



Sponges Revealed: A Synthesis of Their Overlooked Ecological Functions Within Aquatic Ecosystems

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Abstract

While sponges are the oldest still living multicellular animals on this planet and omnipresent within aquatic ecosystems, they have not been studied nearly as much compared to the recognized ecosystem drivers in coral reefs: corals, algae, and fish. We therefore want to take this opportunity to illustrate the diversity, functionality, and sheer survivability of these ancient animals. Beyond its multitude of external shapes and colors, sponges hold a unique internal aquiferous system. This system of afferent and efferent canals is intricately linked to supply its key function as a filter feeder. By filtering both particulate and dissolved material, sponges fill a niche in nutrient cycling. Moreover, the survivability of sponges is demonstrated in the variety of habitats it resides in; from freshwater canals to polar deep seas. In formerly uninhabitable environments, sponges can potentially create biodiversity hotspots by providing habitat complexity and shelter from predators. This review will give insight into the early life history, morphology, diet, and reproduction of sponges. Furthermore, it is imperative to consider their function as habitat facilitator, nutrient cyler, and, last but not the least, their potential for future pharmaceuticals. The emphasis in the proceedings has been specifically put on the role of sponges as nutrient cyler as they play a role in the three essential elements: carbon, nitrogen, and phosphorous. With all this in mind, it should be clear that even though sponges are relatively overlooked marine invertebrates, they should be studied similarly to corals and respected as a key ecosystem driver in novel and established environments.

Keywords

Porifera · Filter feeders · Nutrient cycling · Habitat facilitation · Marine natural products

9.1 Introduction

Ever since marine research has been documented several hundreds of years ago, we usually consider coral reefs as iconic examples of biological hotspots. These reefs have provided potential services to the ecosystem, among them are their services for early humans to maintain nutritional uptake. We have typically considered coral reefs to consist of three big ecosystem drivers: corals, algae and fish. Yet, within these coral reefs lie a less familiar but equally important builder and energy conveyer: sponges. Slowly, recognition develops that sponges are key ecosystem engineers. They have the capacity to retain nutrients and transform them into a bio-available form back into their surrounding habitat while providing protection for motile fauna. In fact, on Caribbean coral reefs, sponges usually show a higher diversity and higher abundance compared to corals (Diaz and Rützler 2001).

However, apart from these iconic coral reefs, there is a multitude of habitats in which sponges thrive (Gili and Coma 1998). Habitats can range from the deep sea to turbulent freshwater canals among cities. Within these various habitats, sponges perform important so-called benthic-pelagic coupling, which is a crucial ecosystem service to recycle pelagic nutrients toward the benthos that would otherwise be unavailable to higher trophic levels (Griffiths et al. 2017). For example, the Caribbean giant barrel sponge *Xestospongia muta* shows a large role in the carbon transfer from the water column to the benthos (McMurray et al. 2017). Moreover, it could be suggested that, in previously uncolonized marine environments, sponges are among the first settlers creating a three-dimensional habitat, allowing benthic ecosystem

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hotspots to develop. However, research is needed to elucidate the potential functional role of sponges as ecosystem engineers.

Apart from the potential functional role sponges fulfill, there is also a wide debate on the phylogenetic relationship among major animal lineages; yet recent research has shown through genomic data that sponges rather than the proposed comb jellies (Dunn et al. 2008) can be interpreted as the sister group to the remaining animals (Nakanishi et al. 2014; Pisani et al. 2015). Considering sponges could be among the first multicellular animals, they are remarkable study objects with respect to evolution. Unlike cnidarians and ctenophores, sponges lack a nervous system but do allow cells to move through layers and accordingly change function (Nakanishi et al. 2014). These characteristics make sponges a unique animal filling niches within the aquatic environment. Yet research regarding sponges until the year 2017 is substantially lower (637 publications) compared to corals (1590 publications) (Fig. 9.1). However, the research regarding sponges is on the rise with projects such as the “EU horizon 2020”-funded SponGES. We hope to appeal to more funding projects in the future to be able to investigate sponges at similar levels to corals.

This review is arranged in four sections. The first section will draw the attention to sponges’ life history, morphology, diet, and reproduction. All these components add to the special position of sponges related to other marine animals. The second section focuses on how sponge morphology plays a role in facilitating habitats for other life forms such as fish, crustaceans, and other invertebrates. Within these habitats, sponges play an important role in the cycling of nutrients to make carbon, nitrogen, and phosphorous bioavailable, which is argued in the third section. Finally, the fourth section will

dive into the human-related prospects of sponges, in both their physical form and at a molecular level as marine natural products valuable to the pharmaceutical industry.

9.2 Sponge Characteristics

9.2.1 History and Phylogeny

Before we can understand the potentially important ecosystem functions of sponges as filter feeders, we need to establish a rudimentary familiarity with the history and morphology of sponges. Sponges (Porifera) have diverged earliest from within the metazoans around 600 million years ago and are one of the most diversified invertebrate phyla present in both the marine (~8000 species) and freshwater (~150 species) environment (van Soest et al. 2018). Yet discussion remains if sponges, rather than ctenophores, are considered the sister group to all the remaining animals (Pisani et al. 2015; Adamska 2016; Simion et al. 2017). There are three classes of sponges which, in general, display bathymetric differences in abundance: Calcarea, Demospongiae, and Hexactinellida (Fig. 9.2) (Reid 1968). Furthermore, later research has shown sponges differ over depth in body size and shape in shallow (Bell and Barnes 2000) and deep areas (Maldonado and Young 1996).

