Chapter 8
Nutrient Fluxes and Ecological Functions of Coral Reef Sponges in a Changing Ocean

Jasper M. de Goeij, Michael P. Lesser, and Joseph R. Pawlik

Abstract Coral reefs are iconic examples of biological hotspots, highly appreciated because of their ecosystem services. Yet, they are threatened by human impact and climate change, highlighting the need to develop tools and strategies to curtail changes in these ecosystems. Remarkably, ever since Darwin's descriptions of coral reefs, it has been a mystery how one of Earth's most productive and diverse ecosystems thrives in oligotrophic seas, as an oasis in a marine desert. Sponges are now increasingly recognized as key ecosystem engineers, efficiently retaining and transferring energy and nutrients on the reef. As a result, current reef food web models, lacking sponge-driven resource cycling, are incomplete and need to be redeveloped. However, mechanisms that determine the capacity of sponge "engines," how they are fueled, and drive communities are unknown. Here we will discuss how sponges integrate within the novel reef food web framework. To this end, sponges will be evaluated on functional traits (morphology, associated microbes, pumping rate) in the processing of dissolved and particulate food. At the community level, we discuss to what extent these different traits are a driving force in structuring shallow- to deep-sea reef ecosystems, from fuel input (primary producers) to engine output (driving and modulating the consumer food web). Finally, as climate change causes the onset of alterations in the community structure and food web of reef ecosystems, there is evidence accumulating that certain biological pathways are triggered, such as the sponge loop and the microbial loop, that may shift reef ecosystems faster than their original stressors (e.g., warming oceans and ocean acidification). Unfortunately,

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these biological pathways receive much less attention at present, which seriously hampers our ability to predict future changes within reef ecosystems.

Keywords Sponges • Nutrient cycling • Sponge loop • Coral reef • Food web • Ecosystem engineers

8.1 Introduction

8.1.1 Sponges as Key Engineers in Changing Coral Reef Ecosystems?

Coral reef ecosystems were originally described as enigmatic hotspots of biodiversity, as seemingly paradoxical highly productive ecosystems residing in marine deserts, and, from a purely anthropomorphic viewpoint, just marvels of natural beauty (Darwin 1842). In the year 2016, 174 years later, it is crystal clear that coral reef ecosystems around the world are rapidly declining because of the combined effects of human activities (e.g., coastal development, overfishing, and eutrophication), including the most detrimental, longer-term effects of climate change (e.g., ocean acidification, increases in seawater temperature, and the intensity and number of hurricanes and tropical cyclones) (Knowlton 2001; Pandolfi et al. 2005; Hoegh-Guldberg et al. 2007; Hughes et al. 2007; Wilkinson 2008; Bender et al. 2010; Hoegh-Guldberg and Bruno 2010). While the overall decline of reefs in response to these stressors has received significant attention, our understanding of ecological processes that shaped coral reefs in the first place and how such processes change with shifting reef states has not received similar attention. Consequently, changing patterns of reef community composition have been well described, but processes shaping these patterns remain poorly understood. In particular, the failure to recognize other key ecosystem drivers other than the "big three" (i.e., corals, algae, fish) by coral reef scientists in recent decades has hampered our ability to predict changes on coral reefs. In this chapter we will recognize a so far largely neglected key ecosystem driver in the cycling of nutrients and energy on coral reef ecosystems: the sponges.

The prevailing view of how highly productive coral reefs maintain such high biomass and biodiversity under oligotrophic conditions was recently challenged with the discovery of the so-called sponge loop pathway (De Goeij et al. 2013), in which sponges efficiently shunt a significant proportion of the ecosystem resources (i.e. defined here as carbon and nitrogen) to higher trophic levels in an otherwise low-food environment. This has provided new insight into how sponges are key ecosystem engineers that act like ecosystem "engines": by efficiently retaining, transforming, and allocating nutrients and energy, they drive communities within the food web framework of coral reef ecosystems. As a result, current reef food web models, without the inclusion of sponge-driven resource cycling, are incomplete and need be

redeveloped. These models are a much-needed foundation to predict future scenarios for tropical, temperate, and cold-water reef ecosystem ecology. However, mechanisms that determine the capacity of sponge engines, how they are fueled, and how they drive reef communities within the food web are at present largely unknown. Moreover, the sponge loop sparked significant interest, controversy, and discussion in the scientific world (Maldonado 2015; Slattery and Lesser 2015; Pawlik et al. 2015a, b). It is therefore time for an integrated review and discussion of viewpoints and knowledge gaps we are currently facing in order to predict how sponge community structure and biomass change under future scenarios of climate change but also how sponges change the ecosystems in which they reside, from shallow-water tropical to cold-water deep-sea coral reefs. In this chapter, we will therefore first (Sect. 8.2) present a summary of known carbon and nitrogen fluxes mediated by sponge communities at ecosystem scale. Secondly (Sect. 8.3), we will discuss critical knowledge gaps at the organismal and ecosystem level concerning the integration of sponges in present food web frameworks. And last (Sect. 8.4), we will end with a perspective on future scenarios of reef development with sponges integrated as key ecosystem engineers.

