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TROPHIC ECOLOGY OF TROPICAL OCTOCORAL: FROM RESEARCH GAPS TO THE STUDY OF TWO DIFERENT ECOZONES.

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RESUMO

Recifes de corais são um dos ecossistemas marinhos mais diversos, complexos, produtivos e economicamente valiosos do mundo, com valor estimado em 352.000 dólares/hectare/ano. Entretanto, mudanças ambientais têm gerado impactos na complexidade e funcionalidade da estrutura dessas florestas marinhas. Diversos locais do mundo estão vivendo uma transição na comunidade marinha, onde organismos mais resilientes estão ocupando espaço e se fixando no ambiente em detrimento daqueles que são mais frágeis. Nessa luta por sobrevivência, os octocorais são vencedores e como resultado têm se tornado mais presentes nos corais marinhos, enquanto os escleractínios estão desaparecendo em algumas regiões, como no mar do Caribe. A habilidade de se alimentarem por heterotrofia parece se destacar como uma das principais características que contribuem para a maior resiliência desses organismo. Entretanto, ainda são necessárias mais pesquisas a área de ecologia trófica para melhorar a compreensão sobre esse tema. Nesse intuito, a tese fornece informações valiosas divididas em 3 capítulos em formato de artigo que objetivam: (capítulo 1) investigar o panorama atual de estudos com ecologia trófica em octocorais tropicais; (capítulo 2) analizar a tendencia trófica dos octocorais *Muriceopsis sulphurea, Plexareulla grandiflora, Phyllogorgia dilatata*, que habitam regiões do Atlântico Sul através de dados bioquímicos (lipídios e carboidratos) e de isótopos estáveis $\delta^{15}N$ e $\delta^{13}C$; (capítulo 3) realizar análise temporal da composição bioquímica (lipídios, carboidratos, proteínas e ácidos graxos) dos octocorais *Plexaurella nutans* e *Pterogorgia anceps* do mar do Caribe. Como resultados, foram pontuadas a necessidade de pesquisas em regiões tropicais do Atlantico Sul, em áreas mesofóticas, identificar a relação entre ecologia trófica e reprodução e investigar os efeitos em conjunto dos disturbios nos octocorais. A partir de análises bioquímicas e isotopos estaveis foram registradas que três espécies de octocorais na região Tropical do Atlantico sul tem tendência heterotrófica e que a análise de dados bioquímicos de espécies de octocorais do mar do Caribe corraboram com dados anteriormente divulgados que confirmam a tendencia autotrófica deles e estão relacionados com aspectos reprodutivos desses animais. Os resultados obtidos oferecem informações inéditas e importantes da ecologia trófica de octocorais em regiões tropicais, cotribuindo para a compreensão da capacidade desses organismos em persistir em ambientes sujeitos a variações ambientais cada vez mais frequentes e intensas.

Palavras-chave: Nível trófico, Aquecimento global, Gorgônias.

ABSTRACT

Coral reefs are one of the most diverse, complex, productive, and economically valuable marine ecosystems in the world, with an estimated value of US$352,000/hectare/year. However, environmental changes have impacted the complexity and functionality of the structure of these marine forests. Several places worldwide are experiencing a transition in the marine community, where more resilient organisms are occupying space and establishing themselves in the environment to the detriment of those that are more fragile. In this struggle for survival, octocorals are the winners and as a result have become more present in marine corals, while scleractinians are disappearing in some regions, such as the Caribbean Sea. The ability to feed by heterotrophy seems to stand out as one of the main characteristics contributing to these organisms' greater resilience. However, more research is still needed in trophic ecology to improve understanding of this topic. To this end, the thesis provides valuable information divided into 3 chapters in article format that aim to: (chapter 1) investigate the current panorama of studies on trophic ecology in tropical octocorals; (chapter 2) analyze the trophic trends of the octocorals *Muriceopsis sulphurea, Plexareulla grandiflora, Phyllogorgia dilatata*, which inhabit regions of the South Atlantic through biochemical data (lipids and carbohydrates) and stable isotopes $\delta^{15}N$ and $C^{\delta 13}$; (chapter 3) perform a temporal analysis of the biochemical composition (lipids, carbohydrates, proteins and fatty acids) of the octocorals *Plexaurella nutans* and *Pterogorgia anceps* from the Caribbean Sea. As result, the need for research in tropical regions of the South Atlantic, in mesophotic areas, to identify the relationship between trophic ecology and reproduction and to investigate the joint effects of disturbances on octocorals was highlighted. Based on biochemical and stable isotope analyses, it was found that three species analyzed of octocorals in the tropical region of the South Atlantic have a heterotrophic tendency and that the analysis of biochemical data from octocoral species in the Caribbean Sea corroborates previously published data that confirm their autotrophic tendency and are related to reproductive aspects of these animals. The results obtained provide new and important information on the trophic ecology of octocorals in tropical regions, contributing to the understanding of the capacity of these organisms to persist in environments subject to increasingly frequent and intense environmental variations.

Keywords: Trophic level, Global warming, Gorgonians.

SUMÁRIO

GENERAL INTRODUCTION

Coral reefs are one of the world's most diverse, complex, productive, and economically valuable marine ecosystems (Connell, 1978; Wyatt *et al*., 2020). The three-dimensional structure and functioning of reefs are constrained by the presence and interaction of ecoengineering species of scleractinian corals (hard corals), hydrocorals, octocorals (e.g., gorgonians), sponges, algae, and other sessile organisms, thus forming marine forests (Rossi, 2013). The richness of biodiversity and its structure resembles forests in the terrestrial environment (Bringloe; Verbruggen; Saunders, 2020); however, they are less accessible, which results in a lack of knowledge about the ecology of the organisms that form coral reefs, especially those that inhabit tropical regions with differentiated environmental conditions such as moderate turbidity, high nutrient content, high productivity, and high temperatures (Halfar *et al*, 2005; Soares, 2020).

This rich forest structure is responsible for the life of several animals and algae that depend on it for their survival, as a source of food, habitat, and nursery (Rossi, 2013; Miller *et al*., 2012). Reefs provide considerable environmental goods and services to humans, acting as a barrier to wave energy, reducing erosion (Sheppard *et al*. 2005), protecting against storm surge, being areas for fish stock renewal, attracting tourism (Rossi, 2013) and sequestering carbon (Krause-Jensen *et al*., 2018), which is essential for mitigating climate change in the ocean (Hoegh-Guldberg *et al*., 2019).

The “trees” of marine forests may correspond, for example, to octocorals, also called gorgonians, which, due to their branched colonies and their attachment methods, allow them to access resources in the water column, providing an advantage compared to other species and reducing competition at the substrate level (Sanchez, 2004). Octocorals are from the subclass Octocorallia, belonging to the Order Alcyonacea from the phylum Cnidaria and are the most diverse group on tropical reefs (Bemayahu, *et al*., 2019; Castro *et al*., 2010). They correspond to the largest known group of corals, with around 3,000 existing species, composed of 47 families and 340 valid genera (Williams and Cairns, 2005; McFadden *et al*., 2006; Daly *et al*. 2007).

Morphologically, octocorals have eight tentacles and eight complete mesenteries in their polyps (McFadden *et al*., 2006) and are characterized by the presence of sclerites, free skeletal elements incorporated into the tissue of polyps and coenenchyma (Daly *et al*., 2007).

The position of sclerites (Lewis & Wallis, 1991) and the junction between elastic and hard calcium carbonate structures (Boller *et al*., 2002), collaborate to flexibility and promote highly resistant to water movements in octocorals. They are commonly referred to as soft corals because they do not produce a rigid calcium carbonate skeleton, which distinguishes them from stony corals (Scleractinia), and visually they are similar to trees, algae, bushes and fans (Bayer, 1961; Khalesi *et al*., 2007).

These characteristics promote the presence of some species in several diverse environments throughout the Caribbean Sea and tropical oceans of the planet (Sànchez, 2016). Furthermore, its lifespan is considered relatively long in some places, reaching more than 50 years (Muricea fruticosa and M. californica) and around 20 to 40 years (Antillogorgia elisabethae) (Goffredo & Lasker 2006, 2008).

The distribution of octocorals is wide in marine and estuarine habitats across all climate zones, both on tropical and subtropical coasts of America and the west coast of Africa (Grasshoff, 1988), and also in temperate waters of the Atlantic (Devictor and Morton, 2010; Perez, Neves, Oliveira, 2011) and in the Mediterranean Sea (Previati *et al*., 2010). However, their abundance in several coral reefs in the Caribbean Sea over the last decades has been increasing more and more, overlapping with Scleractinia corals (such as Acropora spp.), which are in decline as a consequence of climate change and local impacts, such as organic pollution (Schubert; Brown; Rossi, 2017; Ramsby & Goulet, 2019).

Studies suggest that the survival and dominance of octocorals in some coral reefs is due to a set of factors such as greater resistance to bleaching, morphological characteristics, types of symbionts and microbiota, but mainly the less dependence of octocorals on feeding throught autotrophy, being able to obtain food resources through heterotrophy (Rossi & Rizzo, 2021). Still, there is a need for more research in order to better understand what is due to this apparent greater capacity for resistance and recovery of these octocorals, which, with increased occupation of the environment, may cause a change in the structure of coral reefs (Schubert; Brown; Rossi, 2017) as well as in the provision of environmental goods and services, such as less resistance to wave action (increased beach erosion) and less availability of fishing resources.

It is estimated that the value of coral reefs is around US$352,000/hectare/year (Constanza *et al*, 2014), but for reefs to efficiently provide all environmental goods and services, their structure must be highly complex, with a wealth of species, taller and more branched corals, complex and large sponges, among others (Rossi, 2013). And for these forests to reach such complexity, thousands of years were needed to form (Gili & Coma, 1998; Baillon *et al*., 2012), which may have the quality and quantity of goods and services offered compromised if they are degraded (Rossi, 2013).

Ocean warming, acidification and anthropogenic pollution (e.g. microplastics - MPs, sewage and oil spills) are primarily responsible for threatening the integrity of coral reefs (Baker *et al*., 2008) and due to this, research is increasing in the world to understand the effects of such environmental changes.

The study of physiology, growth and survival of coral reefs that are living under stressful conditions in the presence of global warming, for example, is a sine qua non condition for assessing the health of these organisms and the sustainability of these reefs. In this context, healthy coral reefs are necessary for the maintenance of marine life, as well as for the storage of blue carbon, which is essential to contain the impacts of climate change on the planet, which can be harmed by the degradation of the reef ecosystem (Crooks *et al*, 2011; Pendleton *et al*, 2012; Soares, 2020; Mies *et al*, 2020).

Much of the survival of coral reefs is intrinsically related to the nutrition of these organisms. Before climate change events and increased organic pollution, the autotrophy feeding was a advantage to allow corals to adquire nutrients form the water, due to the symbiosis with dinoflagellates of the family Symbiodinacea (LaJeunesse *et al*, 2018) previously described as of the genus Symbiodinium (Ramsby *et al*, 2014). However, the increase in stressful environmental conditions over the years has favored the prevalence of heterotrophic octocorals to the detriment of autotrophic ones, which means that the lower the dependence on symbionts, the greater the survival capacity. (Schubert; Brown; Rossi, 2017).

It is very important to know the food sources that support coral, because their feeding can change due to environmental conditions and the availability of food (Rossi *et al*. 2006a, Gori *et al*. 2007, 2012, Rossi & Tsounis 2007), and this is directly linked to their ability to face challenges in the ocean. Depending on the season and reproductive stage, changes in the food source and thus in the biochemical composition of gorgonians are possible. In tropical environments, coral species could be more heterotrophy in the wet season because of the higher turbidity, low light available, reducing photosynthesis in coral (Nahon *et al*., 2013).

The presence of octocorals can also be influenced by the nutrient content in the marine ecosystem, being more abundant or not in areas of high nutrients and turbidity according to their tolerance capacity (Fabricius *et al*., 2005; Schleyer and Celliers, 2003). Octocoral sea whips have been shown to be more dependent on autotrophy and therefore may be more sensitive to bleaching with increasing temperature in oligotrophic zones (Rossi *et al.* 2018).

The nutritional composition of octocorals is responsible for their ability to face and survive challenges, depending on the balance of their carbohydrates, lipids and proteins (Grémare *et al.*, 1997). Lipids play a crucial role in cell membranes and serve as an energy store for coral growth (Battey & Patton, 1984; Pearse & Muscatine, 1971) and reproduction (Edmunds & Davies, 1986). Most coral's total lipids reside within its polyps (corallites) (Imbs; Dembitsky, 2023), and especially in octocorals, lipids are considered the main components of the energy balance (Zaslow & Benayahu, 1999).

The fatty acids (FA) composition are the main constituents of lipids and have been widely applied in marine food webs as markers of predator–prey interactions, providing useful information on either autotrophic or heterotrophic origin of food (Dalsgaard *et al.*, 2003), according to the dietary sources of FA (Sorokin 1993, Ayukai 1995, Fabricius & Dommisse 2000), presenting different lipid composition (Dalsgaard *et al.* 2003, Bishop & Kenrick 1980, Zhukova & Titlyanov 2003).

In soft corals, the FA composition significantly differed from FA profiles of reef building corals and hydrocorals of the genus Millepora (Imbs *et al.*, 2010a), by the presence of C16 and C24 polyunsaturated FAs (PUFAs) (Imbs *et al.*, 2009), which are different from reef building corals FA profiles (Imbs *et al.*, 2010a). PUFAs were used as the markers of zooxanthellae and the indicators of possible translocation of PUFAs from zooxanthellae to the host in the soft corals (Imbs *et al.*, 2010b).

The lipid profile of corals varies according to several factors, such as reproductive stage, seasonal variations, habitat depth, light availability, and other environmental conditions (Meyers 1979, Saunders *et al.* 2005). Depending on the season and reproductive stage, changes in the food source and thus in the biochemical composition of gorgonians are possible. During the reproduction period, for instance, fluctuations can be observed in lipid content during maturation of the oocytes and spawning processes (Oku *et al.*, 2003; Rossi *et al.* 2006).

Low lipid values could be related to spawning events, otherwise, high levels of lipids are observed in gorgonians as a strategy to store energy, which will be needed for the sexual products (Orejas *et al.* 2002, 2007; Elias-Piera *et al.*, 2013), as observed in several Mediterranean gorgonians (Rossi *et al.* 2006a,b, 2012, Rossi & Tsounis 2007, Gori *et al.* 2012). Therefore, understanding the reproductive cycle of octocoral species is a good indicator of lipid accumulation, which is important to assess their nutritional status and, consequently, predict their survival.

Research on octocoral nutrition has been carried out through analysis of the biochemical balance (protein–carbohydrate–lipid levels) and analysis of stable isotopes. Commonly used in marine ecology, the carbon isotope (δ13C) for discriminating production sources, and (δ15N) nitrogen for estimating nitrogen sources and trophic position. These methodologies have proven to be efficient in offering accurate information on the characteristics of the assimilated food by corals (Iken *et al.* 2001, Jacob *et al.* 2006, Carlier *et al.* 2007, Mintenbeck *et al.* 2007, Mincks *et al.* 2008), allows us to understand how different organisms invest their energy.

Stable isotopes analyses offer advantages over traditional methods like gut contents analyses, because the isotopes compositions are time-integrated, representing material assimilation by consumers over timescales of days to months, whereas hours to days. Additionally, coral tissues contain information about what has been assimilated from the diet, not just ingested (Skinner, *et al.*, 2022). For example, a difference in $\delta^{13}C$ values between coral tissue and his symbiont reflects a low degree of nutrient exchange between the two partners and may indicate heterotrophic tendency in corals (Reynaud *et al.* 2002; Baker, 2015).

Knowledge of trophic tendency in octocorals is essential to identify how these animals are feeding, how this affects their ability to survive in the long term, and consequently, these findings will offer valuable contributions to improving our knowledge of the structure, function and health of the coral reef ecosystem, since heterotrophy has great responsibility for increasing the resilience to thermal stress (Grottoli *et al.*, 2006) and ocean acidification (Edmunds, 2011; Connolly *et al.*, 2012).

However, there are few studies in the literature that investigate feeding interactions in corals, and most of those are aimed at hard corals. Trophic ecology is fundamental to understand how reefs are organized and sustained and could be a central role in the management and conservation of reef ecosystems (Ladd *et al.* 2020). Most studies focus on corals living in oligotrophic tropical reef, in similar habitat conditions, characterized by low turbidity, clear waters, and low temperature variation, in temperate or tropical waters. However, there are coral reefs in regions such as the Tropical Southwestern Atlantic that thrive in extreme conditions, including high turbidity and high-water temperatures.

In general, even in more well-known tropical environments such as the Caribbean, the knowledge of the trophic ecology of octocorals is limited, and in octocorals living under extreme environmental conditions is extremely limited (Rossi *et al.*, 2020; Morillo-Velarde *et al.*, 2018 Ribes *et al.* 1998; Pupier *et al.* 2019).

Researches that aims to study the survival ability of octocorals that live subjected to high nutrient content for example, in the current context of global warming, is necessary and urgent to understand what is happening to coral reefs today and what we can expect in the future if the impacts continue to grow rapidly. For this pourpose, the findings from this thesis may indicate whether octocorals can act as potencial indicator species of the health of the reef environment, providing valuable insights into how these organisms respond to environmental changes in a global context and contributing to the development of national public policies.

In this context, this PhD thesis was structured in three chapters. Chapter 1 was conducted to assess the current state of research in trophic ecology of tropical octocorals. This chapter provided new perspectives through the bibliographic review of the main articles published between 2010 and 2022 that focused on this theme. It was possible to obtain a diagnosis of the current scenario and thus point out improvements required to gain deeper insight into trophic ecology in octocorals. The discovery of these knowledge gaps revealed in this perspective review shows that expanding knowledge of energy store processes is important to gain a deep understanding of the potential resilience of reef octocorals in the face of global change and their role in future seascape composition. This chapter has already been published in the journal Mediterranean Marine Science.

Chapter 2 was thought to offer trophic ecology information of tropical octocoral that inhabit regions considered suboptimal for the reef community (Soares *et al.*, 2018). The Southwest Atlantic Ocean coral reefs form structures significantly different from the well-known coral reef models, wich characteristics that make them a unique system (Mies *et al.*, 2020). Coral reefs live on the limit of physiological stress, under wide temperature variations, moderate turbidity, sediment resuspension, high nutrient input (Kleypas *et al.* 1999; Perry and Larcombe 2003; Halfar *et al.* 2005; Schoepf *et al.* 2015; Chow *et al.* 2019; Soares, 2020). The ability to survive in these environmental conditions appears to provide octocorals with greater resistance and resilience to environmental disturbances, such as thermal stress (Soares, 2021; Mies *et al.*, 2020).

Despite the importance of these habitats, knowledge about the octocoral community is very limited, compared to what is known about corals from the Indo-Pacific and Caribbean Sea. Even less is known about nutritional strategies and there is virtually no information on the trophic ecology of octocorals from Southwest Atlantic Ocean reefs.

In this context, the trophic trends of *Muriceopsis sulphurea, Plexareulla grandiflora, Phyllogorgia dilatata*, three octocoral present in two sites from reefs along the Brazil coast were investigated. For the first time, biochemical composition and δ15N and δ13C isotopes of octocoral from these reefs were analysed and this provides important insights into their biomolecule profile, their trophic position and their potential for resilience in the current climate emergency.

Advancing the study of trophic ecology in octocorals from tropical reefs, chapter 3 performed a temporal analysis of the biochemical composition (lipids, carbohydrates, proteins and fatty acids) of the octocorals Plexaurella nutans and Pterogorgia anceps from the Caribbean Sea to complement previous research by Rossi *et al.* (2020).

The higher presence of octocoral while scleractinians are disappearing is already a reality in the Caribbean Sea and is largely due to the better nutritional efficiency of these soft corals. These analyses offered deep insights into trophic trend of these octocoral species as well as making a connection with reproductive processes.

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CHAPTER 1 - The gaps in knowledge to understand the link between resilience and trophic ecology in tropical octocorals

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Abstract

The structural and functional change of shallow-water coral reefs is a reality that is still not fully understood. In many areas of the world, such as the Caribbean shallow waters, it has been shown that macro algae, sponges, and octocorals occupy the seascape left by stress-sensitive scleractinians, which did not resist human impacts. In this paper, we analyze different drivers for the current-day resilience of one of the “winning” taxa, the octocorals, in the face of changing environmental conditions, paying attention to existing gaps in knowledge. The trophic plasticity of these organisms is recognised as one of the main traits responsible for their stability, allowing them to feed in a more generalist way, along with other biological characteristics (morphology, reproductive strategies, type of symbiont). To investigate the current state of trophic ecology in tropical octocorals, we reviewed 51 articles from 2010 to 2022 to assess new information on this underexplored topic. We categorised data extracted from scientific articles by geographic regions associated with the study site, research objectives, sample collection depth, octocoral family studied, trophic ecology, and impacts of human disturbances. Based on our results, we point out improvements required to obtain greater knowledge about the trophic ecology in octocorals: (A) Expand research on understudied geographic regions (Tropical Southwestern Atlantic); (B) Focus research in mesophotic areas; (C) Investigate the relationship between trophic ecology and reproduction, and describe the reproduction cycles of octocorals, linking energy inputs with energy storage strategies; (D) Analyze the effects of combined and synergistic human disturbances through *ex situ* and *in situ* experiments. Among the gaps of knowledge revealed in this perspective review, expanding the knowledge about the energy budget processes is important for gaining a deep understanding of the potential resilience of reef octocorals in the face of global change and their role in future seascape composition.

Keywords: Soft coral; Bleaching; Marine Forest; Gorgonians; Management.

1. Introduction

The progress of the development of human society promotes serious pressures on marine life and has been causing long-term negative consequences on coral reefs, known as one of the planet's most vulnerable ecosystems (Pandolfi *et al.*, 2003; Hughes *et al.*, 2017). Ocean temperature increase, sea level rise, acidification, marine pollution, overfishing, and land-use changes (Hughes *et al.*, 2003; Hoegh-Guldberg, 2011) are some human-induced disturbances responsible for generating profound changes in tropical coral reefs (Carpenter *et al.*, 2008; Doney *et al.*, 2020).

Many reef-building stress-sensitive scleractinians cannot adapt to this stressful global situation (Hoegh-Guldberg *et al.*, 2007) and, combined with synergistic human pressures, can harm their health (Eynaud *et al.*, 2011). The significant evolutionary adaptation of scleractinians aimed at enhancing energy acquisition through symbiotic photosynthesis (Enríquez *et al.*, 2005), but made these corals more susceptible to bleaching due to their strong autotrophic dependence (Enrìquez *et al.*, 2017; Hughes *et al.*, 2018).

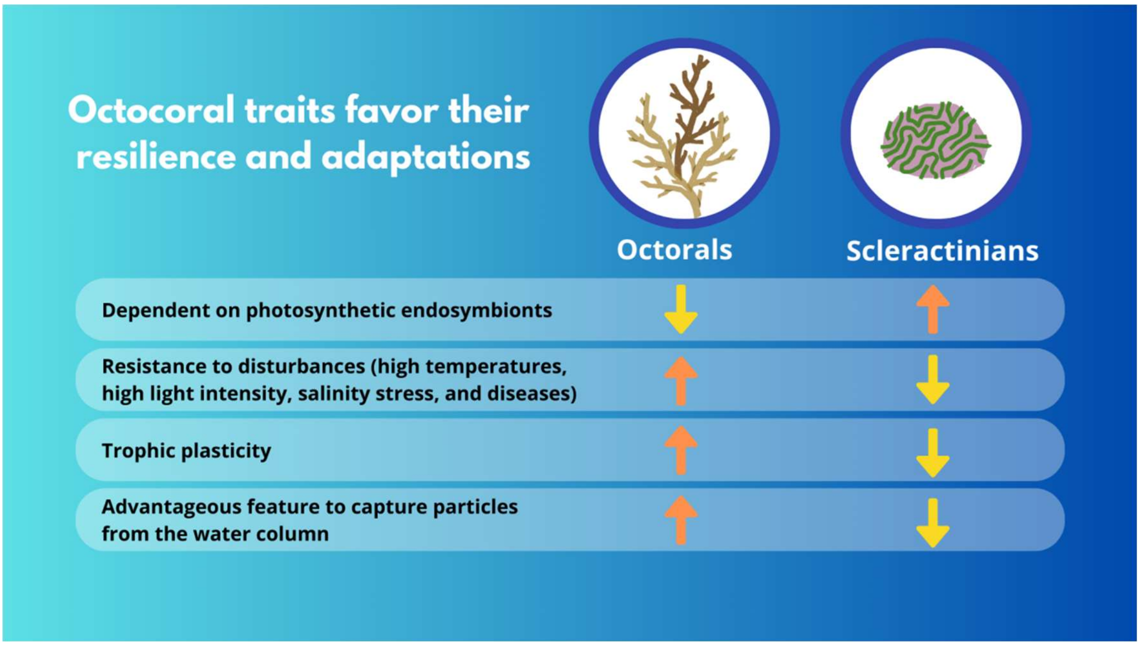
The decline of one functional group, such as reef-building corals, triggers an immediate response from other groups that may be adapted to the changing conditions. This shift threatens the capacity to produce a massive, wave-resistant carbonate platform (Stoddart, 1969) and the ecosystem goods and services delivered by scleractinian corals, considered foundational organisms (Birkeland, 2015). Organisms that survive such environmental changes can remain on reefs and even increase their populations (Norström *et al.*, 2009), leading for example to phase shifts from scleractinians to octocoral dominance in some tropical regions (Hughes, 1994; Fabricius & Alderslade, 2001; Bell *et al.*, 2021). In the Florida Keys, octocorals increased by 138%, 11 years after the 1998 El Niño (Ruzicka *et al.*, 2013) and also are dominant in the Tropical Western Atlantic (Tsounis & Edmunds, 2017).

The significant proliferation of octocorals in the Caribbean, heralds a paradigm shift for reef ecosystems, embodying the "new normal" (Lasker *et al.*, 2020). Over the past several decades, there has been a noticeable decline of scleractinians reported in several coral reefs, accompanied by an increase in the abundance of octocorals, but this phenomenon is not yet fully understood by science (Norström *et al.*, 2009; Lasker *et al.*, 2020; Bell *et al.*, 2021).