Calcarea or calcareous sponges are restricted to shallow environments where it is least demanding to produce calcium carbonate (Vacelet 1988). Demospongiae constitute to about 90% of all sponge species and live in the widest range of habitats (Zenkevich et al. 1960). From the epipelagic until the bathypelagic zone, they thrive in both freshwater and marine environments, under various shapes and sizes (van Soest et al. 2018). Finally, Hexactinellida or glass sponges are the least flexible species. They possess a net of amoebocytes where the epidermal cells would be in other sponge classes. Their cells are interspersed with glass spicules protruding on the outside, which makes them a very rigid class (Barnes 1982). This class is present in polar regions and ocean depths of the abyssal pelagic zone. All three classes have hard skeletal elements called spicules to support their body. The spicules of Calcarea contain calcium carbonate, while the latter two are made up of hydrated silicon dioxide. Recently, the fourth class of sponges has been recognized to be phylogenetically well distinct from their closest relative Demospongiae: Homoscleromorpha (Gazave et al. 2012). They display a relatively simple body structure and with 184 species constitute to only 2% of the sponge species recorded (Hooper and van Soest 2002; van Soest et al. 2018). Therefore, our focus will remain on the three aforementioned classes.

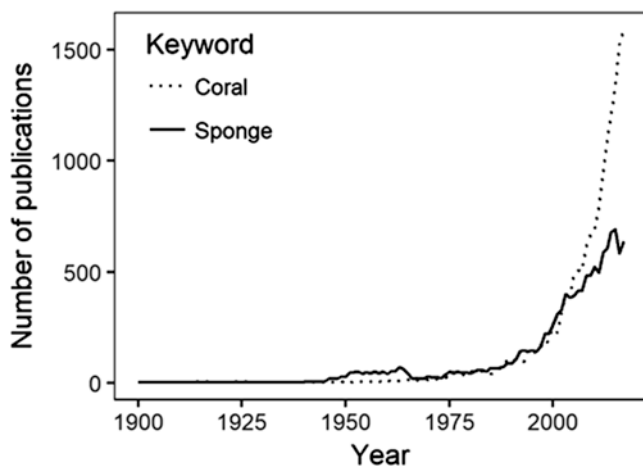


Fig. 9.1 Annual number of scientific publications on the PubMed database including the words “coral” (dotted line) or “sponge” (solid line) in the publication title or as a keyword from 1900 to 2017

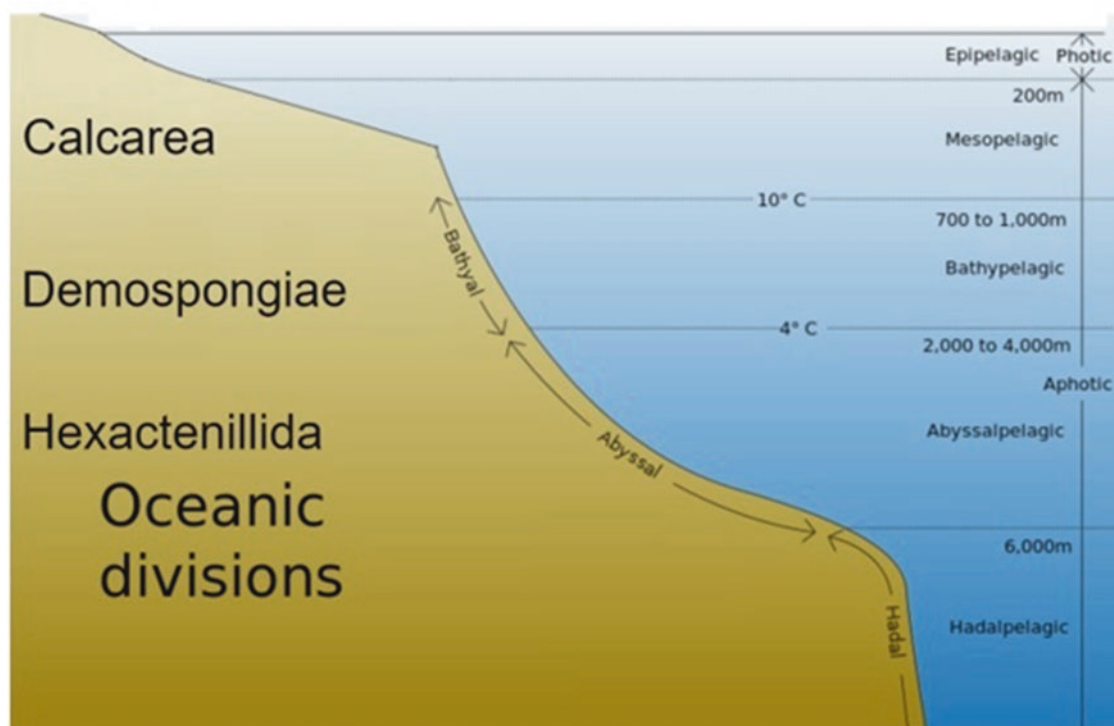


Fig. 9.2 General trend in the bathymetric distribution of three main sponge classes

9.2.2 Morphology

Sponges are radially symmetrical sessile filter feeders with a unique aquiferous system, which is an arrangement of afferent and efferent canals conducting water through chambers lined with flagellate choanocyte cells (Simpson 1984). These choanocyte cells propel water actively through the sponge's aquiferous system. Three conditions of this system exist with increasing size and complexity. Demospongiae are known to display the most complex and folded leuconoid condition, with many inhalant canals (ostia) collared by choanocyte cells together with one or more converging exhalant canals (oscula) (Boury-Esnault and Rützler 1997). This folding increases surface area of cells in contact with the surrounding seawater. A large number of the sponge cells (archaeocytes) are totipotent (Müller 2006), meaning they can change form and function. This is especially useful when perturbations occur surrounding a sessile filter feeder. This totipotency allows cells to migrate over the three different cell types present: pinacocytes, mesohyl cells, and choanocytes (Müller 2006). Sponges unlike more complex multicellular organisms do not have nervous, digestive or circulatory systems. In its place, sponges rely on water flowing through their bodies to nourish them with food and oxygen while simultaneously excreting waste. Furthermore, they do not show bilateral symmetry. Instead, sponges show radial symmetry, which allows for maximal efficiency in water flow around the central cavity of the sponge.

