Symbiotic Relationships in Octocorals: The Role of Gorgonians

Relaciones simbióticas sobre octocorales: el papel de las gorgonias

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Abstract
Octocorals are structurally complex organisms with significant ecological importance. Their morphology allows them to create multiple habitats, promoting their association with other marine species and thereby increasing ecosystem biodiversity. These interactions can be classified as symbiotic relationships or associations with fauna. Symbiotic relationships, being more specialized, can be categorized based on their impact on the host and the duration of the symbiosis, differentiating among three main types: mutualism, commensalism and parasitism. This article aims to highlight the role of octocorals in interspecific relationships within an ecosystem, as well as to emphasize their diversity and importance. Currently, organisms from seven phyla have been recorded inhabiting octocorals; therefore, studies that classify these interactions or utilize non-invasive methodologies for their study are lacking.

Keywords: invertebrates, biodiversity, epibionts, associated fauna.

Resumen
Los octocorales son organismos estructuralmente complejos con una gran importancia ecológica. Su morfología les permite crear múltiples hábitats que fomentan su asociación con otras especies marinas y aumentan la biodiversidad de los ecosistemas como resultado. Estas interacciones pueden ser categorizadas como simbiosis o fauna asociada. Las relaciones simbióticas, al ser más especializadas, pueden clasificarse de acuerdo con el impacto en el hospedero y la duración de la simbiosis. Este artículo tiene como objetivo resaltar el papel de los octocorales en las relaciones interespecíficas de un ecosistema, así como resaltar su diversidad e importancia. Actualmente, se han registrado organismos de siete fila que habitan sobre octocorales; sin embargo, son escasos los estudios que clasifiquen estas interacciones o que utilicen metodologías no invasivas.

Palabras clave: invertebrados, biodiversidad, epibiontes, fauna asociada.

1. Ecology of octocorals

Octocorals (Phylum Cnidaria) are colonial organisms found in all marine ecosystems, from the intertidal zone to depths of up to 6 400 m, with higher diversity in shallow tropical reefs and in deep sea habitats (Pérez *et al*., 2016). These organisms stand out for their diversity, morphological plasticity and interspecific relationships. About 3 500 species of octocorals classified into soft corals, gorgonians and sea pens are recorded (Pérez *et al*., 2016). The highly variable morphology of these organisms makes them visually captivating, ranging from encrusting, filiform, membranous and arborescent forms. Their structural complexity makes them dominant species or engineering species of some benthic communities. Therefore, this work will focus on octocorals of the order Malacalcyonacea (McFadden *et al*., 2022), known as gorgonians or sea fans. The aim of this work is to highlight their role as a microhabitat in an ecosystem by showcasing the several interactions that can be established with other organisms of the community, in order to emphasize the importance of symbiotic relationships in their survival and in the ecosystem.

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The ecological importance of gorgonians is based on the mentioned structural complexity, which allows the formation of three-dimensional planes, creating multiple microhabitats that can be exploited as spawning grounds, nurseries, feeding and refuge areas by other species (Lau *et al*., 2020). These observations have been recorded before the 20th century (Buhl-Mortensen & Mortensen, 2004), with a vague and inconsistent classification, as they were only described as fauna attached to coral branches. Nevertheless, some species are closely associated with sea fans, where the presence of one can even determine the presence of the other (Thiel & Baeza, 2001).

Organisms belonging to seven phylla have been observed as associated or related to octocorals; most are classified as microfauna inhabiting on or within corals, such as sponges, hydrozoans (Calcinai *et al*., 2013; Maggioni *et al*., 2020b), polychaetes, mollusks, crustaceans (Goh & Chou, 1994; Buhl-Mortensen & Mortensen, 2004) or gastropods (Reijnen, 2016). However, there is macrofauna that is found only in close proximity to them, on the substrate or swimming in the water column, such as echinoderms (Metaxas & Davis, 2005) and some fishes (Ben-David & Kritzer, 2005; Reijnen *et al*., 2010).

This work will focus exclusively on the interactions that octocorals maintain with marine fauna. However, it is important to highlight that sea fans also establish close relationships with organisms such as algae and bacteria, with these relationships being crucial for their survival in some cases (Van de Water *et al*., 2018). In the case of algae, the most prominent relationship is found between dinoflagellates of the Symbiodiniaceae family and the polyps of certain genera of octocorals (Jahajeeah *et al*., 2020). These relationships form a mutualistic symbiosis in which microalgae receive inorganic nutrients in exchange for providing photosynthetic products that corals use in biological functions such as calcification (Farag *et al*., 2018).

