

## SYMBIOTIC ASSOCIATIONS IN MARINE SPONGES

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**ABSTRACT** *The characteristics of the sponge structure, homogenous, flexible, and simple, but pervaded by canals and their ability for filter-feeding, may facilitate development of intimate associations with other organisms. This study reviewed the described symbiotic associations between marine sponges and other organisms as well as among marine sponge species. Associations in marine sponges show a wide range of relationships with their symbionts. These can range from mutually beneficial, to commensal, to parasitic or pathogenic. Sponge species also vary in the types of symbionts they host from facultative sponge associates that also live in other sheltered habitats, to obligate sponge associates that occupy a variety of sponge species, to obligate specialists on particular sponge species. The associations can cause the morphological alteration of the symbionts and other adaptive behavior. Observations of new*

*and unique associations were also discussed.*

**Keywords:** *Ecology, aquatic resources, literature review.*

## INTRODUCTION

Only a simple description is needed to define an apparently simple but fascinating group of organisms, sponges. The Phylum Porifera (from the Latin *porus* 'pore' and *fero* 'to bear') includes the simplest and most primitive metazoans (Becerro, 2008). Lacking most of what we commonly associate with the animal kingdom, sponges capture and concentrate dilute resources using a large surface area, like plants but they have the ability to suspension feed effectively, like higher metazoans do (Leys, S. P., & Hill, 2012). Sponges

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have great potential to alter coastal ecosystems. Because of their great abundance, impressive filtering capacity, heterogeneous diet, and complex bacterial associations, sponges could play a significant role both in providing nutrients to planktonic primary producers (Diaz, M. C., & Ward, 1997; Jiménez & Ribes, 2007; de Goeij *et al.*, 2013) and in depleting organic matter from the water column in shallow warm-water and deep-sea cold-water coral ecosystems (Rix *et al.*, 2016; Bart *et al.*, 2021).

Symbiotic associations, in which individuals of two or more species are intimately associated by being adherent to each other or by a host-guest relationship, can range from mutually beneficial, to commensal, to parasitic or pathogenic (Wulff, 2006). Sponge species also vary in the types of symbionts they host from facultative sponge associates that also live in other sheltered habitats, to obligate sponge associates that occupy a variety of sponge species, to obligate specialists on sponge species (Wulff, 2006). As symbionts, microbial communities can be species-specific (specialists), shared among sponge species (generalists), or even cosmopolitan (Taylor *et al.*, 2007). These are considered together because often it is not known exactly how an association affects the participating species. Several associations between sponges and other organisms are due to the aptitude of sponges to be epizoic, that is living or growing on the external surface of an animal, in this way solving the problem of substrate competition (Rützler, 1970). Because of the associations, sponges may be subjected to morphological alteration, while, in other cases, the sponge forces the host to modify its morphological organization (Wulff, 2006).

One of the challenges of studying symbiotic relationships in sponges presents unique challenges, particularly due to their rapid post-mortem disintegration and the absence of durable skeletal structures (Pawlik *et al.*, 2015; Webster & Thomas, 2016). This makes one-time observations insufficient, necessitating time-series studies and integrated methodologies (Pita *et al.*, 2016; Kiran *et al.*, 2018; Carrier *et al.*, 2022). Any interactions including symbiotic associations of sponges with other organisms and among sponges of different species have therefore depended on time-series observations of individuals and communities and combinations of field and laboratory work that elucidate cellular- and molecular-level mechanisms (Wulff, 2006; Björk *et al.*, 2013). A hint that some generalizations about symbiotic associations of sponges may be possible is just becoming evident, as accumulating data are beginning to show taxonomic and geographic patterns. An additional difficulty in the study of symbiotic associations is that the fact that sponges remain an enigmatic group, because they are difficult to identify and to maintain under laboratory as when they die, they tend to disappear very quickly. Many studies at particular sites have not yet reached comprehensive levels, such as how the symbiotic associations involve of the host nor do they have any host preferences to associate with. Consequently, it is very likely that disclosures and surprises will continue to emerge from new studies. In this paper, the described symbiotic associations in marine sponges were reviewed.

