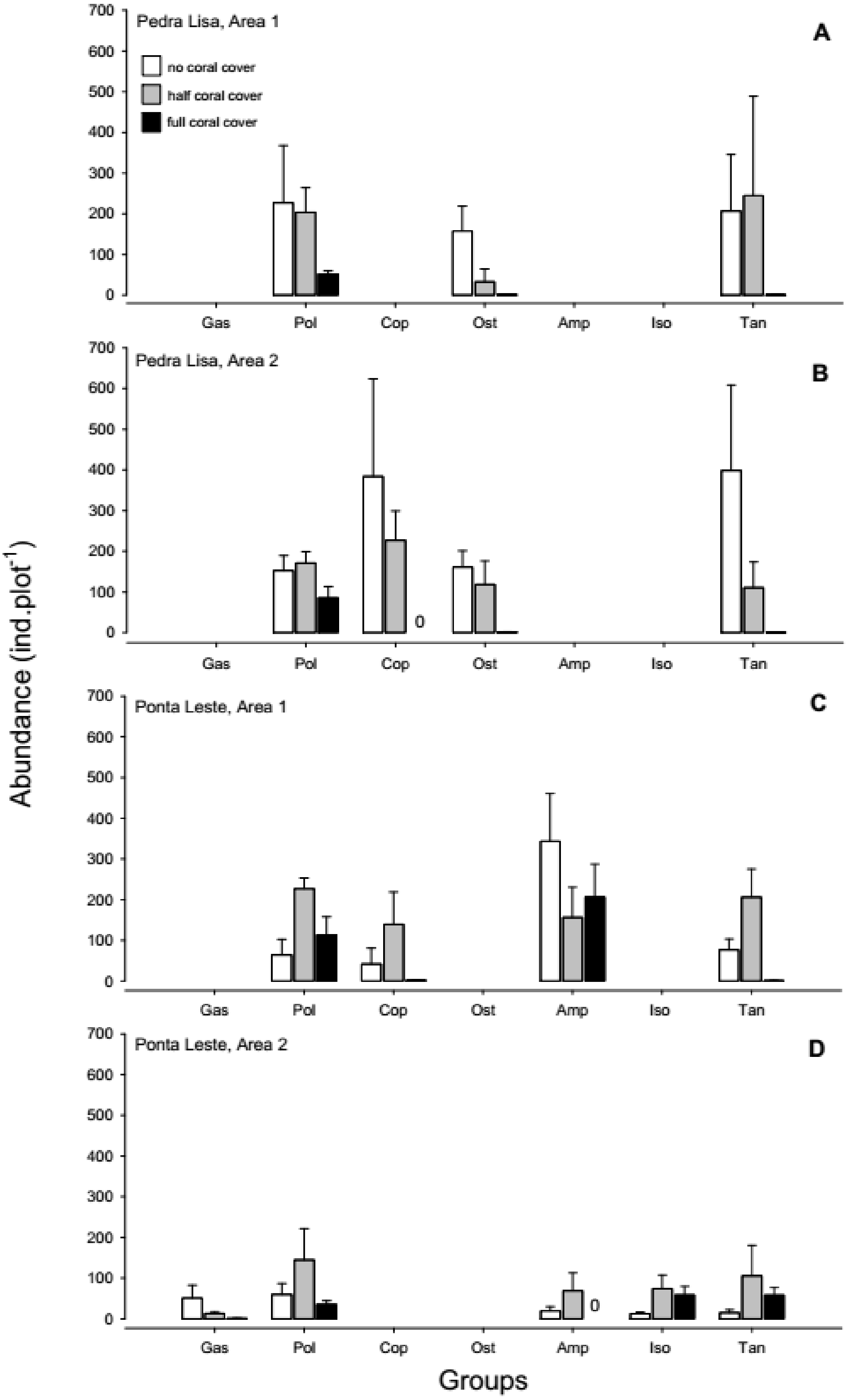

Fig. 2.5 Abundance of taxonomic groups explaining dissimilarities among reef habitats of varying sun-coral cover. Only the groups accounting for specific dissimilarities in each area are represented. Bars and whiskers stand for average values and respective standard errors. Abbreviations of taxonomic groups as in figure 2.3.

Table 2.3 Results of SIMPER analyses to identify the main taxonomic groups of mobile invertebrates responsible for changes in community structure among reef habitats with contrasting sun-coral cover. For each pairwise habitat comparison, cut-offs were set for groups contributing to at least 10% and cumulating 50% of dissimilarities (shaded in gray). Pol: Polychaetes; Tan: Tanaids; Cop: Copepods; Ost: Ostracods; Iso: Isopods; Gas: Gastropods; Biv: Bivalves.