9.2.3 Diet

Traditionally, researchers thought most sponge species relied on particulate food sources such as bacteria and plankton (Kahn et al. 2015). However, a century ago already, suggestions were made that the traditional view of sponges only feeding upon particulate food sources (Reiswig 1971; Pile et al. 1996, 1997), was insufficient to sustain their nutritional requirements (von Putter 1914).

Nowadays, sponges have been suggested to play an important role in dissolved organic matter (DOM) cycling, thereby fueling “benthic-pelagic coupling” (de Goeij et al. 2013; Lesser 2006). This will be discussed in more details in the section on nutrient cycling (see Sect. 9.4). The question remains, however, if this food source is taken up by the endosymbionts abundantly present in the sponge's tissue or by the sponge itself. The presence of microorganisms in marine sponges has been identified already 80 years ago (Dosse 1939). We know now that sponges may host large amounts of microbes (Gloeckner et al. 2014; Taylor et al. 2007), within some cases up to 40% of their body mass (Taylor et al. 2007). High microbial abundance (HMA) sponges harbor as many as 10^8 to 10^{10} cells \cdot g⁻¹ of sponge wet weight, being two to four orders of magnitude higher than microbial abundance in seawater. Low microbial abundance (LMA) sponges contain $<10^6$ cells \cdot g⁻¹ of sponge wet weight. This distinction in microbial abundance could have a considerable effect on their capacity to feed on dissolved compared to particulate

food sources. Sometimes, 48–80% of sponge's energy supply comes from these endosymbiotic microbes (Ruppert et al. 2004).

Apart from these food sources, more feeding modes occur in sponges. Some sponges even host photosynthesizing cyanobacteria as endosymbionts to additionally produce food and oxygen (Taylor et al. 2007). For example, sponges often host green algae to provide them with nutrients (Wilkinson 1992). However, some species living in low nutritious environments have become carnivorous sponges (class Demospongiae; family Cladorhizidae) that prey on small crustaceans (Maldonado et al. 2015). Little is known about their ability to capture prey as they count up to a diverse group of 328 species (van Soest et al. 2018) only present in challenging and remote deep-sea environments (Maldonado et al. 2015). Interestingly, these carnivorous sponges have lost most of their aquiferous system and choanocytes. Therefore, it is unsurprising that they are opportunistic feeders together with their endosymbiotic methanotrophic bacteria, which can act as a complementary food source to these deep-sea sponges (Vacelet et al. 1995).

9.2.4 Life History

Very little is known about the life cycle of sponges with respect to population dynamics, which is very important for conservation (Maldonado et al. 2015). We do know that, similar to other metazoans, sponges can use sexual reproduction through both viviparous and oviparous species. Even though it is more difficult to study viviparous species, due to internal maturation, we know more about their life cycle compared to oviparous species (Leys and Ereskovsky 2006). Moreover, sightings of egg spawning are rare compared to corals, which suggests a more viviparous lifestyle in sponges, but numbers are still largely unknown. Hexactinellida and Calcarea are viviparous, while most oviparous sponges are found in the Demospongiae (Leys and Ereskovsky 2006).

Similar to corals, sponges are hermaphrodites, in which case they release both sperm and eggs. Due to the absence of organs, gametes are, respectively, transformed from the choanocytes and archeocytes. After the capture of sperm by a host, fertilization and hatching usually occur internally after which the larvae swim out until they find a place to settle. In the case of deepwater Hexactinellida, it is difficult to determine the early life history. Yet some studies have found that two of those species are productive year-round (Ijima and Okada 1901; Okada 1928) and one was only seasonally active in early summer (Boury-Esnault and Vacelet 1994). This shows that deepwater environments can be influenced by seasonal fluctuations in some cases.

In contrast, the totipotency of sponge cells also allows for asexual reproduction, by means of four distinct methods: fission, fragmentation, budding, and gemmule formation. Fission creates large clonal populations of especially encrusting sponges, for example *Crambe crambe* (Calderón et al. 2007). Fragmentation usually occurs in turbulent environments, with, for example, high predation pressure or wave action. Similar to fission, fragmentation allows nearby recolonization within a single habitat in the case of some coral reef species where almost 30% of a population consists of the same genome (Wulff 1986). Budding occurs in a limited number of species, such as *Tethya citrina* and *Tethya auranitium* (Gaino et al. 2006). Finally, one special adaptation is the formation of gemmules predominantly by freshwater species during unfavorable conditions (Kilian 1952). These survival pods form due to considerable temperature differences experienced in freshwater environments in comparison to the ocean (Manconi and Pronzato 2016). These pods of unspecialized cells remain dormant until conditions improve, and they either recolonize their parental skeletons or start a new colony.

Depending on where sponges live, they can grow from a few years in temperate regions to hundreds of years in both tropical and deep-sea environments. Some sponges grow only 0.2 mm per year which makes specimens of over 1 m in diameter over 5000 years old (Ruppert et al. 2004).