## SYMBIOTIC ASSOCIATIONS BETWEEN MARINE SPONGES AND OTHER INVERTEBRATES

The diversity and abundance of symbiotic associations between marine sponges and invertebrates is astonishing. The study by Ribeiro *et al.*, (2003) documented an exceptionally diverse invertebrate community—2,235 individuals from 75 species across 9 phyla—associated with the encrusting sponge *Mycale* (*Carmia*) *microsigmatosa* in southeastern Brazil. This finding underscores the sponge's role as a microhabitat supporting rich biodiversity. While specific studies replicating this exact finding are limited, subsequent research has continued to explore the diversity of invertebrate communities associated with marine sponges. Over 14 years, (Macdonald *et al.*, 2006) identified at least 36 species of *Synalpheus* shrimp inhabiting 17 sponge species. More than 50% of these shrimp species were found exclusively in a single sponge species, indicating high host specificity. Another study recorded 14 amphipod species as endocommensals within three sponge species on the Great Barrier Reef (Myers & George, 2017). Notably, three new *Leucothoe* species were each specific to a single sponge host, demonstrating strong host specificity. Likewise, Goren *et al.*, (2021) documented 210 polychaete species from 30 families associated with 11 sponge species in the Mediterranean Sea. The findings highlight significant host specificity and suggest that sponge-associated polychaete assemblages are structured and not random. However, many other associations depict various

mechanisms and different purposes towards different organisms.

### 1. Symbiotic associations between marine sponges and cnidarians

All classes of Cnidarian except the Cubozoa include species that are associated with sponges. In the Anthozoa, the Zoanthids in the genera *Parazoanthus* and *Epizoanthus* appear to be obligate symbionts, thought to gain substratum space in space-limited systems and protection from predators by intimate association with sponge (Swain, T. D., & Wulff, 2007). For example, in the zoanthid *Parazoanthus swiftii* hosted by sponge *Iotrochota birotulata* was determined to be mutually beneficial, with sponge gaining protection from a specialist angelfish predator (West, 1976). In contrast, zoanthid *Parazoanthus parasiticus* hosted by tube sponge *Niphates digitalis* appeared to interfere with host pumping and did not provide predator protection for sponge *Callyspongia vaginalis* (Lewis, 1982). Through molecular phylogenetic analyses, a study reveals that host associations among zoanthids are largely conserved over evolutionary time, indicating a strong phylogenetic conservatism (Swain, 2010). Notably, the research identifies instances where shifts in host species are accompanied by corresponding changes in symbiotic relationships, such as the loss of photosynthetic endosymbionts, highlighting the intricate link between host specificity and symbiotic adaptations. Recent research has delved into the interactions between the sponge *Cinachyrella cf. cavernosa* and the zoanthid *Zoanthus sansibaricus*, particularly focusing on the chemical and ecological dynamics of their association. (Singh & Thakur, 2018) examined how

the presence of *Z. sansibaricus* influences the asexual reproduction (budding) of *C. cf. cavernosa*. The study found that increased coverage by the zoanthids negatively affected the sponge's budding frequency, indicating that spatial competition from the zoanthids can suppress sponge reproduction. Further research by Singh & Thakur (2021) found that the sponge *C. cf. cavernosa* produces  $\beta$ -sitosterol, which acts as an allelochemical causing bleaching and symbiont loss in *Z. sansibaricus*, potentially limiting its overgrowth.

The greatest diversity in the association between Cnidaria and Porifera is found in the Hydrozoa. The most evident example of the association is found in all species of the sponge genera *Hebella* and *Anthohebella* which are associated with hydroid hosts (Boero *et al.*, 1997). When the association with a particular type of host is widespread within a single genus or family, it is highly probable that an adaptive radiation from a single ancestral association occurred and will surely lead to the discovery of new species of hydroids or to the elucidation of life cycles (Puce *et al.*, 2005). In these cases, the ancestors, who once established the association, became the founders of monophyletic clades containing species with similar host preferences. Another study investigated the spatial ecology of the association between the hydrozoan *Nemalécium lighti* and various sponge genera in the coral reefs of Bonaire, Dutch Caribbean. *N. lighti* exhibited generalist symbiosis, associating with 9 of 16 sponge genera across 15 of 16 surveyed sites, with a marked preference for large tubular sponges of the genus *Aplysina* (Gobbato *et al.*, 2022). The prevalence of this association reached over 30% in some

sites, suggesting a significant ecological interaction between these species.