On the other hand, the coral microbiome plays a fundamental role in their health and physiology (Van de Water *et al*., 2018). It has been demonstrated that due to their ability to produce antimicrobial compounds, octocorals have a remarkably stable microbiome, with slight geographical and temporal variations (Lee *et al*., 2012; Haydon *et al*., 2022). Diseases or mass mortality events caused by bacteria and viruses have only been the result of external factors, such as opportunistic pathogens and environmental stress (Huete-Stauffer *et al*., 2011; Quintanilla *et al*., 2018).

2. Symbiosis or associated fauna?

Usually, interspecific interactions that involve a sessile or low-motility macroinvertebrate, such as octocorals, allow distinguishing between host and hostess, where typically the hostess has a larger size and serves as a habitat for the host (Castro, 1988). However, hosts can be classified into symbionts or associated fauna.

The concept of symbiosis has been modified several times, and now has been accepted as "a heterospecific association that is reflected in many adaptive interactions" (Castro, 1988). Over time, some authors such as Ríos (2019) have pointed out other criteria for it to be considered a symbiotic relationship. Such as physical proximity, duration for at least a part of the life cycle of the symbiont, and one of the species have to benefit and develop a degree of dependence.

Consequently, there are multiple organisms that can be found near or interacting with octocorals, but do not fit the conditions of a symbiotic relationship. These organisms are usually dragged by currents and attached to the branches of sea fans, or are found passing through, so their presence is not necessarily related to octocorals and there is no dependence between both species. These are named "associated fauna" and are usually defined by some authors as any animal found in the coral colony or nearby areas (Buhl-Mortensen & Mortensen, 2003).

It may seem arbitrary and complicated to identify those hosts of octocorals that are symbionts from those that are not, but there are some criteria that can be considered. Since symbiosis reflects coevolution, both morphological and behavioral adaptations allow symbionts to go unnoticed by predators by hiding or dwelling on coral branches (Lau *et al*., 2020). These adaptations are usually reflected in a similar coloration between the symbiont and the octocoral, as is the case of the decapod *Quadrella nitida* (Smith, 1869) symbiont of the gorgonian *Muricea fruticosa* (Verril, 1869), both share white coloration in the basal part and red in the upper part (Arcos, 2013) (figure 1). On the other hand, some symbionts even present ornamentations similar to the polyps of the octocoral, an example is the pygmy seahorse, *Hippocampus bargibanti* (Whitley, 1970), which inhabits octocorals of the genus *Muricella* sp., and presents a grayish coloration and small reddish protuberances along the body, which mimics the polyps of the host (Reijnen *et al*., 2010) (figure 2). However, morphological changes are not the only signs of symbiosis or co-evolution between species, Buhl-Mortensen & Mortensen (2004) highlight that some organisms inhabiting the scleractinian coral Lophelia sp. have adapted a very short larval stage in order to ensure the establishment of offspring on the hosts, given their patchy distribution.

FIGURE 1
Q. nitida crab on the branches of its octocoral hostess *M. fruticosa*
Source: Aburto-Oropeza *et al*., 2011.

FIGURE 2
H. bargibanti attached to the branches of a *Muricella* octocoral
Source: Photo by Greg Lecoeur.

These types of adaptations are not observable in the associated fauna. However, since octocorals are typically positioned perpendicular to the currents, some filter-feeding organisms can benefit from it. For example, the basket brittle star of the genus *Gorgonocephalus* (Leach, 1815) is sometimes found on gorgonians. When octocorals are not present, they may attach to branching sponges or hide among benthic rocks (Clippele *et al.*, 2015). Another ecological function of sea fans, as mentioned earlier, is the creation of spawning areas. This can be observed in some organisms such as the cuttlefish *Sepiella inermis* (Van Hasselt, 1835), which often use some octocorals as a substrate for spawning in shallow intertidal regions of the Eastern Arabian Sea (Gaikwad *et al.*, 2021). Cuttlefishes have been reported to attach their eggs to different hard and anchored substrates, seeking areas that provide protection to the capsules, whether it is an octocoral or not (figure 3).