Along with octocorals, there are also reports including other animal groups (e.g., Ascidiacea, Porifera, Zoantharia, and Actiniaria) that are increasing in their presence in shallow reefs, altering the distribution of habitat-forming taxa, the composition of benthic assemblages, and consequently the reef functioning (Sorte *et al.*, 2010; Chen *et al.*, 2011; Hughes *et al.*, 2018; Bell *et al.*, 2022). Furthermore, climate change may be responsible for a higher thermal stratification in the global ocean (Li *et al.*, 2020), intensifying ocean acidification, reducing ocean mixing, and impacting marine food webs. Consequently, some benthic filter feeders may as well be restricted due to low incoming energy (Rossi *et al.*, 2019; Lesser & Slattery, 2020). For decades, research studies have been alerting about the collapse of reef growth and the consequential loss of ecosystem goods and services. A fresh approach to the science, management, and governance of reef ecosystems is urgently needed, considering adapting to forthcoming environmental conditions (Hughes *et al.*, 2017; Rossi *et al.*, 2019; Denis *et al.*, 2024).

Increases in octocoral abundance and distribution have been reported on Caribbean reefs over the last 25 years (Ruzicka *et al.*, 2013; Lasker *et al.*, 2020; Edmunds & Lasker, 2022). However, whether octocoral traits favour their resilience or resistance and adaptations is still unclear. Autotrophic-heterotrophic balance and energy inputs, morphological variability and flexibility, fast growth rates responding to local environmental variability, types of endosymbionts, sexual and asexual reproduction, resistance to emerging microbial diseases and the role of associated microbiota are important characteristics for successful resilience in octocorals to survive against environmental and human-induced disturbances (Fig. 1) (Henry & Hart, 2005; Schubert *et al.*, 2017; Weil *et al.*, 2017; Lasker *et al.*, 2020; McCauley *et al.*, 2020; Rossi & Rizzo, 2021).

Trophic plasticity (i.e., the capability to adapt the energy needs to the available autotrophic-heterotrophic inputs) is considered the main feature among the previously listed traits, providing a survival advantage to many octocoral species due to their capacity to use different nutrient sources to gain metabolic energy (Rossi *et al.*, 2020; Pupier *et al.*, 2021). Unlike scleractinians, they are less dependent on dinoflagellate endosymbionts (Symbiodiniaceae, Lajeunesse *et al.*, 2018) in terms of organic matter translocation, enhanced nutrient acquisition through heterotrophy, compensating for the lack of autotrophy or even being an alternative when the photoautotrophic component is fully functional (Radice *et al.*, 2019). This enables their capability to withstand stress conditions such as global warming, marine heat waves, and ocean acidification (Schubert *et al.*, 2017). However, not all heterotrophic and mixotrophic octocoral species are immune to suffering impacts when subjected to highly stressful conditions (Lasker *et al.*, 2020), heterotrophy in octocorals may give a significant advantage in terms of survivorship (Denis *et al.*, 2024).



Octocoral traits favor their resilience and adaptations

	Octorals	Scleractinians
Dependent on photosynthetic endosymbionts	↓	↑
Resistance to disturbances (high temperatures, high light intensity, salinity stress, and diseases)	↑	↓
Trophic plasticity	↑	↓
Advantageous feature to capture particles from the water column	↑	↓

Fig. 1: Octocoral traits that favor their resilience and adaptations compared to scleractinians

Nevertheless, there is a lack of information about the potential adaptability of this taxonomic group to the net trophic conditions, and such core information is necessary to understand the future seascape composition (Rossi et al., 2019). The available data is far enough to understand a potential advantage from an energetic point of view of octocorals in front of scleractinians. Enhancing our understanding of the diverse species inhabiting various reef environments is crucial for anticipating future seascapes amid global environmental challenges (Rossi et al., 2017a).

In tropical areas, where mixotrophic octocorals are dominant (Schubert et al., 2017), some efforts have been made to understand better the role of heterotrophy and autotrophy in their energy budgets (Ramsby et al., 2014; Baker et al., 2015; Rossi et al., 2017a; Rossi et al., 2020). It is evident, however, that there are many gaps of knowledge bridging core concepts like energy inputs and outputs (e.g., reproduction, growth, metabolism, etc.), morphological performance or optimization of autotrophic and heterotrophic strategies that may answer the potential succession in some tropical areas of scleractinians by these ecosystem engineering species (Tsounis & Edmunds, 2017). In this perspective article, we investigate the relationship between resilience and the trophic ecology of tropical octocorals. We focus on discussing recent advances over the last decade and demonstrate core knowledge gaps for further research.

2. Trophic ecology linked to community shifts (scleractinian- to octocoral-dominated reefs)

On a healthy tropical shallow-water reef, octocorals (e.g., gorgonians), sponges, and scleractinians (reef-building hard corals) are the most common sessile animals (McFadden *et al.*, 2010; Schubert *et al.*, 2017; Lesser & Slattery, 2020). Scleractinians, as engineering species, play a major role in providing structural complexity with their three-dimensional carbonate surfaces, maintaining key roles in reef ecosystems, and providing space, shelter, and food for associated high biodiversity (Srinivasan, 2003; Sale *et al.*, 2005; Raes *et al.*, 2007; Wild *et al.*, 2011). They grow with a stable calcium carbonate framework (Bellwood & Hughes, 2001; Pratchett *et al.*, 2015) that provides the capacity to form a massive, wave-resistant rigid platform (Stoddart, 1969). Moreover, reef rugosity is associated with a high abundance of reef fishes (McClanahan & Shafir, 1990), supporting tourism and fishing activities (Wilkinson, 1996). They can also create geological structures that may become islands or true stone coastal barriers. In other words, there are many benefits offered by a healthy reef-building coral framework that is crucial for the maintenance of marine life in the tropical ecosystem and, in addition, supports ecosystem goods and services that contribute to the livelihoods of tens of millions of people worldwide (Moberg & Folke, 1999).

Gorgonians and sponges also act as ecosystem engineering species (Wild *et al.*, 2011; Maldonado *et al.*, 2017; Rossi *et al.*, 2017a), but their functionality and ecosystem services provided are very different from those of reef building scleractinians (Paoli *et al.*, 2017). They will not protect coastal areas from high-energy events such as storms or hurricanes (Ferraio *et al.*, 2014) and they potentially have less capability to immobilize carbon during long periods (Rossi & Rizzo, 2020), for example. Their ability to optimize light harvesting but having a non-neglectable heterotrophic input even in nutrient-poor and warm environments let them expand worldwide (Ferrier-Pagès *et al.*, 2015; Rossi *et al.*, 2019). Consequently, their role in biogeochemical cycles will be very different from scleractinians (Wild *et al.*, 2011; Lesser & Slattery, 2020). Octocorals create forest habitats for other mobile and sessile reef species, but they do not create a hard and solid carbonate structure like scleractinians and hydrocorals (Jones *et al.*, 1994; Wolff *et al.*, 1999). They are thus not considered carbonate reef-building organisms (Schubert *et al.*, 2017; Steinberg *et al.*, 2022). It is thus clear that the impact on the provision of ecosystem services by octocoral-dominated reefs represents a threat to the sustainability of essential sectors, including fishing, food security, coastal protection, and tourism (Baste & Watson *al.*, 2022).

In particular, focusing on the carbon cycle, a huge disadvantage in the octocoral spreading is related to the reef's function of carbon immobilization (Coppari *et al.*, 2019), also observed in sponges (Coppari *et al.*, 2016), and other active and passive benthic suspension feeders (Rossi & Rizzo, 2021). They together capture and immobilize CO_2 from the atmosphere of both organic and inorganic forms (Nellemann *et al.*, 2009) directly through photosynthesis of the symbiotic cells or indirectly because of the ingesting of particles. Their contribution of photosynthetically fixed carbon provided by dinoflagellate endosymbionts to their host is different between species, being lower carbon flux and the carbon immobilized derived from photosynthesis in octocorals than in scleractinians (Fabricius & Klumpp, 1995; Ferrier-Pagès *et al.*, 2015).

Most shallow tropical corals have a symbiotic relationship with Symbiodiniaceae (Wild *et al.*, 2011; Lajeunesse *et al.*, 2018), translocating photosynthates to their hosts in oligotrophic waters (Muscatine & Porter, 1977). Under stressful environmental conditions (e.g., heatwaves or organic pollution), the symbiosis is affected, with a decrease in the photobiological activity and energy supply to the coral host that needs to be compensated in other ways (Brown, 1997), such as increasing heterotrophic inputs (Douglas, 2003; Baker *et al.*, 2008). Nutritional losses may occur, triggering immunological and nutritional reduction, which could lead to the death of the host if the corals are unable to recover after stopping the stressful cause (Denis *et al.*, 2024). The adaptability of stress-sensitive scleractinians to ocean warming seems to be much restricted by their morphology and associated light scattering (Enríquez *et al.*, 2005; 2017). Therefore, it is important to understand the advantages and drawbacks of octocoral to coral reefs in terms of heterotrophic and autotrophic inputs (Rossi *et al.*, 2020) and their photobiological performance (Rambsy *et al.*, 2014; Rossi *et al.*, 2018) to understand the possible transformation of the reef seascape. This information is still scarce and needs an in-depth understanding of different areas, depths and morphologically different species.

Octocorals are much less dependent on photosynthetic endosymbionts than scleractinians (Fabricius & Klumpp, 1995) as indicated, for example, by the lower contribution of autotrophically acquired carbon to octocoral respiration values (CZAR) in octocorals with Symbiodiniaceae (Fabricius & Dommisse, 2000; Derviche *et al.*, 2021), which contributes to their resistance to many disturbances (Baker & Romanski, 2007) such as high temperatures (Jaap, 1979), high light intensity, salinity stress (Hoegh-Guldberg & Smith, 1989), and diseases (Kushmaro *et al.*, 1998). The three-dimensional structure with octocoral polyps is an advantageous feature to capturing particles from the water column and provides a greater possibility of obtaining food (Gili & Coma, 1998) through a heterotrophic carbon input (Ramsby & Goulet, 2019; Rossi *et al.*, 2020). They also are trophically plastic, acquiring nutrients through autotrophic (symbionts) and heterotrophic (zooplankton, particulate detrital organic matter, phytoplankton or dissolved compounds) feeding (Fabricius & Klumpp, 1995; Rossi *et al.*, 2020).

Such performance enables them to maintain physiological functions when autotrophy is reduced (Falcowski *et al.*, 1984; Anthony *et al.*, 2009), such as during severe bleaching events (Lasker, 2003; Prada *et al.*, 2009) presenting greater resistance than in scleractinian, surviving and recovering endosymbionts after extreme events such as marine heatwaves (Steinberg *et al.*, 2022). They also can survive in mesotrophic-eutrophic tropical shallow waters (Fabricius & McCorry, 2006; Baker *et al.*, 2010) enhancing their heterotrophic potential by increased reliance on heterotrophic input during periods of decreased autotrophy in some polluted areas under urban nutrient-laden run-off (Baker *et al.*, 2015). Because of these abilities, octocorals start to dominate Caribbean tropical reefs, changing marine communities and having the potential to spread to other reefs (Bell *et al.*, 2021).

3. Higher resilience of octocorals: Biological aspects versus environmental conditions

Based on the knowledge of the direct link between feeding characteristics and the permanence of corals in the benthic environment, trophic ecology research with octocorals is being carried out to answer questions that explain the permanence of these organisms, replacing some scleractinians in tropical regions. As a result, it was discovered that besides the trophic flexibility, other morpho-ecophysiological traits contribute as well to the permanence and proliferation of octocorals (Fig. 2). We list some of these here, some also found in stress-tolerant scleractinians: (a) symbiont acquisition by horizontal transmission, promoting association with different symbionts than those of their parents (Lewis & Coffroth, 2004; Fay & Weber, 2012); (b) polyp morphology with a high surface area (polyp and tentacle diameter) to volume ratio (SA/V) improve light-capturing ability and carbon autotrophic input (Porter, 1976; Lewis 1982; Rossi *et al.*, 2018); (c) enlargement of sclerites to increase the internal light field (Prada *et al.*, 2008; Rossi *et al.*, 2018); (d) morphology (i.e., branching patterns, polyp size, spicule distribution, etc.) related to symbiont performance (Rossi *et al.*, 2018); and (e) capability of gorgonians to modify symbiont and holobiont parameters (e.g., Chl-a concentration per symbiont cell, number of symbiont cells per cm^2, etc., Goulet *et al.*, 2017).

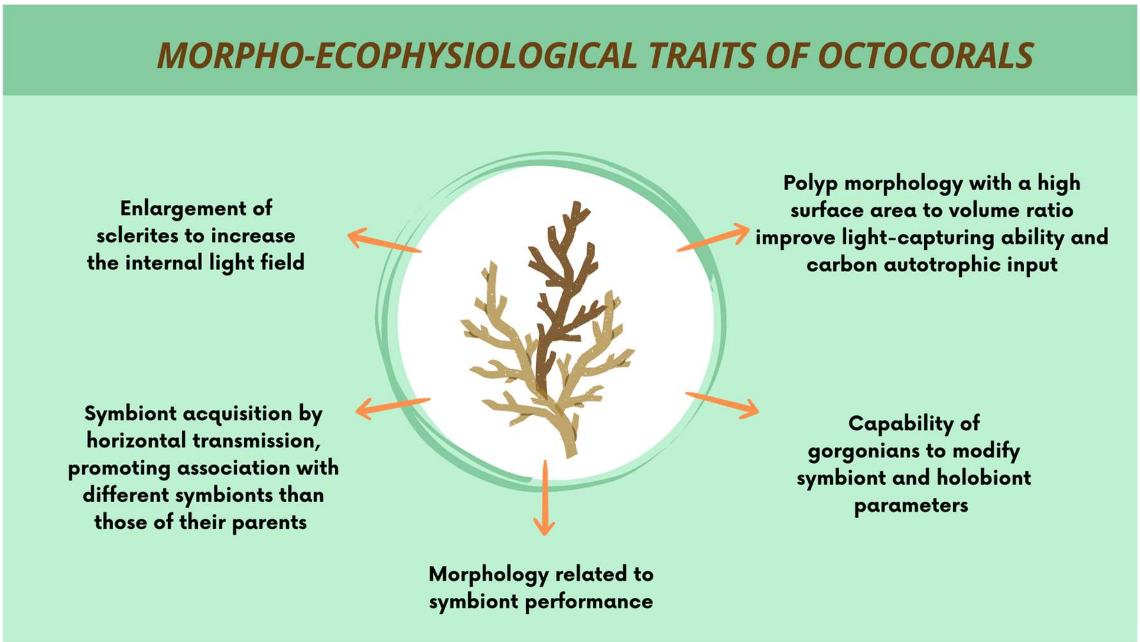


Fig. 2: Morpho-ecophysiological traits that also contribute to the permanence and proliferation of octocorals.

The above-mentioned interpretations have scarce case studies, clearly lacking information to answer to such an Anthozoa substitution. Much research remains to be done to clearly understand what causes octocoral persistence in tropical regions, even those that do not depend that much on symbionts, but environmental conditions are known to have a very important role in their distribution (Fabricius & McCorry, 2006; Abad *et al.*, 2022). Huge knowledge gaps (e.g., seasonal food inputs and trophic ecology of key reef gorgonians) in many aspects make it difficult to interpret such ecological succession, as shown in our literature review, where we looked for recent publications that aimed to investigate the trophic ecology of tropical octocorals.

In the search of recent publications carried out in three databases (Scopus, Web of Science, and ScienceDirect), between 2010 and 2022, we systematically observe the above-mentioned gaps of knowledge and others related to the potential role of trophic ecology in the successful dominance of octocorals under certain circumstances. This recent period was selected due to a noticeable surge in articles addressing this topic in the last decade. Before starting the qualitative review, an unrestricted search was conducted, revealing a surge in relevant articles post-2010. While significant works existed before this period, they were not as closely aligned with our focus. Furthermore, our aim in this perspective article was to acquire up-to-date insights into the research and methodologies employed in studying the trophic ecology of shallow tropical octocorals. The search strategy was limited to keywords in English, and each database had its word sequences according to its own rules. For Web of Science and Scopus, the search strings were performed using the keywords: (octocoral* OR Alcyonacea OR Gorgonacea OR "soft corals" OR "gorgonian") AND (*trophy OR "trophic ecology" OR lipid OR carbohydrate OR physiology OR nutri* OR diet OR "stable isotopes"). For ScienceDirect, we used: (octocoral OR Alcyonacea OR Gorgonacea OR "soft corals" OR "gorgonian") AND (trophy OR "trophic ecology" OR physiology OR nutrition).

In the beginning, we did not confine our search to a specific geographic region to explore the panorama of trophic ecology studies with octocorals in a global context, resulting in a selection of 87 publications from various regions worldwide. When comparing this result with publications on the trophic ecology of scleractinians, it was observed that the amount of research conducted with these hard corals is more substantial in its trophic ecology, health statuts and impact assessment than studies conducted with soft corals (e.g., gorgonians). This observation was confirmed when we conducted a search on Google Scholar using the specified keywords and changed "octocoral" to "scleractinian". The difference in the generated results was three times greater, indicating how much remains to be understood about the ecophysiology and trophic ecology of these organisms. However, since the focus of the respective article is on investigating publications conducted in tropical and subtropical regions, we have selected 51 articles out of the 87 initially found (see Supplementary Material for further details).

As a result, articles published in tropical and subtropical regions obtained on average, about four (4) articles were published per year, with 2012 being the year with the highest number of publications (n = 7), however, in the years 2011 and 2013 no publication was found. Based on the graph created with this result, it is possible to observe the increase in publications from 2016 onwards, which shows that research on this topic has been receiving more attention over the last few years and is expected to have an increasing trend (Fig. 3). We listed geographic regions associated with the study site, sample collection depth, target family of octocorals, trophic ecology, and research objectives to understand the relationship with the trophic ecology and ecophysiology of tropical octocorals.

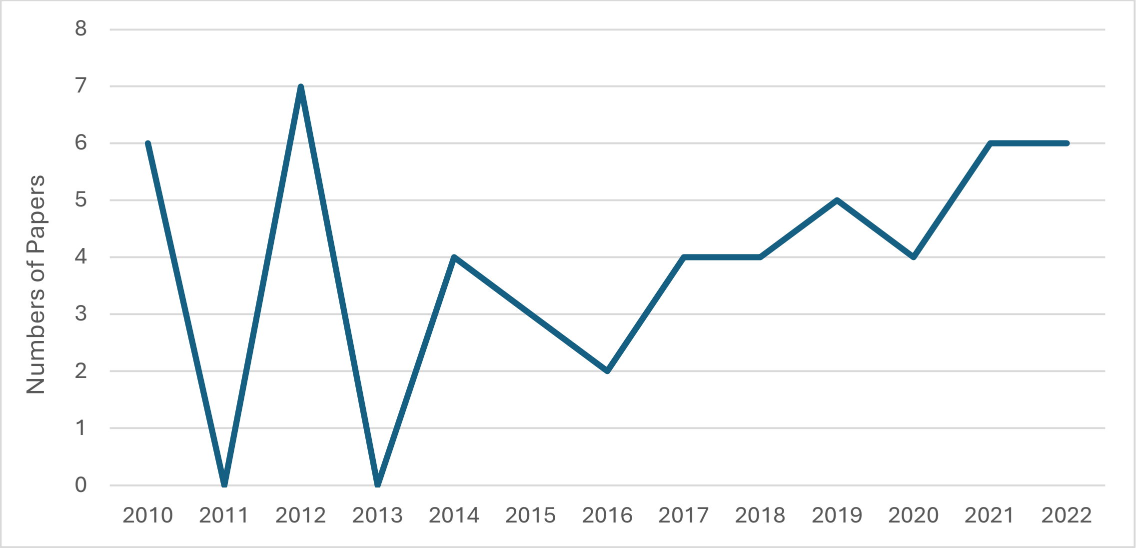


Fig. 3: Number of published studies (trophic ecology of octocorals in tropical and subtropical coasts) included (left axis) in this review per year.

Geographic regions associated with the study site

Observing the regions where the octocoral samples were collected for the research, we obtained the number of publications carried out according to provinces of Spalding *et al.* (2007). The Red Sea and the Gulf of Aden, and the Tropical Northwestern Atlantic (mainly in the Caribbean region) recorded the highest amounts of searches, corresponding to 31% (n = 16 from all 51 publications that collected offshore samples) and 29% (n = 15) respectively. Next, Sunda Shelf was represented by 17% (n = 9); South China Sea and Western Coral Triangle were represented by 5% publications (n = 3 each); Tropical Northwestern Pacific in 4% (n=2); Western Indian Ocean, Lord Howe and Norfolk Islands, Tropical Southern Atlantic had the lowest representation, each appearing in only one study (Fig. 4).

This demonstrates the importance of octocoral-dominated reefs research in these regions, based on the environmental changes they are facing. On the other hand, only one publication represented the Tropical Southwestern Atlantic, revealing a disproportionately applied effort on this topic. We want to highlight this point because this vast region has not yet been properly studied.

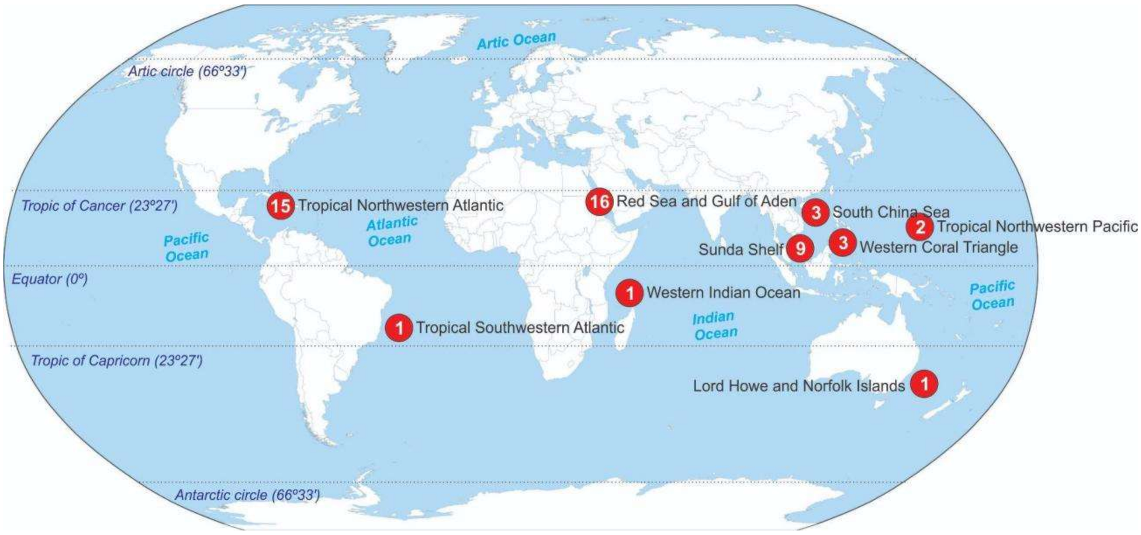


Fig. 4: Number of publications (red circles) about trophic ecology of octocorals in Tropical and Subtropical regions, according to the provinces classification by Spalding *et al.* (2007).

Sample collection depth

The environmental conditions of the sites where octocoral sampling was conducted were not always described in the research studies. However, among the information reported, we can highlight data on the depth of sample collection. The vast majority (79%, n = 40) of the studies analyzed only octocorals that inhabited shallow waters (0.1 to 30 m depth), while 6% (n = 3) of the studies collected samples from shallow and mesophotic waters (30 to 150 m depth) and only 4% (n = 2) from only from the mesophotic area alone. Among all 51 articles, only 11 reported water temperature data, which were recorded in locations ranging from 20°C to 37.7°C. Data on other environmental variables, such as salinity, were scarce or non-existent in most of the studies.

Target family of octocorals

Octocorals chosen for the development of research predominantly (around 90%) belong to the order Malacalcyonacea (new Alcyonacea), represented by 13 families across 46 publications: Gorgonidae, Plexaureliidae Nephtheidae, Lemnaliadae, Sarcophytidae, Sinulariidae, Carijoidae, Nephtheidae, Xeniidae, Paramuriceidae, Melithaeidae, Ellisellidae, and Isididae. Among these, the number of articles that focused on studying Plexaureliidae species stood out, which were present in 24 publications. On the other hand, species from the order Scleralcyonacea were studied in about 10% of the articles, appearing in five publications and representing three species from the families Ellisellidae, Helioporidae, and Briareidae.

Trophic ecology

Identification of the trophic level of the species studied in the articles was not easy to obtain because they did not report the information. In the vast majority, species were simply characterized with or without Symbiodiniaceae, with no specification of how they obtained food. Among the studies that presented trophic ecology, 47.05% (24 publications) classified octocorals as mixotrophic, with tendencies toward either autotrophy or heterotrophy depending on the species. In 15.7% (8 publications), no information was provided about the trophic ecology of octocorals, or whether the species contained Symbiodiniaceae. In the other 37.2% (19 studies), species were identified as either strictly heterotrophic or strictly autotrophic.

Research objectives

Based on the principle that all selected articles involve octocoral trophic ecology, we tried to understand what the main objectives of the analyzed studies were. Some of them focused in investigating purely the trophic level and others aimed to combine this knowledge with other topics of interest involving octocorals, such as the evaluation of resistance to heating and bleaching, and efficiency as indicators of water quality and pollution. Thus, to better understand which scientific topics receive research attention and which are lacking, the objective of the studies was separated into three categories: 1) Research involving only aspects of trophic ecology, or with food strategy, sources of nutrition, and nutritional strategy, were categorized as "trophic ecology", corresponding to 23 publications (45% of the total of 51 studies); 2) Studies evaluating the effects of impacts on the trophic ecology of octocorals were classified under "Environmental Disturbances", accounting for 31% (16 publications); 3) Other research objectives were less represented, such as "Bioindicators" (12%) and "Cultivation Purpose" (6%), while some categories (e.g., "Bioprospecting of Natural Products", "Paleoceanography," and "Reproduction") were each addressed by only one article, corresponding to 2% each.

Research evaluating the effects of impacts on the trophic ecology of octocorals, ("Environmental disturbances" category) began in 2012, though publications were limited, ranging from one to three per year. However, in 2022, the number of studies increased to five publications. Warming seawater and nutrient enrichment were the main human-induced impacts studied, alone or combined, but microplastics and bleaching impacts were also studied. Such an increase highlights the importance of understanding the role of octocorals in the future seascape and the interest that, step by step, makes possible a better understanding of this taxon in the tropical ecosystem functioning.