Pedra Lisa: Area 1

no coral vs. half cover			no coral vs. full cover			half coral vs. full cover		
Taxon	Contrib. %	Cumulative %	Taxon	Contrib. %	Cumulative %	Taxon	Contrib. %	Cumulative %
Tan	26.4	26.4	Tan	20.5	20.5	Pol	39.5	39.5
Pol	16.4	42.8	Pol	18.0	38.5	Tan	29.3	68.7
Ost	13.6	56.4	Ost	15.9	54.4	Amp	16.2	84.9
Cop	13.4	69.8	Cop	13.7	68.1	Biv	4.3	89.3
Gas	10.2	80.0	Gas	10.9	79.0	Ost	3.9	93.2
Amp	9.1	89.0	Amp	9.7	88.7	Iso	3.2	96.4
Oph	3.8	92.9	Oph	4.2	92.9	Gas	1.5	97.9
Iso	2.9	95.8	Iso	2.9	95.8	Cra	1.4	99.4
Cra	2.4	98.1	Cra	2.5	98.3	Oph	0.6	100.0
Biv	1.9	100.0	Biv	1.7	100.0	Cop	0.0	100.0

Pedra Lisa: Area 2

no coral vs. half cover			no coral vs. full cover			half coral vs. full cover		
Taxon	Contrib. %	Cumulative %	Taxon	Contrib. %	Cumulative %	Taxon	Contrib. %	Cumulative %
Tan	33.6	33.6	Tan	27.8	27.8	Cop	34.1	34.1
Cop	23.5	57.1	Cop	25.6	53.4	Pol	15.3	49.4
Gas	10.7	67.8	Ost	14.0	67.4	Ost	15.3	64.8
Ost	9.4	77.2	Gas	8.9	76.4	Tan	14.4	79.2
Amp	7.5	84.7	Pol	6.4	82.8	Iso	8.1	87.2
Pol	6.8	91.5	Iso	6.0	88.8	Gas	4.0	91.3
Biv	3.0	94.6	Amp	6.0	94.8	Biv	3.8	95.0
Oph	3.0	97.6	Oph	2.4	97.2	Amp	2.3	97.3
Iso	1.5	99.1	Biv	2.1	99.3	Cra	1.8	99.1
Cra	0.9	100.0	Cra	0.7	100.0	Oph	0.9	100.0

Table 2.3 Continued

Ponta Leste: Area 1

no coral vs. half cover			no coral vs. full cover			half coral vs. full cover		
Taxon	Contrib. %	Cumulative %	Taxon	Contrib. %	Cumulative %	Taxon	Contrib. %	Cumulative %
Amp	26.6	26.6	Amp	34.3	34.3	Tan	28.1	28.1
Tan	18.4	45.0	Tan	15.6	49.9	Amp	18.9	47.1
Cop	15.7	60.7	Pol	14.6	64.5	Cop	15.7	62.8
Pol	12.7	73.4	Iso	12.6	77.1	Pol	9.4	72.2
Ost	7.2	80.6	Ost	6.1	83.2	Ost	7.3	79.5
Iso	5.5	86.1	Cop	5.6	88.7	Iso	7.3	86.8
Biv	4.7	90.9	Gas	4.4	93.1	Biv	4.5	91.2
Gas	4.1	95.0	Oph	4.0	97.1	Gas	4.4	95.6
Cra	2.5	97.5	Biv	2.1	99.2	Cra	2.7	98.4
Oph	2.5	100.0	Cra	0.8	100.0	Oph	1.7	100.0

Ponta Leste: Area 2

no coral vs. half cover			no coral vs. full cover			half coral vs. full cover		
Taxon	Contrib. %	Cumulative %	Taxon	Contrib. %	Cumulative %	Taxon	Contrib. %	Cumulative %
Pol	23.9	23.9	Tan	23.2	23.2	Pol	25.5	25.5
Tan	18.6	42.5	Iso	21.9	45.1	Tan	20.8	46.2
Iso	12.9	55.4	Gas	19.0	64.1	Amp	15.1	61.3
Amp	11.9	67.4	Pol	13.1	77.2	Iso	12.4	73.7
Gas	10.8	78.2	Ost	7.9	85.1	Cra	9.2	82.9
Cra	7.3	85.5	Amp	7.7	92.8	Biv	6.7	89.7
Biv	6.2	91.7	Cra	2.9	95.7	Ost	4.8	94.5
Ost	4.9	96.6	Oph	2.4	98.1	Gas	2.7	97.2
Oph	2.8	99.4	Biv	1.5	99.6	Oph	2.3	99.5
Cop	0.6	100.0	Cop	0.4	100.0	Cop	0.5	100.0

2.5 Discussion

This study reports for the first time the effects of invasive sun corals on mobile invertebrate assemblages inhabiting subtropical rocky reefs, otherwise dominated by native colonial fouling invertebrates, algal turfs and canopy of varying complexity. Although there were some spatial inconsistencies at different scales, a case is made for a frequent tipping point between half and full coral cover, beyond which main taxonomic groups (i.e. tanaids, copepods and ostracods) become much less abundant or collapse. Most vertical or nearly-vertical walls at Búzios Island present a sun-coral cover varying within this range, indicating that resilience to further increase of sun coral abundance is very unlikely.