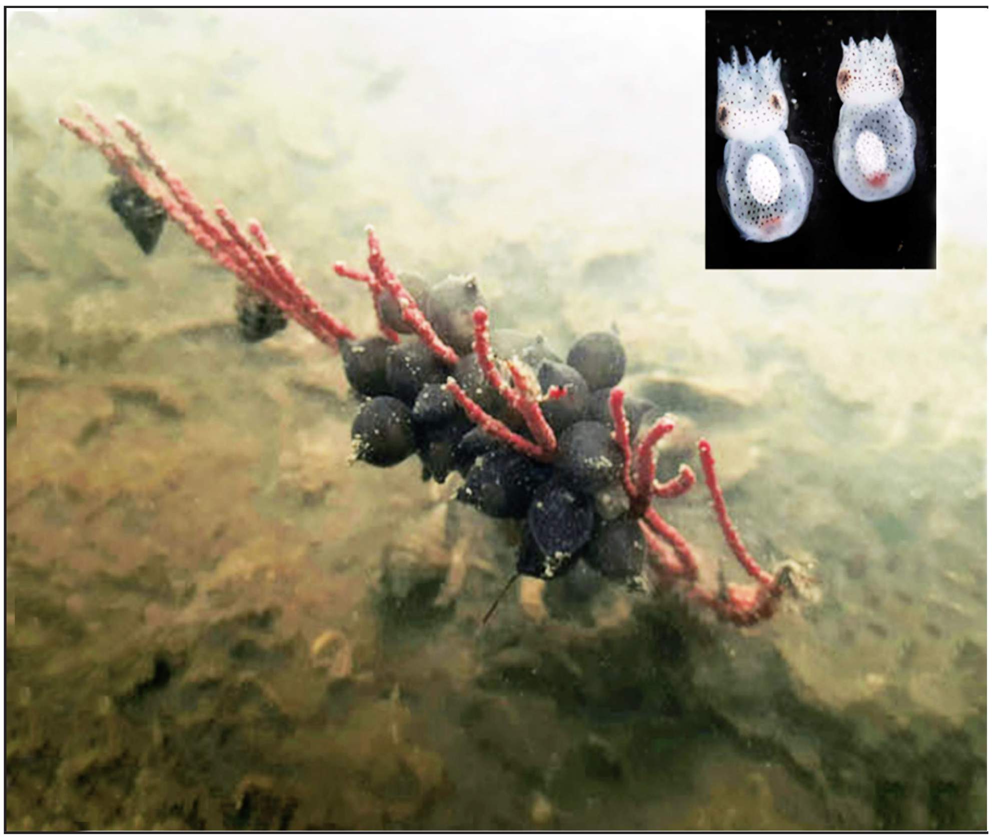

FIGURE 3

Pseudopterogorgia colony with egg capsules of the cuttlefish *S. inermis* attached

Source: adapted from Gaikwad *et al.*, 2021.

3. Effect on hostess and symbiont

Symbiotic relationships are usually classified according to different criteria, including spatial interaction, which distinguishes between endosymbionts and ectosymbionts. The first ones are mostly attached to the octocoral axis, covered by the coenenchyme with an opening to the outside, and are mainly composed of copepods and organisms of the class Ascothoracida (Korzhavina *et al.*, 2021). On the other hand, ectosymbionts live above coral branches. In addition, some authors classify symbionts in terms of exclusivity to the hostess species, where obligate symbionts can only inhabit one species, and facultative symbionts have a wider range of adaptability to different species within the group or genus (Buhl-Mortensen & Mortensen, 2004).

However, the most commonly used classifications are based on two factors: the impact on the hostess and the duration of the symbiotic relationship (Parmentier & Michel, 2013). On this basis, three types of symbiotic relationships with octocorals have been recorded: commensalism, which is the most common and involves a benefit to the host while the hostess remains neutral; mutualism, where both organisms receive benefits, and parasitism, where the host benefits at the cost of damage to the hostess (Castro, 1988; Buhl-Mortensen & Mortensen, 2004).

There are some symbiotic relationships where the effect of both organisms is evident, such as the "hotel" described by Maggioni *et al*. (2020b). This takes place on the octocoral *Bebryce* cf. *grandicalyx* which has as symbionts a sponge completely covering the branches (except for the calyx of the polyp) and the hydrozoan *Zanclea timida*, embedded in the sponge (figure 4). These organisms maintain a three-way mutualistic symbiotic relationship, while the octocoral benefits by obtaining protection from other epibionts covering its polyps, the sponge and the hydrozoans have less competition and a favorable place for food filtration.