8.2 Carbon and Nitrogen Cycling on Reef Ecosystems Mediated by Sponges

Sponges are well known to be efficient filter feeders upon particles, such as nano-and picoplankton (e.g., Reiswig 1971; Pile et al. 1996; Ribes et al. 1999; Lesser 2006; Yahel et al. 2007; McMurray et al. 2016), and their ability to take up and release dissolved nutrients (e.g., Yahel et al. 2003; De Goeij et al. 2008a; Southwell et al. 2008b; Fiore et al. 2013; Mueller et al. 2014a; McMurray et al. 2016). Some species are able to fix carbon (e.g., Wilkinson 1987; Trautman and Hinde 2002; Erwin and Thacker 2007; Fiore et al. 2013) or nitrogen (e.g., Wilkinson and Fay 1979; Wilkinson et al. 1999) through their associated bacteria. They generally show a net release of inorganic nitrogen (e.g., Corredor et al. 1988; Southwell et al. 2008b; Fiore et al. 2013; Keesing et al. 2013), thereby using processes of nitrification (e.g., Diaz and Ward 1997; Southwell et al. 2008a) or denitrification (e.g., Hoffmann et al. 2009; Fiore et al. 2013). Excavating sponges can even influence carbon cycling by physically degrading carbonate structures through bioerosion (reviewed by Schönberg 2008). At the organismal level, these are just few examples of key publications describing sponge-mediated carbon and nitrogen processes (also extensively reviewed by Maldonado et al. 2012).

At the ecosystem level, the influence of sponges in biogeochemical cycles is much harder to assess, as data are lacking or incomplete. But the few studies that have extrapolated sponge-mediated fluxes of carbon or nitrogen to the ecosystem level show the potential of sponge ecological contributions to their ecosystem. Natural assemblages of sponges on the temperate reefs of New Zealand removed a significant part, up to 12.1%, of the available particulate organic carbon pool (Perea-Blazquez et al. 2012). Sponges also have a significant effect on reef biogeochemistry as sources

of dissolved inorganic nitrogen (DIN) (Corredor et al. 1988; Southwell et al. 2008b; Keesing et al. 2013). They contribute 10–18% of the total recycled nitrogen flux across the South Australian continental shelf to a water depth of 100 m (Keesing et al. 2013). Jiménez and Ribes (2007) estimated the DIN release by sponges on a Mediterranean reef to exceed nitrogen primary production demands by 2–7 times. On tropical, shallow coral reefs, the estimated efflux of DIN by the sponge community on a 600 m^2 reef in the Florida Keys—note: excluding cryptic (i.e., living in caves, cavities, crevices, etc.) and non-cryptic encrusting sponges—is approximately 15 mmol N m^{-2} day^{-1} (Southwell et al. 2008b), which is higher than the reported average release rates of the entire coral ecosystems (2–6 mmol N m^{-2} day^{-1}) (Atkinson and Falter 2003). But even in the deep sea, sponges exhibit very high grazing capacity, showing the highest ever reported grazing rates on particulate organic carbon as compared with any other filter-feeding organism within their ecosystem (Kahn et al. 2015). The total organic carbon uptake rates through these deep-sea glass "sponge grounds" (150–342 mmol C m^{-2} day^{-1}); (Kahn et al. 2015) are in fact in the same order of magnitude as total organic carbon uptake rates through the cryptic sponge communities on tropical coral reefs (90–350 mmol C m^{-2} day^{-1}) (De Goeij et al. 2013).

8.2.1 Sponges and Dissolved Organic Matter (DOM)

DOM is, by far, the largest source of organic matter (>90% of total) on reefs and is operationally defined as organic matter passing a fine filter (typically glass fiber filter GF/F with ±0.7 μm pore size or polycarbonate filter with 0.2 μm pore size) (Benner 2002; Carlson 2002). Sponges consistently possess the highest feeding efficiencies and even selective preferences for pico- and nanoplankton in comparison with DOM (e.g., De Goeij et al. 2008b; Mueller et al. 2014a; McMurray et al. 2016). However, when taken into account as food source, DOM generally encompasses the majority (56–97%) of a sponge's daily carbon intake (Table 8.1) on shallow reefs. It is striking that when one only considers studies that have *measured* DOM as food source (Table 8.1), 17 out of 20 investigated species show DOM uptake. Even more striking are the largely absent massive growth forms—see also Sect. 8.3 of this chapter; 5 out of 20, of which *Theonella swinhoei* (Yahel et al. 2003), *Agelas conifera* (Slattery and Lesser 2015), and *Xestospongia muta* (McMurray et al. 2016) are confirmed to take up DOM—and the complete lack of data from the Indo-Pacific coral reef region.