4. Challenges in trophic and ecophysiological octocoral research in tropical and subtropical areas

Our review highlighted that research concentrates mainly in shallow waters of the Red Sea and the Tropical Northwestern Atlantic, focusing on the order Malacalcyonacea, but rarely presenting information on the trophic level of the studied species. Seawater temperature rise and nutrient enrichment are the main environmental impacts addressed worldwide. Based on the results obtained in this article we suggest four main research directions to improve knowledge about octocorals and their biology (Fig. 5).

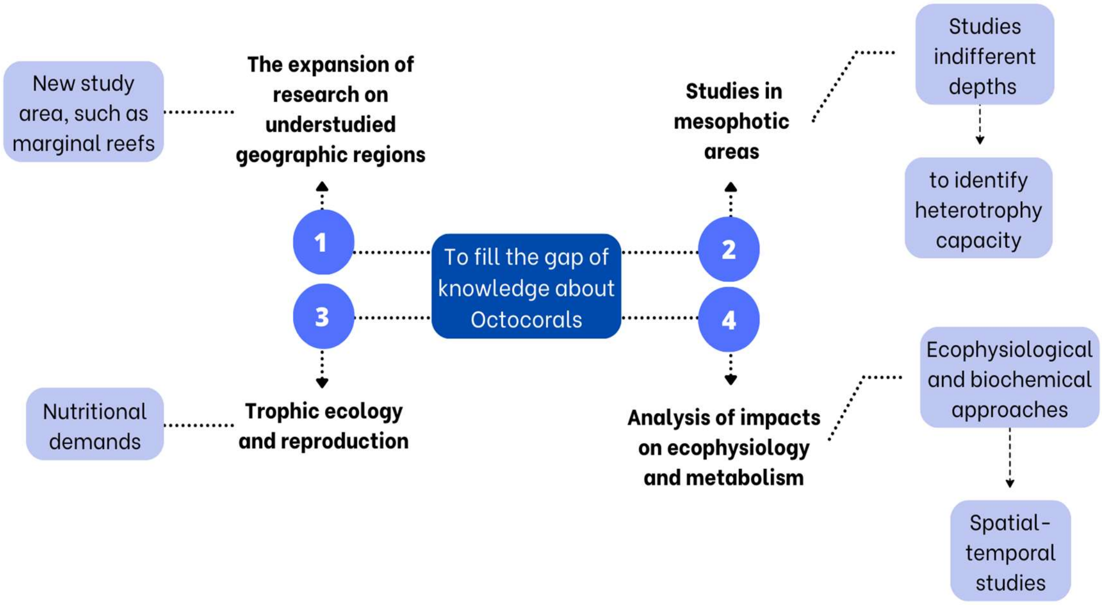


Fig. 5: Recommended actions to improve knowledge about octocorals and their biology.

A. Expanding research in under-studied geographic regions

Human-induced disturbances in marine ecosystems vary across different ecoregions, and the impacts of climate change will depend not only on the specific activities occurring in each region but also on the local adaptation of octocoral species. These factors together shape the resilience potential of octocoral populations, influencing their ability to withstand and recover from environmental changes. Research on the trophic ecology of octocorals was concentrated in only a few ecoregions. The Caribbean Sea has been going through profound ecological reef changes in recent decades (Gardner *et al.*, 2003; Mora, 2008), and some studies come from this area. Other places have been less studied (e.g., South Atlantic), so the information is scarcer. However, it has to be highlighted that the knowledge of octocoral ecology was neglected for decades (Lasker *et al.*, 2020). Therefore, what can we say about other places that didn’t show phase shifts?

Among these underrepresented regions, Southwestern Atlantic reefs off the Brazilian coast, serves as a prime example. Home to the richest and largest reef complexes in the South Atlantic (Leão *et al.*, 2016; Bastos *et al.*, 2018) they form structures significantly different from the well-known reef models (i.e., Caribbean and Indo-Pacific), with low coral richness and a high proportion of endemic species (Castro & Pires, 2001; Floeter *et al.*, 2008). On 3,000 km of the coast of Brazil, there is a rich, abundant, and endemic octocoral fauna, which is subject to various human impacts, but little is known about how they behave with these changes. Coastal runoff and urban development, tourism, trading of reef organisms, predatory fishing, the installation of industrial projects, and fossil fuels exploitation (Maÿal, 1986; Coutinho *et al.*, 1993; Leão *et al.*, 2003) in addition to recent threats like oil spill events (Soares *et al.*, 2020) and microplastics (Corinaldesi *et al.*, 2021), are severe disturbances that promote octocoral vulnerability or abundance. The extent to which these factors influence octocoral populations remains uncertain and requires further investigation through applied studies (Tsounis & Edmunds, 2017; Aued *et al.*, 2018; Cant *et al.*, 2024).

In the Southwestern Atlantic, octocoral habitats have high nutrients and moderate turbid waters, with particular environmental characteristics different from the oligotrophic and clear waters found in the Indo-Pacific and Caribbean areas (Mies *et al.*, 2020). Although Brazilian coastal reefs experience coral bleaching episodes less frequently and with lower intensity compared to other regions (Mies *et al.*, 2020), catastrophic declines in coral cover recently put in doubt the resilience of these reefs (Duarte *et al.*, 2020). But as most attention is focused on hard corals (Leão *et al.*, 2010), it remains unknown what happens with octocoral population adaptations, because they are not always so resistant and can also be threatened by environmental conditions. Invasion of octocoral species into the Southwest Atlantic, Brazil, has instigated profound and enduring alterations within benthic ecosystems, not only catalysing significant shifts in the composition, and dynamics of benthic communities, but also threatening macroalgal-dominated rocky reefs (Lages *et al.*, 2012; Altvater & Coutinho, 2015; Menezes *et al.*, 2021).

In tropical and subtropical coasts of Africa, as well as in extensive areas of Asia, increasing pressures have been observed threatening the reef species and mesophotic ecosystem (Soares *et al.*, 2019). In Sodwana Bay, South Africa soft corals were more susceptible to bleaching than hard corals during 2000 and 2001 (Floros *et al.*, 2004). However, as in the Southwest Coast of the Atlantic, a deep gap of knowledge is present in these areas, where very few references were found to include information about the presence/absence, taxonomic classification or distribution among habitats of these cnidarians (Pérez *et al.*, 2016; Santos *et al.*, 2016; Moura *et al.*, 2023)

Knowledge about the trophic ecology of octocorals under different environmental conditions, such as extreme reefs, will help to better understand their resistance, but also the study of what we consider “normal” reefs is deeply lacking in the scientific agenda. Unlike other tropical regions, in the South Atlantic, we have not yet been able to obtain an overview of the current or future prevalence of octocorals, nor even an estimation of their distribution and taxonomic description.

B. Focusing in mesophotic areas

The study in mesophotic areas has to be seen as an essential step needed to better understand the whole functioning of habitat connections (Turner *et al.*, 2019; Soares *et al.*, 2020). Shallow and mesophotic reefs have many functioning and distribution aspects in common, but the differences regarding the shared species in terms of trophic ecology and ecophysiology are still very scarce (Turner *et al.*, 2019). As seen in this review, very few studies investigate trophic ecology at mesophotic depths in tropical reefs. The study of octocorals at different depths made possible to identify heterotrophy capacity in shallow-water octocorals, showing that they are not restricted to autotrophy exclusively. Pupier *et al.* (2021) showed that these anthozoans are not restricted to heterotrophy in deeper areas, because octocoral performance of the same species could change depending on the depth, and consequently, the conditions to which they are exposed, when considered in shallow and mesophotic habitats, but many more studies are needed to make a better comprehension of this point.

In addition, mesophotic environments may present a greater richness of octocorals than shallow environments (e.g., in the Red Sea), contributing to increasing knowledge about marine biodiversity (Shoham & Benayahu, 2017). Making use of advanced technologies can facilitate research in deeper environments, collecting octocorals for trophic analysis using remotely operated vehicles (ROV) for example (Ferrier-Pagès *et al.*, 2022), but we need more confrontation with shallow habitats to understand how they will respond to climate change and how they behave in terms of trophic ecology.

C. Investigating trophic ecology and reproduction

The heterotrophic nutrition of octocorals depends on the available food in the near bottom seston (Gili & Coma, 1998; Rossi & Gili, 2009). Such seston may have a different balance in their particles regarding carbohydrates, lipids and proteins (Grémare *et al.*, 1997), and the alteration of these compounds can lead to difficulties in facing challenges, causing disease and even mortality (Imbs & Yakovleva, 2012; Scanes *et al.*, 2018). The reproductive process is linked to the nutrition of the species, as there is a great demand for energy storage and lipids during this physiological stage, including the formation of eggs and planula larvae (Rinkevich, 1989; Arai *et al.*, 1993; Ward, 1995; Rossi *et al.*, 2006; Viladrich *et al.*, 2022a).

Research that investigates gonadal development throughout the year and aspects of trophic ecology such as protein, carbohydrate and lipid content answer questions about the reproductive time and gonadal production (Gori *et al.*, 2012), being a good tool to integrate seasonal and environmental factors. Carbohydrates, but especially lipids, are a very good indicator of species' reproductive performance and health status after stress events (Rossi *et al.*, 2017b), being one of the pendant gaps of knowledge that have to be addressed in tropical octocorals (Shirur *et al.*, 2014). Thus, understanding the strategy used by octocorals to capture food must be considered, since reproduction is metabolically costly, and any alteration that occurs with the ability to store energy in the animal influences its reproductive efficiency (Gohar, 1940; Fabricius & Alderslade, 2001; Rossi *et al.*, 2017b). If there is a deficiency in particle capture or photobiological performance, this biological process will also be limited and all its development will be harmed (Denis *et al.*, 2024).

In tropical seas, it has been shown that the seasonal coupling with environmental and biological variables of the water column is essential to understanding the carbon and nitrogen fluxes (Rossi *et al.*, 2020). However, there is still a long road to arrive and understand how such seasonality effectively affects octocoral life cycles and trophic constraints, as has been suggested in scleractinians (Scheufen *et al.*, 2017). In line with this energy input (feeding rates, photobiology) there has to be a strategy of energy output (i.e., the quantity of energy or carbon used to breath, reproduce, etc.) (Rossi *et al.*, 2017b). In octocorals, reproductive strategies are surface brooding, internal brooding and broadcast spawning (Ribes *et al.*, 2007; Kahng *et al.*, 2011). Regeneration abilities, high fecundity, and polyp pulsation are reproductive processes carried out by some octocorals that promote rapid reef colonization (Ben-David-Zaslow *et al.*, 1999; Nadir *et al.*, 2023).

However, for the efficient development of these animals, the environmental conditions in which they are found must be suitable for their needs. Environmental shifts or disturbances can alter the reproductive capacity of octocorals (Gori *et al.*, 2007; 2013). Pollution, habitat destruction and climate change are responsible for reducing the reproductive ability of gorgonians (Lin *et al.*, 2012) and increases in water temperature can affect the reproductive capacity of octocorals species, acting differently between sexes (Arizmendi-Mejia *et al.*, 2015). Water warming causes a greater reduction in the number of fertile polyps in females of *Paramuricea clavata* (Risso, 1827), but males did not react in the same way (Linares *et al.*, 2008). To the best of our knowledge in tropical areas, few observations are scarce (De Putron & Ryland, 2009; Michaelik-Wagner & Willis, 2001), only shallow and mesophotic reproductive cycles have been described (Liberman *et al.*, 2018) with light as a driver factor of potential changes in the water column (and thus the photosynthetic performance).

Reproduction is compromised when animals are trying to survive, as an energy that should be devoted to their natural biological processes, such as reproduction and growth, is being devoted to adapting to stressful conditions (Brown & Bythell, 2005). Larval fitness depends on the mother's care of female gorgonians and the energy transferred for the first life stages (Viladrich *et al.*, 2017; 2022a), but such an approach has been only barely considered during the last decades (Viladrich *et al.*, 2022b). In the review carried out in Lasker *et al.* (2020), only one article assesses the effects on reproductive processes, trophic ecology and the effects on the next generations in tropical octocorals (Lin *et al.*, 2012). The simplest information, which is the reproductive cycle of the species, is lacking or very scarce (Kahng *et al.*, 2011).

Investigating how trophic ecology can affect the reproductive capacity and the impact on the next generations of octocorals in different natural or simulated conditions is essential to obtaining knowledge about the ability of animals to perpetuate themselves (Liberman *et al.*, 2018; Viladrich *et al.*, 2022a), even more even in this current context of so many environmental threats to which they are subjected (Rossi *et al.*, 2017b).

D. Analyzing impacts on ecophysiology and metabolism

As expected, there is a significant gap in knowledge regarding the consequences of combined disturbances on the physiological performance of octocorals, unlike scleractinians, for which many studies document the harmful effects of these disturbances, such as high mortality associated with oceanic events and ocean acidification (Hoegh-Guldberg *et al.*, 2007).

However, the gorgonian response to impacts appears to be species-specific, as observed in the available literature.

Among the 16 reviewed articles that investigated the trophic ecology of octocorals in front of environmental impacts, the majority researched isolated impacts, mainly nutrient excess and water temperature increase. Only five analyzed combined stressors, also focused on the impacts of nutrient excess and warming increased. For example, octocorals were demonstrated to be impacted when subjected to high temperatures and different dissolved N forms together, causing increased assimilation of N (Pupier *et al.*, 2021), when in high temperature and UVR *Pseudoplexaura porosa* (Houttuyn, 1772) and *Eunicea tourneforti* (Milne, Edwards & Haime, 1857) reduced the sclerite content and Symbiodiniaceae densities showing they have a greater ability to withstand future conditions of increasing temperature and acidification (McCauley *et al.*, 2018).

Octocorals are subjected to multiple stressors at the same time and, therefore, their ability to deal with them is not segmented: survival depends on their relationship with all of them at once (cumulative effect). Because of this, studies that aim to investigate the impacts on octocorals when subjected to stress factors together are needed, crucial to understanding the future of coral reefs (Goulet *et al.*, 2017). Octocorals exposed to various treatments in the laboratory can provide information regarding changes in growth (Enochs *et al.*, 2016; Guzman *et al.*, 2019), C and N content (Pupier *et al.*, 2021), symbiotic dinoflagellate density, lipids and FA composition (Imbs & Yakovleva, 2012) and gonadal-energy storage (Gori *et al.*, 2013). During short or long-term experimental analyses, it is possible to insert stressing factors, and with observation, routinely see how octocorals respond to adversities (Bramanti *et al.*, 2013; Gori *et al.*, 2013), understanding the stages of these responses, following step by step the symptoms that organisms show over the time. However, the above-mentioned experiments have been made with warm temperate octocorals, not fully representative of what may happen in tropical or subtropical areas. This makes the initial detection of these symptoms think about the application of strategies to reverse or minimize the source of impact (Dellisanti *et al.*, 2021).

In laboratory experiments, however, environmental conditions are not the same with those the octocorals deal with in natural reef habitats. In the laboratory, one or two variables are usually applied, putting the animals in a challenge and observing how they act at the same time, but it is not possible to observe the cyclical fluctuations in the environmental conditions that the organisms face in the natural environment. Therefore, observing octocorals in their habitat of origin may be better if we can make an *in situ* approach, with punctual ecophysiological methods (e.g., respiration, Coma *et al.*, 2002) or with long-term-integrating variables such as the biochemical balance (Rossi *et al.*, 2006).

Such ecophysiological approaches are lacking in tropical areas for octocorals (Schubert *et al.*, 2017). Very few research groups consider this possibility, centred in a few coral reef areas such as the Red Sea or the Caribbean. The studies, for example, looking at respiration/production only rarely make a seasonal approach in tropical areas (Rossi *et al.*, 2020), being centred on experimental designs (Baker *et al.*, 2015; Pupier *et al.*, 2019). The use of the biochemical approach is also scarce in tropical octocorals, being also centred in a few areas and only rarely considering a seasonal approach (Ben-David Zaslow & Benayahu, 1999; Shirur *et al.*, 2014; Pupier *et al.*, 2021). Spatial-temporal studies are necessary to understand the capability of these species to optimize their reproductive output in terms of larval release and performance (Viladrich *et al.*, 2017), being an essential path to understanding if they will be successful in the recruitment processes.

Such tools may be used to clarify the potential response and adaptation to the fast-changing conditions of the water column and the associated physical-biological factors in different areas to clarify the potential gain, loss or maintenance of the populations due to climate change.

5. Conclusions

Based on our literature review, we have identified in this perspective paper, knowledge gaps that need to be filled to advance our understanding of trophic ecology in tropical octocorals. With the knowledge gained from these studies, it is possible to obtain more precise information on the longevity and persistence of these organisms in coral reefs, because the marine community shift caused by the overlap of these animals to the detriment of the scleractinians can have serious consequences.

Our premise has been that learning about octocoral trophic ecology in tropical reefs is important to better understand their future role in reef areas in all regions and different habitat conditions. These animals have been living under environmental and direct human impacts for a long time and seem to have adapted well, according to the few studies carried out. There is still a range of tropical octocoral species that we do not have the slightest knowledge of. They inhabit different environmental conditions that need to be discovered and described, and we need to know how they are dealing with the current global situation. Octocorals and other stress-tolerant organisms could flourish in the short term in some places, but to what extent? This is why we need to rethink and update reef ecosystem management, which must adapt to the new changes, and for that, it is necessary to improve knowledge about the species that are changing the landscape of tropical and subtropical reefs.

In this perspective article, we highlight some research that needs to be conducted to provide insights into understanding the future trends of coral reefs and thus help public authorities in the development of new actions, encouraging more trophic ecology studies, to better understand how the octocorals are dealing with the speed and intensity of changes brought about by the Anthropocene.

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Competing interests

The authors declare no competing interests.

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SUPPLEMENTARY MATERIAL

All 51 literatures used in the review:

	Title	**Reference**	**Year**	**Publication**
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33	Divergent Capacity of Scleractinian and Soft Corals to Assimilate and Transfer Diazotrophically Derived Nitrogen to the Reef Environment	Pupier, C. A., Bednarz, V. N., Grover, R., Fine, M., Maguer, J. F., & Ferrier-Pagès, C.	2019	Frontiers in Microbiology
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48	Reef-Building Corals Do Not Develop Adaptive Mechanisms to Better Cope With Microplastics.	Rades, M., Schubert, P., Wilke, T., & Reichert, J.	2022	Frontiers in Marine Science
49	The pulsating soft coral *Xenia umbellata* shows high resistance to warming when nitrate concentrations are low	Thobor, B., Tilstra, A., Bourne, D. G., Springer, K., Mezger, S. D., Struck, U., ... & Wild, C.	2022	Scientific Reports
50	The widely distributed soft coral *Xenia umbellata* exhibits high resistance against phosphate enrichment and temperature increase	Mezger, S. D., Klinke, A., Tilstra, A., El-Khaled, Y. C., Thobor, B., & Wild, C.	2022	Scientific Reports

51	Symbiotic stony and soft corals: Is their host-algae relationship really mutualistic at lower mesophotic reefs?	Ferrier-Pagès, C., Bednarz, V., Grover, R., Benayahu, Y., Maguer, J. F., Rottier, C., ... & Fine, M.	2022	Limnology and Oceanography

CHAPTER 2 - Trophic Ecology of three octocorals in “Marginal” Reefs of the Southwestern Tropical Atlantic

RESUMO

A maioria dos recifes do planeta encontram-se em transformação devido às mudanças ambientais globais com o branqueamento e a mortalidade de corais formadores de recifes, e estabilidade ou aumento de outros grupos como os octocorais. Em recifes turvos, determinadas espécies recifais aparentam ter maior resiliência às mudanças climáticas como as ondas de calor. Estudos que abordem o metabolismo dos octocorais provou ser uma ferramenta essencial para compreender os seus ciclos biológicos e a sua capacidade de lidar com períodos de fome ou stress. Nesse contexto, análises bioquímicas e de isótopos estáveis dos tecidos dos corais, incluindo os corais moles, são ferramentas conhecidamente eficazes para a identificação de suas fontes de alimentos. Porém, a maioria desses estudos são com escleractíneos sendo limitados os estudos com octocorais; em especial em recifes de águas moderadamente turvas. Sabendo disso, amostras de três espécies de octocorais (*Muriceopsis sulphurea, Plexareulla grandiflora, Phyllogorgia dilatata*) dominantes foram coletados ao longo da costa do Atlântico Sudoeste Equatorial em 2020 e 2021. Dados de lipídios, carboidratos, isótopos $\delta^{15}N$ e $\delta^{13}C$ foram obtidos. O conteúdo de lipídio variou entre 154 ± 56 (ug/mgAFDW) e 380 ± 72 (ug/mgAFDW) correspondendo a 15% e 38% AFDW. Resultados de $\delta^{13}C$ encontrados foram entre -15.44‰ e -20.32‰, e valores para $\delta^{15}N$ se apresentaram entre 3.64‰ à 6.16‰. Essas análises indicam que essas espécies de ocotocorais apresentam tendência heterotrófica, sendo capazes de enfrentar com maior resiliência as situações de estresse, decorrentes de mudanças globais e locais. Esse é o primeiro estudo com ecologia trófica de octocorais no Atlântico Sudoeste Equatorial e fornece importantes insights sobre o perfil das biomoléculas, sua posição trófica em recifes turvos e seu potencial de resiliência na atual emergência climática.

Palavras-chave: Nível trófico, Aquecimento global, Gorgônias.

ABSTRACT

The majority of coral reefs worldwide are transforming due to global environmental changes such as bleaching and mortality of reef-building corals, as well as stability or growth of other groups such as octocorals. In turbid reefs, certain reef species appear to be more resilient to climate change, such as heat waves. Studies addressing the metabolism of octocorals have proved to be an essential tool for understanding their biological cycles and their ability to cope with periods of hunger or stress. In this context, biochemical energy storage molecules and stable isotope analyses of cnidarian tissues, including soft corals, are known to be effective tools for identifying their capability to accumulate reserves and understand their food sources. However, most of these studies have been with scleractinians, with studies with octocorals being limited, especially in coral reefs with moderately turbid waters. Considering this, samples of three species of octocorals (*Muriceopsis sulphurea, Plexareulla grandiflora, Phyllogorgia dilatata*) were collected along the Southwest Atlantic Equatorial coast in 2020 and 2021. Data on lipids, carbohydrates, $\delta^{15}N$ and $\delta^{13}C$ isotopes were obtained. The lipid content was between 154 ± 56 (ug/AFDW) and 380 ± 72 (ug/AFDW) corresponding to 15% and 38% AFDW. Results of $\delta^{13}C$ were between -15,44‰ and -20,32‰ and $\delta^{15}N$ values ranged from 3,64‰ to 6,16‰. These analyses indicate that these octocoral species have a heterotrophic tendency, being able to face greater resilience to stress situations resulting from global and local changes. This is the first study on the trophic ecology of octocorals in the Southwest Atlantic Equatorial and provides important insights into their biomolecule profile, their trophic position on turbid reefs and their potential for resilience in the current climate emergency.

Keywords: Trophic level, Global warming, Gorgonians.

1. Introduction

Octocorals (Cnidaria, Anthozoa), belonging to the subclass Octocorallia, are one of the most common benthic organisms, occupying environments ranging from shallow tropical waters to deep-sea habitats, and from the Tropics to the Poles (Benayahu and Loya 1981; Fabricius and Alderslade 2001; Benayahu *et al.,* 2019; Schubert *et al.,* 2017). Many species exhibit a tree-like or bushy morphology, forming dense three-dimensional communities, often referred to as "animal forests." Along with other benthic communities like mussel beds, black coral fields, or sponge grounds, these structures provide essential habitats for hundreds of associated organisms (Rossi *et al.,* 2017a; Sánchez 2016; Jones *et al.,* 1994; Orejas *et al.,* 2022).

They provide essential resources for various marine species, including fish and nudibranchs, offering food, shelter, protection, and nurseries for reproduction (Tsounis *et al.,* 2020; Avila *et al.,* 1999; Pratchett 2005; FitzPatrick *et al.,* 2012; Epstein and Kingsford 2019). By doing so, they contribute to increased biodiversity (Reaka-Kudla 1997). Additionally, octocorals transfer energy and nutrients between pelagic and benthic systems by capturing particles or transforming light and CO_2 into organic matter and releasing organic this matter in the form of mucus (Coma *et al.,* 1998; Rossi *et al.,* 2017b). However, the ecosystem services provided by octocorals differ from those of scleractinian on coral reefs. For example, soft corals do not form the massive, wave-resistant reef platforms that stony corals do (Stoddard, 1969), and their ability to act as carbon immobilizators is less efficient due to the structure of their skeletons and a lower capability to store carbon (Rossi and Rizzo, 2020).

In tropical coral reefs, octocorals are diverse and abundant and have become dominant in certain areas in response to global environmental changes (Inoue *et al.,* 2013; Ruzicka *et al.,* 2013; Lenz *et al.,* 2015; Lasker *et al.,* 2020). They dominated environmental left by reef-building scleractinian corals, which do not have the same resilience capacity in the face of multiple human-related disturbances, as marine heatwaves and repeated bleaching (Hoegh-Guldberg *et al.,* 2007; Hughes *et al.,* 2017), which increased scientific interest in studying these reef animals, which historically received significantly less attention compared to scleractinian corals (Schlichter 1982; Burris 1983).

Various octocoral traits, such as their morphology with sclerites, reproductive strategies, thermal tolerance through symbiosis with *Symbiodinacea*, higher growth rates (Yoshioka & Yoshioka, 1991; Cadena & Sanchez 2010), and robust immune systems (van de Water *et al.,* 2018) are considered to contribute to this current resilience. However, their feeding strategy has been identified as the most significant competitive advantage that allows them to thrive in disturbed reef environments (Lasker, Cocito *et al.,* 2013; Rossi *et al.,* 2018). Feeding by heterotrophic and mixotrophic modes enhances their resilience and adaptability, reducing reliance on light energy and symbionts for food acquisition through autotrophy (Ribes, Coma & Gili, 1998). They also perform better against bleaching effects compared to scleractinian, which have the advantage of being more efficient in light harvesting but are also more sensitive to temperature and nutrient shifts (Schubert *et al.* 2017).