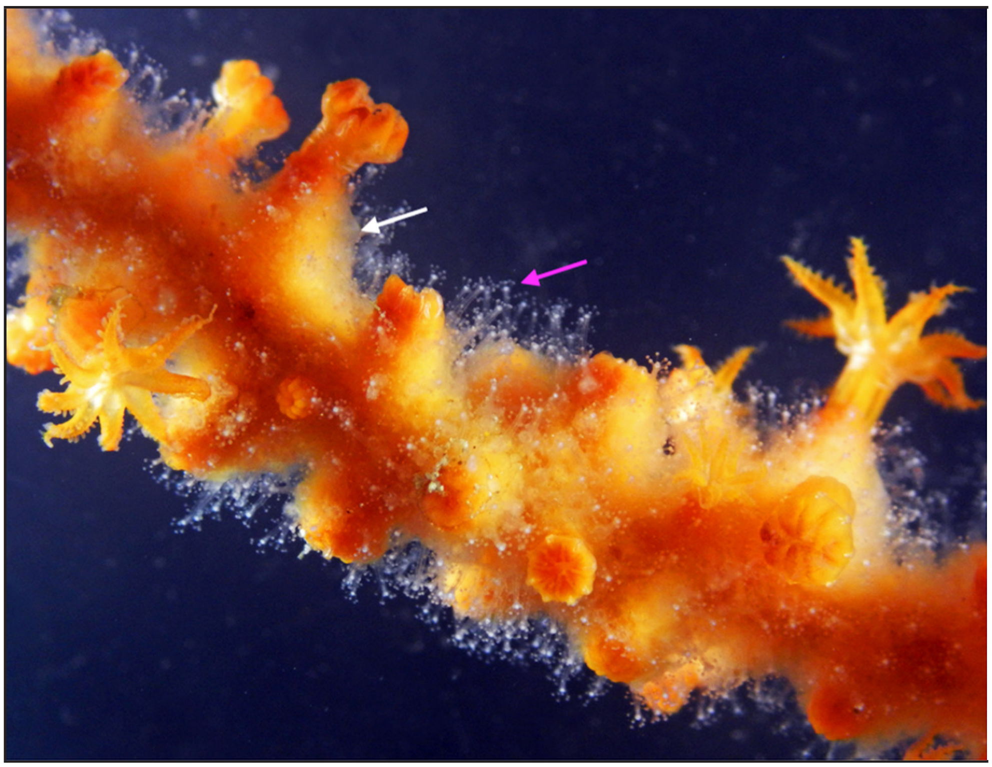

FIGURE 4
Branch of the octocoral *B. cf. grandicalyx*, covered by a suberitid sponge (White arrowhead) and *Z. timida* hidroids (Pink arrowhead)
Source: adapted from Maggioni *et al*., 2020a.

Another example of a mutualistic relationship is the case of two invasive species: the octocoral *Carijoa riisei* and the demosponge *Desmapsamma anchorata*. These species are native to the Atlantic Ocean; however, since 1972, they have successfully spread throughout Indo-Pacific reefs. Their success is attributed to their mutualistic symbiosis, where the sponge covers the coral colony except for the polyp calyx, avoiding competition for space, while the octocoral is protected from predators such as ovulids and nudibranchs. Additionally, the filter-feeding behavior of the sponge increases the availability of particles for the coral polyps (Calcinai *et al*., 2004; Galván-Villa *et al*., 2023).

In contrast to these examples, it has been pointed out that not all symbioses can be limited to a single classification, as they are all in continuity, and sometimes a boundary between categories cannot be established (Parmentier & Michel, 2013). This is supported by the fact that the effect on the host is often unclear. Such is the case with some polychaetes of the family Polynoidae, which are symbionts of octocorals responsible for cleaning organic matter from the surface of the branches. But also, they often feed on food particles that are trapped by the polyps, so they could be considered both mutualistic and parasitic (kleptoparasitism) (Buhl-Mortensen & Mortensen, 2004). Also, some shrimp of the family Palaemonidae, which are usually classified as commensalisms, can feed on the tissue of octocorals hostess when food is scarce, so some classify them as kleptophagous or pseudoparasites (Wirtz & d'Udekem-d'Acoz, 2001). Symbiotic relationships such as the above call into question the supposed commensalism of most of the species recorded as symbionts on sea fans, since this categorization could be due to a lack of studies.

4. Reflection of evolution

All symbiotic relationships begin as associated fauna, and depending on the benefits obtained from this interaction, they have the capacity to transform into dependent relationships through evolutionary adaptations. These interactions initially serve a primary purpose: to minimize intraspecific competition for resources, thereby seeking the exploitation of a new habitat (Baeza, 2007). Once these facultative associations form, natural selection begins to act on those organisms that exhibit characteristics allowing them to better adapt to the new hostess, leading to diversification compared to other organisms of the species that continue living independently. Consequently, the biodiversity of the ecosystem increases (Cerrano *et al*., 2006).