Changes in the abundance and of main invertebrate groups and community structure are apparently related to the loss of the intricate physical structure of several native fouling species, as the sun coral cover becomes predominant. Compared to temperate shallow reefs where most complex habitat consists of large brown macroalgal beds, namely fucoids and kelps (Vermeij, 1978; Witman & Dayton, 2001), tropical and subtropical rocky reefs are usually dominated by a complex mosaic of very diverse assemblages of small macroalgae, mostly red, colonial fouling invertebrates, such as sponges, ascidians and bryozoans, and both soft and hard corals (Witman & Dayton, 2001; Oigman-Pszczol et al., 2004; Porter et al., 2013). In southeastern Brazil, filamentous and articulated coralline algal turfs, together with canopy-forming algae such as *Sargassum*, *Hypnea*, *Laurencia* and *Padina* build up major habitats within healthy reefs (Oigman-Pszczol et al., 2004), and aggregate diverse fish assemblages (Floeter et al., 2007) at higher densities compared to other important coastal systems (Eggersten et al., 2017). It is still unclear whether fish use those reef vegetated habitats as shelter or foraging grounds, but the latter is very probable as seaweeds tend to aggregate very high densities of potential prey (Tano et al., 2016). The complex structure of most seaweeds also favours the accumulation of sediments and detritus coming from land by frequent rain showers and local hydrodynamics, adding environmental heterogeneity at spatial scales within the range of body sizes of common accompanying fauna (Airoldi, 2003). The mixed matrix of algal tissues and trapped sediments is preferential habitat for an array of invertebrate groups, including tanaids, ostracods and copepods (Berghe & Bergmans, 1981; Danielpool et al., 1996; Pereira et al., 2014). This likely explains why those groups were almost absent at patches saturated by sun corals in Búzios Island. Interestingly, the effects on amphipods, which include several species that directly graze on host algal tissues (Neckles et al., 1993; Duffy & Hay, 2000), were not affected in any evident way. This reinforces the notion that the provision of physical complexity, not the supply of algal tissues to mesoherbivores, drives the abundance and distribution of the main invertebrate groups found in samples.

The crustacean groups that were most affected by the sun coral invasion at Ilha de Búzios are all very important prey for larval and juvenile nearshore fish. Tanaids were the most abundant group in areas with only partial or no sun coral cover. Because they rank among the most important food items for intermediate fish size-groups (5.0-10.0 cm; Pereira et al., 2014), their exclusion as patches develop to sun coral saturation may negatively impact fish populations. Tanaids have also low dispersal capacity (Pereira et al., 2014) and therefore migration from seaweed to coral-dominated habitat (i.e. recolonization) is very unlikely. Ostracods and harpacticoid copepods are not only consumed by early fish stages but also considered important trophic links in bentho-pelagic food webs. Ostracods are a major food source for many vertebrate and invertebrate species (Mbahinzireki et al., 1991) and harpacticoids, the most abundant copepods in this study, are an important food source for penaeid shrimp and many larval and juvenile fish species (Nelson & Coull, 1989; Pinto et al., 2001). Unlike the complex seaweed architecture, sun coral colonies do not provide interstitial spaces compatible to the size of small crustaceans, and do not retain sediments or detritus that can be used as food sources (Airoldi, 2003;

Berghe & Bergmans, 1981; Danielpool et al., 1996). The rapid invasion of *Tubastraea* spp. may therefore alter the nearshore trophic web and lead to the loss of endemic fauna and flora. In the worst case-scenario declines of small mobile invertebrate groups which are prey for demersal consumers may affect whole ecosystem services, particularly artisanal fisheries aiming reef species.

Polychaetes were also affected by the presence of sun corals but this group was present in all samples, including patches fully covered by the orange cup coral. Effects on lower taxonomic levels, not addressed in this study, may underlie their generalized occurrence at the different reef habitats. Polychaetes exhibit remarkable functional diversity (Wouters et al., 2018), with many groups successfully colonizing hard bottoms (Hutchings, 1981; Gobin, 2010). On reef habitats, polychaetes are mostly found in crevices or holes within calcareous rock (Nogueira et al., 2001), providing shelter against predators and the supply of different food sources, including debris, small invertebrates and algae. Nogueira and Martin (2002) found that the endemic Brazilian brain coral *Mussismilia hispida* (Verril, 1868) supports a very rich and diverse assemblage of polychaetes, similarly as reported by others for coral habitats in the Mediterranean Sea and the Indian Ocean, as well as other Atlantic regions (Mccloskey, 1970; Kohn & Lloyd, 1973; Arvanitidis & Koukouras, 1994). While providing important physical structure to reef habitats, sun corals may also exert strong negative allelopathic effects. For instance, Creed (2006) showed that sun corals infringe necrosis on *Mussismilia hispida* colonies up to a distance of five centimetres. Negative allelopathy through the release of water-borne toxic substances (Coll et al., 1982; Sammarco et al., 1983; Gunthorpe & Cameron, 1990) may not only intensify interspecific competition for the occupation of primary space, but also restrict coral habitat to species that tolerate the presence of toxic substances to some extent. It is known that some polychaete species are associated to toxic sponges (Skilleter et al., 2005), and can absorb low concentrations of different toxins and heavy metals (Bryan & Hummerstone, 1971; Mebs, 1998). It is possible that the widespread occurrence of polychaetes over the different reef habitats at Búzios Island is a result of their generalized tolerance to water-borne allelochemicals.

The trends discussed above are however prone to substantial change at the spatial scales examined. Most important, the effects of sun coral abundance were clearer at Pedra Lisa (PEL) compared to Ponta Leste (POL). PEL is a relatively sheltered area, facing north, while POL is close to the eastern end of Búzios Island, and thus more frequently exposed to the larger swell that build from prevailing easterly winds (Fontes & Castro, 2017). Because this coastal region is often oligotrophic (Ciotti et al. 2010), wind-driven upwelling and wave-action more likely impacting POL may substantially increase nutrient supply and the flow of feeding particles to invertebrate consumers. Those effects may partially obscure the effects of sun coral cover. Smaller scale inconsistencies, as shown for richness, are more difficult to interpret. Differences in richness are often dictated by the distribution patterns of rare groups, which, in turn, may reflect the occurrence of the host biogenic habitat, such as sponges, ascidians and particular algal canopies to name a few microhabitats that may play an important role in rocky reef systems. Even at nearly saturated coral patches, secondary habitat built by filamentous algae, solitary ascidians *Phallusia nigra* or even small clumps of mytilid bivalves *Isognomon bicolor*, may host distinct species assemblages. Clearly, further work is needed to tease apart potential factors that may operate at smaller spatial scales.