9.3 Sponges as Habitat Providers

Aggregations of sponges are observed in many different environments: coral reefs, mangrove forests, deep sea regions and polar regions. Sponge aggregations have been shown to increase habitat complexity and consequently increase the abundance and biodiversity of benthic associated species (Maldonado et al. 2015). Sponges provide associated species with various services such as shelter from predation, food availability, breeding grounds, and substratum to settle on.

9.3.1 Tropical Habitat Providers

On tropical coral reefs, much habitat complexity is provided by corals. However, sponges may also contribute to habitat facilitation either directly or indirectly. For example, on Caribbean reefs, 39 sponge-dwelling fish species were found (Tyler and Böhlke 1972). Different degrees of sponge associations were described by Tyler and Böhlke (1972). Some goby species are classified as obligate sponge-dwellers with some even showing morphologically specialized features for living exclusively inside sponges (Tyler and Böhlke 1972). Other fish species of various families are

simply fortuitous sponge-dwellers. They only use sponges for the deposit or brooding of eggs and usually live outside of sponges.

Tube- and vase-shaped sponges on coral reefs off Key Largo, Florida, offer a physical barrier that lowers fish predation pressure on brittle stars (Henkel and Pawlik 2005). A chemical defense to deter fish predators is lacking in these sponges, which might make them a preferred surface for deposit feeders next to a predation refuge (Henkel and Pawlik 2005). Sponge-associated brittle stars are known to consume detrital particles adhering to the sponges' surface (Hendler 1984).

Indirectly, sponges in Bahamian caves contribute to increased herbivore abundance on coral reefs. The cave sponges provide corals and algae with enhanced nutrient levels. Coral cover and diversity was higher close to cave openings compared to similar sites further away (Slattery et al. 2013). The increased habitat complexity (through corals) and increased food availability (through algae) result in increased herbivory.

9.3.2 Deep-Sea Habitat Providers

In the deep sea, scarcity of complex structural habitat makes sponge grounds one of the most important hotspots for biodiversity (Hogg et al. 2010). Demosponges (Klitgaard 1995; Maldonado et al. 2015) and glass sponges (Beaulieu 2001) have been described as abundant deep-sea habitat providers for associated fauna. Klitgaard (1995) found 242 species associated with deep-sea demosponge aggregations in the North Atlantic. The majority of the sponge-associated fauna used the sponges as substratum.

Biohermal glass sponge reefs increase habitat complexity through biohermal growth. Glass sponges are able to fuse their spicules by a process called secondary silicification. Young sponges settle on the silica skeletons left behind by their ancestors. Fish, crustaceans, nudibranchs, and infaunal polychaetes were found to be more abundant in biohermal glass sponge reefs compared to surrounding areas (Maldonado et al. 2015). This could be due to the improved hydrodynamics of the boundary layer and the shelter the glass sponge reef topography provides to the benthic fauna. Additionally, the energy and nutrient cycling which increases benthic-pelagic coupling (see Sect. 9.4) could also help increase local benthic biodiversity.

Lithistid sponges are known to form rigid massive silica skeletons, which do not easily dissolve. New lithistid sponge recruits can settle on these skeletons, which results in biohermal growth much like glass sponge reef growth. Lithistid sponge mounds on the seabed attract fish and various macro-invertebrates (Maldonado et al. 2015).

In the deep sea off California, USA, 139 taxa of marine organisms were found to be associated with glass sponge stalks (Beaulieu 2001). These micro cryptic habitats were dominated by zoanths and polychaetes that used the stalks as a hard substratum to grow on.

Carnivorous cladorhizid sponges on the Macquarie Ridge live among many other invertebrates (Maldonado et al. 2015). However, cladorhizid sponges might not increase biodiversity by increasing habitat complexity. Because of their carnivorous characteristics, cladorhizid sponges might prevent larvae from settling.

9.3.3 Arctic Habitat Providers

Seabed gouging is a process that is described as drifting ice going through the benthos with the keel when passing through shallower waters. Seabed gouging is known to disturb glass sponge aggregations in the Weddell Sea, Antarctica, leaving behind sponge spicule mats, which serve as a substratum for other organisms (Maldonado et al. 2015). Muddy, soft seabeds were linked to species-poor communities, while solid sponge spicule mats were linked to species-rich communities (Hogg et al. 2010).

9.3.4 Habitat for Commercially Important Species

Sponges provide structural habitat which harbors food and/or provides shelter from predators for fishes and crustaceans (Butler et al. 1995; Ryer et al. 2004; Miller et al. 2012). Some sponge-associated species are also commercially important for fisheries.

High mortality of sponges after cyanobacterial blooms in Florida Bay had consequences for juvenile Caribbean spiny lobster living around these sponges. These lobsters are important to commercial fisheries. The spiny lobsters were exposed to increased predation due to the lack of shelter that was previously provided by sponges (Butler et al. 1995).

Other sponge-associated species are threatened by fishing activities (such as trawling and dredging). When fishing gear (such as nets and long lines) is towed across the seabed, it removes and damages large epibenthic organisms, including sponges. Groundfish (such as cod and ling) are often caught in trawl nets along with sponges (Hogg et al. 2010). Cod, ling, halibut, and Pacific Ocean perch are commercially important fish species that might face negative consequences of sponge habitat loss. Regulation is needed to protect sponge aggregations and the species living in close proximity to them.