Studies have shown that heterotrophy constitutes a substantial portion of gorgonian energy input (Ribes *et al.,* 1998, 2003; Tsounis *et al.,* 2006; Gori *et al.,* 2012b), and depending on environmental conditions, they may shift toward an almost exclusively heterotrophic diet, unlike scleractinian (Schubert *et al.,* 2017; Pupier *et al.,* 2021). Research methods such as analyzing the biochemical balance (protein–carbohydrate–lipid composition) and stable isotope values of octocoral tissues provide insights into the trophic level and characteristics of their assimilated food sources (Crandall *et al.,* 2016; Pupier *et al.,* 2019; Jacob *et al.,* 2006; Carlier *et al.,* 2007; Mintenbeck *et al.,* 2007; Mincks *et al.,* 2008).

The use of stable carbon and nitrogen isotope ratios ($\delta^{13}C$ and$\delta^{15}N$) has been largely efficient in identifying the trophic level of coral. When $\delta^{13}C$ values of corals and their symbionts are similar, it means that there is an exchange of nutrients between them (e.g., Muscatine *et al.* 1989; Reynaud *et al.* 2002), demonstrating a tendency for autotrophy in corals. On the other hand, $\delta^{15}N$ enrichment observed in host coral, relative to their symbionts, are generally correlated with the heterotrophic food sources. For example, accumulation of $\delta^{15}N$ and $\delta^{13}C$ in *Plexaura homomalla* and *Eunicea flexuosa* from eutrophic sites indicated a greater reliance on heterotrophy, on the other hand, clean sites had lower $\delta^{13}C$ values, consistent with autotrophic nutrition (Ward-Paige *et al.,* 2005).

However, knowledge about the trophic ecology of octocorals, especially in tropical reefs, remains limited compared to temperate zones. Given that these organisms inhabit a wide range of environmental settings, it is essential to conduct nutritional studies to understand how they survive under various reef-associated conditions, such as different temperatures, turbidity and latitude. Despite octocorals have the same feeding apparatus, using eight tentacles to capture particulate food carried by water flow (Lewis, 1982), they can change their diets due to environmental conditions such as depth (Lasker *et al.* 1983; Gori *et al.* 2012) and substrate type (Sherwood *et al.* 2008).

Temporal analyses of trophic ecology also could elucidate benthopelagic coupling processes, shedding light on natural diet, feeding rates, reproduction, and growth. For example, the biochemical composition of *Corallium rubrum* and *Paramuricea clavata* varied throughout the year (Rossi *et al.,* 2006), indicating that this latter species is an opportunistic feeder even though gut content analysis showed a higher proportion of ciliates than present in the environment (Coma *et al.,* 2001). Seasonality has been demonstrated to be an excellent approach to better understand life cycles and the potential coupling with the available energy of different organisms (Rossi *et al.* 2017b), being able to describe the needs of a species, resilience potential, and the potential constraints.

Most studies on octocorals have focused on species inhabiting shallow waters or the upper edge of the mesophotic zone, environments considered optimal for coral growth due to oligotrophic waters, stable temperatures, low nutrient levels, and clear waters (Ferrier-Pagès *et al.,* 2022; Soares *et al.,* 2021; Hughes *et al.,* 2018). In contrast, octocorals living under different conditions, with high sediment inputs, high and variable temperature, and in high-latitude reefs - conditions considered undesirable for these organisms - have received far less attention (Schoepf *et al.,* 2023).

In the literature, coral reefs that occur in environments under these extreme conditions are referred to as marginal reefs, because they are present in a “sub-optimal” environment condition, compared to corals reefs that inhabit clear waters. They are typically characterized by low biodiversity, reduced habitat complexity, and low coral cover, and are dominated by stress-tolerant and weedy coral communities (Browne & Bauman, 2023). The considered turbid environments within the “marginal coral reef” description are characterized by elevated siliciclastic sedimentation and turbid waters (Camp *et al.,* 2018; Burt *et al.,* 2020; Soares, 2020).

Recent research indicates that while interest in the trophic ecology of octocorals has grown in Tropical regions, most studies remain concentrated in the Tropical Northwestern Atlantic and Red Sea, where octocorals are becoming dominant on shallow water coral reefs (Harland *et al.*, 1993; Grossowicz & Benayahu, 2012; Pupier *et al.,* 2019; McCauley & Goulet, 2019; Klinke *et al*., 2022; Lucas, 2022). However, there is a near-absence of research on the nutrition of octocorals in turbid-zone coral reefs in the Tropical Southwestern Atlantic (Leão *et al.,* 2003; Francini-Filho *et al.,* 2013).

To better understand the potential shifts in species dominance and the role of octocorals in future seascapes, the aim of this study is investigating the contribution of autotrophy and heterotrophy to the nutrition of three octocorals from Tropical Southwestern Atlantic, living under extreme conditions. We hypothesize that heterotrophy plays an important role in supporting these species' survival in such turbid-zone conditions. We also wanted to understand the role of energy storage in these Southwest Atlantic Tropical species. To test these hypotheses, octocoral colonies were sampled, and their nutritional composition, as well as autotrophic and heterotrophic sources, were analyzed through biochemical and isotopic analysis of coral tissues. This will contribute to a better understanding of octocoral ecological cycles in this poorly studied coral reef region but also in unique environmental conditions.

2. Material and Methods

2.1 Study site and environmental data

The study was conducted on the coast of Bahia state and Alagoas state in Brazil (Figure 1), the only country with true biogenic coral reefs known in the South Atlantic Ocean (Paulay, 1997; Castro & Pires, 2001). Both reefs are inside Marine Protected Areas.

Specifically, the sampling was carried out in three localities:

In region 1 - Maragogi (Alagoas): Samples were collected in January and October 2021, in a spot called "Pedra da Virada", belonging to the Marine Protected Area Costa dos Corais (APACC), 5 km off the coast and at approximately 3 m depth. This area is known as the first and the largest marine conservation unit in Brazil, spanning 120 km along the Northeast coast, covering regions in both Pernambuco and Alagoas states (Maida, Ferreira, 1997; Miranda *et al.,* 2020). In this area, a large range of different ecosystems are present such as shallow reefs, mangroves, seagrass beds, rhodolite/sponge beds and mesophotic reefs from the coast to the break of the continental shelf (Maida, Ferreira, 1997; Pereira *et al.,* 2018).

In region 2- Recife de Fora: Recife de Fora Marine Park (RFMP, Bahia), a spot that is located 9 km off the coast, at approximately 3 m depth, 30 minutes away with motorboat transport, with samples collected in November 2020 and November 2021. This Marine Protected Area (i.e. equivalent to category II of the International Union for Nature Conservation – IUCN) (Tedesco *et al.*, 2018) covers an area of 19.68 km^2 (Lima *et al.,* 2021) with reefs developing parallel to the coast, forming several natural pools where species of hard and soft corals live, besides algal cover and others that form the richness of reef biodiversity, as in the APACC also (Castro & Zilderberg, 2016).

In region 3 - Costa: On the coast of Mucugê Beach (Bahia). Near Coral Research Center, 100 – 200 m from the coast, on shallow water, in interdital zone at approximately 15-50 cm of depth at low tide, with samples collected also in November 2020 and 2021.

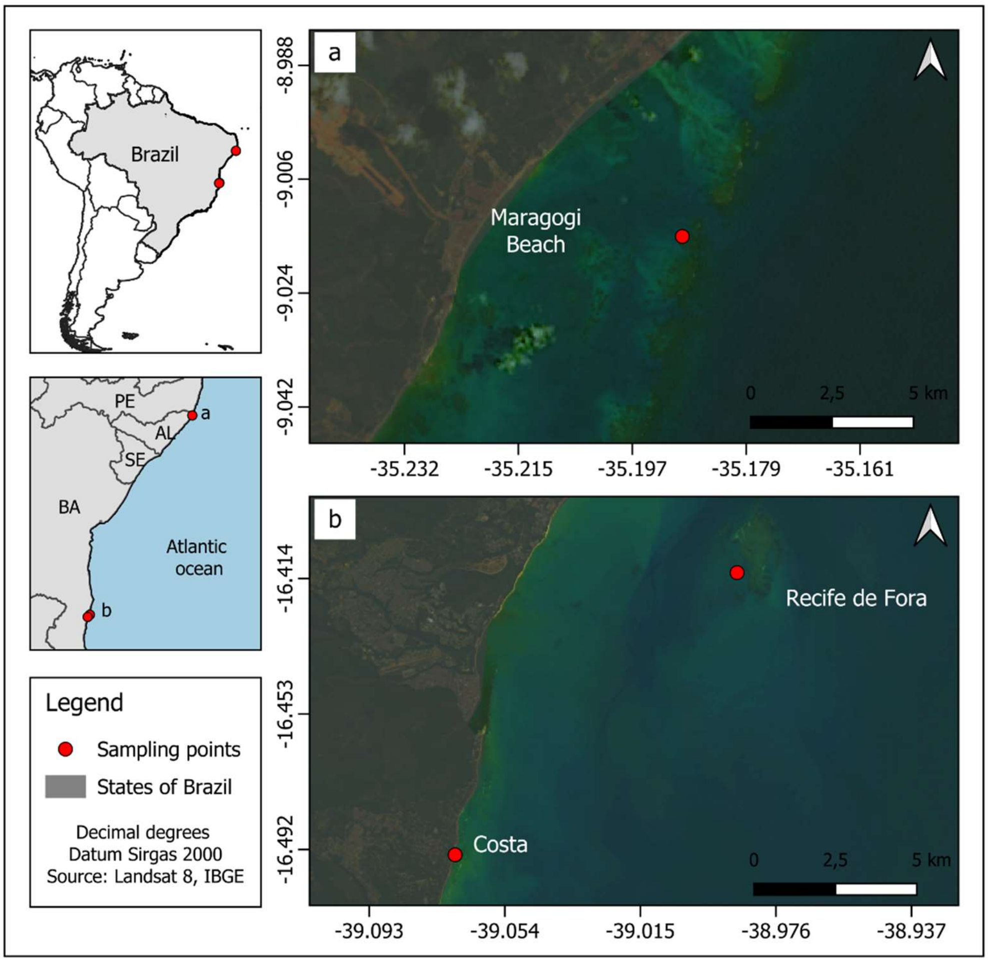

Figure1: Study site in Maragogi on the Marine Protected Area Costa dos Corais, the coast of Alagoas states, and in Recife de Fora and Costa do Mucugê, the coast of Bahia state, both in northeast Brazil, South Atlantic.

In Maragogi (region 1), environmental data on water temperature (°C) and luminosity (Lux) was provided through surveys conducted on-site, such as those carried out to assess the health of *Siderastrea stellata (*Paulino *et al*, 2023). Environmental data in Bahia from regions 2 and 3 were obtained by Coral Vivo for August and December 2020. In 2021, data received was from August, November and December (Table 1).

Table 1. Summary of water analysis performed on Bahia and Maragogi: Min (Minimum); Max (Maximum); Med (Medium); DO (dissolved oxygen); WT (water temperature); O (October); A (August); D (December); N (November). The physical-chemical parameters in Maragogi were measured using a Ysi 6600V2 sonde.

	2019	2020	2021
Costa da Bahia		Min 27,09 °C (A) Max 28,39 °C (D) Min 18.171,87 lux (A) Max33.879,62 lux (D)	Min 26,26 °C (D) Max 27,96°C (O) Min16148,476 lux (D) Max 24340,91 lux (D)
Recife de Fora		Min 25,83 °C (A) Max 27,6 °C (D) Min 20.525,88 lux (D) Max33.628,90 lux (A)	Med 28,87 °C (N) 27436,513 lux(N) 31788,262 lux (N)
Maragogi	April (rainy season): 29.55°C (WT), 8.6 (pH); 33.25 (salinity), 0.1 NTU (turbidity), 104.6% (DO) September (dry season): 28.76 °C (WT); 9.1 (pH); 32.98 (salinity); 0 NTU (turbidity); 147.8% (DO)		

2.2 Sample collection

Samples of three octocoral species, *Muriceopsis sulphurea,* and the two endemics from Brazil cost *Plexareulla grandiflora* and *Phyllogorgia dilatata* (Figure 2), were collected in three above-mentioned regions chosen on the coast of the states of Alagoas and Bahia, in the Northeast of Brazil: Maragogi (1), Recife de Fora (2), Costa (3).

Samples were collected with scuba diving (SCUBA) and manual removal in the shallow region (< 5 m deep). Branches (5 - 8 cm length) were cut with scissors. 20 different colonies of each species (and each place where they were present) were collected and transported in plastic bags in a cooler with ice and immediately brought to the laboratory.

All fragments were cleaned with sterile artificial seawater (salinity: 35) to reduce the risk of sample contamination. Branches were divided into two subsamples, with the apical part being frozen at -80 °C for nutritional analysis: organic matter, biochemical analysis and stable isotopes (Rossi *et al.* 2006; Rossi *et al.* 2018). The basal part was fixed in 6% formalin in 50 mL Falcon for future analysis. Samples were identified and transported to the laboratory, where all apical parts were freeze-dried and ground to powder with a mortar and pestle and stored at -20 °C.

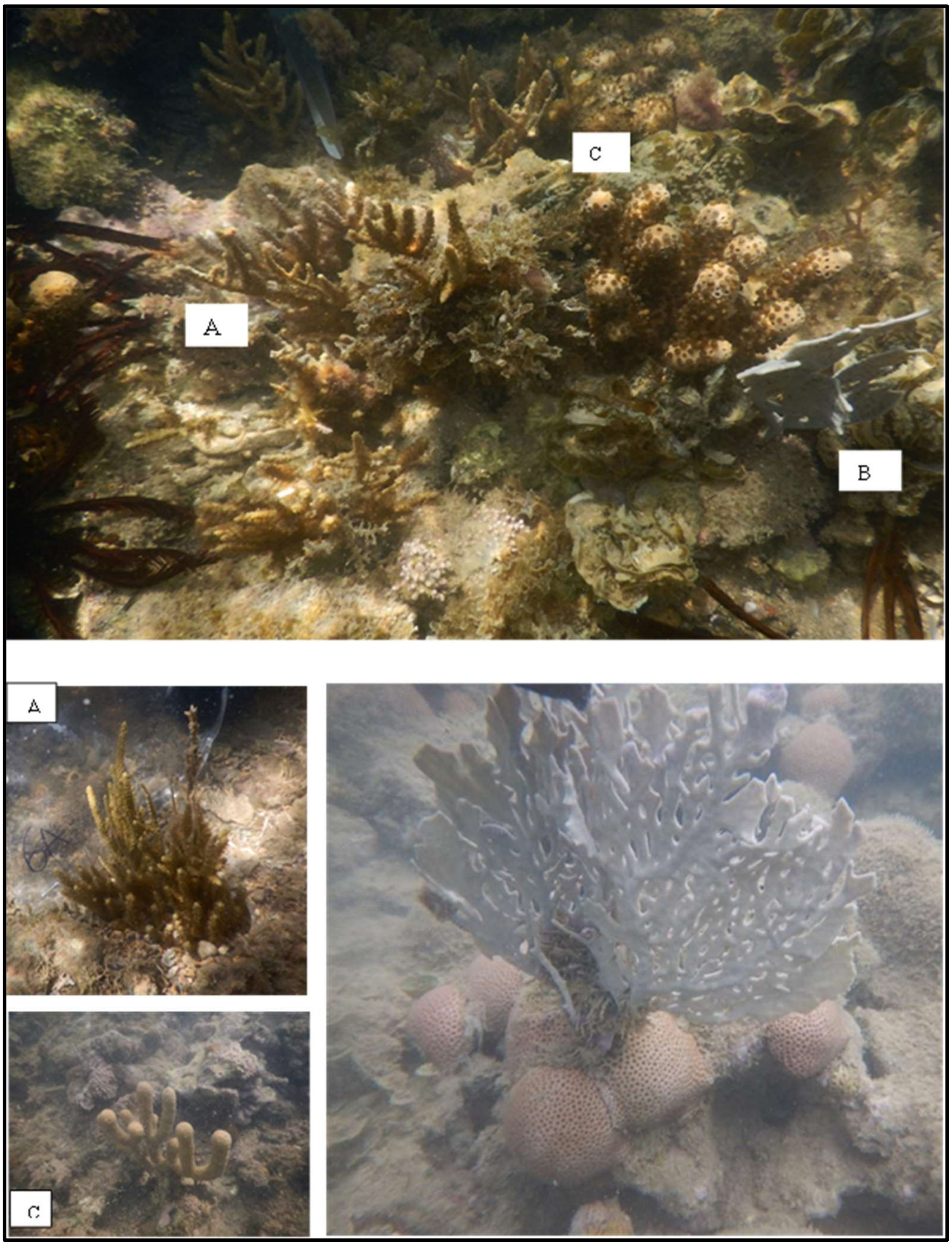

Figura 2: Three octocoral species from the Southwest Atlantic Equatorial coast: (A) *Muriceopsis sulphurea* (B) *Phyllogorgia dilatata* and (C) *Plexaurella grandiflora*. Source: Prepared by the authors (2022).

2.3 Nutritional analysis

2.3.1 Organic Matter

The organic matter (ash-free dry weight, AFDW) content was determined by subsampling 10 mg of the coenenchyme of the freeze-dried tissue (N = 10 per species) weighted, burned and weighted again (Slattery and McClintock 1995; Rossi *et al.* 2006). Samples were combusted in a muffle furnace (Relp 2H-M9) at 500 °C for 4 h, the remaining inorganic ash was weighed, and the organic content was obtained (Slattery and McClintock 1995; Rossi *et al.*2006).

2.3.2 Biochemical analysis

Biochemical energy balance (carbohydrates and lipids) was carried out with two colorimetric protocols (spectrophotometry) with a methodology previously used successfully in octocorals (Servetto *et al*, 2017, Rossi *et al*, 2006). Freeze-dried tissue (N = 20) from each species, location and period was used. For carbohydrates, 8 - 10 mg pieces of tissue were homogenized in 3 mL of distilled water and quantified by the method Dubois *et al.* (1956), using glucose as a standard. For lipids, 10 mg pieces of freeze-dried tissue (N = 20) were homogenized in 3 mL of chloroform-methanol (2:1). All data were normalized to ash-free dry weight (AFDW) for three species. They were quantified according to the method of Barnes and Blastock (1973), using cholesterol as a standard.

Tissue samples from up to 20 different colonies of each octocoral species were initially targeted for each region and period, but the number of samples successfully processed varied between species, location, and sampling period (Table2)

Table 2. Number of samples used for biochemical analyses (lipids and carbohydrates) of the three species of octocorals studied according to the sample collect period and region. Nov = November; Jan = January; Oct = October.

Analysis	**Species**	**Area and Period**		
		Bahia Costa Nov20/ Nov21	**Recife de Fora Nov20/ Nov21**	**Maragogi Jan21/ Oct21**
Lipids	*Muriceopsis sulphurea*	11/ 10	11/ 14	12/ 13
	Plexareulla grandiflora	12/ 20	14/ 14	15/ 13
	Phyllogorgia dilatata	9/ 12	-	13/ 16
Carbohydrates	*Muriceopsis sulphurea*	16/ 10	8/ 19	13/ 13
	Plexareulla grandiflora	8/ 15	14/ 19	7/ 10
	Phyllogorgia dilatata	8/ 16	-	17/ 16

2.3.3 Stable Isotopes analyses

Sample preparation for stable isotopes analysis

Two subsamples of 10 mg were weighed from 3 freeze-dried samples of each species by region and date. In one subsample for δ^{15}N determination, no treatment was carried out. But, in the other subsample to δ^{13}C determination, it was necessary to acidify to remove inorganic calcium carbonate to not interfere in results, by adding 10 % HCl drop-by-drop until effervescence ceased, to complete the acidification, and then were oven-dried at 50 ºC for 72 h.

Afterward, three replicates of each subsample were weighted with a precision balance (± 0.001 mg) into tin capsules (11 x 4 mm, Elementar Microanalysis) to conduct the isotopic composition analyses to obtain carbon and nitrogen values using a mass spectrophotometer, following protocol according to the Elias-Piera *et al*. (2013).

Performing Stable Isotope Analyses

All samples were performed using the Elementar IsoPrime 100 isotope ratio-mass spectrometry (IR-MS) instrument (IsoPrime Ltd.) coupled to a CNS elemental analyzer (Elementar Vario Pyro Cube EA CNS; Elementar Analysensysteme GmbH). Stable carbon isotopic values (δ13C) were quality checked and calibrated by using the reference materials Glucose (BCR-657) and Polyethylene (IAEA-CH-7), while for the stable nitrogen isotopic (δ15N) values potassium nitrate (USGS32) and ammonium sulfate (USGS25) were used.

Stable isotope ratios ($\delta^{13}C$ and δ15N) were expressed as parts per thousand (%) (difference from a standard reference material) by the following equation:

$$\delta^{13}C \; or \; \delta^{15}N \; (‰) = \left[\frac{R \; sample}{R \; standard} - 1\right] x1000 \qquad (1)$$

where R corresponds to 13C/12C or 15N/14N of the analyzed sample (Rsample) and standard used (Rstandard). Standard R values for 13C were from Vienna Pee Dee Belemnite (VPDB) and 15N from atmospheric N2 (Air). Each sample was analyzed 3 times and the standard deviation calculated was < 0.50 ‰ for $\delta^{15}N$ and < 0.20 ‰ for $\delta^{13}C$.

2.4 Statistical Analyses

Data were tested for normality using the Shapiro-Wilk test. Analysis of variance (one-way ANOVA) allowed for the determination of significant differences ($p < 0.05$) for each parameter. For the comparison of differences between carbohydrates and lipids of different places and time, a Tukey HSD Post-hoc test was used. The statistical analyses were conducted using Statistica 7.0 and Past 4.03.

3. Results

3.1 Species occurrence

In Bahia, we sampled all three species studied: *Muriceopsis sulphurea*, *Plexaurella grandiflora*, and *Phyllogorgia dilatata*. Unfortunately, in Maragogi, we were unable to find any colonies of *P. dilatate*. Only *M. sulphurea* and *P. grandiflora* were found and collected. As a result of the sex determination of octocoral, polyps from three species across different periods were dissected, but no gonads were found.

3.2 Nutritional analysis

Lipid and carbohydrate content (mean ± SD) for the 3 species studied in three regions in two periods are presented in Figure 2. Lipids content from *Muriceopsis sulphurea* decreased significantly compared to Costa and Recife de Fora. The average lipid composition in the Bahia Costa ranged between 354 and 380 ug lipid/mg AFDW while in Recife de Fora, the values ranged from 154 to 242 ug lipid/mg AFDW. In Maragogi, the results were very similar, showing no differences between periods, they ranged from 229 to 238 ug lipid/mg AFDW (Table 2). The carbohydrate composition on the Bahia Costa ranged from 187 to 291 ug carbohydrate/mg AFDW. In Recife de Fora, it ranged from 129 to 404 ug carbohydrate/mg AFDW, and in Maragogi, from 131 to 204 ug Carbohydrate/mg AFDW.

In *Plexaurella grandiflora*, the average lipid composition on the Bahia Costa ranged between 227 and 270 ug Lipid/mg AFDW. In Recife de Fora, the values ranged from 285 to 290 ug lipid/mg AFDW, while in Maragogi, they ranged from 234 to 269 ug lipid/mg AFDW. The average carbohydrate composition on the Bahia Costa ranged from 158 to 397 ug carbohydrate/mgAFDW. In Recife de Fora, it ranged from 192 to 368 ug carbohydrate/mg AFDW, and in Maragogi, from 117 to 231 ug carbohydrate/mg AFDW.

In *Phyllogorgia dilatata*, the average lipid composition on the Bahia Costa ranged from 260 to 286 ug lipid/mg AFDW. In Recife de Fora, the values ranged from 301 to 357 ug lipid/mg AFDW. The average carbohydrate composition on the Bahia Costa ranged from 370 to 427 ug carbohydrate/mg AFDW. In Recife de Fora, it ranged from 351 to 359 ug carbohydrate/mg AFDW.

Table 3. Composition of lipid and carbohydrates per ash-free dry weight (% AFDW) in branches of Brazilian tropical octocorals *Muriceopsis sulphurea*, *Plexareulla grandiflora* and *Phyllogorgia dilatata.* Showing the difference in contents between the regions and periods analyzed. Bahia Costa in November 2020 and 2021; Bahia Recife de Fora November 2020 and 2021; Maragogi January and October 2021.