Scyphozoans inhabit a variety of sponges such as the polyps of crown jellyfish *Nausithoe punctata* which are strictly associated with horny sponges in a non-parasitic and mutualistic association and might contribute to their skeletal structures (Uriz *et al.*, 1992). This finding was also supported by Meroz, E., & Ilan, (1995) who found an exclusive dependency of *N. punctata* on a common Red Sea coral reef sponge, *Mycale fistulifera* for its development and survival.

Recent research has expanded our understanding of symbiotic relationships involving scyphozoans (true jellyfish), particularly focusing on their associations with dinoflagellate symbionts. While direct associations between scyphozoans and sponges are not well-documented in recent literature, studies have highlighted the complex symbioses between scyphozoans and dinoflagellates, which may indirectly influence sponge communities through shared ecological interactions. (Enrique-Navarro *et al.*, 2022) conducted two studies revealing that *Cotylorhiza tuberculata* hosts *Symbiodiniaceae* dinoflagellates in a UV-protected, photosynthesis-enhancing symbiosis, and that scyphozoan-dinoflagellate associations in Mediterranean and Brazilian waters show host-specificity shaped by environmental factors—highlighting the complexity and ecological relevance of these relationships, despite limited knowledge on scyphozoan-sponge symbioses.

Symbiosis between sponges and octocorals has rarely been recorded. There is however an unusual association of a sponge *Desmapsamma anchorata* with

octocoral *Carijoa riisei* has been reported from Indonesia (Calcinai *et al.*, 2004). In this case, the sponge receives support structure to grow vertically avoiding competition for space, while octocoral gains protection against predators. Intriguingly, both the sponge and the octocoral might have invaded the tropical Pacific as a pair since they are originally Caribbean species. A decade later, a study finds the phenotypic plasticity of sponges and describes 28 species associated with octocorals *Carijoa riisei*, *Paratelesto rosea* and *Alertigorgia hoeksemai* in Indonesia, Hawai'i, and Vietnam—including four new species (*Chondropsis subtilis*, *Hymedesmia spinata*, *Hymedesmia (Stylopus) perlucida*, and *Mycale (Aegogropila) furcata*)—revealing that 21.4% are new records for the regions and underscoring the role of epibiosis in enhancing marine biodiversity (Calcinai *et al.*, 2013).

## 2. Symbiotic associations between marine sponges and echinoids

When predation on brittlestars is often intense, the association with sponges may provide brittlestars with a refuge from fish predation (Hendler, 1984). Henkel & Pawlik, (2005) observed that the brittlestar *Ophiothrix lineata* predominantly inhabits the sponge *Callyspongia vaginalis*, utilizing its tubular structure as a physical barrier against predators. Despite *C. vaginalis* lacking chemical defenses, its morphology offers effective shelter, highlighting the importance of physical refuge in brittlestar habitat selection. In addition, many sponges produce secondary metabolites that deter predation by reef fishes and may serve as a chemical as well as a physical barrier from predation (Pawlik *et al.*, 1995; Loh & Pawlik,

2014). Sponges also provide greater access to food particles for suspension-feeding brittlestars (Henkel & Pawlik, 2005) and a feeding surface for deposit feeding (Hendler, 1984). Thus, brittlestars may select sponge habitat because it provides both predation refuge and access to food.

## 3. Symbiotic associations between marine sponges and bryozoans

Symbiotic association between sponge and bryozoans has been rarely recorded. Interestingly, Harmelin *et al.* (1994) reported about 90% of the colonies of the bryozoans *Smittina cervicornis* were overgrown by the encrusting sponge *Halisarca dujardini* in a variety of habitats in the northwestern Mediterranean. The bryozoans provided support to the sponge to be high above the substratum in the same way as skeletal fibers or spicules provided support, while the feeding currents appear to be strengthened for both partners.