8.2.2 The Sponge Loop Pathway

Coral reefs are complex three-dimensional structures, of which most available space for settlement or excavation of benthic communities, such as sponges, lies underneath the reef (Garrett et al. 1971; Jackson et al. 1971; Ginsburg 1983). "The largest, but least explored coral reef habitat" (Richter et al. 2001) consists of framework cavities and

Table 8.1 Overview of dissolved organic matter (DOC) feeding by all 20 known species for which DOC was measured as part of the total organic carbon (TOC) intake by the sponge

Sponge	Location	Habitat	HMA/LMA	Shape	Net DOC uptake	% DOC on TOC	Net detritus production	Reference
Dysidea avara	Mediterranean, Spain	Temperate, shallow	LMA	Encrusting, mound	No	Net release	NA	Ribes et al. (1999, 2012)
Theonella swinhoei	Red Sea, Israel	Tropical, shallow	HMA	Massive, tubular	Yes	>90	Yes	Yahel et al. (2003)
Aphrocallistes vastus	NE Pacific, Canada	Cold, deep	LMA	massive, Branching	No (bulk DOC NA)	NA	NA	Yahel et al. (2007)
Rhabdocalyptus dawsoni	NE Pacific, Canada	Cold, deep	LMA	Massive, tubular	No (bulk DOC NA)	NA	NA	
Halisarca caerulea	Caribbean, Curaçao	Tropical, shallow	LMA	Encrusting, sheet	Yes	92	Yes	De Goeij et al. (2008a, b, 2013)
Mycale microsigmatosa	Caribbean, Curaçao	Tropical, shallow	LMA	Encrusting, sheet	Yes	93	NA	
Merlia normani	Caribbean, Curaçao	Tropical, shallow	LMA	Encrusting, sheet	Yes	94	NA	
Agelas oroides	Mediterranean, Spain	Temperate, shallow	HMA	Encrusting, globular	Yes	NA	NA	Ribes et al. (2012)
Chondrosia reniformis	Mediterranean, Spain	Temperate, shallow	HMA	Encrusting, globular	Yes	NA	NA	

(continued)

Table 8.1 (continued)

Sponge	Location	Habitat	HMA/LMA	Shape	Net DOC uptake	% DOC on TOC	Net detritus production	Reference
Chondrilla caribensis	Caribbean, Curaçao	Tropical, shallow	HMA	Encrusting, globular	Yes	NA	Yes	De Goeij et al. (2013)
Haliclona vansoesti	Caribbean, Curaçao	Tropical, shallow	LMA	Encrusting, mound	Yes	NA	Yes	
Scopalina ruetzleri	Caribbean, Curaçao	Tropical, shallow	LMA	Encrusting, mound	Yes	NA	Yes	
Cliona delitrix	Caribbean, Curaçao	Tropical, shallow	LMA	Excavating	Yes	81	NA	Mueller et al. (2014a)
Siphonodictyon sp.	Caribbean, Curaçao	Tropical, shallow	HMA	Excavating	Yes	83	NA	
Agelas conifera	Caribbean, Bahamas	Tropical, shallow	HMA	Massive, branching	Yes	56–97	NA	Slattery and Lesser (2015)
Hymedesmia coriacea	NE Atlantic, Norway	Cold, deep	LMA	Encrusting, sheet	Yes	NA	Yes	Rix et al. (2016a)
Mycale fistulifera	Red Sea, Jordan	Tropical, shallow	LMA	Encrusting, mound	Yes	NA	Yes	Rix et al. (2016a, b)
Hemimycale arabica	Red Sea, Jordan	Tropical, shallow	LMA	Encrusting, mound	Yes	NA	Yes	Rix et al. (2016b)
Chondrilla sacciformis	Red Sea, Jordan	Tropical, shallow	HMA	Encrusting, globular	Yes	NA	Yes	
Xestospongia muta	Caribbean, Florida Keys	Tropical, shallow	HMA	Massive, barrel	Yes	71	No	McMurray et al. (2016)

Shown are their location, habitat, whether they are high or low microbial abundance (HMA or LMA) species, their shape, and if detritus production has been established. *NA* not analyzed

