Mediterranean Marine Science

Vol 26, No 2 (2025)

Special issue, 2025 Marine Animal Forest of the World (MAF WORLD)

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doi: 10.12681/mms.36099

To cite this article:

MATOS RIBEIRO, E., GARCIA, T. M., SOARES, M. O., & ROSSI, S. (2025). The gaps in knowledge to understand the link between resilience and trophic ecology in tropical octocorals. *Mediterranean Marine Science*, *26*(2), 312–326. https://doi.org/10.12681/mms.36099

Review Article

Mediterranean Marine Science
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
www.hcmr.gr
DOI: https://doi.org/10.12681/mms.36099

Contribution to the Special Issue: Marine Animal Forest of the World (MAF WORLD)

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

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Contributing Editor: Vasilis GEROVASILEIOU

Received: 08 December 2023; Accepted: 25 November 2024; Published online: 21 March 2025

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 macroalgae, 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 (e.g., 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 mixotrophic 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 article,, 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.

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 and mortality 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 reef 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*.,

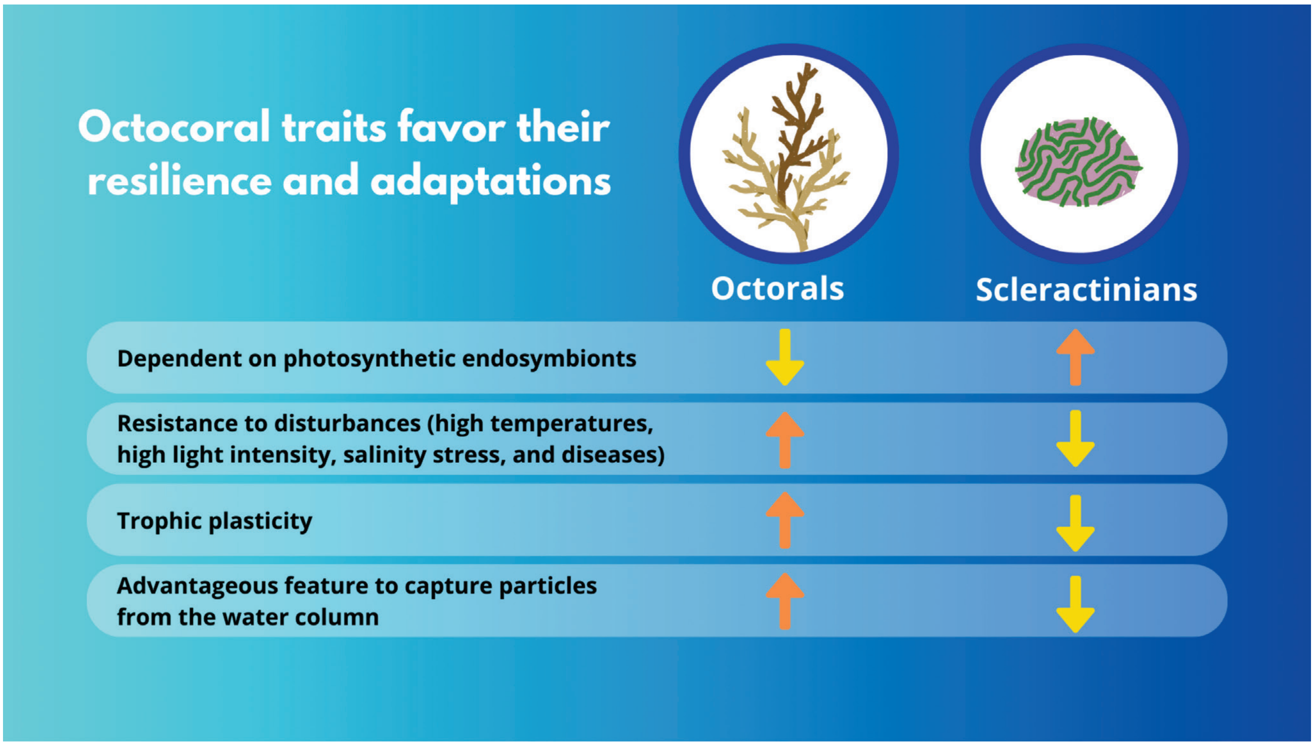

Fig. 1: Octocoral traits that favor their resilience and adaptations compared to scleractinians.