## 4. Sponges associated with crustaceans

Mutualism association was recorded in hermit crabs and suberitid sponges, where the sponges encrust gastropod shells inhabited by hermit crabs and then continue to grow, apparently relieving the crabs of the necessity of finding new shells as they grow (Wulff, 2006). Nevertheless, another study on these kinds of associations in the northern Gulf of Mexico revealed that mutual benefit might be a hasty conclusion in some cases, as hermit crabs left sponge-covered shells in favor of clean shells (Sandford, 1995). A more obvious assumption of mutual benefit is made in the case of sponge-decorated decorator crabs in which case camouflage seems to be a purpose of the interaction

(Schejter & Spivak, 2005). In the other case, seasonal preference for decoration with the sponge *Hymeniacidon heliophila* may confer predator protection to decorator crabs in North Carolina in winter and spring when their preferred algal decoration, *Dictyota menstrualis*, is unavailable, as this sponge is inedible to local fishes (Stachowicz, J. J., & Hay, 2000).

Sponge-dwelling snapping shrimps have attracted attention as the only known example of eusocial marine organisms, which have three characteristics: overlapping generations, reproductive division of labour and cooperative care of young (Duffy, 1996). A classic example of symbiont that relies on the sponge's water current for supply of suspended food particles was a pair of *Spongicola* that inhabit the hexactinellid sponges *Euplectella*. The shrimp enter the sponge when they are young, only to become trapped in their host's glass-like case as they grow too large to escape (Brusca & Brusca, 2003). This entrapment promotes a monogamous relationship, as the shrimps remain confined within the same host (Saito *et al.*, 2002). Research indicates that the transition from pair-living to eusociality in synalpheid shrimps is closely linked to their symbiotic relationships with sponges. The sponges provide a stable and defensible habitat, which, combined with limited larval dispersal and high relatedness among colony members, fosters the evolution of complex social behaviors (Subramoniam, 2023). Eusocial species tend to be ecological generalists, suggesting that a broad ecological niche may provide the stability necessary for the development of complex social behaviors (Duffy & Macdonald, 2010). The evolutionary models suggest that eusocial and communal breeding are

distinct evolutionary endpoints that evolved independently from pair-forming ancestors, rather than communal breeding serving as an intermediate stage toward eusociality (Chak *et al.*, 2017). This indicates multiple evolutionary pathways leading to complex social systems in snapping shrimps. Chak *et al.* (2021) discovered that eusocial *Synalpheus* species possess larger genomes with a higher content of transposable elements compared to their non-eusocial counterparts, a genomic expansion attributed to reduced effective population sizes resulting from reproductive specialization, highlighting a complex interplay between social structure and genome evolution in these organisms.

Barnacles from the subfamily Acastinae are known to inhabit sponges, embedding themselves within the sponge tissue (Yu *et al.*, 2019). These barnacles exhibit host specificity and have been studied for their larval biology and symbiotic relationships with their sponge hosts. High numbers of copepod crustaceans have been reported to inhabit sponges that lack a defined aquiferous canal system but possess internal cavities, which the copepods use for shelter and feeding (Chin *et al.*, 2020).

### 5. Sponges associated with polychaetes

Polychaete worms are common sponge symbionts. Non-filter feeding polychaete species may feed on their hosts, such as the small errant polychaete *Branchiosyllis oculata* was found to live and feed on 9 of 16 sponge species surveyed in Bermuda (Pawlik, 1983). The colour of *B. oculata* matched the colours of two host sponge species, *Tedania ignis* and *Cinachyra alloclada*, as the result of the worms ingesting their hosts. There are

consistent differences between temperate examples, which a few large worms, not necessarily have obligated association with a particular host sponge, and tropical examples which huge numbers of small worms completing their entire life cycle within their sponge host (López *et al.*, 2001).

Numerous polychaete species, particularly from the family Syllidae, inhabit sponge canals and cavities, often completing their entire life cycles within the host sponge. A notable example is *Ramissyllis multicaudata*, a branching syllid polychaete discovered in Darwin Harbour, Australia that lives entirely within the tissues of sponges from the genus *Petrosia*, with its intricate branching body occupying the sponge's internal canals (Glasby *et al.*, 2012). A study on sponge-associated polychaetes (*Haplosyllis* spp.) in Nha Trang Bay, Vietnam, found that these polychaetes select, incorporate, and enrich parts of their host sponges (*Clathria reinwardti*, *Amphimedon paraviridis*, *Neofibularia hartmani*, and *Aaptos suberitoides*)' microbiomes, resulting in species-specific bacterial communities.