		Bahia Costa		Bahia Recife de Fora		Maragogi	
		nov/20	nov/21	nov/20	nov/21	jan/21	oct/21
Muriceopsis sulphurea	Lipids	38%	35%	24%	15%	23%	22%
	Carbo	29%	18%	12%	40%	13%	20%
Plexareulla grandiflora	Lipids	22%	27%	28%	29%	23%	26%
	Carbo	39%	15%	38%	19%	11%	23%
	Lipids	28%	26%	30%	35%		

Phyllogorgia dilatata	Carbo	37%	42%	35%	35%

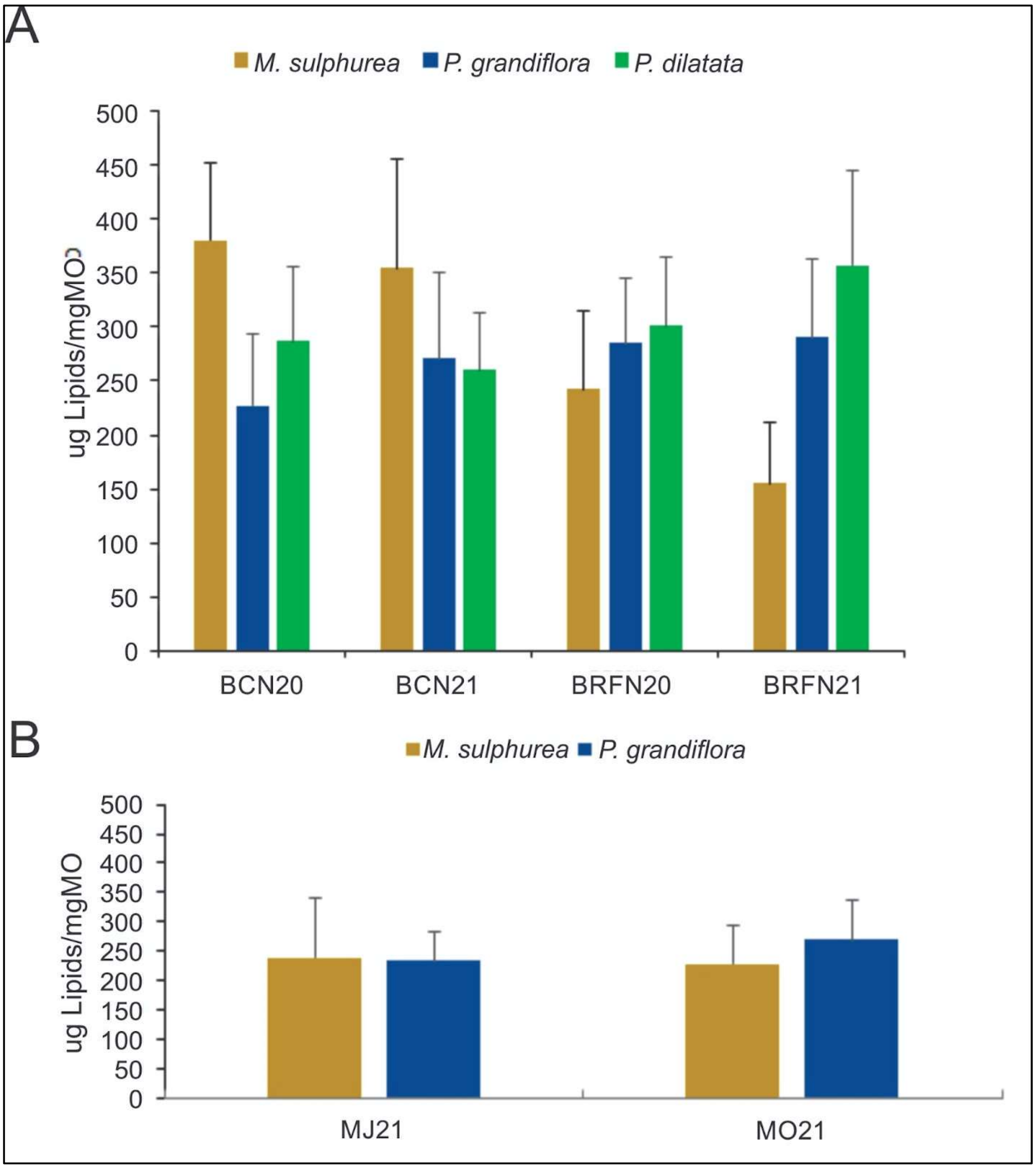

Figure 2. Lipid (average contents ± SD) in branches of Brazilian tropical octocoral *Muriceopsis sulphurea*, *Plexareulla grandiflora* and *Phyllogorgia dilatata.* in sample from colonies in three sites and two periods. BCN20: Bahia Costa November 2020; BCN21: Bahia Costa November 2021; BRFN20: Bahia Recife de Fora November 2020; BRFN21: Bahia Recife de Fora November 2021; MJ21: Maragogi January 2021; MO21: Maragogi October 2021.

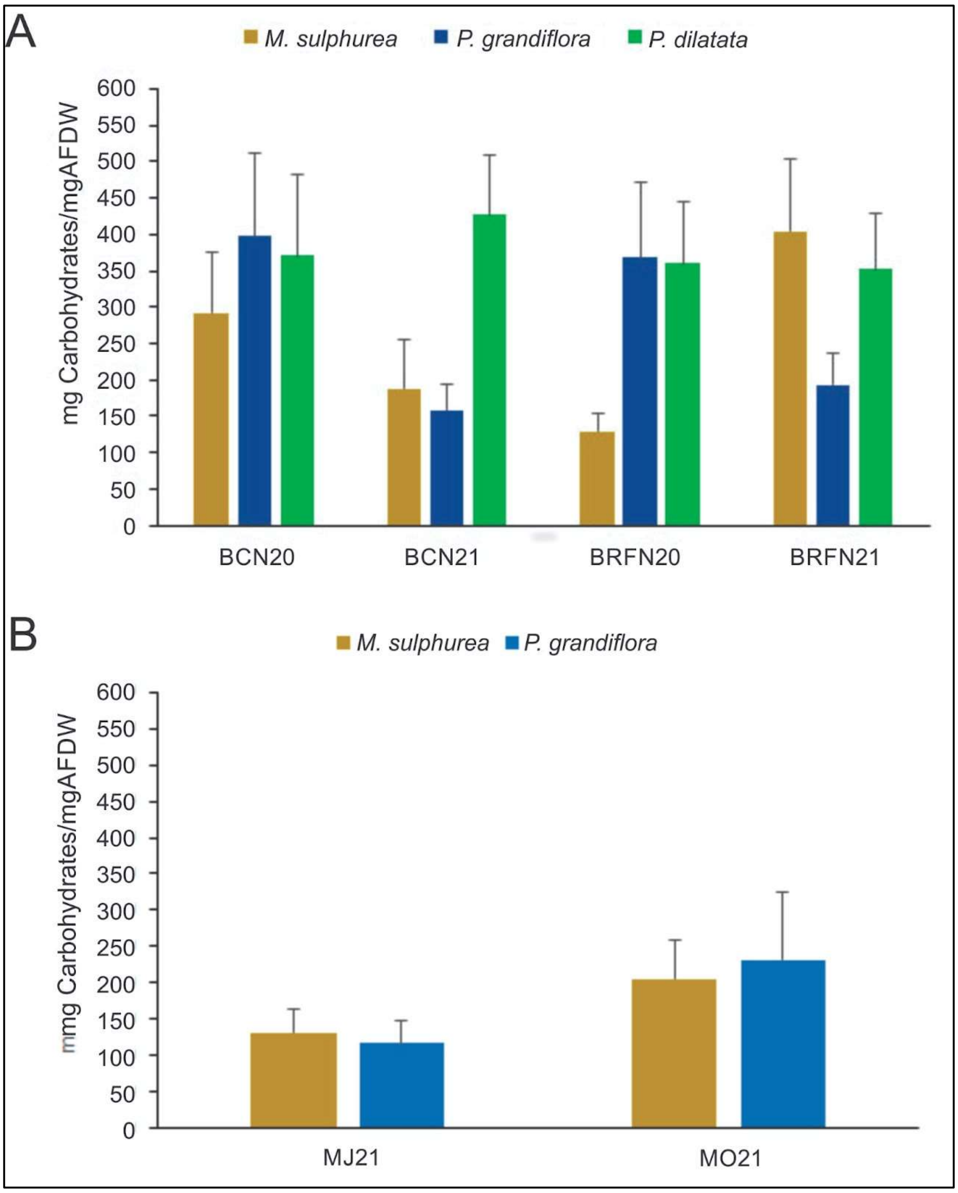

Figure 3. Carbohydrates per ash-free dry weight (% AFDW) (average contents ± SD) in branches of Brazilian tropical octocoral *Muriceopsis sulphurea*, *Plexareulla grandiflora* and *Phyllogorgia dilatata* in sample from colonies in three sites and two periods. BCN20: Bahia Costa November 2020; BCN21: Bahia Costa November 2021; BRFN20: Bahia Recife de Fora November 2020; BRFN21: Bahia Recife de Fora November 2021; MJ21: Maragogi January 2021; MO21: Maragogi October 2021.

3.3 Stables isotope

Carbon and nitrogen stable isotope ($\delta^{13}C$ and $\delta^{15}N$) conducted on *Plexareulla grandiflora, Phyllogorgia dilatata and Muriceopsis sulphurea* and are shown in Figure 4.

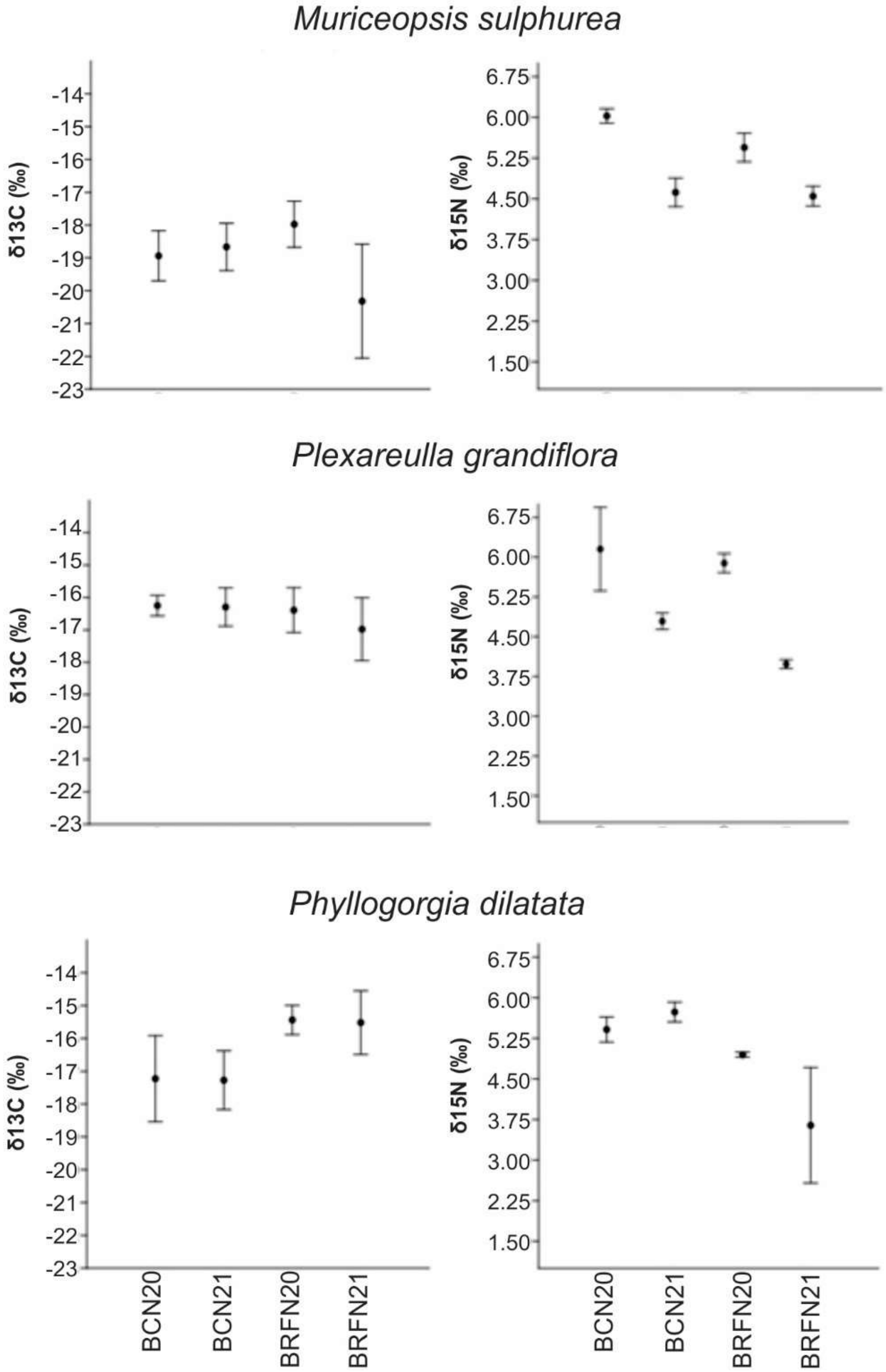

Figure 4. Mean δ^{13}C and δ^{15}N of of Brazilian tropical octocoral *Muriceopsis sulphurea*, *Plexareulla grandiflora* and *Phyllogorgia dilatata* in 2 sites and 2 different periods: BCN20: Bahia Costa November 2020; BCN21: Bahia Costa November 2021; BRFN20: Bahia Recife de Fora November 2020; BRFN21: Bahia Recife de Fora November 2021.

Results of δ^{13}C were between -15,44‰ and -20,32‰. The lowest measured δ^{13}C value was for *P. dilatata* in BPRFN20 and the higher was for *M. sulphurea* in BRFN21 sampled. δ^{15}N values ranged from 3,64‰ to 6,16‰. The lowest measured value was for *P. dilatata* in BPRFN21 and the organism most enriched in δ^{15}N was for *P. grandiflora* in BRFN20 (Table 3).

No result was obtained for the samples collected from Maragogi region because no values were recorded for these samples after processing them with the spectrophotometer.

Table 3. Mean δ^{13}C and δ^{15}N of of Brazilian tropical octocoral *Muriceopsis sulphurea*, *Plexareulla grandiflora* and *Phyllogorgia dilatata* in 2 sites and 2 different periods: BCN20: Bahia Costa November 2020; BCN21: Bahia Costa November 2021; BRFN20: Bahia Recife de Fora November 2020; BRFN21: Bahia Recife de Fora November 2021.

	δ^{113}C (VPDB)				**δ^{15}N (Air)**			
	BCN20	**BCN21**	**BRFN20**	**BRFN21**	**BCN20**	**BCN21**	**BRFN20**	**BRFN21**
M. sulphurea	-18,93	-18,66	-17,97	-20,32	6,03	4,62	5,45	4,55
P.grandiflora	-16,25	-16,30	-16,39	-16,98	6,16	4,79	5,89	3,98
P. dilatata	-17,22	-17,27	-15,44	-15,52	5,41	5,73	4,95	3,64

In Figure 5 is possible to see the average results of δ^{15}N and δ^{13}C from all groups analyzed (three samples each). The BRFN21 was the only group more distant than others and with a big standard deviation for δ^{15}N.

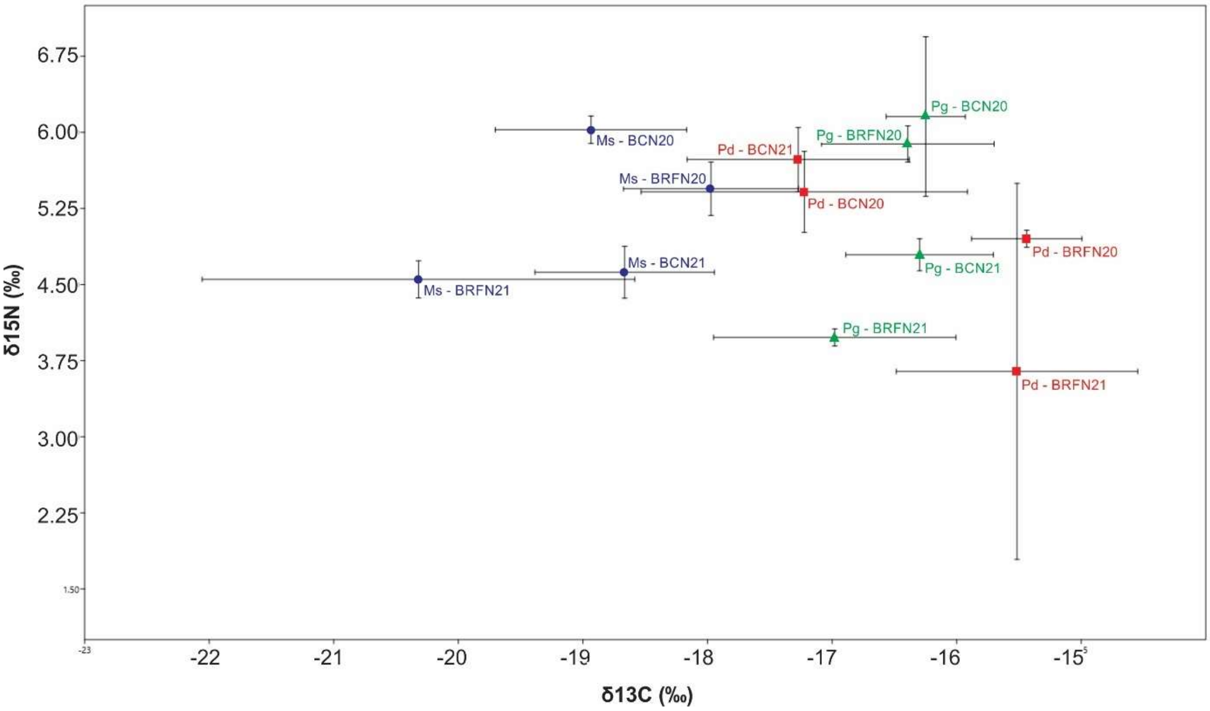

Figure 5. $\delta^{15}N$ and $\delta^{13}C$ of all groups analyzed together. Each spot represents the mean ± SE (n=3). The corresponding values of the species are differentiated by colors: green color: *Plexaurella grandiflora*; red color: *Phylogorgia dilatata*; blue color: *Muriceopsis sulphurea.* BCN20: Bahia Costa November 2020; BCN21: Bahia Costa November 2021; BRFN20: Bahia Recife de Fora November 2020; BRFN21: Bahia Recife de Fora November 2021.

The biochemical content from *M. sulphurea* and *P. grandiflora* was statistically different. All samples *P. dilatata* were collected only in Bahia and they didn’t show a statistical difference between them, neither in carbohydrates nor in lipids (Supplementary material).

M sulphurea: All carbohydrates contents from Bahia Coast 2020 showed a significant difference ($p < 0.05$) between all other regions, and periods. Compared with same place but one year later (BCN21), difference was p=0.001, not so distance when compared to other groups tested: BRFN20 (p=0.0001); BRFN21 (p=0.0001); MJ21(p=0.0001); but with exception of group MO21(p=0.02), the closest to the p=0.05 threshold. Carbohydrates content of BRFN21 were also different from all others compared: BCN21 (p=0,0001); BRFN20 (p=0.0001); MJ21(p=0.0001); MO21(p=0.0001). Valeus from Maragogi didn’t show a statistically significant difference between years, but also were both similar from those BRFN20 and BCN21. About lipids, samples from Bahia Coast in the two years (2020 and 2021) had no statistical difference between them, and they showed the same value p=0,1. However they showed differences with all other locations and periods. Samples from Maragogi didn’t change statistically lipid’s content in the two sampling periods and showed statistical similarities from Recife de Fora (p>0,05).

P. grandiflora: Lipids content did not show significant differences between region and periods. Otherwise, we had a variability in results from Carbohydrates. They showed significant difference between Bahia Coast Nov. 2020 and almost all locations and periods analyzed, except those from BRF20. Results from BCN21 show significant differences only from BCN20 (p=0,0001) and BRFN20 (p=0,0001). BRFN20 content was also statistically different from almost all groups, except for BCN21. Contents from Maragogi were statistically different between samples from the same location, but in two different periods (p=0,01), and also from BCN20 and BRFN20. They were statistically similar to other groups (BCN21 and BRFN21) in the same year 2021.

4. Discussion

Biochemical analysis of storage biomolecules

For the first time, the present study investigated the trophic tendencies of three species of tropical octocoral living in extreme conditions on reefs in the Southwestern Tropical Atlantic through the biochemical composition and stable isotope concentration, comparing species, locations and considering different times of the year. The biochemical composition, and isotopic signatures showed the heterotrophic importance in the overall energy budget of these species in the studied locations, supporting the hypothesis that the reduced reliance on symbionts increases the likelihood of these species persisting in the environment.

In the literature, research focusing on trophic ecology of octocorals in tropical regions is already reduced when compared to works with Scleractinia, and results obtained from octocorals in coral reefs that living in extreme environmental conditions are practically non-existent. For example, in this type of coral reefs of Southwestern Atlantic, *Carijoa riisei* was, to the best of our knowledge, the only octocoral species that had its trophic ecology recorded (Lira *et al*, 2009; Gomes *et al.,* 2012).

This is first-time using isotopes signatures to characterize trophic relationships in octocoral species, so our comparative analysis with the present literature was restricted to the results found for octocorals from other places such as Caribbean, China, Red Sea or Vietnam. Regions with different environmental conditions from those found in the study region, however, also deal with adversities such as global warming, pollution or intensive tourism (Rise *et al.,* 2022; Dearden & Manopawitr, 2011; Lasker, 2005; Gil *et al*, 2015; Cai *et al.,* 2024). Nutritional aspects in octocorals are highly variable and depend on several factors, such as region (season, depth, light availability, etc.) and species (Imbs, 2013). While some species can obtain sufficient carbon from particulate organic matter (Murdock, 1978; Coffroth, 1984), they still rely on nitrogen supplied through *Symbiodinium* photosynthesis (Wainwright, 1967). These dinoflagellates transfer a significant portion of lipids to their coral hosts, a process closely linked to light availability (Crossland *et al.,* 1980). On tropical ecosystems, this ability of octocorals to utilize autotrophic and heterotrophic energy sources has been reported (Sorokin 1991; Fabricius and Klumpp 1995; Ribes *et al.* 1998) and this characteristic presents itself as a great survival advantage in facing variations in stressful environmental conditions.

The total lipid found in this study comprises a major constituent of coral carbon content acting as the main energy reserve in them, considerably greater than that reported for Hydrozoans and Scyphozoans (Joseph, 1979) and has become a primary benchmark for evaluating the chemical makeup of biological in corals (Imbs & Dembitsky, 2023; Harland *et al*, 1993). The total pool of coral lipids consists of macromolecules produced by both the coral host and its symbionts (Sikorskaya *et al., 2021*) and could range from 9% to 47% of tissue dry weight of coral polyps (Yamashiro *et al*. 1999), which means the total weight of tissue with ashes. In our results, lipid content was calculated from AFDW (the weight without ash and water) in *Plexaurella grandiflora, Phyllogorgia dilatata and Muriceopsis sulphurea* showed a variation ranging from 154 ug to 380ug, corresponding to 15% - 38% of ash free dry weight tissue, values that match with symbiotic coral, such was found in soft coral *Lobophytum crassum* from Subtropical Okinawa Island with 23.5% total lipid content (Yamashiro *et al.,* 1999)

In *P. grandiflora* the lipid content ranged between 22% – 29%, a similar value compared to record found in Caribbean symbiotic gorgonian *Plexaura homomalla*, such lipids represented by 22% of dry weight (Joseph, 1979), both originated from same order Malacalcyonacea, but different families. All three specie's lipids showed values that are consistent with coral species that perform symbiosis, very contrasting from lipid content in Caribbean *Eunecia tourneforte* which was 5.2% of dry weight, as low as asymbiotic tropical gorgonians from Vietnam *Bebryce indica and Mopsella aurantia* that had lower lipid values ranging from 1.24% to 3.80% of dry weight (Lam et.al, 1981; Imbs & Dembitsky, 2023). Shallow-water Antarctic soft corals also have low lipids content 5.2–12.6% (Slattery & McClintock, 1995), as showed in in *Malacobelemnon daytoni* (between 100 and 164 mg lipid mg1 OM) (Servetto *et al.,* 2017).

Lipids play a crucial role in the majority of biochemical and physiological processes in corals (Rodrigues, 2008; Seemann, 2013) and can fluctuate due to a variety of factors, such as reproductive stage, seasonal variations, habitat depth, light availability, and other environmental conditions (Meyers 1979, Saunders *et al*. 2005). Because the largest amount of lipids in corals is derived from the organic carbon transferred between Simbiodyniacea and coral tissues in symbiotic corals, when there is a decline in dinoflagellate populations - such as during thermal stress or bleaching events - there is often a corresponding decrease in the coral's lipid content, more than 75% of their original total lipid content (Yamashiro *et al.,* 1999; Imbs and Yakovleva, 2012; Liu *et al.,* 2022)

This was observed in an experiment with the symbiotic gorgonian *Eunicella singularis*, where lipid levels dropped from ~4 mg cm^{-2} to ~2 mg cm^{-2}, when the temperature increased from 18°C to 26°C (Ezzat *et al.,* 2013). Coral bleaching events further exacerbate this decline in hard corals, with lipid content decreasing from 26.5 ± 2.3% for normal corals, and was 9.0 ± 1.5% for bleached samples such as *Stylophora pistillata*, *Porites cylindrica*, *Montipora aequituberculata*, *Goniastrea aspera*, *Fungia fungites*, *Montipora digitata*, and *Montipora informis* after 1998 bleaching event (Yamashiro *et al.,* 2005).

Total lipid content is also correlated with reproduction, because this process involves a major energy investment, and is related to the nutritional storage of the gorgonians (Stimson 1987; Harland *et al*. 1992; Ben-David-Zaslow and Benayahu 1999; Rossi *et al*. 2006), which therefore depends on food availability. Analyzing total lipid content in animal tissue provides insights into nutritional status, can improve understanding about reproductions cycles and consequently octocoral dynamic population (Gori *et al.,* 2013).

Lipid accumulation could increase during maturation of the oocytes and lipid content remains high until spawning (Oku *et al.,* 2003; Rossi *et al*. 2006). Shallow-water Mediterranean gorgonian species have an increased lipid content during the spring, linked to the principal bloom in Mediterranean primary and secondary production, otherwise, there is a lipid decrease during summer period of water stratification as well as in late autumn, when the quality of food decreases due to storms and rainfall (Gori *et al.,* 2007; Rossi *et al.,* 2006). In *Junceella fragilis* and Junceella *juncea* lipid concentrations in late-stage oocytes were lower than those of early stage oocytes, indicating the potencial use of this nutrient as an energy source by oocytes (Lin *et al.,* 2012).

Studies on the reproductive cycle of *Phyllogorgia dilatata* from the coast of Bahia do not appear to present a synchronous pattern in gamete production, but did present reproductive peaks, one in the dry period (September to January) and another possibly in the rainy period (April and May) (Ferreira, 2009). In this current study, the lipid contents of *P. dilatata* from Maragogi were carried out in January and October, corresponding to dry season. The statistical similarity found of lipids between samples collected in two different months but from the same climate season could be a small indicator that they could be going through the same biological process, possibly in spawning season as was reported in same species in Bahia. However, we don't have enough data to provide conclusive information on the reproductive cycle of these animals. Unfortunately, there is no information in literature about the reproductive biology of *P. grandiflora* and *M. sulphurea* until now.

Carbohydrate content in octocoral tissue was also another biochemical compound analyzed and showed a great variability between species from Bahia. The values obtained were much higher than those observed in other species not consistent with the fact that Carbohydrates is a minor constituent in gorgonian branches, behind Proteins and lipids, responsible for the biggest energy reserves in cnidarians (Fitt and Pardy, 1981; Slattery and McClintock, 1995; Ben-David-Zaslow and Benayahu, 1999; Rossi *et al*. 2006; Shirur *et al.,* 2014).

Shirur *et al*. (2014) analyzed the biochemical composition of organic matter in eight Caribbean gorgonian species, belonging to the families Plexauridae and Gorgoniidae, and found carbohydrates ranging from 1% to 7% of the organic matter, formed a minor constituent in gorgonian branches. In the same study, the carbohydrate content in *Antillogorgia americana* and *Pterogorgia anceps* was found to be two to six times lower than in the other gorgonian species examined.