Invasive species can be considered a great threat to marine ecosystems, displacing native species and ultimately causing overall changes of community structure, food-web topologies and ecosystem functioning (De Paula & Creed, 2005; Molnar et al., 2008). Moreover, invasive species such as sun corals are autogenic engineers, as long as their own physical structure modifies the surrounding environment (Jones et al., 1994). We report severe impacts of the sun coral invasion on populations of major invertebrate groups, chiefly tanaids, ostracods and copepods, deeply modifying community structure when coral cover exceeds 50%. Our findings add to the results of Mizrahi and colleages (2016), who suggested higher impacts at habitat patches where the diversity of native fouling assemblages is highest and reinforce the perception that the sun coral invasion will have far-reaching consequences. Vast areas of shallow-water reef habitat at Búzios Island, as well as other places (e.g. Ilha Grande, RJ), are invaded by sun-corals beyond tipping point estimates and there is no evidence supporting any reversals of past invasive trends. Given that long-standing reef ecosystem services might be compromised, including artisanal fisheries, this study further highlights the need to control the sun coral spread and its eradication at places where its occurrence is still restricted and removal efforts feasible.

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Chapter 3

Food web associated with the habitat-modifying and invasive sun coral *Tubastraea* spp.

3.1 Abstract

The sun coral, *Tubastraea* spp, is an azooxanthellate coral that is rapidly invading North and South Atlantic tropical coasts. It is also an ecosystem engineer that once established, tends to dominate altering the local community structure and function. However, there are no studies on the food web associated to the colonies of *Tubastraea* spp. At the basis of this coral another invasive species is very often found, the bivalve *Leiosolenus aristatus*, a borer species that perforates the base of hard corals. Stable isotopic analysis was applied to all organisms occurring at the microhabitat built by *Tubastraea* spp to 1) provide the first trophic characterization of the food web facilitated by *Tubastraea* spp., while also 2) elucidating if *L. aristatus* receives nutrition from its coral host *Tubastraea* spp. Stable isotopic analyses showed that the food web that accompanies this invasive coral seems to be mostly composed of suspension feeders, confirming that the new community established after *Tubastraea* spp. invasion is dominated by heterotrophs. It was also concluded that both *Tubastraea* spp. and *L. aristatus* are suspension feeders consuming similar resources. This way, *L. aristatus* seems to profit from the expansion of *Tubastraea* spp. because the coral provides it with a structure to live, but not a source of nutrition. As *Tubastraea* spp. progresses in its invasion of new areas, this borer bivalve should follow.

Keywords**:** Exotic species, ecosystem engineer, predator-prey interactions, stable isotopes.

3.2 Introduction

The sun coral is the most rapidly invading species of the Brazilian rocky shore, negatively affecting the native biodiversity, as evidenced by the decreasing population of the endemic Brazilian brain coral *Mussismilia hispida*. (Creed, 2006). The natural range of the sun coral *Tubastraea* spp. is the Indo-Pacific region and it has two main species (*T. coccinea* and *T. tagusensis*), which are at the epicentre of the invasion in Brazil (Creed et al., 2016). The two species are very difficult to distinguish and thus we will refer to them as *Tubastraea* spp. The sun coral invasion started in the Caribbean Sea (first recorded in 1943 by Vaughan & Wells) and began its descent towards Southwestern Atlantic (late 1980s), passing by the Gulf of Mexico and Florida (1977) (Castro et al., 1999; Cairns, 2000; De Paula & Creed, 2004; Fenner & Banks, 2004). In Brazil, the first sun coral colonies were found in offshore oil platforms in Campos oil basin, Rio de Janeiro. Is notorious the rapid invasion by the scleractinian along the Brazilian shore, from north to south, in the last thirty years (De Paula & Creed, 2004; Mantelatto et al., 2011).

In general terms, both species are hermaphrodites with a vast reproductive strategy – with sexual and asexual reproduction –, early reproductive maturity, a great planulae release, a great fixing capacity in natural (cave ceilings and undersides of big rocks) or artificial (dock pilings and buoys) substrate, high recruitment and growth rates and settlement preference in vertical surfaces (Cairns, 2000; Creed & De Paula 2007; De Paula et al. 2014; Mizrahi et al. 2014 (b); Creed et al., 2016). The orange cup coral is, also, able to produce antifouling chemical compounds which prevent the fish and invertebrate predation (Creed et al., 2017). All the features previously mentioned, are the responsible for giving the "invasive species" status to the sun coral, thus, are gathered all the conditions for a successful and rapid establishment and proliferation in regions outside of their native range. An example of the rapid expansion of this coral (De Paula et al., 2014) is the notorious invasion in areas where the presence of sun coral was rare and started to be abundant or dominant and, was estimated, in Ilha Grande (RJ, Brazil) region an expansion rate of 2.1km/year (Lages et al., 2011; Creed et al., 2017).