## 6. Sponges associated with molluscs

Associations of sponges with dense populations of molluscs have been widely described in most oceans. A commensal-protective mutualism of an unspecialized and probably facultative nature between scallops and sponges was reported in the end of 1970's in Ireland. The scallop *Chlamys varia* were widely found associated with an enveloping epizootic growth of the sponge *Halichondria panicea* (Forester, 1979). Further study found that scallop *Chlamys hastata* often hosts epibionts like sponges and barnacles on its shell; while sponge encrustation, particularly by

*Myxilla incrustans* and *Mycale adhaerens*, provides the scallop with protection against predators such as the sea star *Pycnopodia helianthoides*, barnacle encrustation increases the scallop's vulnerability to predation (Farren & Donovan, 2007). This suggests that sponge encrustation offers a mutualistic benefit by enhancing scallop survival, whereas barnacle encrustation may be detrimental.

In South Australia, sponges encrusting scallop shells not only deterred asteroid predators but also prevented damage from boring sponges, leading to faster scallop growth. Additionally, in both Ireland and Australia, sponges facilitated scallop escape from predators; notably, in Australia, one sponge species inhibited starfish predation even when scallops were immobilized, suggesting the involvement of physical or chemical defenses (Pitcher & Butler, 1987).

In another association that seems to benefit both partners, sponges of 19 species inhabit shells of bivalve *Arca noae* in the Mediterranean. The sponges may benefit from water flow generated by the bivalve, and all six species of boring sponges that were present on the rocks were missing from the shells (Corriero *et al.*, 1991), suggesting that non-boring sponges might protect shells from borers. Also, the sponge *C. crambe* encrusting *A. noae* shells inhabited predation on their hosts by a starfish, a non-native invasive snail and octopus (Marin & Belluga, 2005).

## 7. Sponges associated with other sponges

Association among highly efficient filter feeders of multiple sponge species is especially fascinating. However, many sponges clearly thrive in the intimate association with each other. In Caribbean

coral reef, *Iotrochota birotulata*, *Amphimedon rubens* and *Aplysina fulva* share an erecting branching growth form but differ in tissue and skeletal characteristics sufficiently to be able to decrease their loss rate adhering tightly to sponges of species that differ from them in chemistry, tissue density and skeletal construction, thereby survival of hazards (Wulff, 1997). Further complicating these associations was reported by Wulff, (2008) as the unusually quickly growing and readily fragmented sponge *Desmapsamma anchorata* can act as a parasite on species that participate in mutualism, gaining benefits without reciprocating.

#### 8. Symbiotic associations with microorganisms

A comprehensive global survey analyzing 804 sponge samples from 81 species across various oceans revealed that sponges harbor exceptionally diverse microbial communities (Thomas *et al.*, 2016). These communities include thousands of operational taxonomic units (OTUs) per host, with both generalist and specialist symbionts contributing to the microbiome (Webster & Thomas, 2016). The study highlighted that sponge-associated microbial communities are distinct from those in surrounding seawater and sediments, emphasizing the unique symbiotic relationships sponges maintain with their microbiota (Sacristán-Soriano *et al.*, 2020). These symbiotic microorganisms—including bacteria, archaea, fungi, and viruses—can constitute up to 35% of a sponge's biomass (Egan & Thomas, 2015), forming a tightly integrated holobiont that contributes to the sponge's nutrition, defense, and ecological resilience.

Among many endosymbionts associated with sponges, bacteria and unicellular

algae are found to provide substantial ecological advantage for they provide their hosts with an ample food resource. This advantage is indicated by the ability of encrusting sponge species host to enormous populations of cyanobacteria to grow rampant over live reef corals on stressed reefs (Rützler, K., & Muzik, 1993). Cyanobacteria's adaptable photosynthetic systems enable them to thrive in low-light environments, making them ideal symbionts for sponges across diverse habitats. Recent research has identified two major cyanobacterial clades, *Candidatus Synechococcus spongiarum* and *Oscillatoria spongeliae*, which are found in unrelated sponge hosts across widely separated geographic locations, suggesting potential host specificity and global distribution (Usher, 2008). These findings highlight the complex biogeography, phylogeny, and ecological roles of cyanobacterial symbionts in sponges, underscoring the need for further studies on their photophysiology and contributions to sponge survival.