In this study, mean carbohydrate content of branches of gorgonian species was (12 – 42%) very higher than reported in Caribbean gorgonian, highlighting the significant variability in biochemical composition among octocoral species. The smallest carbohydrate content found was from *P. grandiflora* in Maragogi (Jan 2021) and the highest content found was from P. *dilatata* in Bahia Coast (Nov 2021). Antarctic gorgonian species *Primnoisis* sp. showed a high value 80.7 ± 28.7 µg carbohydrate mg−1 OM while *Fannyella nodosa* showed an average value of 12.0 ± 6.0 µg carbohydrate mg−1 OM (Elias-Piera *et al.,* 2013).

Carbohydrate levels in gorgonian could also change in coral tissue according to the season. *Alcyonium acaule* (Octocorallia, Alcyonacea) changed from a high carbohydrate content ranged 32.69 ± 1.50 µg mg^{-1} OM (winter season) to 21.94 ± 1.51 µg mg-1 OM (autumn season) (Rizzo *et al.,* 2021). *Paramuricea clavata* also revealed change from 61 ± 10 SD µg mg^{-1} to 71 ± 11 SD µg mg^{-1} OM in summer-autumn and winter-spring season of the same year (Rossi *et al.,* 2005).

Otherwise, other species have very low carbohydrates content such *Heteroxenia fuscescens* from the Red Sea that showed mean 0.6% carbohydrates (Ben-David-Zaslow and Benayahu 1999), as low as 0.5 – 0.7% found for three shallow water Antarctic soft coral species *Alcyonium paessleri, Clavularia frankliniana and Gersemia antarctica (*Slattery & McClintock, 1995). Carbohydrates values are very low compared to what we found in octocorals in this study.

Just like lipids, carbohydrates can also change their composition according to environmental disturbances, which raises the importance of carrying out more biochemical research to verify the changes that can occur with octocoral species from extreme conditions reefs. After thermal stress event, gorgonians decreasead carbohydrate in 58% in *P. clavata* and 45% in *E. cavolini* over time may indicate that *P. clavata* had higher depletion of its energy reserves which could lead to a reduced investment in antimicrobial defense and microbiota regulatory capacities by the coral host (Tignat-Perrier *et al.,* 2022). This is consistent with the reported mortality of this species after heat events (Coma *et al.,* 2009). In our case, maybe the accumulation of carbohydrates is a response to photobiological conditions, coupled with the heterotrophy of the different gorgonian species analyzed (Schubert *et al*. 2017).

A differential antioxidant capacity was revealed by Scleractinian after a bleaching event, with a significant increase in the carbohydrate metabolic capabilities of bacteria in *Acropora* and *Goniastrea* corals in the Great Barrier Reef (Littman *et al.,* 2011) and the South China Sea (Sun *et al.,* 2020).

Spatial and temporal comparisons

The octocoral species analyzed in this study belong to coral reefs located in Southwestern Tropical Atlantic, a biogeographic region whose reef communities have received limited scientific attention and are consequently underrepresented in global coral reef research. These regions are commonly called marginal reefs, as they refer to reef environments that develop under conditions considered suboptimal for the growth and survival of coral reefs (Schoepf *et al.,* 2023; Zweifler *et al*, 2021).

However, this concept isn't entirely true. Certainly, these environmental conditions are not optimal for Caribbean or the central Indo-Pacific, that depends on high-water clarity, stable temperatures, and carbonate saturation to promote coral growth (Spalding, 2004; Quezada-Perez, *et al*, 2023). Otherwise, many coral species are highly adapted to the environmental conditions of these reefs.

Southwestern Tropical Atlantic — particularly along the Brazilian coast – octocoral and coral species, including other reef organisms live well adapted to high turbidity, significant terrigenous sediment input, greater thermal amplitude, and salinity variability (Soares, 2020; Sánchez *et al*, 2019) typically characteristics by these reefs. This habitat is not sub optimal or marginal to them, but rather optimal and essential for their survival and ecological success. This means that the concept of "marginal" carries a reductionist bias that overlooks the adaptive complexity and resilience of local species. So, it is more appropriate to recognize these reefs as functionally distinct systems, operating within a different set of environmental constraints that have shaped unique ecological strategies and morphologies.

Conducting research on trophic ecology on Brazilian coastal reefs contributes to understanding how coral communities can survive in extreme environmental conditions, aiding global conservation efforts for reef survival. For this purpose, sampling sites were chosen along the Brazilian coast of Bahia and other points on more distant reefs in Bahia and Maragogi.

Human impacts and environmental conditions may influence these sites differently, with coral reefs closer to the coast having worse indicators of coral cover and health compared to those further from the coast (Kikuchi *et al.* 2010). A priori, it was hypothesized that these variations in environmental conditions would lead to different patterns in the trophic ecology of octocorals. Statistical analyses had significant differences in the biochemical composition of the colonies between sites, but not in all species, so it was not possible to establish a pattern due to environmental variations.

Coral Reefs APA – Maragogi, are impacted by human activities such as tourism, fishing, and capture of ornamental marine organisms (Steiner *et al.,* 2006), pollution from domestic sewage and high rates of sedimentation and turbidity (Leão *et al.,* 2010; Silva, 2022). Eutrophication caused by these factors increases the planktivores, limits the amount of light available, reducing the density of zooxanthellae, resulting in an impact on the feeding of coral, especially those most dependent on autotrophy, promoting bleaching events and diseases in corals (Anthony *et al.,* 2011; Maynard *et al.,* 2011; Ishizaka, 2010).

In general, coral reefs with an intense human presence have macroalgae predominated to the detriment of corals and other benthic organisms (Mendonça, 2004), but the spot named "Pedra da Virada", chosen in Maragogi for this research, is not a site designated for tourism, so it does not suffer as much direct impact as the others like on the Bahia Coast, for example. Furthermore, the water temperature recorded in this site is from 24°C in raining period to 30.5°C in dry season (Maida & Ferreira, 1997), with the highest rainfall volume in July (~526 mm), while the lowest is in December (~81 mm) (Torres & Machado, 2011). This means that the period of capture of octocoral samples carried out in January and October 2021, corresponds to the dry season. Samples of *M. sulphurea* didn't show a statistical difference between the month periods in all compounds, but in *P. grandiflora* carbohydrates showed statistical differences between the periods.

On the Recife de Fora Park – Bahia, annual temperature fluctuation ranged between 24.00 °C (min) and 29.00 °C (max) in 2016 (Santos *et al.,* 2014), and the average water temperature recorded on the studied period was 26.88 °C in 2020 and 28.87°C in 2021 (data provided by the Coral Vivo team). Recife de Fora is located about 9 km off Porto Seguro city (Leão & Dominguez, 2000), a with 20m maximum depth (Laborel, 1969), and during low tide, natural pools are formed with depths between 1 and 2m (Arantes, 2012), but only one is open to tourism. The spot chosen for this current research is not a place frequented by tourists, so the direct human impact is reduced in comparison to the Bahia Coast.

However, the site chosen for the sample capture was located before the largest reef, facing land. According to a previous study, higher nitrogen levels (up to 1.16 μmol L−1) were recorded at a very nearby point, in contrast to the values of points located on the other side of the reef, facing the sea (Marangoni *et al.,* 2019), which means that they are probably more influenced by pollution (Costa 2007; Smith *et al.,* 1981). Anthropogenic nutrient pollution of coral reefs in Southern Bahia, Brazil. *Brazilian Journal of Oceanography*, *55*, 265-279. This can be observed due to high δ^{15}N levels recorded for all three species, with higher values obtained in samples from the Coast.

M. sulphurea seems to be the species most influenced by environmental conditions than *P. grandiflora*, because it was the only species that had lipids and carbohydrates composition with statistical differences between Bahia Coast (2020) and Offshores reefs (RF and Maragogi) in both 2020 and 2021capture periods. Carbohydrate contents in Coast (2020) showed higher value than Coast (2021) and RF (2020), around 300 ugcarbohydrates mg AFDW, except for RF (2021) with 400 ugcarbohydrates mg AFDW. Otherwise, *P. grandiflora* did not have this same pattern, despite the difference in carbohydrates from Coast to Offshore, they present statistically equal lipid levels between all regions and periods. An inference can be made about the fact that individuals that inhabit the Bahia Coast must suffer greater human impact due to easy accessibility, in addition to facing more extreme environmental conditions, since they are in intertidal zones, often being covered and uncovered by water.

The period of the COVID-19 pandemic may have also influenced the results of the analyses in Bahia, considering that the first analysis was conducted in 2020 and the second in 2021.The first period took place as soon as the quarantine period (Covid) ended in 2020, and the other was one year later. In other words, in the first collection, even the beaches were closed to the movement of people, with practically no impact caused by tourism on the coast or on the offshore reefs and in the second collection period the place had entered a new phase with greater reopening and fewer restrictions. Considering this, we observed that the carbohydrate contents of the species *M. sulphurea* and *P. grandiflora* collected from the Coast in 2020 showed a statistical difference compared to the other groups in 2021. But we didn't have the same pattern as for the lipids.

Stable Isotope analysis

Stable isotopes signature of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) found in the three gorgonians provide evidence of the importance of heterotrophy in these octocorals, particularly based on the carbon values, originated from particulate living and dead organic matter (POM) and the absorption of dissolved organic material (DOM) (Widdig & Schlichter (2001). These results are especially compelling when compared to the $\delta^{13}C$ values found in other coral species inhabiting tropical regions.

$\delta^{13}C$ composition in corals is very related to their dietary sources, since it is known that the $\delta^{13}C$ values produced by *Symbiodiniaceae* differ significantly (Jacob *et al.,* 2005) with plankton, and is possible to distinguish whether the carbon is acquired from autotrophy or from heterotrophy based on the carbon content found in its tissues (Fry and Sherr, 1984). For instance, the $\delta^{13}C$ of fatty acid 18:4ω-3 values in zooplankton were from -22.0‰ to -25.0‰, while zooxanthellae were from -11.5‰ to -13.8‰, close to found in scleractinian *Porites astreoides* (-12.2‰ and -15.8‰) (Teece *et al.,* 2011).

In our results $\delta^{13}C$ were between -15,44‰ and -20,32‰ and $\delta^{15}N$ values ranged from 3.64‰ to 6,16‰. They are similar to those found in nine heterotrophic Caribbean octocoral with $\delta^{13}C$ content ranged between -13.8‰ and -17.7‰ and $\delta^{15}N$ between 4.2‰ and 7.5‰ (Rossi *et al.,* 2018), as similar in *G. ventalina* $\delta^{15}N$ values high as 7.7‰ (Baker *et al.,* 2010).

In Caribbean Sea, 11 gorgonians species collected in Bocas del Toro exhibited natural $\delta^{13}C$ of -17.3‰. However, when in dark and light exposure experiment, *Plexaurella fusifera* and *Plexaurella nutans,* had an increase of $\delta^{13}C$ content, going from -8.2‰ to 35.9‰ and -5.7‰ to 23.8‰, respectively. But comparing with the huge increasing of 400% $\delta^{13}C$ value in *Gorgonia ventalina* and *Pterogorgia anceps* it is undeniable the great autotrophic tendency of this two gorgonians. On the other hand, the two first *Plexaurella* species have a more heterotrophic tendency, which was congruent also with morphological aspects like larger polyps, lower ratio of surface area to volume (SA/V) and lower energy production with photosynthesis/respiration (P/R) <1.0, different from the others with smaller polyps and P/R > 1.5, that is, highly autotrophic (Baker, 2015).

Considering that *Plexaurella fusifera* and *Plexaurella nutans* belong to the same genus *Plexaurella* (Kölliker,1865) as well as the studied *Plexaurella grandiflora* with mean -16‰C like of natural $\delta^{13}C$ from them and also have a similar morphology, this may be a strong indication that they present a lower SA/V, and probably also a greater heterotrophic tendency. This hypothesis that unites morphology with energy acquisition has been reported since Cary (1918), who found highest rates of respiration in 12 Caribbean species with the highest SA:V.

Along with carbon analysis, knowing the nitrogen levels in octocoral tissue through measurements of stable N isotopes ($\delta^{15}N$) allows identifying the origin of these N sources and thus evaluating the influence of nutrients on animals (González-De Zayas *et al*, 2020). Nitrogen parameters have been examined in gorgonians (Ward-Paige *et al.,* 2005; Baker *et al.,* 2010; Risk *et al.,* 2014). Sources of nutrient could be originated from wastewater effluents, stormwater runoff, synthetic fertilizers, and atmospheric deposition due to the burning of fossil fuels (Piñon Gimate *et al.,* 2008; Ochoa-Izaguirre and Soto-Jiménez, 2013; González-De Zayas *et al.,* 2012a,b).

In high turbidity and low light conditions heterotrophy tends to increase (Anthony, 2000; Anthony and Fabricius, 2000). *P. grandiflora* and *M. sulphurea* samples from this research lives in eutrophicated ambient and $\delta^{15}N$ signatures ranged from 3 to 6‰, probably originated from the heterotrophic feeding. Typical $\delta^{15}N$ values range from -3 to 0‰ for newly fixed N, 6 to 22‰ for dissolved inorganic N (DIN) derived from untreated (6 to 9‰) and treated (10 to 22‰) sewage (Heaton, 1986; McClelland *et al.,* 1997; McClelland and Valiela, 1998; Kendall *et al.,* 2007; Sherwood *et al.,* 2010; Ochoa-Izaguirre and SotoJiménez, 2013). *Plexaura homomalla* and *Eunicea flexuosa* wich showed higher $\delta^{15}N$ (> 3‰) and lower $\delta^{13}C$ values in dirty sites from tropical islands of Florida (Atlantic Ocean), indicative of greater reliance on heterotrophy (Ward-Paige *et al.,* 2005). The same is reported to scleractinian as Seemann (2013) that found higher $\delta^{15}N$ values (> 4.0‰), indicating that the supply of nitrogen was on a higher trophic level and less from the *Simbiodiniacea*.

Tropical and subtropical oceans have a low primary productivity in general because of the low nutrient concentration in the surface (Sigman & Hain, 2012). However, in areas of upwelling and continental shelves it is the opposite due to the large amount of nutrients and light favoring photosynthesis processes. The Tropical Atlantic Ocean shows a large seasonal variability and is influenced by many different local physical and chemical forcing factors such as equatorial and coastal upwelling, large inputs of freshwater, and African dust (Carpenter *et al*, 2004; Barkley *et al*, 2019).

In addition to offering information about the trophic level of octocorals, knowledge about nitrogen can help to evaluate pollution impacts on coastal and marine ecosystems. González-De Zayas *et al.* (2020) measured the isotopic composition of N in gorgonians from Cuba and México and found lower values in less impacted ecosystems for *Pterogorgia anceps and Gorgonian flabellum*, with values from 4.34‰ to 3.90 ‰ $\delta^{15}N$ respectively. On the other hand, in higher impacted ecosystems they had an increase of 6.55‰ $\delta^{15}N$ and 7.53‰ $\delta^{15}N$ respectively. For *Plexaurella nutans* the variation was smaller between sites, ranging from 3.8‰ to 4.25‰ $\delta^{15}N$. This shows that *P. nutans* does not have as great a heterotrophic capacity as other species, because even though it has a greater quantity of nutrients available, it did not assimilate as much as other animals.

Results from other Caribbean gorgonians showed levels of nitrogen ranging from 1.8‰ to 7.5‰ from the least impacted to the most impacted environment (Ward-Paige *et al.* 2005; Ward-Paige *et al.* 2005; Baker *et al.* 2010; Risk *et al.* 2014). Reported values from $\delta^{15}N$ signals in sentinels (macroalgae, gorgonian, coral, seagrass) inhabiting oligotrophic waters (-1 to +2h) are lower than those exposed to urban wastewater pollution (6-11h, typically > 6h) (González-De Zayas *et al.,* 2020).

The nitrogen values from the studied octocoral species correspond with the environmental conditions of the reefs where they live. In the Southwestern Atlantic Ocean, variations in precipitation and high amount of rainfall or dry periods, has a relationship if el Niño (Nobre *et al.,* 1986; Gan, 1992) that influences the amount of continental freshwater runoff and the biogeochemicall process (Ciotti *et al.,* 1995). These characteristics contribute to promote moderately turbid waters with high sedimentation rates (Segal and Castro, 2011), in contrast to clear-water from oligotrophic waters, such as Indo Pacific and Caribbean areas (Hughes *et al.,* 2017; Hughes *et al.,* 2018).

In addition to dealing with turbid waters, these octocorals have to struggle to survive facing intense ocean warming in the Southwestern Atlantic, wish is increasingly intensifying during the past decades (Marcello *et al.,* 2018; Rodrigues *et al.* 2019; Gramcianinov *et al*, 2023). Bleaching in coral reefs from Brazil have been recorded (Miggotto 1997), but is becoming more frequent and intense, like the bleaching happened in 2019, when occurred a record-breaking heatwave event, with bleaching frequency 88.01% of the colonies recorded and mortality of many corals (Banha *et al.* 2019), including the studied octocoral *M. sulphurea* and *P. dilatata* and those considered highly resistant to thermal stress hard coral *Siderastrea stellata* (Duarte *et al.,* 2020; Gaspar *et al*, 2021).

CONCLUSION

Stable isotopes signature of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) found in the three gorgonians and lipids content provide evidence toward heterotrophy in these species. This is the first research with stable isotopes measurements to evaluate trophic ecology in three octocoral species in extreme environmental conditions reefs from Southwestern Atlantic Ocean. The understanding of nutritional requirements of octocoral that inhabit eutrophic regions is crucial to understand how marine life is developing. Knowledge about octocoral health and resilience are important to understand how these organisms are dealing with the constant environmental challenges that pose your life at risk.

In recent years, high temperature events are occurring with more frequency and intensity, affecting the marine community, and causing mass bleaching in Scleractinia and Octocoral. Our study provides data on the biochemical properties of gorgonian species and advances our knowledge of the fauna from Southwestern Tropical Reefs. Understanding that heterotrophy offers an alternative to the energy autotrophic input, by reducing dependence on

Symbiodiniaceae, is understanding an advantage to survive in face environmental disturbance, crucial to establish themselves on marine environment, in contrast to other exclusively autotrophic coral.

These new data on the feeding preferences of octocoral that lives under extreme environmental conditions contribute to understanding trophic interactions in coral reefs. Octocoral corals in general appear resilient to many threats such as pollution and global climate change, however the survival potential of a marine community may decrease with the greater the frequency and intensity of impacts. This study brings relevant advances on feeding of reef octocoral and highlights the importance of new research to promote knowledge about octocoral species for the maintenance of marine reef communities.

Research that focuses on octocoral that lives in extreme environments and how they are behaving in the face of global changes are needed and essential to any management strategy. Knowledge about other octocoral species from other regions of the Brazilian coast, the relationship between biological coral process such as reproduction and nutrition, are some topics lacking information and are extremely recommended for future research. We therefore recommend that there be greater dissemination of information about the importance of octocorals for local community in order to spread awareness for the conservation and preservation of these important animals.

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SUPPLEMENTARY MATERIAL

Statistical results after ANOVA for *Muriceopsis sulphurea* between groups:

1) Carbohydrates

	BCN20	BCN21	BRFN20	BRFN21	MJ21	MO21
BCN20		0,006975	0,000142	0,000313	0,000128	0,019865
BCN21	0,006975		0,512517	0,000127	0,427853	0,992727
BRFN20	0,000142	0,512517		0,000127	1,000000	0,181811
BRFN21	0,000313	0,000127	0,000127		0,000127	0,000127
MJ21	0,000128	0,427853	1,000000	0,000127		0,105966
MO21	0,019865	0,992727	0,181811	0,000127	0,105966	

2) Lipids

	BCN20	BCN21	BRFN20	BRFN21	MJ21	MO21
BCN20		0,974878	0,001495	0,000130	0,000850	0,000315
BCN21	0,974878		0,019519	0,000131	0,012255	0,004233
BRFN20	0,001495	0,019519		0,078265	0,999999	0,998722
BRFN21	0,000130	0,000131	0,078265		0,085511	0,151810
MJ21	0,000850	0,012255	0,999999	0,085511		0,999668
MO21	0,000315	0,004233	0,998722	0,151810	0,999668	

Statistical results after ANOVA for *Plexaurella grandiflora*:

1) Carbohydrates

	BCN20	BCN21	BRFN20	BRFN21	MJ21	MO21
BCN20		0,000130	0,947145	0,000130	0,000130	0,000291
BCN21	0,000130		0,000130	0,758240	0,859770	0,168584
BRFN20	0,947145	0,000130		0,000130	0,000130	0,000557
BRFN21	0,000130	0,758240	0,000130		0,262853	0,769590
MJ21	0,000130	0,859770	0,000130	0,262853		0,045006
MO21	0,000291	0,168584	0,000557	0,769590	0,045006	

2) Lipids didn't show statistical differences

CHAPTER 3 - Seasonal biochemical balance and fatty acid composition of the Caribbean octocorals *Plexaurella nutans* and *Pterogorgia anceps.*

RESUMO

Em diversas partes do mundo observa-se uma mudança na composição das espécies em recifes de corais de ambientes tropicais, principalmente em áreas rasas. Em particular, no Mar do Caribe, os octocorais estão a tornar-se cada vez mais abundantes, substituindo os escleractínios em vários locais. Estudar a ecofisiologia dos octocorais comparando-os com os corais duros é uma ferramenta valiosa para compreender essas alterações. Este artigo avalia a variação sazonal interanual da composição bioquímica (lipídios, carboidratos, proteínas e ácidos graxos) de duas gorgônias *Plexaurella nutans* e *Pterogorgia anceps* no Mar do Caribe. As maiores concentrações de lipídios, proteínas e carboidratos para *Pterogorgia anceps* foram correspondentes a 809 ug mg^{-1} AFDW, 251 ug mg^{-1} AFDW e 7 ug mg^{-1} AFDW, enquanto *Plexaurella nutans* foram 640 ug mg^{-1} AFDW, 423 ug mg^{-1} AFDW e 20 ug mg^{-1} AFDW. Foram encontrados um total de 27 ácidos graxos, com grande quantidade de marcadores de AG 16:0 e 14:0 em ambas as espécies. Os dados presentes são complementares a estudos anteriores nos quais o aporte energético dessas espécies mixotróficas é estudado, corroborando a tendência autotrófica como principal estratégia alimentar desses corais moles, sendo a heterotrófica, no entanto, um importante suprimento energético. Além disso, os padrões encontrados na composição lipídica ao longo do ano também estão de acordo com os padrões reprodutivos da espécie.

Palavras-chave: Nível trófico, Branqueamento, Aquecimento global, Gorgônias.

ABSTRACT

In several parts of the world, a community change in species composition is observed in coral reefs from tropical environments, mainly in shallow areas. In particular, in the Caribbean Sea, octocorals are becoming increasingly relevant as ecosystem engineering species, replacing scleractinians in several locations. Studying the ecophysiology of soft corals by comparing them to hard corals is a valuable tool for understanding these changes. The present chapter provides the biochemical composition (lipids, carbohydrates, proteins and fatty acids) of two gorgonians (*Plexaurella nutans* and *Pterogorgia anceps*) from the Caribbean Sea during a seasonal sampling. The highest lipid, protein and carbohydrate concentrations to *Pterogorgia anceps* were correspondent to 809 ug mg-1 AFDW, 251 ug mg-1 AFDW and 7 ug mg-1 AFDW while *Plexaurella nutans* were 640 ug mg-1 AFDW, 423 ug mg-1 AFDW and 20 ug mg-1 AFDW. A total of 27 fatty acids were found, with large amount of FA markers 16:0 and 14:0 in both species. The present data are complementary to previous studies in which the energy input of these mixotrophic species is studied, corroborating the autotrophic tendency as the main feeding strategy of these soft corals, being the heterotrophic one, however, an important energy supply. In addition, the patterns found in the lipid composition throughout the year are also in agreement with the reproductive patterns of the species.

Keywords: Trophic level, Bleaching, Global warming, Gorgonians.

INTRODUCTION

There is evidence of a huge change in several coastal and oceanic areas of the world of the dominance of the marine animal forests, based on the so called "ecosystem engineering species" (Rossi *et al* 2017a). A deep biotic composition change is present along the latitudinal gradient, and most of the problem may come not only from direct human impacts (e.g., bottom trawling), but also from the deep changes in the energy fluxes due ongoing climate change (Rossi *et al*. 2019; Campanyà-Llobet *et al* 2017). In particular, tropical shallow areas, have witnessed a profound change in species composition, being in many places substituted the reef-building corals (e.g., scleractinians) by other taxonomic groups like octocorals, porifera or macroalgae (Done 1992, Bak *et al*. 1996, Griffith 1997, Hughes *et al*. 2007). The extreme efficiency of the symbiotic performance in hard corals may be one of the keys to understand their regression, being the global warming and marine heat waves a clear controller of their presence (Enrìquez *et al*. 2015), but not the only one (Jackson 2014). Such global environmental changes have a direct impact on the capability of these ecosystems to regulate biogeochemical cycles, stock carbon or create the optimum conditions for biodiversity conservation (Paoli *et al* 2017), because of the clear difference between a scleractiniandominated habitat or the one dominated by sponges, octocorals and macroalgae (Alvarez-Filip *et al*. 2009). Understanding in such a framework the importance of the trophic ecology (e.g., seasonal changes) will be essential to envisage the seascape transformation that is already ongoing (Denis *et al*. 2024).

Coral reefs are susceptible to global and local human impacts (bleaching, acidification, diseases, pollution, sedimentation, overfishing) and all the interaction between these will impact negatively on marine animal forest health (Baker *et al.,* 2008, Hoegh-Guldberg *et al.,* 2007, Hughes *et al.,* 2003, Ateweberhan *et al.,* 2013). In the tropics, a high proportion of octocoral species in shallow coral reefs are mixotrophic (Schubert *et al*. 2017), obtaining energy through autotrophic and heterotrophic sources (Sorokin 1991; Fabricius and Klumpp 1995; Ribes *et al*. 1998; Baker *et al*. 2015). This ability to not depend solely on one type of feeding strategy has proven to be an efficient strategy for the survival of these animals in the face of environmental disturbances (Schubert *et al*. 2017, Rossi *et al.,* 2019a; Mies *et al.,* 2018; Sully & Woesik, 2020). It has been suggested that the shift from autotrophy to heterotrophy may be essential to explain the resilience of these organisms to bleaching or excess nutrient loading in the water (Baker *et al* 2015; Rossi *et al* 2020).