Juvenile halibut showed a strong preference for habitats with a 16% sponge coverage compared to habitats with bare

sand in laboratory experiments (Ryer et al. 2004). This strong preference could be due to less predation vulnerability for halibuts. Ryer et al. (2004) observed predators being impeded on their prey pursuit by the sponges.

Rockfishes, including the Pacific Ocean perch, are associated with sponges in the southeastern Bering Sea (Miller et al. 2012). The sponges are thought to support diverse and abundant macroinvertebrate communities that serve as prey for rockfish next to providing shelter from predators (Miller et al. 2012).

9.4 Nutrient Cycling by Sponges

9.4.1 Sponge Loop

Nutrient cycling is essential to maintain a balance between food and waste for all species in an ecosystem food web. In marine environments, primary producers on reefs, such as corals and algae, release 50% of their mucus, of which 80% is dissolved directly into the adjacent seawater (Wild et al. 2004, 2008). DOM, consisting of, e.g., carbohydrates, lipids, and proteins, is an abundant potential food source on reefs for microbes (Azam et al. 1983), yet largely unavailable to most heterotrophic reef inhabitants (de Goeij et al. 2013).

Conventionally, microbial degradation of DOM in the water column and sediment has been considered the primary pathway in DOM cycling (Harvey 2006; Wild et al. 2004, 2009). However, decades ago already, suggestions were made that the traditional view of sponges only feeding upon particulate food sources, such as bacteria and plankton (Reiswig 1971; Pile et al. 1996, 1997), was insufficient to sustain their nutritional requirements (von Putter 1914).

Recently, sponges have been discovered to take up DOM, thereby providing an important role in benthic-pelagic coupling (de Goeij et al. 2013; Lesser 2006). Only 42% of the dissolved carbon taken up from the ambient water is respired by sponges. Therefore, the remainder is most likely either assimilated, used for reproduction, or converted into particulate organic matter (POM) through cell shedding (Alexander et al. 2014; de Goeij et al. 2009). Assimilation, in the form of growth, takes place very little in encrusting sponges; thus, conversion to POM is considered the preferred route. This shedding takes place mainly among the choanocytes which, unsurprisingly, also show high proliferation rates (Alexander et al. 2015) 2900 times faster compared to their normal growth rate of other cells (Ayling 1983). A recent study has revealed that these other cells, specifically from the mesohyl, contribute additionally to the production of POM (Maldonado 2016). This high cell turnover can be a clever mechanism to prevent permanent damage to the sponge caused by environmental stress (de Goeij et al. 2009) and creates the opportu-

nity for higher trophic levels to feed on these cells (de Goeij et al. 2013).

The turnover of DOM by sponges is faster than by microbes (van Duyl et al. 2008) and equals the order of magnitude of the gross primary production in the Caribbean reef ecosystem (de Goeij et al. 2013). Thus, apart from the conventional microbial loop (Azam et al. 1983), accounting for only 10% of nutrient cycling, a sponge loop (de Goeij et al. 2013), accounting for 90%, now supports a major role in the DOM reincorporation pathway. The produced POM is, thereafter, most likely consumed by detritivores, which can be present as associated sponge fauna in so-called consumer-resource interactions (de Goeij et al. 2013; Rix et al. 2016).

Most food web models do not include the role sponges have in cycling resources in their environments, which makes the many current models incomplete. Future food web models can be improved by adding sponge energy and nutrient cycling. Moreover, sponges carry out benthic-pelagic coupling, which is crucial to retain nutrients within an environment. Within this section, we will focus on the three important cycles of: carbon, nitrogen and phosphorous, as key components to sustaining life.

9.4.2 Carbon Cycling by Sponges

Carbon is one of the main components of biological life forms, and sponges play an important role in carbon cycling in aquatic ecosystems. They take up and release carbon to their environment in several ways (Rix et al. 2017).

Organic matter dissolves in water after extracellular release or cell lysis by primary producers such as phytoplankton, macrophytes, and coral symbionts. Dissolved organic carbon (DOC) concentration can differ in space and time in aquatic ecosystems: 0.7 to 45 mg · L⁻¹ in rivers, 0.7 to 330 mg · L⁻¹ in lakes, and 0.5 to 3.0 mg · L⁻¹ in the ocean (Mulholland 2003). DOC is a large energy resource in aquatic environments and makes up a large part of DOM (Wild et al. 2004). For example, on coral reefs, more than 90% of the total organic matter consists of DOM (Carlson 2002). However, the carbon fraction of DOM is not readily available to most organisms. Mostly sponges and microbes utilize DOC as an energy source. The DOC uptake of Caribbean coral reef sponges is estimated to be 90 to 350 mmol C · m⁻² · day⁻¹ (de Goeij and Van Duyl 2007), which is comparable to the gross primary production of 200 to 600 mmol C · m⁻² · day⁻¹ on coral reefs (Hatcher 1990). DOC removal on coral reefs is mostly accounted for by sponges compared to only 5 to 50 mmol C · m⁻² · day⁻¹ of microbial DOC uptake (de Goeij and Van Duyl 2007; Haas et al. 2011). Total organic carbon (TOC) uptake of coral reef sponges consists predominantly (56 to 97%) of DOC (de Goeij et al. 2017). Next to filter feeding on carbon sources, some sponge species host

photoautotrophic symbionts, which photosynthesize and transfer carbon into the sponge's tissue (Wilkinson 1983; Fiore et al. 2013). Wilkinson (1983) found that the carbon fixation rate in coral reef sponges containing symbiotic cyanobacteria was only 2.4 to 6.6% in dark conditions compared to light conditions. However, sponges usually do not rely chiefly on the symbionts for nutrition. Additionally, apart from dissolved food sources, particulate sources such as bacteria can act as a food source (Kahn et al. 2015).