The adaptation of the host to the hostess faces multiple challenges, to which natural selection responds with highly specific mechanisms, resulting in magnificent and diverse symbiotic relationships. Problems such as the exploitation of resources obtained from the hostess, specifically food, have been solved by reducing the size of parasitic hosts, avoiding excessive damage and ensuring a food source for their lifespan. This phenomenon is observed in all octocoral parasites. Another adaptive mechanism is evident in the larval stages of some symbionts, with specializations such as a short larval period. This adaptation prevents the progeny from being carried away by currents to areas where octocoral hosts are not distributed, thus increasing the probability of survival. Finally, some adaptations are observed in aggressive or territorial behaviors, which help avoid competition with other symbionts. Such behaviors are observed in multiple octocoral symbionts, typically occurring with only 1 to 2 specimens per octocoral colony, often consisting of a female and male (Zann, 1987; Thiel & Baeza, 2001).

Symbiotic relationships are often described as involving a process of coevolution, where two organisms undergo a process of reciprocal natural selection. However, this has been put to debate, Clayton *et al*. (2016) point out that commensalistic relationships may not exhibit coevolution. They suggest that adaptations leading to increased dependence on symbiosis are expressed only in the organism benefiting from the relationship, indicating an unidirectional evolutionary change.

This interpretation, however, might be due to the mismatch of life expectancy between octocorals and their symbionts. Since symbionts typically have faster generational rates, evolutionary transitions may occur at different scales. This does not necessarily negate the possibility of coevolution entirely. In this context, the defense mechanisms of octocorals, which have played a crucial role in their evolutionary success, such as chemical adaptations, may need to evolve towards compounds with greater toxicity to prevent the association of organisms on coral branches. While such adaptations have been observed in response to certain predatory fishes or epibiont algae (Sammarco & Coll, 1992), they have not been observed in those octocorals that maintain symbiosis with other invertebrates, so it may be a clear sign of coevolution.

Therefore, some studies have aimed to identify the extent of this reciprocal evolution. For example, the parasitism observed between many gastropods of the family Ovulidae and octocorals, which has gained significant attention due to their notable morphological and physiological adaptations (figure 5). The specialization of this group when associated with sea fans leads to distinct changes in their shells, such as complex colorations or patterns, polyp-like structures, or physiological adaptations focused on avoiding the toxicity of compounds produced by some octocorals (Goh & Chou, 1994; Schiaparelli *et al*., 2005). Despite these adaptations, phylogenetic studies have shown that evolutionary changes in ovulid hosts have not been reciprocated by octocorals (Reijnen, 2016). As a result, conducting phylogenetic studies in other types of symbiotic relationships between fauna and octocorals becomes necessary to determine the degree of coevolution they may exhibit. Alternatively, such studies might lead to the conclusion that, regardless of the type of symbiosis, the effects induced by the hosts are not significant enough to drive the evolution of the octocoral group.

FIGURE 5
Morphological diversity of gastropod symbionts of octocorals
Source: adapted from Sánchez *et al*., 2016; Reijnen & Van der Meij, 2018.

Prospective analysis

Octocorals play a fundamental role in many marine ecosystems, performing a significant ecological function by providing microhabitats, spawning areas, nurseries, feeding grounds and shelter areas. This facilitates their association with numerous species of marine fauna. Their wide distribution in the oceans reveals the remarkable adaptability and high morphological and chromatic plasticity of certain genera, making them a complex and under-studied group.

In this theoretical framework, it is crucial to conduct studies that provide information about the role of octocorals as microhabitats, that distinguish between symbiotic hosts and associated fauna, or studies that include phylogenetic analyses to identify the line that separates these interactions. These studies will highlight the ecological importance of sea fans within an ecosystem, encouraging better management and protection of these organisms.

Additionally, it is important to note that existing studies on these associations tend to be highly specific, focusing on symbiotic relationships, and most of these studies have been conducted in the Indo-Pacific region. This underscores the need for research focused on the community structure of both symbionts and associated fauna with octocorals in various regions around the world.

Finally, it is essential to carry out these studies using methodologies that do not have a negative impact on octocoral communities, taking into account their vulnerability to environmental changes and their characteristic low resilience which is typical of sessile organisms with extremely slow growth rates, like corals.

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