Little is known about the relationship established between borer bivalves and the organisms they perforate. *Leiosolenus aristatus* (Dillwyn, 1817) is a borer bivalve which its native range is the Caribbean Sea but with a large worldwide distribution. Is possible to find this specimen in the Pacific and Atlantic Ocean (from Portugal to Senegal on the North Atlantic and from North Carolina to Venezuela in the Western part of the Atlantic) (Simone & Gonçalves, 2006; Lopes., 2011). In Brazil, the first record of the invasion was in 2005 in two States, Rio de Janeiro e São Paulo (Simone & Gonçalves, 2006). *Leiosolenus aristatus* is the accepted scientific name nowadays but the genus of this mytilid it was, already, recognize as *Litophaga* (Röding, 1798) and *Myoforceps* (Fischer 1886) (Lopes, 2011). Despite this species had been several names in the past, its primary recognition is very simple if we look to the pointed, crossed tips at the posterior part of the shells, which cross like fingers (Lopes, 2011; Ignacio et al, 2012). The preferential habitat of the bivalve is hard surfaces, such as shells, corals and barnacles (Lopes, 2011), boring substrata and soft rocks from intertidal to 5m depth (Simone & Gonçalves, 2006; Ignacio et al., 2012). Having regard to the preferred habitat, is acceptable to admit that we are talking about a species which needs to perforate to survive. Such perforation may have possible damage to native species, because the "datemussels" (common name for the posterior part of the shells being crossed like fingers) perforate the living shells, causing deformation of the host and even its death (Simone & Gonçalves, 2006). Because of its habit of penetrating corals and because its presence often goes unnoticed initially, it may significantly change the structure of local coral communities and is considered an invasive species (Lopes, 2011). Mariculture can be the primary (even if is not an intended biological introduction vector) vector for the introduction of the species in the Brazilian coast but, also, ballast water and hull fouling are other potential vectors (Ignacio et al., 2012).

L. aristatus is native to the tropical Northwest Atlantic, thus the two species (the bivalve and the sun coral) do not overlap at their native distribution range. The association between the two only occurs when their invasive ranges of distribution meet. There is no information on the trophic relations between these two invasive species.

Stable isotopic analysis was applied to all macro-organisms occurring at the microhabitat built by *Tubastraea* spp. agglomerates to 1) provide the first trophic characterization of the food web facilitated by *Tubastraea* spp. while also 2) elucidating if *L. aristatus* receives nutrition from its coral host *Tubastraea* spp.

3.3 Materials and Methods

3.3.1 Study area

The study area is in the Búzios Island (23 48’ 11” S; 45 08’ 21” W), off the southeast coast of Brazil (Fig.3.1). The island has 7.5 km^2 and is scarcely inhabited, mostly by traditional fishermen. The climate is wet tropical. Summers in this area are typically warm and wet, with frequent tropical storms. The numerous heavy rain showers (often more than once a day) mean that the input of terrestrial matter is highly variable on a fine temporal and spatial scale. This way, punctual collection of particulate matter (POM) for stable isotope analyses will necessarily result in highly variable values. This also applies to phytoplankton and zooplankton. For this reason, sampling did not include POM, phytoplankton and zooplankton.

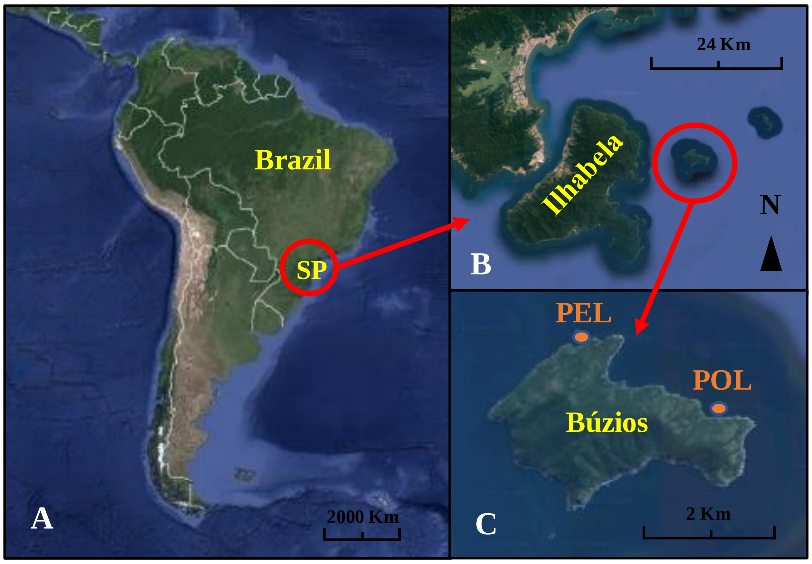

Fig. 3.1 Representative map of (A) Brazil and São Paulo location in South America, (B) Búzios Island location at Northeast of Ilhabela and (C) Samplig sites region in Búzios Island: Pedra Lisa (PEL) and Ponta Leste (POL).