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).

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.

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 ornature-based 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 runoff (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).

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 inter-

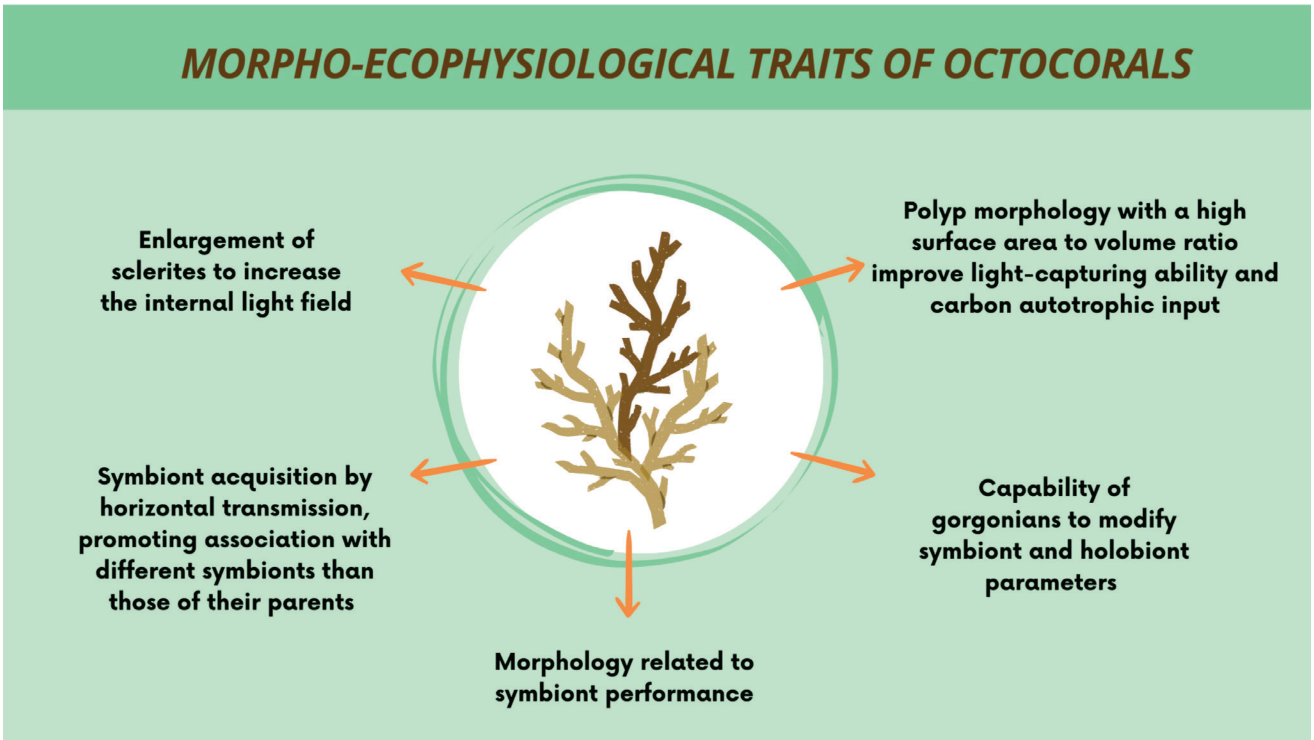

Fig. 2: Morpho-ecophysiological traits that also contribute to the permanence and proliferation of octocorals.

nal 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).

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.