(sub)marine caves (m-scale) to intraskeletal holes made by worms and excavating sponges (cm-scale), to interstitial sediment pores (μm-scale). One square meter of projected open reef can hide up to 8 m^2 of cryptic habitat (Richter et al. 2001; Scheffers et al. 2004). The volume of this framework is estimated to be 75–90% of the total reef volume (Ginsburg 1983). That framework is responsible for the uptake of 16–47% (Indo-Pacific, East Kalimantan, Indonesia) and 60–175% (Caribbean, Curaçao) of the gross primary production rates of an entire coral reef system (based on 200–600 mmol C m^{-2} day^{-1}; Hatcher 1990) (De Goeij and van Duyl 2007). The majority of organic carbon removal by the reef framework, >95% for both Indo-Pacific and Caribbean regions, was accounted for by dissolved organic carbon (DOC) (De Goeij and van Duyl 2007). Framework walls are almost completely covered by a wide variety of living organisms, mostly communities of crustose coralline algae and suspension or filter feeders, dominated by sponges (e.g., Jackson et al. 1971; Wunsch et al. 2000; van Duyl et al. 2006). These cryptic sponges, the majority millimeter-thick encrusting species, were not only shown to explain the uptake of (predominantly dissolved) organic matter (De Goeij et al. 2008a), but also that a significant part of that organic matter was subsequently released as detritus (De Goeij et al. 2013; Alexander et al. 2014). Whereas the majority of DOM is not readily available to most heterotrophic reef inhabitants, sponge-derived detritus, as it passively settles down on reef sediments and reef surfaces, is entering the classical food chain through detritivores. In this way, the cryptic sponge communities of Caribbean coral reef ecosystems may turn over the carbon equivalent of daily reef gross primary production (De Goeij et al. 2013).

In addition to a Caribbean reef ecosystem, the DOM-sponge-detritus pathway has now been shown for a Red Sea coral reef ecosystem but also in the deep, cold, and aphotic waters of a North Atlantic coral reef ecosystem (Rix et al. 2016a). However, the generality of this pathway remains, at the least, unclear and has triggered many questions and uncertainties (Maldonado 2015; Slattery and Lesser 2015; Pawlik et al. 2015a, b). Do all sponges (massive to encrusting, cryptic to open reef) contribute equally, or at all, to the sponge loop? What is the role of sponge-associated microbes in the processing of DOM? How does depth or light availability affect food availability on reefs, and how will that impact total reef fluxes of carbon and nitrogen?

8.3 The Role of Sponges in Ecosystem Biogeochemistry (Controversies and Knowledge Gaps)

8.3.1 Critical Knowledge Gaps at the Organism Level

8.3.1.1 Sponge Functional Diversity in Processing of (Dissolved) Organic Matter

At present, there are considerably more sponge species on Earth—8846 valid species in the World Porifera Database, distributed over five phylogenetic classes (Van Soest et al. 2017)—than mammals (5416) (Wilson and Reeder 2005). These sponge

species exist in habitats ranging from marine deep seas to freshwater mountain lakes and from pristine tropical coral reef waters to aquatic ecosystems adjacent to urban centers with millions of people, such as the Amsterdam canal system. It is common to distinguish between the differences in biological and physiological function of two mammal species, even when they occur at the same trophic level within a food web. For sponges, however, it is common to study "sponges," irrespective of their phylogenetic or trophic position. For example, it is unknown whether all sponges contribute (similarly or at all) to nutrient cycling within reef ecosystems through the sponge loop. There are, most likely, different types of sponges that possess functional traits that aid in the utilization and processing of DOM. And, most likely, physiological processes will occur at different rates between sponges living in different ecosystems, e.g., cold deep sea versus tropical shallow sea. Depending on their local biomass, this could determine their impact on the biogeochemical cycling of nutrients within those ecosystems. It is important to identify sponge functional types, since the current lack of knowledge on factors controlling DOM processing by different sponge types prohibits a comprehensive assessment of sponge DOM fluxes and will result in incorrect predictions of coral reef ecosystem biogeochemistry. Here, we will discuss three possible functional traits: associated microbes, morphology, and pumping activity.