3.3.2 Sampling

Sampling took place during summer, in February of 2017, at two sites, PEL (S 23°47′54.2” - W 45°09′24.6”) and POL (S 23°48′6.79“- W 45° 7′21.65“) distanced approximately 3 km (Fig 3.1). Both sites have vertical rock walls covered with *Tubastraea* spp. At each site, a diver collected all organisms, with a chisel and an air-lifting device coupled to SCUBA tanks (Munro, 2013), from two 0.5 m^2 squares distanced approximately 5 m. Sampling was conducted at a mean depth of 5 m. Samples were preserved on ice and taken to the laboratory at CEBIMar (Centre for Marine Biology of the University of São Paulo).

3.3.3 Laboratory Procedures

Tentacles of *Tubastraea* spp. were plotted for stable isotope analysis. Muscle tissue samples were dissected from molluscs and crustaceans. Tissues of all species were dried at 60ºC and ground to fine powder with a mortar and pestle.

The isotopes analysed were $\delta^{13}C$ and $\delta^{15}N$. These isotopes are commonly used for the description of food webs in a wide variety of ecosystems because they allow the estimation of the food sources used by organisms over time, allowing a characterization of their feeding habits and trophic levels (Peterson et al., 1985; Riera & Richard, 1996; Kwak & Zedler, 1997; Baeta et al., 2009; Vinagre et al., 2015).

The carbon and nitrogen isotopic composition of the samples was determined using a Flash EA 1112 Series elemental analyser coupled on line via Finningan ConFlo III interface to a Thermo delta V S mass spectrometer. The carbon and nitrogen isotope ratios are expressed in delta (δ) notation, defined as the parts per thousand (‰), a deviation from a standard material (PDB limestone for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$): $\delta^{13}C$ or $\delta^{15}N = [(Rsample/Rstandard) - 1] \times 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. The precision in the overall preparation and analysis was better than 0.1‰ for $\delta^{13}C$ and 0.3‰ for $\delta^{15}N$.

3.3.4 Data Analysis

Analyses of variance (ANOVA) were conducted to test if *Tubastraea* spp, *L. aristatus* and *Cassostrea virginica* showed isotopic differences. Both *Tubastraea* spp, *L. aristatus* have never been isotopically characterized, so we compared their values not only between each other but also with the oyster *C. virginica*, which is a well-known suspension feeder and could thus be used as a reference. The ANOVA assumptions were previously investigated. Normality was investigated through the Shapiro-Wilk's test and homoscedasticity through Levene's test. A significance level of 0.05 was considered in all test procedures.

3.4 Results

The food web associated with *Tubastraea* spp. seems to be dominated by primary consumers, most of them suspension feeders, like the ascidian *Phallusia nigra*, the sun sponge *Hymeniacidon heliophila*, the barnacle *Tetraclita stalacifera* and the oyster *Crassostrea virginica*.

Eleven species/groups were analysed in this study (Table 3.1, Fig 3.2). Two macroalgae were analysed, the red macroalgae *Amphiroa* sp. and "turf", a mix of small intertwined filamentous macroalgae that are difficult to separate and were thus analysed as a bulk. *Amphiroa* sp. is clearly not contributing to this food web, since its isotopic values are clearly distinct from those of all consumers. The isotopic values of the mix we called "turf" are consistent with it being consumed by the two non-suspension feeding species analysed, the speck-claw decorator crab *Omalacantha bicornuta* and the sea snail *Morula nodulosa* (Table 3.1, Fig 3.2). Worms of the Nereididae family may also be feeding on turf. The barnacle *Tetraclita stalactifera* is also a well-known suspension feeder, however its isotopic values are more enriched in $\delta^{13}C$, than the other suspension feeders analysed (Table 3.1, Fig 3.2). The isotopic values of *Tubastraea* spp., *L. aristatus* and *C. virginica* did not present significant differences, neither in $\delta^{15}N$ (F=3.023, P=0.068), nor in $\delta^{13}C$ (F=1.229, P=0.311) (Fig. 3.3).

Table 3.1 Number of individuals/plots analysed and their mean δ15N and δ13C values (standard deviations in brackets).

Taxa		N	$\delta^{15}N$	$\delta^{13}C$
Macroalgae				
	Amphiroa sp.	3	1.65 (1.12)	-3.68 (0.18)
	Turf (mix)	5	7.71 (0.70)	-15.84 (0.76)
Porifera				
	Hymeniacidon heliophila	4	8.18 (1.14)	-18.49 (0.66)
Cnidaria				
	Tubastraea coccinea (tentacles)	6	8.24 (1.16)	-18.27 (1.38)
Polychaeta				
	Nereididae	14	9.72 (2.16)	-18.39 (1.14)
Gastropoda				
	Morula nodulosa	6	10.09 (0.55)	-16.37 (1.14)
Bivalvia				
	Crassostrea virginica	8	7.40 (1.04)	-19.34 (0.81)
	Leiosolenus aristatus	12	7.01 (0.90)	-19.13 (1.55)
Crustacea				
	Omalacantha bicornuta	3	9.37 (0.76)	-17.52 (1.33)
	Tetraclita stalactifera	6	8.67 (1.59)	-14.47 (1.89)
Ascidiacea				
	Phallusia nigra	3	5.35 (0.03)	-20.16 (0.07)