The trophic ecology from Caribbean gorgonian species has been studied compared with gorgonians from other regions (Ribes *et al*. 1998; Rambsy *et al*. 2014; Kupfner Johnson & Hallock, 2020; Rossi *et al*. 2018; Rossi *et al*.,2020). These studies show the importance of autotrophy, but also in some cases the presence of a non-neglectable amount of energy coming from heterotrophy. Sometimes, the punctual experimental design or sampling has to be complemented with an integrator, a way to understand during a sesonal observation what if the origin of the energy input and the importance of the energy storage coupled with the ecophysiology of the species (Rossi *et al*. 2017b). Among other things, the seasonal biochemical balance may be a cue to understand the ability of these anthozoans to close reproductive cycles, confront starvation or simply allocate energy for different outputs as suspension feeding organisms (Rossi *et al* 2017b; Rossi *et al*. 2019b). The quantity and quality of lipids, carbohydrates and proteins in animal tissue depends on their trophic strategy and this impacts the animal's reproduction, as well as other processes such as growth and health of the individuals/colonies to face environmental disturbances such as heatwaves (Szmant & Gassman 1990, Anthony & Connolly 2004, Grimsditch & Salm 2006; Kahng *et al*.,2011; Gori *et al*., 2013). Furthermore, nutritional conditions of parental colonies may also affect the survival of their offspring because they translocate lipids and other storage macromolecules to the new potential settlers (Strathmann 1985; Simpson 2009; Viladrich *et al* 2017).

The health status of the mother octocoral colony will be essential for the future larvae (Viladrich *et al* 2022), and this depends on being able to store energy along the annual cucle (Rossi *et al*. 2019b). The stress induced by different environmental conditions or the natural life cycle of the species can be reflected in its ability to store molecules such as lipids and carbohydrates (Rossi *et al*. 2017b), the authentic integrators of the water column physical and biological conditions.

Analyses of biochemical balance (protein-lipid-carbohydrate) and stable isotopes are thus useful tools to assess energy origin (Rossi *et al*. 2006; Gori *et al*, 2012; Viladrich *et al.,*

2016) and this information may help explaining octocorals prevalence in different reef areas of the Caribbean, for example (Schubert *et al.,* 2017). Fatty acids (FAs), the main components of lipids detected in corals (Imbs, 2013), are also a very good descriptor of the origin of the energy inputs, as well as the status of the species in terms of potential mobilizing lipids throughout the year (Imbs & Dang, 2021; Gurr *et al*., 2002). They are considered trophic markers because the primary producers have a specific fatty acid signature that is transferred to primary consumers, and subsequently along the food chain, allowing for the tracing of dietary sources across trophic interactions (Dalsgaard *et al*. 2003, Iverson *et al*. 2004).

Studying the seasonal trends of nutritional input represents an important approach to understanding the trophic ecology of reef species, particularly the variation of biochemical compounds, which strategies they are using to feed, helping to elucidate reproductive cycles, energy investment in respiration, and population dynamics (Ribes *et al*. 1999; Rossi *et al*. 2004; Rossi *et al*. 2006; Tsounis *et al*. 2006). Nutritional sources may vary according to the animal's environmental conditions, biological processes and season (Rossi *et al* 2017b). In mixotrophic species, such as many Caribbean gorgonians, under elevated nutrient environmental conditions, there is an enrichment of Symbiodiniaceae (Borell and Bischof, 2008) also the *Symbiodinium* type is decisive for the octocoral fitness (Mieog *et al*. 2009). Improved nutritional status and higher energy reserves in soft corals could promote a better adaptation to survive in eutrophicated nearshore sites (Seemann *et al.,* 2013). In this context, lipid reserves can help to overcome stress events such as severe bleaching and marine heatwaves , as previously discovered (Szmant & Gassmann, 1990).

Octocorals show depletion of lipids and carbohydrates (Grottoli *et al.,*2004; Rossi *et al* 2006), during periods of starvation (Harland *et al.,*1992; Szmant Froelich and Pilson, 1980) or under ambient food and/or light constraints (Ben-David-Zaslow and Benayahu, 1999; Rossi *et al.,*2006; Rossi *et al*. 2019b). They are tightly coupled with reproductive cycles, being the more favorable elapsed time through the year the one that couples with the higher accumulation of energy (Rossi *et al* 2017b; Rossi *et al*. 2019b). In fact, this pattern of lipid fluctuation offers critical information on the seasonal variability of these species, closely tied to their reproductive strategies that are in general related with the capability to capture more food (see a specific model for hydrozoans in Rossi *et al.,* 2012). Such insights enrich our understanding of the biological processes underpinning what may be the fate of the tropical coral reefs, advancing knowledge of how these organisms allocate energy across different life stages and respond to environmental pressures.

Integrating knowledge of reproductive processes with biochemical composition content, particularly lipids, provides valuable insights into the physiological dynamics of octocorals (Topçu & Öztürk, 2016). During the reproduction period, animals spent a high quantity of energy to drive this process, and consequently there is a change in lipid levels.

This is especially true for sessile benthic suspension feeders, that have to allocate a high quantity of reserves to be successful in their sexual output, relying on currents to make the difference in terms of being capable to maintain their populations (Rossi *et al.,* 2019b). Initially, lipid stores increase in preparation for reproduction, followed by a significant depletion post-reproductive phase, that could be 85–100% decreased (Ward 1995, Leuzinger *et al.,* 2003).

To better understand the role of these ecophysiological factors and their coupling with reproductive processes, two different species from shallow coral reefs of Caribbean gorgonians were chosen for the present study: *Plexaurella nutans* and *Pterogorgia anceps* (Fig.1). Despite both are mixotrophic, they have different Symbiodinium's associations (Goulet & Coffroth, 2004). While *P. nutans* is considered commensalist, *P. anceps* is more mutualistic with symbionts transferring higher portions of photosynthetic Carbon to the host (Baker *et al*. 2015). This difference may influence reproduction cycle and the ability to deal with environmental disturbances, since *P. anceps* had already shown decrease in colony size, as observed in Florida Keys since 1990's (Thanopoulou, 2022).

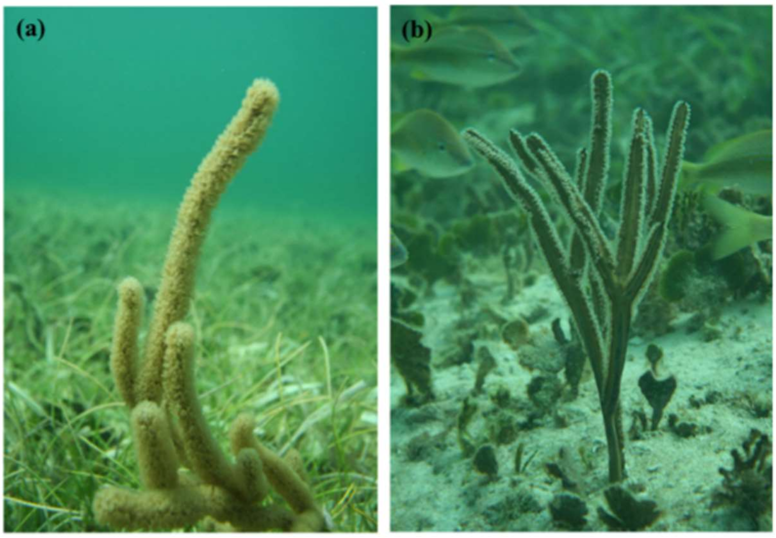


Figure 1: Pictures of octocorals (a) *Plexaurella nutans* and (b) *Pterogorgia anceps* in the Mexican Caribbean reef lagoon of Puerto Morelos. Sources taken from Rossi *et al.*2020.

To understand how these Caribbean gorgonians behave during an annual cycle in terms of trophic ecology, Rossi *et al* (2020). in a previous study, discovered that autotrophy plays the primary means of obtaining energy in both species, but with different patterns according to the season, probably related to the reproduction periods. For this purpose, they investigated zooplankton capture rate by gut content examination, photobiological performance through the year, signatures of stable isotopes $\delta^{13}C$ and $\delta^{15}N$ and Symbiodiniaceae influence (cell densities, pigment contents, and host respiratory demand).

Despite knowledge of reproduction aspects of Caribbean gorgonians *Plexaurella nutans* and *Pterogorgia anceps* are based on single observations, the available data is enough to understand their reproductive cycles. *Pterogorgia anceps* reproduce by surface brooding embryos sparse in the branch surface during autumn (October) (Ritson-Williams 2010), whilst *Plexaurella nutans* reproduces by broadcast spawning in summer (July) (Kahng *et al.* 2011). Up to now, except a single paper made on a single moment of the year (Shirur *et al.,* 2014), there is no data available about the seasonal biochemical variation of these Caribbean gorgonians in this period as we proposed here.

Investigating how the biochemical content (lipids, protein, carbohydrates and fatty acids) is distributed over the course of a year (interannual variation) and the relationship with reproduction, contribute to increasing knowledge about the potential role of gorgonians as dominant organisms in Caribbean coral reefs. In this way, the present study presents novel information from the reported study by Rossi *et al* (2020), presenting the biochemical composition (lipids, carbohydrates, proteins and fatty acids) of *Plexaurella nutans* and *Pterogorgia anceps* during an annual cycle.

MATERIAL AND METHODS

Sampling site and collection

Samples from two octocoral species, *Pterogorgia anceps* (Pallas 1766) and *Plexaurella nutans* (Duchaissaing and Michelotti 1860) were collected monthly in annual cycle, since April 2014 to April 2015, in the same area at ~ 2 m depth in the Puerto Morelos reef lagoon, Mexican Caribbean (20° 50’ 57.8659” N, 86° 52’ 34.6967” W).

The lagoon experiences seasonal variations in temperature (mean temperature range 25–30°C) and light (max. daily intensity range 200–1800 µmol quantam^{-2}s^{-1}), data that were obtained from the Oceanographic and Meteorological Academic Service (SAMMO) of the UNAM Coral Reef Systems Academic Unit in Puerto Morelos. The monthly variation in light level at collection depth was calculated, using the reported light attenuation coefficient for the lagoon (Kd = 0.2 m-1; Enrıquez and Pantoja-Reyes 2005), showing light levels of 67% of incident light at 2 m depth and a variation in mean seasonal maximum light intensity between 620 and 880μmol quanta m^{-2} s^{-1}.

Branches of ten different colonies (5–8 cm height; n = 1 per colony) of each of the two species were monthly collected, kept in cool conditions in a plastic bag (with ice, temperature 6-8°C) and afterward taken immediately to the laboratory, where they were divided into two subsamples. The apical part was frozen at – 80°C for subsequent analyses of organic matter content and biochemical composition.

Organic matter

The organic matter (OM) content was described by Rossi *et al* (2020). The analyses consist by subsampling 300–500 mg of the coenenchyma of the freeze-dried tissue (n = 10 per species and month). Samples were combusted in a muffle furnace (Relp 2H-M9) at 500 C for 4 h, and the remaining inorganic ash was weighed. The OM content (ash-free dry weight, AFDW) was calculated from the difference between dry weight (DW) and ash weight (AW) (Slattery and McClintock 1995; Rossi *et al*. 2006 for gorgonian treatment).

Biochemical analysis: seasonal variation of carbohydrates, proteins, lipids, and fatty acids

Biochemical analyses (carbohydrates, proteins and lipids) were processed using a spectrophotometer consisting of colorimetric quantifications (Servetto *et al*, 2017, Rossi *et al*, 2006). Results are presented in μg carbohydrate-protein-lipid mg $AFDW^{-1}$ of ± standard deviation (SD), using monthly samples. The axis was separated from all the samples before measurement.

The freeze-dried tissue (10 – 15mg) frozen at – 80°C were processed for proteins, one analysis per colony, during the 12 months inboth species. The tissue peeled from the axis was weighed using a microbalance (precision: 0.01 mg), homogenized in 6ml 1N NaOH. and quantified following the method of Lowry *et al*. (1951), using albumin as standard.

Carbohydrates (~10mg) were quantified using the phenol-sulfuric acid method, homogenizing tissue in 3 mL of distilled water and quantified using glucose as standard by the method Dubois *et al*. (1956).

For lipids, 10 mg pieces of freeze-dried tissue were homogenized in 3 mL of chloroform-methanol (2:1). and total lipids were quantified colorimetrically, using cholesterol as a standard (Barnes & Blackstock,1973). All data were normalized to ash-free dry weight (AFDW) for both species. These protocols have been widely used with corals and have proven good results (Elias-Piera *et al.,*2013; Gori *et al.,*2013, 2007; Rossi *et al.,*2006a).

FAs determination was made using 3 samples of 3 colonies of each species from approximately 10 - 12 mg (±0.1 mg) of each dry weight sample. Samples were collected in April 2015.FA were identified and quantified with gas chromatography (GC) (Agilent Technologies 7820 A GC). Analysis was performed in splitless injection mode using a Thermo Trace GC instrument fitted with a flame ionization detector, and a DB-5 Agilent column (30 m length, 0.25mm internal diameter and 0.25µm phase thickness). Helium was used as a carrier gas at a constant flux of 33 cm s^{-1}. For the FAs fraction, the oven temperature was programmed to increase from 50°C to 320°C at 10°C min^{-1}, and held at 320°C for 17 min. Injector and detector temperatures were kept constant through the analysis at 300°C and 320°C, respectively. Methyl esters of fatty acids (FAME) were identified by comparing their retention times to those of anexternal standard (37 FAME compounds, Supelco® Mix C^4-C^{24}). The reproducibility of the procedure was evaluated by injecting blanks and internal standards at different concentrations. A blank sample was analyzed in every batch of 14 samples to monitor background levels of FAME during the analysis. Fatty acids were quantified by integrating areas under the peaks in the gas chromatograph traces (Chromquest 4.1 software) with calibrations derived from internal standards (Gori *et al.,* 2012; Viladrich *et al.,* 2016).

RESULTS

Biochemical analyses

Caribbean gorgonians exhibited higher values of lipids in contrast to protein and carbohydrates (Fig.2). In *Pterogorgia anceps*, lipids ranged from 190 to 809 µg lipid/mgAFDW, proteins ranged from 94 to 251 ug protein/mgAFDW and carbohydrates ranged from 3 to 7 µg carbohydrate/mgAFDW. In *Plexaurella nutans* lipids ranged from 211 to 640 µg lipid/mgAFDW, proteins ranged from 207 to 423 ug protein/mgAFDW and carbohydrates ranged from 12 to 20 µg carbohydrate/mgAFDW.

The highest lipid concentrations were observed in August 2014 for both species *P. anceps* (809 ug mg^{-1} AFDW ± 275) and *P. nutans* (640 ug mg^{-1} AFDW ± 233). And lowest concentrations were July 2014 for *P. nutans* (211 ug mg^{-1} AFDW ± 63) and April 2014 to *P. anceps* (190 ug mg^{-1} AFDW ±80).

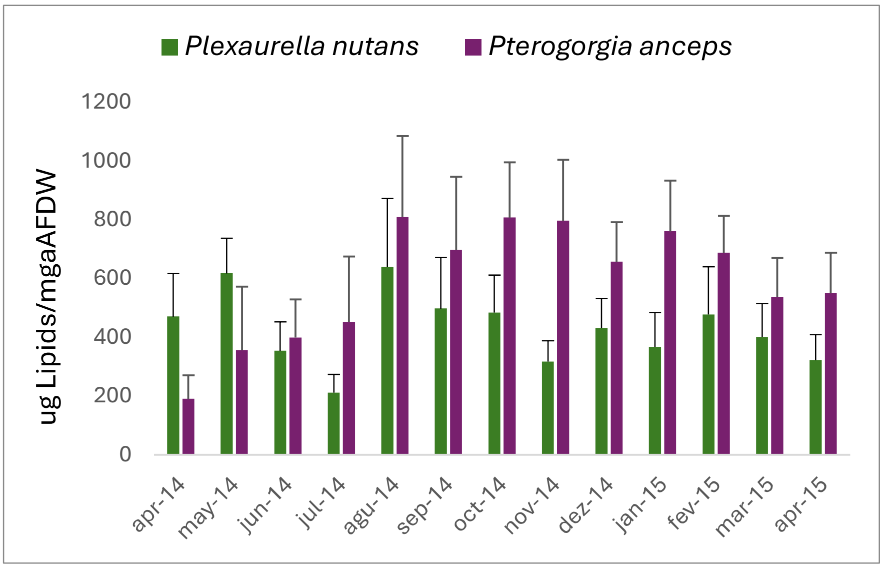
The highest protein concentration was observed in May 2014 in *P. nutans* (423 ug mg^{-1} AFDW ± 60) and in April 2015 for *P. anceps* (251 ug mg^{-1} AFDW ±95), while the lowest protein concentration to *P. nutans* was in April 2014 (207 ug mg^{-1} AFDW ± 64) and the lowest value in *P. anceps* was in July 2014 (94 ug mg^{-1} AFDW ±30). Finally, the highest carbohydrate values in May 2014 (7 ug mg^{-1} AFDW±2,6) in *P. anceps,* contrasts with February 2015 (20 ug mg^{-1} AFDW± 6,8) in *P. nutans.* The lowest carbohydrate concentrations were observed in July 2014 (3 ug mg^{-1} AFDW±1) in *P. anceps* compared to those of in April 2014 (12 ug mg^{-1} AFDW±3) in *P. nutans.*

Fatty acid composition

The range of FA from apr-2014 to apr-2015 varied from 11 to 35 ug mg^{-1} AFDW in *P. nutans* and from 11 to 42 ug mg^{-1} AFDW in *P. anceps.* The higher presence of FA in *P. nutans* was in aug-2014 and in *P. anceps* was in nov-2014. The lowest FA composition in *P. nutans* as in dez-2014 and in *P. anceps* was in apr-2014 (Fig.3)

We detected up to 27 fatty acids in *P. nutans* and in *P. anceps*. Among these, the main FA in both *P. nutans* and in *P. anceps* were: C12:0; C14:0; C16:1(n-9); C15:0; C17:0; C18:3(n-6); C18:2(n-6); C18:1(n-9); C18:0; C20:5(n-3); C20:4(n-6); C20:3(n-6); C22:6(n-3); C22:1(n-11); C22:2 (n-6). (Table1).

The higher presence of FA compositions in *P. nutans* was for C16:0 (0,72 ug mg^{-1} AFDW ±0,10), but others FA were characterized by a high (>0,1 ug mg^{-1} AFDW) presence of C:14:0; C20:5(n-3) and C18:0. The higher amount for *P. anceps* was C16:0 (0,21 ug mg^{-1} AFDW ±0,18), but others FA had a high presence (>0,1 ug mg^{-1} AFDW): C17:1; C18:1(n-9); and C18:0.


🟩 Plexaurella nutans
🟪 Pterogorgia anceps
ug Lipids/mgaAFDW
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400
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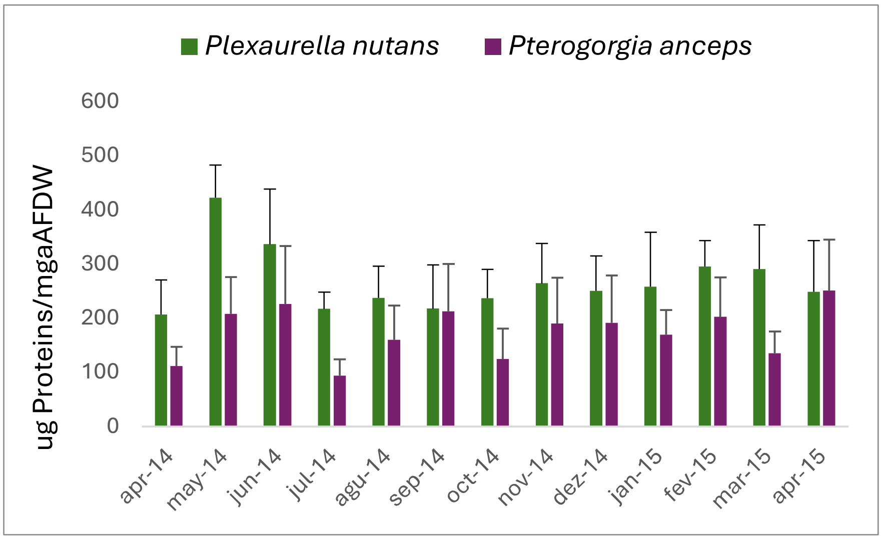
🟩 Plexaurella nutans
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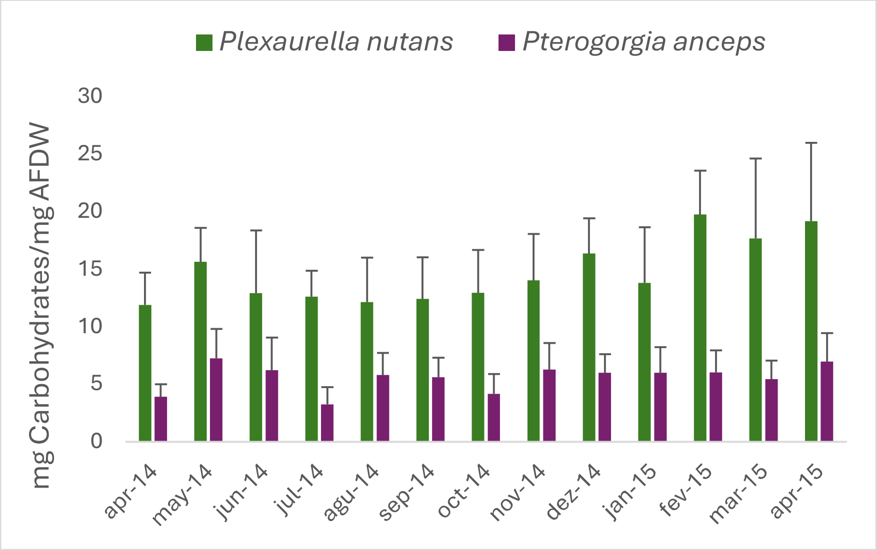
🟩 Plexaurella nutans
🟪 Pterogorgia anceps
mg Carbohydrates/mg AFDW
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may-14
jun-14
jul-14
agu-14
sep-14
oct-14
nov-14
dez-14
jan-15
fev-15
mar-15
apr-15

Figure 2. Biochemical parameters in branches of Caribbean gorgonians *Plexareulla nutans and Pterogogia anceps.* Average contents (±SD) of lipid, protein and carbohydrates per ash-free dry weight (% AFDW) in sample from colonies during annual cycle since April 2014 than April 2015.

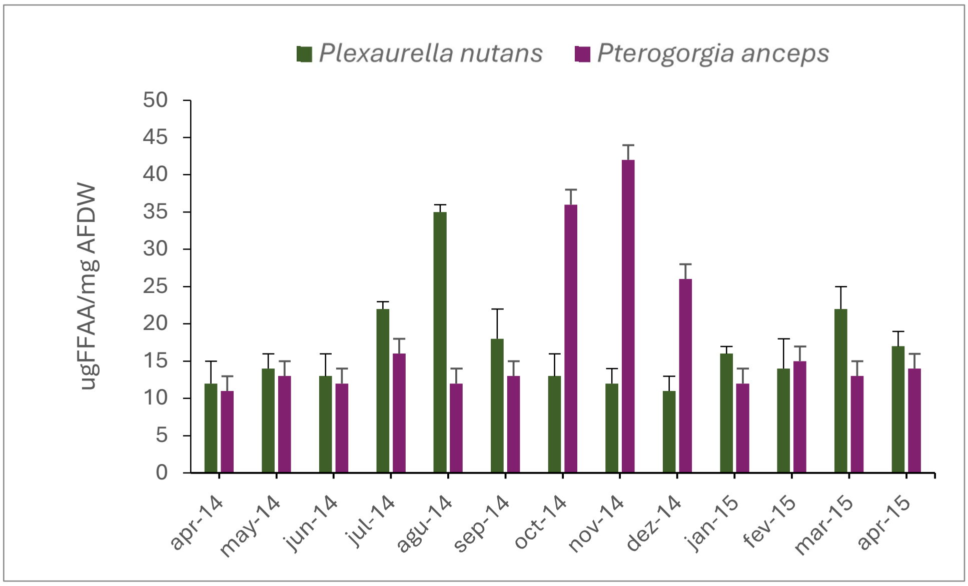

Figure 3: Fatty acid (FA) content (ug/mgAFDW) (mean ± SD) in tissue of *Pterogorgia anceps* and *Plexaurella nutans* colonies (n = 3) since april 2014 to april 2015.

Table 1: Composition of the different fatty acids (FA) detected in both samples from *P. nutans* (n=3) and *P. anceps* (n=3) in April 2015 (ug/mgAFDW). Mean and standard deviation (SD).

P. nutans			***P. anceps***		
FA	MEAN	SD	FA	MEAN	SD
C12:0	0,0025	0,00043	C12:0	0,0014	0,00061
C14:0	0,1235	0,02752	C14:0	0,0220	0,00241
C16:0	0,7198	0,10681	C16:0	0,2163	0,18241
C16:1(n-9)	0,0281	0,00942	C16:1(n-9)	0,0064	0,00188
C15:0	0,0062	0,00131	C15:0	0,0052	0,00001
C17:0	0,0152	0,00234	C17:0	0,0195	0,00066
C18:3(n-6)	0,0240	0,01034	C18:3(n-6)	0,0243	0,01337
C18:2(n-6)	0,0359	0,00245	C18:2(n-6)	0,0149	0,01149
C18:1(n-9)	0,0584	0,02008	C18:1(n-9)	0,1419	0,04668
C18:0	0,2423	0,03835	C18:0	0,1103	0,01540

C20:5(n-3)	0,1352	0,04274	C20:5(n-3)	0,0982	0,05089
C20:4(n-6)	0,0113	0,00442	C20:4(n-6)	0,0313	0,03799
C20:3(n-6)	0,0054	0,00147	C20:3(n-6)	0,0103	0
C22:6(n-3)	0,0204	0,00938	C22:6(n-3)	0,0113	0,00902
C22:1(n-11)	0,0085	0,00574	C22:1(n-11)	0,0073	0,00265
C22:2 (n-6)	0,0012	0	C22:2 (n-6)	0,0077	0,00786

DISCUSSION

This study analyzed variations in biochemical composition and FA content in two Caribbeans gorgonian species during a year. The highest lipid, protein and carbohydrate concentrations in *Pterogorgia anceps* were correspondent to 809 ug mg^{-1} AFDW ± 275 in aug-2014; 251 ug mg-1 AFDW±95 and 7 ug mg-1 AFDW±2,6; while the lowest lipid, protein and carbohydrates were 190 ug mg^{-1} AFDW±80 in apr-2014; 94 ug mg^{-1} AFDW ±30 and 3 ug mg^{-1} AFDW±1.