Little is known about viruses in sponges, although virus-like particles were observed in cell nuclei in *Aplysina cavernicola* (Thiel & Imhoff, 2003). It was suggested that these particles could be involved in sponge cell pathology. Infection of a sponge *Ircinia strobilina* derived alpha proteobacterium by a bacteriophage isolated from seawater has also demonstrated (Lohr *et al.*, 2005), although the susceptibility of this siphovirus to infect the bacterium in nature is not known (Taylor *et al.*, 2007). Net primary productivity and stable isotope analyses of microbial and host sponge fractions showed that unicellular Parasynechococcus-like cyanobacterial species are commonly reported in sponges and play a role in this carbon transfer process (Burgsdorf *et al.*,



2022). While direct evidence for archaea-to-sponge carbon transfer is limited, these findings suggest a broader potential for nutrient sharing between sponges and their microbial symbionts. Genomic studies have shown that many sponge-associated *Thaumarchaeota* possess unique genes for ammonia oxidation, carbon fixation, and stress response, suggesting a high level of adaptation to symbiotic life (Haber *et al.*, 2021). Some sponges exhibit host-specific symbiont strains, implying coevolution or vertical transmission, from parent to offspring (Carrier *et al.*, 2022). In deep-sea environments, certain sponges, such as *Aphrocallistes* sp., *Farrea* sp., and *Paratimea* sp., host specific *Nitrosopumilaceae* lineages. This specificity suggests potential vertical transmission of these symbionts, differing from the more generalist associations observed in shallow-water sponges (Garritano *et al.*, 2023). These findings raise new research questions about microbiome resilience, sponge adaptation to climate stress, and biotechnological applications like biofiltration.

## SYMBIOTIC ASSOCIATIONS BETWEEN MARINE SPONGES AND OTHER NON-INVERTEBRATES

Different associations have been reported, in which sponges live on vascular plants, such as seagrass blades in estuaries (Fell & Lewandrowski, 1981) and water hyacinth roots (Tavares *et al.*, 2005). In these cases, the plants serve primarily as substrata and the plant life cycle can impose a degree of ephemerality on the life history of the sponges

(Fell & Lewandrowski, 1981). Mangrove roots, particularly those of *Rhizophora* mangle, provide stable, long-lived substrates that support diverse and abundant sponge communities (Hunting *et al.*, 2010). These associations are complex, involving mutualistic interactions where sponges benefit from the structural support and nutrient-rich environment of the roots, while mangroves may gain protection from root-boring organisms and enhanced nutrient cycling facilitated by the sponges (Engel & Pawlik, 2005). Sponges living on mangrove roots have been recognized to increase root elongation rate and decrease root infestation by boring isopods (Ellison & Farnsworth, 1990). Stable isotope analyses also suggest transfer of dissolved inorganic nitrogen from sponge to mangrove and transfer of carbon from mangrove to sponge (Ellison *et al.*, 1996; Engel & Pawlik, 2005).

## CONCLUSION

Symbiotic associations in marine sponges are very diverse and abundant. Most commonly represented in the associations with marine sponges are crustaceans, polychaetes, molluscs and cnidarians. However, many other marine sponges' associations involving many organisms illustrate various mechanisms and different purposes. Even though mostly the participating species support each other, the associations can range from mutually beneficial, to commensal, to parasitic or pathogenic. These are considered together because often it is not known exactly how an association affects the participating species. Furthermore, the associations with a particular type of host may create an adaptive morphology and modify its morphological organization. Therefore,

different host preferences may lead to the discovery of new species symbionts. Intriguingly, it is still illustrated in this review that a few studies in marine sponge association are just becoming evident from accumulating taxonomic data and geographic patterns from a few groups of organisms. Therefore, well-illustrated field manuals for large geographic areas are still needed to gain more comprehensive levels of symbiotic associations. Moreover, studying the symbiotic associations in marine sponges is becoming more challenging when some new and unusual associations in marine sponges are discovered. It is likely that new studies will provide more surprises in the associations between these organisms.

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