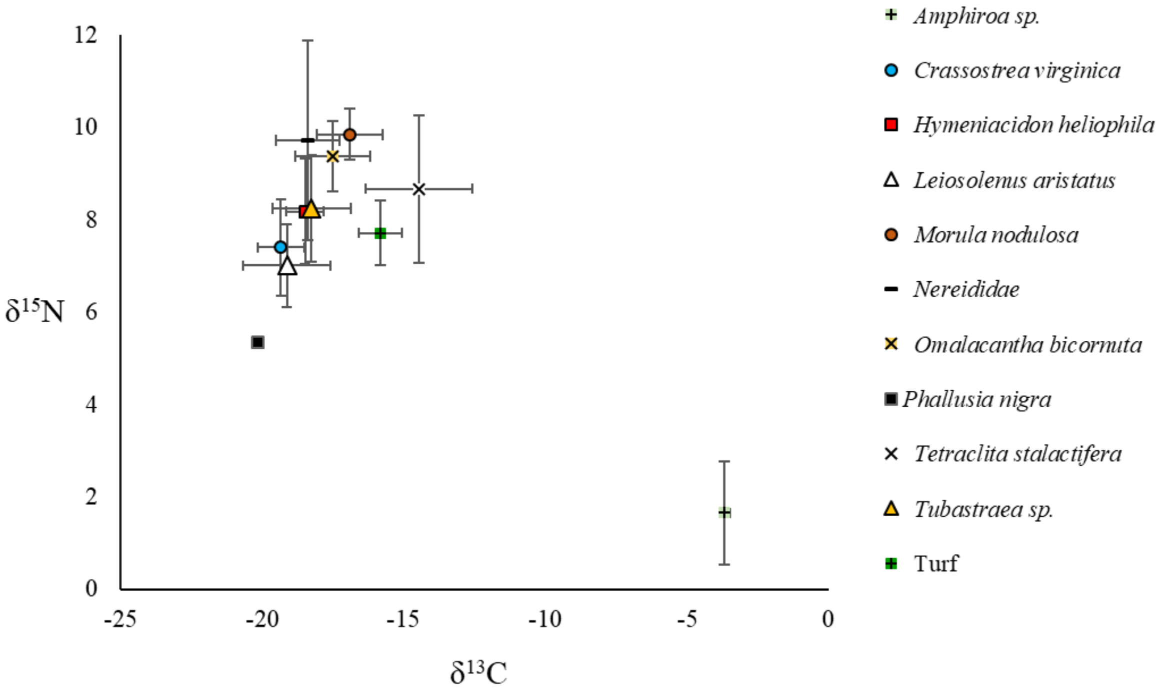

Fig. 3.2 Biplots of the mean (±SD) δ13C and δ15N values of the organisms analysed.

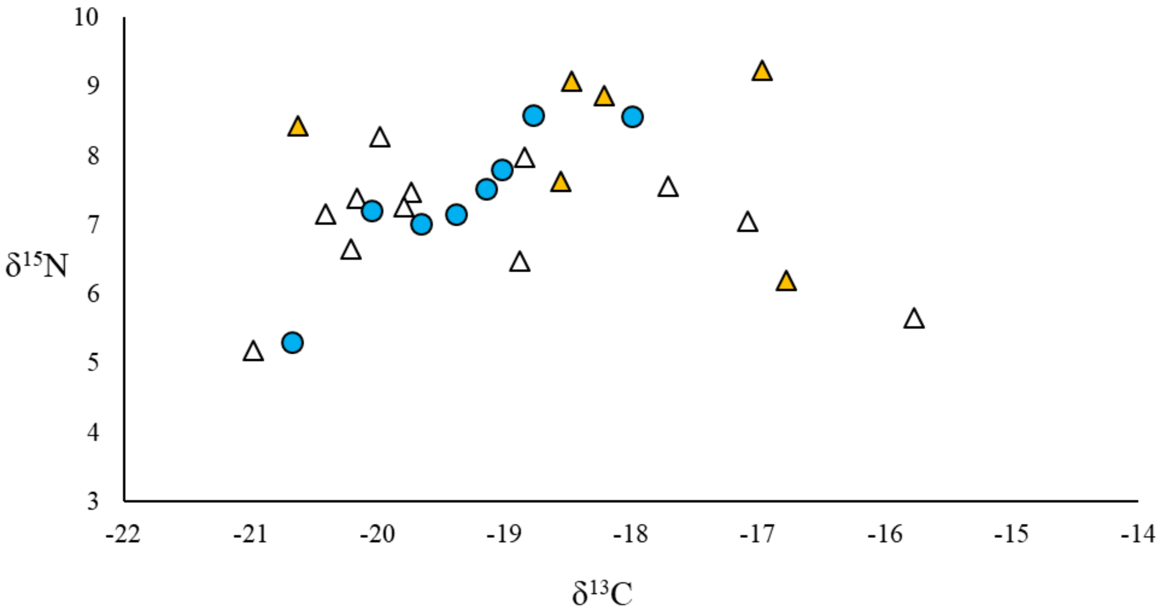

Fig. 3.3 Biplots of individual isotopic values of *Tubastraea* spp. (yellow triangles), *L. aristatus* (white triangles) and *C. virginica* (blue circles), collected from the Búzios Island, Brazil, in February 2017.