After DOC uptake, 3.7 to $14.7 \mu\text{mol DOC} \cdot \text{mmol C}_{\text{sponge}}^{-1} \cdot 12 \text{ h}^{-1}$ is assimilated inside sponge cells and sponge-associated microbe cells (Rix et al. 2017). Carbon fixation in sponges is not restricted to the abundance of associated microbes because LMA sponges also take up DOC (de Goeij et al. 2017). Part of the carbon taken up by sponges is respired; another part is used to grow. De Goeij et al. (2017) estimated a daily net biomass increase of 38% for *Halisarca caerulea* if all assimilated carbon (61% of the TOC uptake) would be used for growth. However, sponges do not grow as fast as expected. Only 2.2% of TOC uptake was used for a daily biomass increase of 1.3% (Alexander et al. 2015). Instead, sponges show a rapid cell turnover. An average cell cycle of only 6 hours was determined for *H. caerulea* (de Goeij et al. 2009). This cell turnover is the result of rapid cell proliferation and shedding of old cells. Fifteen to 24% of the carbon assimilated by sponge holobionts is released as particulate organic carbon (POC) (Rix et al. 2017). This is how sponges transform energy in the form of DOC to POC. Carbon becomes available to detritivores (such as ophiuroids, crustaceans, snails, and polychaetes) that consume sponge-derived POC (de Goeij et al. 2013; Rix et al. 2017).

Alternatively, sponges make carbon available to their environment through bio-erosion. Excavating sponges break down calcium carbonate chemically by dissolution and mechanically by chip production (Zundevich et al. 2007).

9.4.3 Nitrogen Cycling by Sponges

Apart from carbon, nitrogen is important in marine ecosystems as it is essential to produce amino acids which in turn make proteins and DNA. Moreover, it is often a limiting nutrient to meet energy requirements in tropical reefs (Muscatine and Porter 1977; Delgado and Lapointe 1994; Fiore et al. 2013). Paradoxically, the abundance of nitrogen in air (78%) remains unavailable for animals unless nitrogen-fixing bacteria, e.g., cyanobacteria, or to a lesser extent, lightning converts nitrogen to a biologically available form. The (re)cycling of inorganic nitrogen is therefore imperative and occurs via different pathways both in surface waters and the deep sea. Nitrification is considered a source of bioavailable nitrogen, whereas denitrification is considered a sink.

These processes are of importance to species-specific ecosystem services to the surrounding environment. For example, benthic microbial nitrifiers provide nitrate to the root nodular system of macrophytes.

Former studies have shown that inorganic nitrogen cycling in sponges takes place and is mediated by the microbial biofilm present in the sponge's tissue (Taylor et al. 2007; Hoffmann et al. 2005; Fiore et al. 2010; Schläppy et al. 2010; Gloeckner et al. 2014). For example, Mediterranean sponges can actively switch between aerobic and anaerobic metabolism by inhibiting water flow over time (Hoffmann et al. 2008). This could induce anaerobic environments to trigger supposed "coupled nitrification-denitrification," meaning a part of the nitrified nitrate is subsequently transformed into nitrogen gas.

Unsurprisingly, the two most present processes to consider in microbial nitrogen cycling in sponges are nitrification and denitrification (Southwell et al. 2008) (Fig. 9.3). Nitrification is a two-tiered process where ammonia-oxidizing bacteria (AOB) perform the first, often rate-limiting, step from ammonium to nitrite, while the nitrite-oxidizing bacteria (NOB) oxidize the latter to nitrate. AOBs are usually beta- and gamma-proteobacteria, and NOB belong to *Nitrobacter* and *Nitrococcus* family (Bayer et al. 2008). Factors that affect nitrification include metabolic interactions in the microbial community and respiration rates but most importantly oxygen concentrations (Müller et al. 2004). If oxygen is lacking, nitrification cannot take place. Sponges, like many other marine invertebrates, usually excrete ammonium as a waste product (Brusca and Brusca 1990). Therefore, the unexpected excretion of nitrate was the first evidence of microbial nitrification within the sponge (Diaz and Ward 1997; Jiménez and Ribes 2007).

Apart from aerobic nitrification, anaerobic processes such as denitrification or anaerobic ammonium oxidation (anammox) also occur regularly in sponges and have, for example, been shown in the tropical sponge *Xestospongia muta* (Fiore



Fig. 9.3 Simplified diagram of nitrification and denitrification superimposed on a vertical slice of a sponge *Geodia barretti*

et al. 2013). First, to confirm the presence of anaerobic zones within sponge tissue, Hoffmann et al. (2005) have investigated bacterial metabolic activity *ex situ* within the HMA sponge *Geodia barretti*. Their research revealed a steep oxygen profile within intact sponges in which anoxic microenvironments could allow denitrifying bacteria to reduce nitrate in nitrogen gas. Furthermore, Fiore et al. (2013) found a negative efflux of nitrate, indicating that either denitrification or anammox was taking place inside the sponge. However, the Caribbean sponge *X. muta* was actively pumping during the study contradicting the earlier hypothesis of Fiore et al. (2010) where lack of pumping would equal denitrification. Finally, Hoffmann et al. (2009) discovered both nitrification and denitrification in *G. barretti* with rates of 566 and 92 nmol N · cm⁻³ sponge · day⁻¹, respectively. However, this research was performed with explants (3 cm³ radial cylinders of cut sponge tissue). Even though sponges are known for their totipotent cells and quick regeneration after damaging (Alexander et al. 2015), using explants alters the aquiferous system to such extent that pumping is most likely inhibited.