Associated microbes—The processing of DOM in surface waters of the ocean is mediated through bacterial uptake and transfer to higher trophic levels through the well-established microbial loop (Azam et al. 1983; Graham et al. 2014). DOM is divided into specific functional groups: labile, semi-labile, and refractory. The latter is the largest part (70–80%) of the total pool but has very low bioavailability—i.e. defined at present as availability as carbon source for bacteria—giving it a residence time of years to centuries (Amon and Benner 1996; Carlson 2002). The semi-labile part of the DOM pool is more bioavailable, with a turnover rate of months to years (Anderson and Williams 1998). Labile DOM includes amino acids, sugars, and other low molecular weight compounds, which are most bioavailable to microbial degradation and have a turnover rate as low as several minutes (Carlson et al. 1994). Key studies on DOM processing within coral reef ecosystems have therefore focused, almost exclusively, on microbial degradation of DOM (e.g., Wild et al. 2004a, b; Nelson et al. 2011; Haas et al. 2011). Additionally, sponges contain diverse microbial communities within their tissues (e.g., Webster et al. 2001; Hentschel et al. 2002, 2003; Taylor et al. 2007). Those have been, not surprisingly, suspected as being responsible for the ability of sponges to process DOM (e.g., Reiswig 1971, 1981; Yahel et al. 2003; Ribes et al. 2012; Maldonado et al. 2012). In fact, (^{13}C–) isotope tracer experiments show that sponge-associated bacterial cells assimilate DOM (De Goeij et al. 2008b; Rix et al. 2016a, b). But, the same experiments show that also sponge cells can rapidly assimilate DOM.

In particular, the *relative abundance* of associated bacteria does not provide clear-cut evidence that DOM processes are strictly microbial. Sponges are roughly divided into two categories based on their number of associated microbes: the high microbial abundance (HMA) sponges, with 10^8–10^{10} bacteria per gram sponge, representing 20–35% of the sponge biomass (Reiswig 1981; Hentschel et al. 2012;

Gloeckner et al. 2014), and the low microbial abundance (LMA) sponges, with bacterial numbers per gram sponge roughly equivalent to ambient seawater concentrations (10^5–10^6 cells mL^{-1}) (Hentschel et al. 2006; Gloeckner et al. 2014). Surprisingly, 9 out of 17 sponges known to process DOM are LMA, *not* HMA species (Table 8.1). In conclusion, the capacity of sponges on coral reefs to process DOM may not solely be attributed to the number of associated microbes.

Another major gap in our knowledge is the relative contribution of sponge cells and associated microbial cells in physiological processes (including carbon and nitrogen cycling) within the sponge holobiont and whether these processes are symbiotic in nature. Molecular analyses show that sponge-associated microbes should be capable of a broad repertoire of carbon and nitrogen transformations as well as other types of metabolic interchanges (Hentschel et al. 2012; Fiore et al. 2015). However, symbiotic relations in the uptake and processing of energy and nutrients within the holobiont are often suggested, but direct evidence is still largely unavailable. To the best of our knowledge, only one isotope tracer experiment has shown the transfer of nitrogen from the associated microbes to the sponge host (Fiore et al. 2013). Few more studies have shown carbon transfer between host and phototrophic-associated microbes (Wilkinson 1983; Erwin and Thacker 2008; Weisz et al. 2010; Fiore et al. 2013). Photosynthetic cyanobacteria are among the most abundant group of sponge-associated microbes (e.g., Steindler et al. 2005; Usher 2008; Thacker and Freeman 2012). Transfer of photosynthate in the form of glycerol and organic phosphate from cyanobacterial symbionts to the sponge host has also been demonstrated (Wilkinson 1979). Additionally, despite the suggestion that the photoautotrophic symbionts of *Xestospongia muta* are commensal in nature (López-Legentil et al. 2008), the use of $H^{13}CO_3$ isotope tracer has shown the autotrophic uptake of dissolved inorganic carbon (DIC) by the bacterial symbionts of *X. muta* and subsequent transfer of that fixed carbon to the host (Fiore et al. 2013).

Sponge communities of the Indo-Pacific have been reported as being dominated by species that are phototrophic, meaning that they contain photosynthetic symbionts that are net primary producers (Wilkinson and Cheshire 1989; Wilkinson and Evans 1989; Powell et al. 2014; Pawlik et al. 2015b; Freeman and Easson 2016). While 20–58% of Caribbean sponges have been shown to contain photoautotrophic microorganisms (e.g., cyanobacteria, *Chloroflexi*, *Symbiodinium*) (Diaz and Rützler 2001), the photoautotrophic potential of species that have been intensively studied is lower than for foliose phototrophic Indo-Pacific sponge species (Erwin and Thacker 2008; Freeman and Thacker 2011). Photoautotrophic sponges have been previously classified as exhibiting production to respiration [P/R] ratios >1.5 (Wilkinson and Trott 1985) supplying up to 50% of a sponge's energy budget and 80% of its carbon budget (Wilkinson 1983; Cheshire et al. 1997). However, before classifying two geographical regions (Caribbean and Indo-Pacific) as distinct in terms of sponge photoautotrophy, this is an area of sponge biology that requires additional study: the use of a P/R cutoff of 1.5 by Wilkinson and Trott (1985) was not justified in the context of the most common cutoff for a positive P/R being a value of ≥1.0. Moreover, many technical problems are associated with short-term measurements to calculate P/R values, as were done in the abovementioned publications (see discussion in

Lesser 2013 for corals that also applies to sponges), so without doubt, quantitative data on sponge primary production from all coral reef regions in the world is needed to improve coral reef carbon budgets (Thacker and Freeman 2012; Pawlik et al. 2015a). The degree of distinction between geographical regions will be further discussed in the knowledge gaps at the ecosystem level.