3.5 Discussion

This work shows that the food web associated with the sun coral is dominated by primary consumers, most of them suspension feeders, like ascidians, sponges, bivalves and barnacles, confirming the work by Lages et al. (2011), which stated that invaded rocky shores in Brazil change from being dominated by macroalgae and zooxanthellate cnidarians, autotrophic organisms, to being dominated by heterotrophic organisms. Furthermore, the non-suspension feeders analysed in the present study were also heterotrophic organisms, the gastropod *M. nodulosa*, polychaetes from the Nereididae family and the crab *O. bicornuta.*

The only autotrophs found were the macroalgae *Amphiroa* sp and the mix of filamentous algae we designated by "turf". Fractionation at the base of this food web seems to be within what is usually assumed between trophic levels, which is an increase in 2.5-4.5 from prey to predator (Owens, 1987; Peterson & Fry, 1987). That can be observed between ascidians, sponges, "turf", and the primary consumers, namely *M. nodulosa*, Nereididae polychaetes and *O. bicornuta*. However, the distinct isotopic values of *Amphiro*a sp indicate that this species does not contribute as nutrition for the primary consumers. Only ascidians, sponges and "turf" had isotopic values consistent with being consumed by organisms higher up the food web.

It must be pointed out that *Tubastraea* spp. isotopic values do not rule it out as a potential food source for the primary consumers analysed in the present study, quite the opposite, its values are very similar to those of other species (sponges) that were pointed as probable food sources for the primary consumers. However, this species has been described as having no natural predators (Campbell, 1983). Its rapid invasion capacity certainly suggests that it is free from predation, however studies on the feeding behaviour of the gastropods, polychaetes and small crustaceans observed here, should elucidate if *Tubastraea* spp. has a role as food source for any consumers in its associated food web. Since no significant differences, neither in δ^{15}N, nor in δ^{13}C, were detected among *Tubastraea* spp., *L. aristatus* and *C. virginica*, it can be concluded that they share the same food source or a similar mix of food sources. Since, the oyster *C. virginica*, is a well-known suspension feeder, it can be concluded that these species are probably also feeding on suspended materials. The barbacle, *T. stalactifera* is also a well-known suspension feeder, however its isotopic values were very distinct from those of the previously mentioned suspension feeders. *T. stalactifera* presented considerably more enriched δ^{13}C values.

This wide difference in δ^{13}C values at the food web basis is common in other coastal food webs and indicates the existence of two energy pathways, pelagic and benthic (Darnaude, 2005; Le Loc'h et al., 2008; Vinagre et al., 2015). The pelagic pathway originates in the photosynthetic activity from phytoplankton while the benthic pathways is based on detritus, carried from by currents and/or transported by terrestrial drainage (Rafaelli & Hawkins, 1999). Marine producers (especially phytoplankton) have more enriched δ^{13}C values than terrestrial primary producers, this way allowing the tracing of the origin of carbon in coastal environments (Haines & Montague, 1979; Riera & Richard, 1996; Bouillon et al., 2000). *T. stalactifera* enriched δ^{13}C values in comparison to the other suspension feeders indicates that this species is probably mainly consuming phytoplankton, while the others are mostly consuming detritus.

Since the isotopic evidence presented here suggests that *L. aristatus* is a suspension-feeder, feeding on the same source as its host *Tubastraea* spp. it can be concluded that this invasive borer bivalve has its invasion facilitated by *Tubastraea* spp. because the coral provides structural refuge, not because it is a source of nutrition. As the coral expands its invasion range, it creates a structural niche for the invasive bivalve to occupy. It should thus be expected that *L. aristatus* will follow *Tubastraea* spp. as it rapidly invades new coasts.

3.6 References

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Chapter 4

4.1 Final Considerations

The present work demonstrates, for the first time, how the sun coral can act as an ecosystem engineer, both affecting the rocky bottoms associated macrofauna and the local food web structure. The results suggest a higher abundance, diversity and richness of species in areas without or partially covered by the sun-coral and on macroinvertebrates, such as tanaids, ostracods and copepods. On the other hand, an invasive bivalve is often found on the hard basis of *Tubastraea* spp. and the community structure associated to the sun coral is, mainly, composed by heterotrophs instead of autotrophs organisms. These are clear evidences that the sun coral is an ecosystem engineer, acting as excluder of some species and facilitator for other species, changing the habitat and all surrounding life.

This study adds to the knowledge on the impact of the sun coral on the rocky shores of Brazil. Further research should lead to new insights into how environmental features, such as food availability, temperature, depth and hydrodynamics, affect the invasion of this coral. It is also important to understand if there are mechanisms of sun coral exclusion. A potential bio-mechanism to slow down the invasion is if the invasive bivalve *L. aristatus* makes the corals hard basis more likely to break because of its perforation. The mytilid could make the calcareous coral basis weaker and prone to break down during storms. This would be a potential mechanism of exclusion of both invaders, the coral does not have the ability to survive without a foundation and the bivalve would not have a sheltered place to live, protected from predators. It is also possible that some native fish prey on the sun coral, like showed by Mirzrahi et al. (2018) for the damsel *Abudefduf saxatilis*, in the same study area. Such fish, or any other predators, could eventually lower the rate of invasion of the sun coral.

If the sun coral invasion does not stop (naturally or due to human intervention), the southwest Atlantic rocky bottoms are likely to continue to be severely invaded. The main consequence of this will be a deep alteration of the local habitats, which means a radical change on the native biotic assemblages. In general terms, an important alteration in the rocky shore food webs and marine biodiversity is taking place at an accelerated rate, affecting the balance of the ecosystems and possibly the local economy via a potential interreference with fisheries.