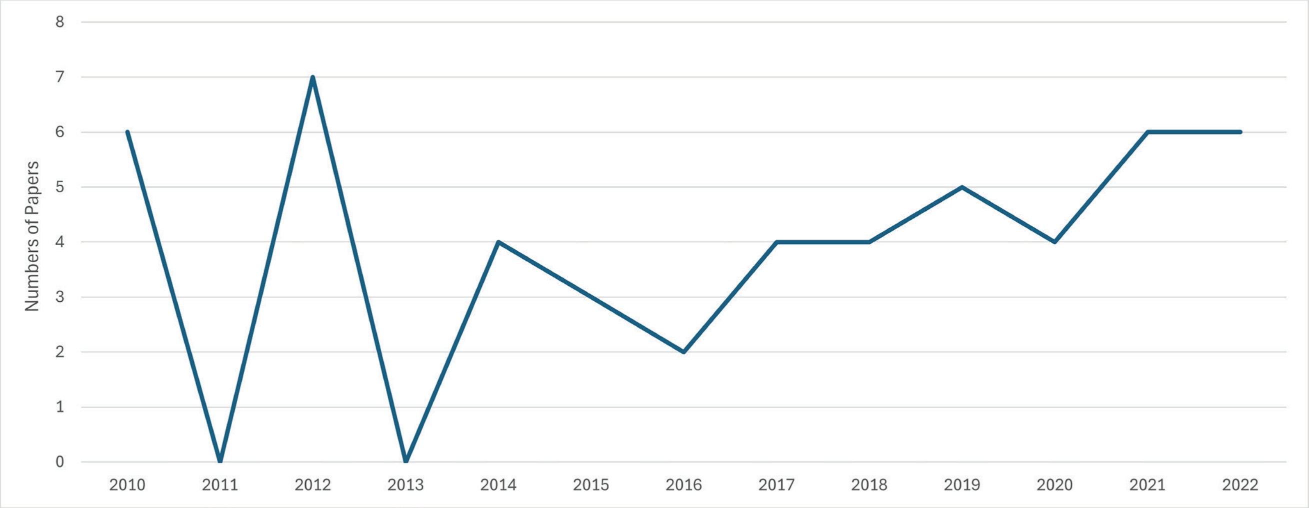

Fig. 3: Number of published studies (trophic ecology of octocorals in tropical and subtropical coasts) included (left axis) in this review per year.

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.

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.

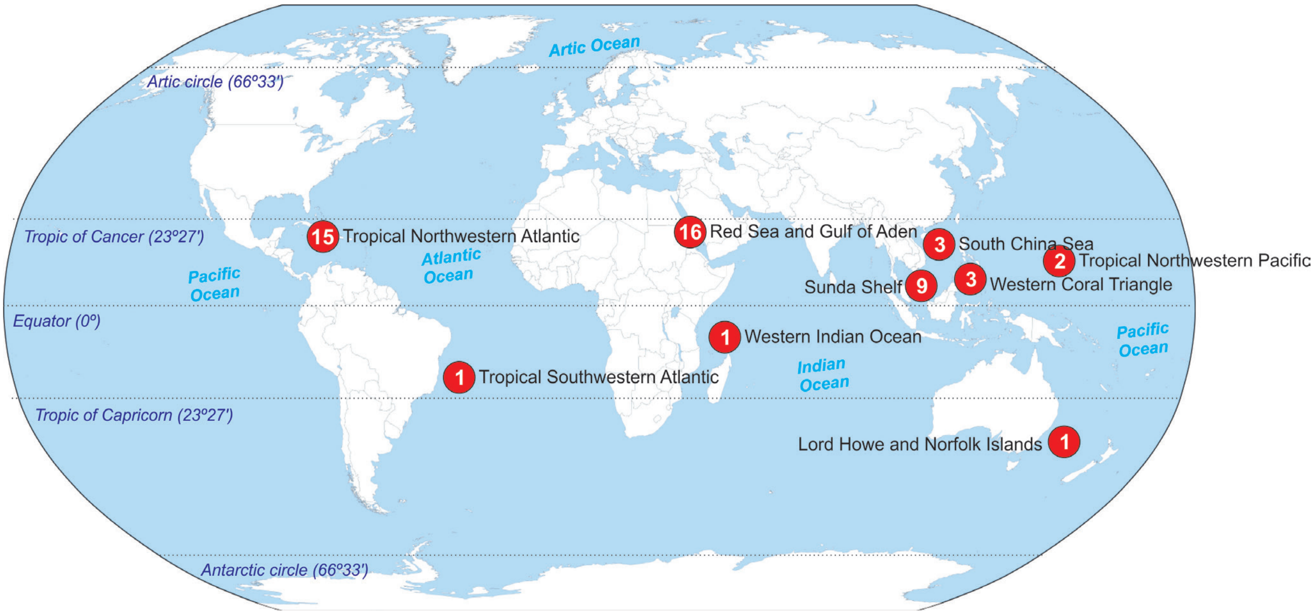

Fig. 4: Number of publications (red circles) about trophic ecology of octocorals in Tropical and Subtropical regions, according to the provinces classification by Spalding *et al.* (2007).