Although the deep sea is often viewed as an uninhabitable environment, particular areas like hydrothermal vents, cold seeps, and sponge grounds actually harbor complex ecosystems (Klitgaard 1995; Roberts et al. 2006; Cathalot et al. 2015). Their dependence on nitrogen is influenced by the influx of inorganic and organic nitrogen from surface waters through vertical mixing (Romera-Castillo et al. 2016) and bottom water advection (Davies et al. 2009). Regarding nitrogen cycling, deep-sea sponges (DSS) can be of particular interest, as in some areas they make up 90% of the benthic biomass (Klitgaard and Tendal 2004; Murillo et al. 2016) and are important filter feeders (Kutti et al. 2013). However, the relevance of DSS is only currently emerging with studies showing that sponges have the potential to recycle essential elements like carbon and nitrogen (Witte et al. 1997; van Oevelen et al. 2009; Rix et al. 2016). As mentioned before in Sect. 4.1, in shallow tropical reefs, sponges are known to retain carbon through the sponge loop, whereas they release nitrogen (de Goeij et al. 2013). Rix et al. (2016) were the first to examine that DSS might have a similar potential in fueling the ecosystem with nitrogen resembling their warm water counterparts. However, she only performed this in *ex situ* aquarium experiments. Whether a potential cold water sponge loop also takes place in the deep sea is yet to be confirmed, especially regarding the cycling of inorganic nutrients.

9.4.4 Phosphorous Cycling by Sponges

Finally, phosphorous is essential for the biological synthesis and for the transfer of energy (Tyrreell 1999). In aquatic environments, phosphorous budgets consist of three compo-

nents: particulate phosphorous, dissolved inorganic phosphate, and dissolved organic phosphate (Maldonado et al. 2012). We know that of these three, the latter is present most abundantly (Dyhrman et al. 2007). However, phosphorous cycling has not undergone comprehensive research as the two nutrients aforementioned. Therefore, data is limited to a few studies which have only concluded that both low and high microbial abundant sponges act as a net source of phosphate reviewed in Maldonado et al. (2012). Further research into phosphorous cycling by sponges would give us more insight into the potential limiting factors of sponge habitats.

9.5 Marine Natural Products from Sponges

9.5.1 Introduction

Since the early Egyptian times, sponge skeletons have been harvested for its cleaning properties and as hygienic tools (Pronzato 2003). Likewise, the earliest medicinal feature, in Greek times, a cold wet sponge placed on the heart, would resurrect the fainted (Jesionowski et al. 2018). However, these days, the capacities of sponges have shifted from a bio-material to a biomolecular source (Jesionowski et al. 2018). Within the last 20 years, the detection of marine natural products (MNP) has increased, with an estimate of 15,000 MNPs discovered until 2010 (Hu et al. 2011). In the search for bioactive compounds in the marine environment, vertebrate animals such as fish, sharks, and snakes have been examined. Among the invertebrates, more groups have been examined including tunicates, echinoderms, algae, mollusks, corals, and sponges. Finally, microorganisms were examined, and of those several bacteria, fungi, and cyanobacteria showed potential (Alonso et al. 2003). The fact that sponges can harbor high densities of microorganisms in the mesohyl layer makes them very potent study objects for novel bioactive compounds (Alexander 2015). Moreover, sponges lack an immune system, protective armor, and mobility which pressed on the evolution to synthesize compounds for defensive purposes. For example, instead of an immune system, when invaded with foreign material, sponges produce a range of chemicals, such as 3-alkyl-pyridinium, that inhibits movement of surrounding cells preventing the use of the sponge's internal transport system (Sepčić et al. 1999).

Interestingly, there is considerable debate about whether sponges are the true producer of these compounds and not just hosts to the true producers: microorganisms (Jensen and Fenical 1994; Bultel-Pončć et al. 1997; Hentschel et al. 2006 reviewed in Mehbub et al. 2016b). It would not be a surprise if the majority of these compounds are a result of the symbiotic microorganisms rather than the host, considering in HMA sponges the body mass could be accounted for by bac-

teria to up to 40% (Taylor et al. 2007). Either way, it is important to investigate the possibilities for MNPs within the holobiont as they ultimately provide the compound as a whole organism. This holobiont approach does lead to some discussion about the true producer and if they can do so without each other's presence. Several reviews have discussed this. In Jensen and Fenical (1994), the problem is mentioned that the sponge does contain a microbial community distinct of the surrounding water, implying that bacteria need the sponge host to be initially present. A prime example of misjudgments of the true producer was found after flow cytometric separation of sponge and microbial fraction localizing the true producer: a prokaryotic cell (Unson and Faulkner 1993).

9.5.2 Potential for Exploitation

The potential to exploit marine sources for pharmaceuticals has been of major importance in recent times since we cannot only rely on terrestrial sources alone. Moreover, it is of importance to investigate these potential pharmaceuticals, because infectious microorganisms constantly evolve a resistance against current pharmaceuticals. Several reviews have focused on MNPs in general (Faulkner 2000; Blunt et al. 2017, 2018); yet some have also focused only on sponge-specific MNPs (Mehbub et al. 2016a).

The reason for sponges to entail such a vast majority of the MNPs found in the marine environment could well be caused by their survival over the past 580 million years. During this time, they have undergone huge environmental changes which induced specialization and formation of vastly different species over the entire aquatic environment. Sponges are at present divided into 4 distinct classes, 25 orders, 128 families, and 680 genera (Abad et al. 2011). These specializations over all the different groups together with their capacity to hold endosymbionts led to the production of a large range of (secondary) metabolites.