Morphology and pumping rate—Sponges possess an extensive variety of growth forms and morphologies, from millimeter-thin sheets to meter-wide barrels, balls, or tubes (e.g., Hooper and Van Soest 2002; Van Soest et al. 2017). A comparison of sponge morphology as a function of LMA versus HMA status reveals no particular pattern. Sponges of all morphological types were represented across these two categories (see Table 1 in Pawlik et al. 2015a and Tables 8.1 and 8.2 in this study). In general, body morphologies have a significant effect on the supply of food (i.e. the availability of food size fractions) to benthic organisms (Abelson et al. 1993). A high body surface-to-volume ratio is particularly important in the uptake of dissolved substances, such as DOM (e.g., Siebers 1982; Azam et al. 1983). The high surface-to-volume ratio of encrusting sponges may thus provide an advantage in DOM uptake, as compared with the lower surface-to-volume ratio of ball- or barrel-shaped non-encrusting sponges (Fig. 8.1). The difference in volume-to-surface area ratio between a thin sheet encrusting and a massive ball growth form can be two orders of magnitude (Fig. 8.1). This may explain why all LMA species in Table 8.1 that take up DOM are all (thin) encrusting. But there is another important functional trait to consider here. The denser tissue and finer filter system of HMA species, as compared to LMA species, increases seawater contact time, causing lower pumping rates, which may allow a more important role for DOM in their diet (Weisz et al. 2008). However, this consequently means that, although DOM processing by LMA sponges may be limited by their lower concentrations of associated microbes, they likely process more water in a shorter time frame than HMA sponges. In terms of net carbon and nitrogen fluxes mediated by sponges, there was no significant difference found in bulk DOM assimilation rates between LMA and HMA sponge species (De Goeij et al. 2008a; Rix et al. 2016a, b). To adequately assess different functional types of sponges, i.e. the role of associated microbes, morphologies, and pumping rates to biogeochemical fluxes, "sponge" research should shift more from traditional descriptive to rigorous functional studies to address these issues.

8.3.1.2 Sponge Loop Controversies: Sponge Growth, Cell Turnover, and Detritus Production

Sponge growth—The original sponge loop pathway is based on the prerequisite that assimilated (predominantly dissolved) organic matter is shunted to higher trophic levels in the form of detritus. Production of detritus is hypothesized to derive from a high turnover of sponge cells under so-called "steady-state" growth conditions, i.e. defined as negligible net biomass increase (De Goeij et al. 2009, 2013; Alexander et al. 2014; Alexander et al. 2015a, b). The "steady-state" definition is confusing and certainly does not hold for the overwhelming number of open reef sponge

Table 8.2 Overview of detritus production (yes or no) by all 22 known species for which detritus was taken into account as part of the total organic carbon (TOC) budget by the sponge

Sponge	Location	Habitat	HMA/LMA	Shape	Net detritus production	Reference
Tethya crypta	Caribbean, Jamaica	Tropical, shallow	LMA	Massive, mound	Yes	Reiswig (1971)
Mycale sp.	Caribbean, Jamaica	Tropical, shallow	LMA	?	Yes	
Verongula gigantea	Caribbean, Jamaica	Tropical, shallow	HMA	Massive, vase	Yes	
Thenea abyssorum	NE Atlantic, Norway	Cold, deep	HMA?	Massive, ball/cup	Yes	
Thenea muricata	NE Atlantic, Norway	Cold, deep	LMA	Massive, ball/cup	Yes	
Theonella swinhoei	Red Sea, Israel	Tropical, shallow	HMA	Massive, tubular	Yes	Yahel et al. (2003)
Aphrocallistes vastus	NE Pacific, Canada	Cold, deep	LMA	Massive, branching	No	Yahel et al. (2007)
Rhabdocalyptus dawsoni	NE Pacific, Canada	Cold, deep	LMA	Massive, tubular	Yes	
Negombata magnifica	Red Sea, Israel	Tropical, shallow	LMA	Massive, tubular	No	Hadas et al. (2009)
Halisarca caerulea	Caribbean, Curaçao	Tropical, shallow	LMA	Encrusting, sheet	Yes	De Goeij et al. (2013) and Alexander et al. (2014)
Chondrilla caribensis	Caribbean, Curaçao	Tropical, shallow	HMA	Encrusting, globular	Yes	
Haliclona vansoesti	Caribbean, Curaçao	Tropical, shallow	LMA	Encrusting, mound	Yes	
Scopalina ruetzleri	Caribbean, Curaçao	Tropical, shallow	LMA	Encrusting, mound	Yes	
Clathria sp.	Caribbean, Curaçao	Tropical, shallow	LMA	Encrusting, sheet	Yes	
Monanchora arbuscula	Caribbean, Curaçao	Tropical, shallow	LMA	Encrusting, sheet	Yes	
Mycale microsigmatosa	Caribbean, Curaçao	Tropical, mangrove	LMA	Encrusting, mound	Yes	
Chondrosia reniformis	Mediterranean, Spain	Temperate, shallow	HMA	Encrusting, globular	Yes	