P. nutans higher values were 640 ug mg^{-1} AFDW ± 233(lipid) in aug-2014, 423 ug mg^{-1} AFDW ± 60 (protein) and 20 ug mg^{-1} AFDW± 6,8 (carbohydrate). The lowest values were 211 ug mg^{-1} AFDW ± 63(lipid) in jul-2014; 207 ug mg^{-1} AFDW ± 64 (protein) and 12 ug mg^{-1} AFDW±3(carbohydrate). A total of 27 fatty acids were found, with large amount of FFA markers 16:0 and 14:0 in both species. FA composition in *P. nutans* varied from 11 to 35 ug mg^{-1} AFDW and in *P. anceps* from 11 to 42 ug mg^{-1} AFDW. The results confirm the autotrophic tendency and reproductive patterns of these soft corals.

Biochemical composition linked to autotrophic tendency and reproduction

The Puerto Morelos reef lagoon had been reported to have higher abundances in zooplankton density during summer/autumn (Alvarez-Cadena *et al*. 2009), which was proven through the main occurrence of crustaceans found by gut content analysis in both species *Plexaurella nutans* and especially in *Pterogorgia anceps,* as reported in the previous study by

Rossi *et al* (2020). The abundance of zooplankton is a key factor for gorgonian energetic balance, as its presence is definitively an important food source, especially when present in food pulses (i.e. high amount of available nutrients for the octocorals in a short, elapsed time, Rossi and Rizzo 2021). This may explain the high lipids content found during summer in both species analyzed in this study, that is, in the same period that higher densities of zooplankton were previously found.

On the other hand, in warm seasonal seas such as the Mediterranean, the trend is having a high amount of food available in late winter and spring, being the summer and autumn a moment in which the energy inputs diminish drastically, leading octocorals in a dormancy state, with the lowest rate investment in growth and reproduction of the year (Coma & Ribes 2003). The anthozoans thus take the more frequent pulses of seston presence in winter-spring in the Mediterranean to store energy (Rossi *et al*. 2006) in form of lipids because of the phyto- and zooplankton blooms.

The environmental conditions of each region are intrinsically connected with the development of coral species and influence their ability to store energy and reproduce. Lipid levels in the tissues of coral vary depending on the contribution of energy from the Symbiodiniaceae and energy consumption during coral breathing, cell replenishment, and release of reproductive material (Ward, 1995). In our results it was possible to observe the variation in lipid composition in both species, *P. anceps* exhibid higher lipid values than *P. nutans,* and this may suggest advantages in terms of energy storage, trophic strategies or physiologic aspects, such as reproduction.

There is a direct transfer of lipids from the parental colonies to the sexual products (Dalsgaard *et al*. 2003; Richmond 1987) observed through the decrease in lipid content after gamete release in Caribbean mesophotic corals (Hosteil *et al.,* 2016). Breeding depends on environmental conditions and is species-specific, with some species reproducing throughout the year, such as *Gorgonia ventalina* (Fitzsimmons-Sosa *et al*. 2004), while others during specific periods (Lasker *et al*. 1996a).

In our results, lipids composition in *P. nutans* showed highest values in May and August of 2014, followed by a drop in composition. In July 2014 was the month with the lowest amount of lipid found, with August showing the highest followed by slight decline until November with a more balanced variation. This information suggests that may have been at least two spawning during the year investigated. *Plexaurella nutans* from Panama have a breeding period reported in July (Kahng *et al*. 2011), a period similar to *Plexaura homomalla* and *Plexaura kuna* in May

– August (Kinzie 1970; Goldberg & Hamilton 1974; Fitzsimmon-Sosa *et al*. 2004; Bastidas *et al*. 2005; Lasker & Kim 1996). This is a great match with the higher values of the lipids from *P. nutans* found in our results.

Pterogorgia anceps have been found brooding in its surface during autumn (October) (Ritson-Williams, 2010). This is, to the best of our knowledge, the only observation made in this Caribbean species. In April 2014, the beginning of the period analyzed in the research, it was recorded the lowest lipid value for *P. anceps*. After this month, lipid value increased until the maximum in August 2014 followed by a small decrease and maintaining low variability in the following months. In fact, August, October and November presented the highest lipids composition, could be related to reproduction time, like was recorded by Ritson-Williams, 2010. However, only temporal reproductive monitoring studies can offer more conclusive statements.

The relationship between nutrition and reproduction in other coral species has also been recorded. Caribbean gorgonians *Junceella juncea* and *Junceella fragilis* were found to have decrease in total lipid content with oocyte developmental stages (Lin *et al*, 2012). In the Scleractinia *Goniastrea aspera* from Okinawa Island showed minimum lipid content (%dry weight) in December–January (21–25%) and maximal in June–September (35– 42%), and this higher value is probably related to oocyte maturation, although no significant changes were observed after the summer spawning (Oku *et al.,*2003). In Mediterranean gorgonians this observation has been also made in different species, being the "mother care" related with the quantity of lipids that can be stored and translocated to the future generations (Viladrich *et al*. 2022). In general, we can couple our results (higher lipid contents, especially fatty acids) with the reproductive cycle.

Gorgonians studied here thus far are either broadcast spawners or brooders with varying synchronized gametogenic cycles (Fitzsimmons-Sosa *et al*. 2004; Kahng *et al*. 2011) and seems to have a higher proportion of FA in maturing oocytes than Scleractinians (Lin *et al*, 2012; Lin *et al.,* 2013). The higher presence of FA found in *P. nutans* was in aug-2014, the same month that we found higher lipid content. *P. anceps* follow the same pattern, with higher amount of FA in aug-oct and nov-2014, when lipids were higher too. This synchrony seems to be a good indicator of the period before spawning.

Again, the coupling with reproduction is an essential cue to understand the capability of the species to be successful in its new recruitment strategy (Rossi *et al* 2019b). There is a fine tuning between the available energy input (in terms of autotrophy and/or heterotrophy) and the successful larvae, that needs substantial energy to drift, colonize the substrate and grow competing with the other sessile organisms. The fact that lecithotrophic larvae contain energy reserves that allow them to settle, metamorphose and also grow the first polyps without the need to feed (Benayahu & Loya 1984; Viladrich *et al.* 2017), suggests that post-larvae might already have developed efficient feeding anatomical structures when food availability increases. Therefore, size and nutritional condition (i.e. energy stored) of lecithotrophic larvae might be a key factor to understand larval survival and thus recruitment, as well as new settlers' mortality (Isomura & Nishihira, 2001; Viladrich *et al.* 2017; Rossi *et al.* 2019b).

However, besides that, spawning period is not the only responsible for lipids values. In hard coral *Pocillopora damicornis* the decrease in lipids was more influenced by environmental changes (Ward, 1995). Marine heat waves events, bleaching could reduce lipids content in both octocorals and hard coral (Yamashiro, 2005; Rossi *et al* 2006; Lange *et al.,*2023). The non-symbiotic species *Paramuricea clavata* had a 30% decrease in lipid reserves after heat stress (Rossi *et al* 2006; Lange *et al.,*2023) and it has been suggested that *Corallium rubrum* may respond to heat waves with oartial mortalities that reflect a drop in lipid contents (Rossi and Tsounis 2007). The symbiotic gorgonian *Eunicella singularis* had reduction in lipid content when exposed to increased temperature from 18 to 26°C (Ezzat et.al, 2013), having a clear distinction of these lipid concentration when has symbiotic cells in its tissue (mixotrophic strategy) or not (heterotrophic strategy) due to the location of their colonies along a depth gradient (Gori *et al* 2012). Soft coral *Sinularia capitalis* lost up to 95% of their Symbiodiniacea and the total lipid content dropped by 3,2 times after increased of temperature (Imbs & Yakovleva, 2012).

In our results, the variation observed in total lipid content may also have been influenced by environmental conditions. Puerto Morelos reef, the sample collection site, is one of the most biodiverse regions of the Caribbean (Miloslavich *et al.* 2010) and is a popular tourist destination, experiencing a rapid urbanization process and consequently suffering many impacts over the years such as sewage, land-use change, fisheries and port activities (Sánchez-Quinto, *et al.*, 2020; Velázquez-Ochoa & Enríquez, 2023). Additionally, this coral reefs experiences extreme weather events such as heat waves, tropical storms and hurricanes (Silva *et al*, 2002; Caballero-Aragón, eta al., 2020). All this may reflect in nutrient content on the marine community, affecting the structure and functioning of the biological communities, leading to biodiversity mortality (Hautier *et al*., 2009).

When in stressful conditions the balance between the energy that is produced and what is consumed is broken (Grottoli *et al.,* 2004), and there could be a decrease in lipid content because the organism needs to use the source of energy to combat the consequences of the stress (Seemann *et al.,* 2013). Monitoring total lipid content in corals is crucial to understanding how animals develop, since this biochemical compound is a good indicator of coral stress and coral mortality can be induced by a high reduction of lipids (Anthony *et al.,* 2009).

In addition to analyzing lipid values, protein and carbohydrates levels also provided informative results in this study. While the highest values for lipids in *P. anceps* were in August, October, and November 2014, the highest protein levels did not follow this pattern. Higher proteins content was in June and September 2014 and April 2015, and carbohydrates showed higher values in May and November 2014 and April 2015. The lowest values found were during spring/summer, with the lowest protein value between April and July 2014, carbohydrates in July and April 2014 and lipids in July and April 2014. This period corresponds to the dry season, that is, characterized by lower precipitation, which may have an influence on the availability of food for the gorgonians studied.

Carbohydrates values were correspondent to the minor constituent in gorgonian branches, as seen in other Caribbean gorgonians between 1 and 7%gOM (Shirur *et al*., 2014). In our results, carbohydrate values correspondent to 0,3 to 0,7%gOM in *P. anceps* and 1,2 to 1,9%gOM in *P. nutans.* These levels for *P. nutans* are within the results found in the literature for other gorgonians, but carbohydrates in *P. anceps* were lowest than 1,81%gOM recorded before (Shirur *et al*., 2014). Not all species follow same patterns, heterotrophic octocoral from mediterranean *Paramuricea clavata* showed higher values ranged from 56 to 68 ug carbohydrate/mgAFDW (Rossi *et al*., 2006), which corresponds to 5.6 to 6.8%. Carbohydrates are much more mobile in metabolic terms than lipids. They easily enter in the Krebs cycle and are rapidly used for respiration. Over the three-year study period, carbohydrate and lipid levels exhibited two distinct seasonal trends in the octocoral *Paramuricea clavata* (Rossi *et al*. 2006).

These biomolecules showed consistent accumulation during the winter–spring months, likely reflecting periods of increased energy storage. Conversely, during the summer–autumn months, their levels underwent significant depletion, corresponding to heightened energy demands associated with increased metabolic activity, reproduction, or other ecological factors. No clear seasonal trend was found in the two studied Caribbean species, so we suggest the carbohydrates produced are rapidly used for different purposes as respiration. Very low concentrations of carbohydrates are closely related with potential stress (Rossi *et al*. 2006b), in which stress proteins negatively correlates with the presence of these macromolecules.

Proteins levels results corresponded to 20 to 42%gOM in *P. nutans* and 9,3 to 25%gOM in *P. anceps*. The protein composition found in *P. nutans* exhibited values much higher than those found in other gorgonians from Caribbean Sea, from 2 – 12,85%, but *P. anceps* corroborated to 12,85%gOM recorded before (Shirur *et al*., 2014). The maximum values of protein-lipid-carbohydrates could coincide with higher disponible to food concentration/quality (Rossi *et al*., 2006), and the lowest values with starvation period (Willmer *et al*., 2000). In laboratory studies investigating feeding constraints, Fitt and Pardy (1981) demonstrated that protein catabolism in anemones subjected to starvation was negligible. This finding highlights the organism's ability to conserve structural and functional proteins during periods of food scarcity, likely relying on alternative energy reserves such as lipids and carbohydrates to meet metabolic demands. This adaptive strategy underscores the resilience of anemones in fluctuating environmental conditions. The present study also focused on investigating FA concentration and composition in one single moment, July 2015, to identify energy mobilization and food sources in a specific period. It was not possible to make a full seasonal approach of the markers, only of the total amount of FFAA. The FFAA analysis is long and expensive in comparison with the colorimetry, so we decided to make a specific approach of the different FAA only in April 2025. However, the present results, also with a statistical approach, may give some cues about the potential mobilization of FFAA during the year (total amount, Figure 3), and the possible origin (Table 1). These biomarkers contribute to indicating the trophic level of the coral, as well as being useful to differentiate soft corals from reef building corals by the presence of tetracosa polyenoic FA (TPA) 24:5n6 and 24:6n3 (Vysotskii *et al.,*1990; Imbs *et al.,* 2010).

Value of fatty acid biomarkers could indicate organic matter (OM) origin and help contributed for environmental health (Bianchi and Canuel, 2011; Prahl *et al.,* 1997; Shi *et al.,* 2001; Weijers *et al.,* 2009). Presence of C22:0 e C24:0, can indicate organic material derived from coastal runoff or sediment. PUFA (polyunsaturated fatty acid) is present in coral lipids and can be originated from external food sources, such as plankton or Symbiodiniacea also (Meyers 1979; Papina *et al.* 2005, Treignier *et al.* 2008). However, species without Symbiodiniacea have a higher proportion of unsaturated fatty acids compared with species with the presence of Symbiodiniacea (Patton *et al.* 1983, Latyshev *et al.* 1991, Yamashiro *et al.* 1999), suggesting that the majority of PUFA is originate from external food sources.

The higher presence of cis- and trans-isomers of 7- methyl -6-hexadecenoic acid in the FA of Caribbean soft corals (Carballeira *et al*. 2002) and in corals from Vietnam (Imbs, 2010) could be related with the absence of Symbiodiniaceae and it is believed this compound is most probable originated by a specific group of bacteria (Imbs *et al.,* 2007, 2009). In octocorals were recorded FA 24:5n-6 and 24:6n-3 and 7,10,13,16-onadecatetraenoic acid (19:4n-3), recognized as a peculiar identified in Caribbean gorgonian corals *Eunicea fusca and E. laciniata* (Carballeira *et al.,* 1997).

In our results, it was possible to observe that there was a strong predominance of fatty alcohol 16:0 in both species that represent a marker of Symbiodiniaceae (Figueiredo *et al.,* 2012) suggesting greater dependence on autotrophy sources. However, there was also a high presence of 14:0 and 18:1(n-9), which means a great contribution to copepods and other crustaceans (14:0) and other marine animals. This result corroborates previously obtained data on stable isotopes that showed the greater autotrophic tendency of these species, but also with heterotrophic contribution (Rossi *et al*, 2020).

CONCLUSION

The present results provided information that contributes to understanding biological process in two gorgonians from the Caribbean Sea through its ecophysiology. The composition of lipid, carbohydrate, proteins and fatty acid markers were successfully recorded during a seasonal period and provided important information about the autotrophic tendency and reproduction of these species.

The patterns found in lipid composition throughout the year provided support to suggest that *P. nutans* reproduction occurs between May and August, a behavior recorded before in the literature. In the same way as high lipid values in autumn recorded by *P. anceps* are consistent with the same breeding season recorded previously. The results found for FA biomarkers corroborated what was recorded by the literature. The largest amount of FA markers 16:0 and then 14:0 found in both species demonstrated that autotrophy was the main energy source for them with an input contribution from heterotrophic sources, supporting the results recorded by Rossi *et al* (2020). Lipid and FA content in *P. nutans* showed the same pattern, with high values during summer/autumn. Proteins didn't show the same pattern, with high values in spring for

P. nutans and P. anceps. Among the three compounds, carbohydrates exhibited the smallest composition, as seen in other Caribbean gorgonians, but with very reduced values for *P. anceps.*

It is clear that these biomarkers are useful to shade light to the seasonal patterns of ecophysiological activity in these two specie. Knowledge of the nutritional pattern of octocorals and monitoring the composition of lipids, proteins, carbohydrates and fatty acids can provide information about the balance of these nutrients in the animal, which can infer about their ability to survive and reproductive possibilities (Rossi et al. 2017b).

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CONCLUSIONS AND FINAL CONSIDERATIONS

Trophic ecology studies have provided important contributions to improving knowledge about the feeding and survival capabilities of octocorals (Baker *et al*., 2010; Imbs & Yakovleva, 2012; Pupier *et al*., 2021). Studying the energy inputs (feeding capabilities and stored energy) and outputs (reproduction, growth, respiration, etc.) makes it possible to better understand the real constraints that these organisms may face or the opportunities they may find in the near future, as other suspension feeders (Rossi *et al*. 2019a). From the nutrient-scarce oligotrophic coral reefs to the highly productive yet seasonally dynamic Antarctic ecosystems, octocorals—recognized as the primary eco-engineers of the animal forest—have developed an array of adaptive feeding strategies (Gili and Coma 1998).

These strategies are finely tuned to the unique environmental constraints of their habitats, enabling them to thrive despite challenges such as fluctuating resource availability or extreme conditions. This evolutionary flexibility not only underpins their survival but also contributes significantly to the remarkable biodiversity observed within these ecosystems (Rossi *et al*. 2017a). By shaping the structure and function of their surroundings, suspension feeders play an essential role in maintaining ecological balance and fostering the resilience of these diverse underwater landscapes (Coma *et al*. 2000).

In coral reefs community, if the cnidarian dietary needs are not met, the energy supply to maintain their biological processes becomes inefficient, so health and, consequently, the life of these animals may be compromised (Fabricius and De'ath 2008). It is in this context that the ability of octocorals to have two feeding modes is crucial to allowing them to remain in the environment even under stressful conditions, especially because they may not rely on autotrophy as much as scleractinians do (Rossi *et al*. 2020).

These living structures serve as vital hubs for nutrient exchange, actively capturing and retaining essential elements such as carbon, nitrogen, and other key nutrients. Through complex biological processes, these elements are integrated into their living tissues and contribute to the development of their intricate three-dimensional morphology (Rossi *et al* 2017b). This dual function not only sustains the organisms themselves but also enhances the overall productivity and nutrient cycling within their ecosystems, reinforcing their critical role in supporting biodiversity and ecosystem stability (Gili and Coma 1998). The ability to utilize both heterotrophic and autotrophic food sources by octocoral, switching from one to the other in a flexible way (Baker *et al*. 2015), provides a significant adaptive advantage to the organisms, allowing them to persist on coral reefs despite the environmental disturbances they face (Ruzika *et al.* 2013), in contrast with most scleractinians that lack this trait and ultimately fail to withstand such challenges.

Scleractinians used to rely in the autotrophic energy input much more than the soft corals, being extremely efficient in light harvesting (Enríquez *et al* 2005). Gorgonians from many tropical oligotrophic shallow-water have been observed feeding on particulate organic matter, zooplankton, and microplankton from the water column, becoming more independent of autotrophic *Symbiodinacea* source, but the feeding tendency of gorgonians from extreme environmental reefs is still unknown. In mesotrophic-eutrophic waters, they may withstand with much more flexibility, shifting in its mixotrophic strategy toward omnivore (Rossi *et al.* 2018; Gonzàlez de Zayas *et al* 2020).

Analysis of the biochemical balance, mainly of lipids, makes it possible to discover the trophic tendency of these organisms (Imbs *et al.*, 2010; Pupier *et al.*, 2021). The biochemical balance of octocorals, as in other species, provides a powerful framework for understanding the impact of feeding input periods on their nutritional condition (Rossi *et al.* 2006). This approach encapsulates a range of trophic processes occurring over short to medium-sized time frames, offering valuable insights into how organisms adapt to changes in resource availability. Proteins play a fundamental role, primarily contributing to structural integrity, enzymatic activity, transport mechanisms, and cellular regulation (Lesser, 2013). Carbohydrates, on the other hand, act as the primary and immediate source of energy, being rapidly catabolized to meet basic metabolic demands (Fitt and Pardy, 1981; Davies, 1991; Kochman *et al.*, 2021). In contrast, lipids serve as the main reservoirs of long-term energy, significantly influencing key biological processes such as survival, reproduction, and growth (Ward, 1995; Pupier *et al.*, 2024).

Consequently, an organism's biochemical balance not only reflects its current nutritional status but also serves as a vital indicator of its capacity to withstand environmental fluctuations and maintain physiological functions over time (Rossi *et al.* 2017a). The implementation of more precise techniques that allow the identification of the signature of stable isotopes carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) that offers precise information on the characteristics of the assimilated food in octocorals has also driven the growth of research in this area, since other methods such as gut-content analyses are time-consuming and imprecise.

The use of this method provides a comprehensive understanding of several critical aspects of an organism's ecology. It allows researchers to describe how food is incorporated into the organism's body, determine its trophic position within the food chain, and partially reveal how the assimilated energy is utilized (Valiela, 1995). Unlike the transient and short-term insights offered by gut content analysis, stable isotope analysis offers a more integrated perspective on long-term nutritional patterns (Valiela, 1995). This technique captures a broader picture by reflecting the characteristics of the assimilated food over extended periods, providing deeper insights into dietary sources and trophic interactions (Carlier *et al.*, 2007). All this information contributes to understanding how organisms obtain their energy according to the environmental conditions in which they live and how this can impact their permanence in the environment.

Low food availability in water for example could be responsible for the lipid storage in Antarctic benthos (Elias-Piera *et al* 2013; Servetto *et al.* 2017). A complementary approach to identifying dietary components is the analysis of fatty acid (FA) composition (Kelly and Scheibling, 2012). Fatty acids serve as robust biomarkers and have been extensively employed in studies of both pelagic and benthic food webs (Imbs & Dang, 2021; Kim *et al.*, 2021). They are particularly useful for identifying food sources—such as diatoms, flagellates, and bacteria—and characterizing the diets of zooplankton (Kelly and Scheibling, 2012). The FA profiles of diatoms and dinoflagellates, for instance, exhibit distinct differences, and zooplankton tend to incorporate and retain dietary FAs in their tissues. In pelagic systems, where phytoplankton represents the dominant primary producer, the use of FAs to trace dietary inputs is relatively straightforward. However, benthic systems are underpinned by a more diverse array of primary producers, including macroalgae, phytoplankton, and bacteria. This diversity enables the use of specific FAs as natural biomarkers to trace, identify, and even quantify the types of diets supporting these ecosystems.

Further, the study of FA quantity (total FA content), quality (relative proportions of saturated fatty acids [SFA], monounsaturated fatty acids [MUFA], and polyunsaturated fatty acids [PUFA]), and composition (specific FA components) provides valuable insights. This information can elucidate the balance between autotrophic and heterotrophic inputs, as well as highlight the primary sources of heterotrophic organic matter in a given system. Such data are essential for understanding energy flow and trophic dynamics across marine and benthic ecosystems.

To understand the current state of research on trophic ecology of octocorals in tropical regions, in chapter 1 we find out the necessity to expand researches to understudied geographic regions like Tropical Southwestern Atlantic and mesophotic areas, investigate the relationship between trophic ecology and reproduction in octocorals, linking energy inputs with energy storage strategies and also analyse the effects of combined and synergistic human disturbances through *ex situ* and *in situ* experiments. These studies will provide more accurate information about the longevity and persistence of octocorals on coral reefs.

Most studies are conducted in temperate regions, and when in tropical regions, most attention is given to coral reef ecosystems in clear, warm, low-latitude oligotrophic waters. These conditions are considered optimal for promoting high coral cover on the reef substrate and high species richness, characteristics very different from turbid reefs, which live in conditions of extreme temperatures and salinities, with moderate turbidity that results in lower coral richness, but with greater resilient to environmental variation.

The Brazilian reefs are the only coral reefs in the Southwestern Atlantic, with small numbers of coral constructors, and high degrees of endemism, where they are adapted to survive in extreme conditions very different from those found in the Caribbean region, known for offering optimal conditions for coral growth. Recognizing the need for studies addressing trophic ecology in octocoral from this type of reefs served as the primary motivation for conducting research with three gorgonians from Southwestern Tropical Atlantic. In the present work, I presented the first approach with such tools to understand spatial-temporal potential differences of the energy storage capability and the adaptation to the energy inputs present in NE Brazilian coast.

The investigation conducted in chapter 2 analyzed the biochemical compositions and stable isotopes signature of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in *Muriceopsis sulphurea, Plexareulla grandiflora and Phyllogorgia dilatata.* The results found demonstrate the heterotrophy of these species, offering these animals greater survival advantages to deal of environmental disturbances, crucial for establishing themselves in a marine environment, in contrast to other exclusively autotrophic corals.

Measurements of seasonal and latitudinal changes in stable isotope composition and biochemical balance help to understand the ecology of benthic organisms and how they invest their energy in biological processes (i.e. growth, respiration, reproduction) during a year. It was observed in some studies with cnidarians, that the energy storage strategy may also be related to the reproductive traits. Even with few studies focused on investigating the relationship between trophic ecology and reproduction in octocoral, it is undeniable that the ability to store food is essential for the reproduction and propagation of the species.

In this context, chapter 3 was focused on investigation of the biochemical composition (lipids, carbohydrates, proteins and fatty acids) of two gorgonians *Plexaurella nutans* and

Pterogorgia anceps from the Caribbean Sea during a seasonal sampling. The values found provided support to confirm the autotrophy as the main feeding strategy and the heterotrophic as the second on these gorgonians, complementing the study carried out by Rossi *et al*., 2020.

The patterns found in lipid composition throughout the year provided support to suggest that *P. nutans* reproduction occurs between May and August, a behavior recorded before in the literature. In the same way as high lipid values in autumn recorded by *P. anceps* are consistent with the same breeding season recorded previously. Additionally, the investigation of the temporal analyses of proteins, carbohydrates and lipids showed that *P. nutans* may have better conditions for storing energy during dry season. Finally, the majority found of FA marker 16:0 and then 14:0 in both species demonstrated that autotrophy was the main energy source for them with an input contribution from heterotrophic sources, supporting the results recorded by Rossi *et al*., 2020.

As a general conclusion it was possible to verify the solidity of studies with trophic ecology, and how the information generated can be useful to understand and elucidate the different processes that occur with octocorals, and thus the implications of their presence in coral reefs communities.

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