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.

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).

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

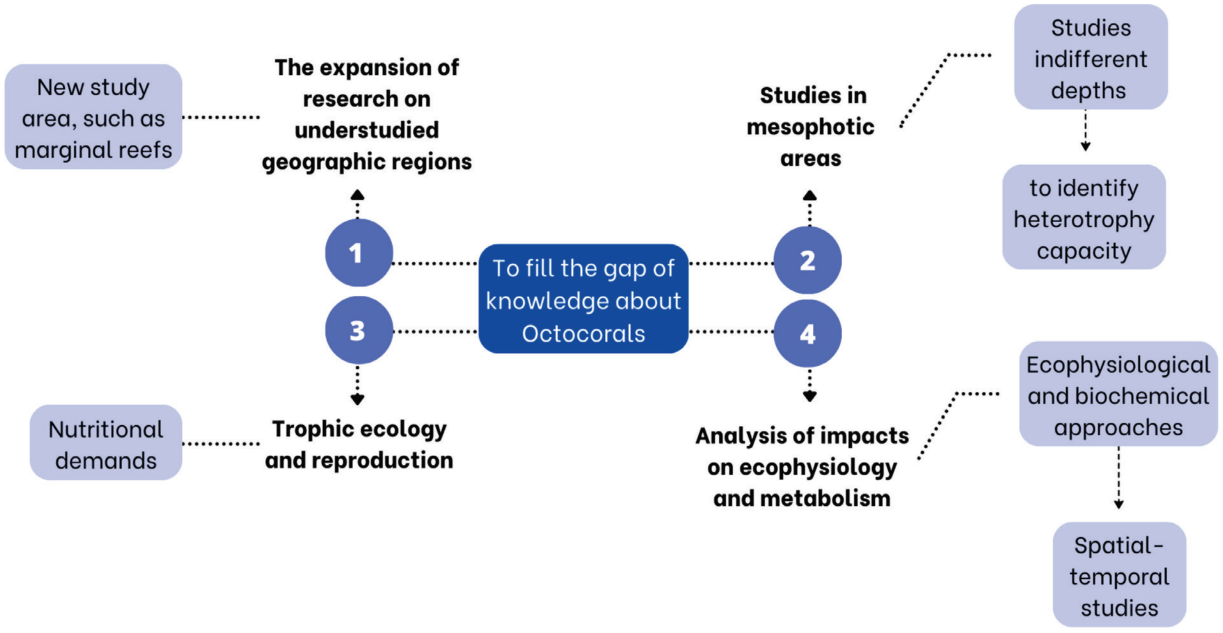

Fig. 5: Recommended actions to improve knowledge about octocorals and their biology.

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 and marginal 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.

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.

Acknowledgements

This publication is based upon work from COST ACTION Marine Animal Forests of the World (MAF-WORLD), CA20102, supported by COST (European Cooperation in Science and Technology). EMR thanks to Fundação Cearense de Apoio ao Desenvolvimento Científico e Tecnológico (Funcap) for the EMR doctoral scholarship. This research was supported by PELD Costa Semiárida do Brasil-CSB (National Council for Scientific and Technological Development CNPq No. 442337/2020-5 and Cearense Foundation for Scientific and Technological Development Support FUNCAP N. PEL-00177-00005.01.00/21). MS also thanks CAPES-PRINT, CAPES-Alexander Von Humboldt Foundation, CAPES-COFECUB, INTEGRAMAR (CNPq, 441226/2023-0), REMAR-BRAS (CNPq, 444172/2024-6) and FUNCAP (Chief Scientist Program) for their financial support. This paper is a contribution to the project European OCEAN CITIZEN project (“Marine forest coastal restoration: an underwater gardening socio-ecological plan”, Horizon Europe HORIZON-MISS-2021-OCEAN-02-01, Contract Number 101093910).

Competing interests: The authors declare no competing interests.

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Supplementary Data

The following supplementary information is available online for the article:

List of the 51 references used in the review.