(continued)

Table 8.2 (continued)

Sponge	Location	Habitat	HMA/LMA	Shape	Net detritus production	Reference
Mycale fistulifera	Red Sea, Jordan	Tropical, shallow	LMA	Encrusting, mound	Yes	Rix et al. (2016a, b)
Hemimycale arabica	Red Sea, Jordan	Tropical, shallow	LMA	Encrusting, mound	Yes	
Chondrilla sacciformis	Red Sea, Jordan	Tropical, shallow	HMA	Encrusting, globular	Yes	
Hymedesmia coriacea	NE Atlantic, Norway	Cold, deep	LMA	Encrusting, sheet	Yes	
Xestospongia muta	Caribbean, Florida Keys	Tropical, shallow	HMA	Massive, barrel	No	McMurray et al. (2016)

Shown are their location, habitat, shape, and whether they are high or low microbial abundance (HMA or LMA)

Fig. 8.1 Volume-to-surface area ratio of a thin encrusting sheet-shaped sponge *Halisarca caerulea*, a massive tubular sponge *Aplysina archeri*, and a massive ball-shaped sponge *Ircinia strobilina*. Shown are their representative geometrical forms (*thin cuboid*, *hollow cylinder*, and *dented ball*) and volume-to-surface area ratio based on hypothetical (but representative) sponge sizes. *l* length, *w* width, *h* height, *r* radius (all in cm)

species on coral reefs in which sponge growth (i.e. measured as linear extension or as a volumetric increase in mass) is substantial (Hoppe 1988, Wulff 2001, Lesser 2006, Trussell et al. 2006, McMurray et al. 2008, Gochfeld et al. 2012, Lesser and Slattery 2013 and references within). Even the sponge *Halisarca caerulea*, which is the encrusting species exhibiting high cell turnover that triggered the sponge loop theory in the first place, shows an average 1.3% daily growth under the same experimental conditions at which cell turnover was determined (i.e. 10–34 cm^2 multioscular and pumping specimens attached to coral rock cleared of epibionts) (Alexander 2015). To clear up any confusion, De Goeij et al. (2009, 2013) initially defined "steady-state" growth conditions from a carbon budget perspective. They estimated the total organic carbon uptake rates for *H. caerulea* at 1026 mmol C m^{-2} day^{-1} (De Goeij et al. 2008a). If all assimilated carbon would be turned into growth (i.e., 61% or 626 mmol C m^{-2} day^{-1}), those sponges would have shown an average daily 38% net biomass increase (based on the *H. caerulea* tissue carbon content of 1666 mmol C m^{-2}; De Goeij et al. 2008b). The measured 1.3% daily growth is *not* slow, considering those sponges may theoretically increase their biomass approximately five times yearly, but only represents 2.2% of the assimilated daily carbon budget (14 mmol C m^{-2} day^{-1}). In this example, detritus is, by far, the largest excretion product with or without considering growth. However, future sponge carbon or nitrogen budgets should include net biomass increases to avoid any confusion, which may differ significantly from species to species, and the term "steady state" should be avoided or clearly defined.

Cell turnover—The conversion of (predominantly dissolved) organic matter into detritus is proposed to occur through a high sponge cell turnover (De Goeij et al.