Among all marine species, sponges are the most investigated with nearly 30% of all MNPs discovered (Mehbub et al. 2016a). This accounts for a total of 4851 compounds of which 1499 isolated only between 2008 and 2012. The compounds were classified into 18 chemical classes among them: acids, alkaloids, esters, fatty acids, and further less relevant groups (Mehbub et al. 2016a). These compounds contain a wide variety of bioactivities: anticancer, antiviral, antibacterial, anti-inflammatory, and many more neural activities (Chakraborty et al. 2009). The latter is of importance because of the vast presence of patients with neurodegenerative diseases especially in high-income countries (Global Health Estimates 2016). Moreover, many studies have investigated the neuroprotective capacities of the MNPs in sponges. Compounds were found with activities such as modulation

of the neurotransmitters acetylcholinesterase and glutamate, decreasing oxidative stress, enrichment of serotonin, and neurite growth (Alghazwi et al. 2016). However, none of these compounds have yet been developed as a finalized marine pharmaceutical.

9.5.3 Culturing of Sponges

Since the eighteenth century, reconstructive growth of sponges has been recorded, with major advances made at the beginning of the twentieth century by Henry Moore in Florida (Jesionowski et al. 2018). Later research has investigated the potential of secondary metabolites regarding their antimicrobial activity (Thompson et al. 1985) acting as therapeutic drugs, collagen, and optical equipment (Munro et al. 1999). However, this has so far been held back by what is referred to as "the supply problem" (Osinga et al. 2003). The supply problem states that we are limited by the small amount of chemical present within the sponge compared to its biomass. Moreover, the dilution effect of the ocean requires compounds to be very stable and highly active (Abad et al. 2011) which would explain the low quantities found. To overcome this, we are required to grow enormous sponge biomass to perform acceptable preclinical and clinical trials. As harvesting the enormous sponge biomass from the environment would not be sustainable, therefore we have to look at alternatives. Thus, opportunities in biotechnological methods are progressively favored to avoid the supply problem. One possible solution is to have the sponge-associated microorganisms to flourish independently of their host to produce larger quantities of MNPs. Another growing area is the use of sponge cell cultures, which avoids the complex environment necessary for whole organisms (Müller et al. 2000). Yet some advance has been made to express these biosynthetic pathways of interest in more easily cultivatable hosts to overcome the supply problem (Wilson et al. 2014). Nevertheless, large-scale production of sponge biomass for MNPs remains unsuccessful.

As mentioned afore, sponges can grow in vastly different natural environments, from the deep sea to tropical reefs. At present, in situ culture has been the only successful approach at harvesting considerable biomass of sponges. The usual method is to use asexual reproduction by fragmentation which creates explants hanging from buoy lines in the water column (Osinga et al. 2003). However, in situ culturing has serious drawbacks such as incoming diseases, abrupt weather changes, or habitat disruption. This has impeded large-scale in situ production. Therefore, Osinga et al. (2003) started to experiment with growing sponges in vivo in bioreactors. They succeeded to grow a tropical sponge *Pseudosuberites andrewsi* on a single marine diatom species either intact or as a filtered crude extract. However, unlike freshwater sponges

Ephydatia fluviatilis and *Spongilla alba*, which have shown to grow successfully on a stock of *Escherichia coli* (Francis et al. 1990), the lack in further culture literature might explain that proper food source or mixture to grow marine sponges is still elusive. Though discussion remains even on the selection of one food source, we know marine sponges feed on several food sources simultaneously, such as: picoplankton, bacteria, viruses and dissolved organic substrates (de Goeij et al. 2013). It could well be that the quality of the particulate food sources and the composition of these dissolved organic substrates are decisive. Yet apart from food sources, there are abiotic variables (such as temperature, salinity, and light) that can determine growth. Therefore, more research should be undertaken finding the balance in food sources while breeding marine sponges under various laboratory conditions.

9.6 Conclusions

In this review, we have tried to outline the importance of sponges to their environments as well as to humans. Sponges are a diverse phylum (consisting of more than 8000 species). In this phylum, a broad range of morphologies, feeding habits, and reproduction strategies are present. Much about these various characteristics of sponges is yet to be discovered and understood. These future discoveries are not only interesting for sponge-specific knowledge but also of importance to a wider understanding of evolution and aquatic ecosystems in general.

Sponges are important to their environment for multiple reasons. Sponges provide habitat and food for fish, crustaceans, and many other animals in a variety of ecosystems ranging from tropical coral reefs to deep-sea sponge grounds. Among these sponge-dwelling organisms are even commercially important species.

Additionally, sponges shape the communities surrounding them by playing a significant role in the cycling of energy and nutrients. Sponges make carbon, nitrogen, and potentially phosphorus available to higher trophic levels. By doing so, these elements are retained within the ecosystems sponges live in and would otherwise not be available to many organisms.

Lastly, sponges are also important to humans in upcoming pharmaceutical research. The high abundance of symbiotic microorganisms living within sponges makes sponges good candidates for novel bioactive compound discovery. It is expected that sponge-associated marine natural products have potential as bioactive compounds in drugs. Therefore, it is important to invest time in uncovering the importance of this phylum within all aquatic ecosystems.

Appendix

This article is related to the YOUMARES 9 conference session no. 11: “Sponges (Porifera): Fantastic filter feeders.” The original Call for Abstracts and the abstracts of the presentations within this session can be found in the Appendix “Conference Sessions and Abstracts”, Chapter “9 Sponges (Porifera): Fantastic filter feeders”, of this book.

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