2009; Alexander et al. 2014, 2015a, b). This turnover is the result of the balance between rapid cell proliferation (biomass gain) and cell shedding (biomass loss). However, direct evidence linking cell turnover and detritus production has not yet been established due to the degraded nature of freshly shed organic material, which includes cell remnants and undigested organic matter (discussed in Alexander et al. 2014, 2015a, b; Maldonado 2015). In addition, Maldonado (2015) pointed out that mitotic cells in transmission electron microscopy (TEM) tissue sections were largely absent, which seems to contradict the data of De Goeij et al. (2009, 2013) and Alexander et al. (2014, 2015a, b), especially concerning the highly proliferative choanocytes (the collar cells of sponges that actively filter seawater; mitotic choanocytes are occasionally found; de Goeij, personal comment). However, this is not necessarily the case. Tissue that has been fixed for TEM or light microscopy represents only a snapshot in time, whereas the DNA synthesis assays used in abovementioned studies were determined over a 6-h period. The significantly lower chance of observing a choanocyte undergoing mitosis using TEM, despite these cells being highly proliferative, suggests a very short mitosis (M) phase of the cell cycle in sponge cells. In fact, *H. caerulea* choanocytes have a very short cell cycle of approximately 6 h and a short DNA synthesis (S) phase of only 30 min (De Goeij et al. 2009; Alexander et al. 2015a). The M phase of eukaryotic cells is approximately 4–10% the length of the cell cycle (Reece et al. 2014; Cooper and Hausman 2016), meaning that in *H. caerulea* choanocytes, it is likely to last between 10 and 30 min. Additionally, nuclear division and the formation of daughter cells (cytokinesis) only last a fraction of the total length of the M phase. Maldonado (2015) also suggests that high rates of choanocyte proliferation may be a side effect of 5-bromo-2′-deoxyuridine (BrdU) labeling (the cell proliferation marker used), which may increase rates of cell division. However, increases in cell proliferation rates as a result of BrdU labeling (as suggested by Maldonado 2015) have not been reported in the literature nor supported by any data we are aware of. In contrast, although BrdU can be toxic in high doses (at least three orders of magnitude higher than applied in the cell proliferation studies described above), its toxicity has been found to be related to *delayed* cell division by lengthening the cell cycle and the inability of cells to divide (e.g., Taupin 2007; De Almeida et al. 2010; Duque and Rakic 2011). Furthermore, several additional studies have shown choanocyte proliferation using different labeling techniques, i.e., titrated thymidine (Shore 1971; Efremova and Efremov 1979) and 5-ethynyl-2′-deoxyuridine (EdU) (Kahn and Leys 2016).

Detritus production—Net detritus production has been established in 19 out of 22 sponge species (Table 8.2). Table 8.2 shows only those studies where detritus was considered as part of the (particulate) organic carbon budget of sponges. Rates of detritus production are not given since it is still largely unresolved how sponge-derived detritus (i.e. all organic matter egested by sponges, including indigested organic matter) should be properly measured. Technological constraints currently hamper a proper quantification of detritus production. In principle there are three techniques published to measure detritus processing by sponges: (1) the direct incurrent-excurrent (IN-EX) method, measuring differences in organic matter concentration (collected on GF/F filters) between water samples entering (IN)

and exiting (EX) the sponge (Reiswig 1971; Yahel et al. 2003, 2007; Hadas et al. 2006; McMurray et al. 2016); (2) the indirect "open pot" method, in which sponges are placed in open-topped pots in running seawater aquaria and detritus is collected on GF/F filters directly from the pots and compared to detritus sampled from pots containing only seawater (Alexander et al. 2014); and (3) the indirect incubation method, in which sponges are placed in flow chambers and detritus is collected on GF/F filters by filtering the entire water content of the chamber (compared to seawater control incubations) (De Goeij et al. 2013; Rix et al. 2016a, b). The latter two methods are integrated over a much longer time frame (24 h for "open pots" and 6 h for incubations) than the first (i.e. minutes) and are suited for small (max 1.5 g dry weight specimens), multi-oscular sponge species. The IN-EX method is generally not suited for those mostly encrusting sponges, since oscula (outflow openings) are too small to sample properly. Using the IN-EX method, detritus may be easily missed within the time frame of sampling (although multiple replications did not show any net detritus production for *Xestospongia muta*; McMurray et al. 2016), just not caught since detrital particles can consist of large detrital clumps or mucal strings or because detritus is washed away from the sponge (or drops down). A fourth method (the "funnel" method; de Goeij, personal comment) has been tried, in which sponges are positioned upside down over a glass funnel, connected to a collection tube. Results are in the same order of magnitude as the "open pot" and incubation method, but not properly tested yet (i.e. the effect of altering the position of sponges in space). Caution thus has to be taken whether the absence of detritus in a measurement actually means "no detritus production" and all methods have issues with proper quantification (detritus may be partly lost through the pores of the GF/F filters and by too high suction pressure; de Goeij personal observation). Of course, it is highly likely that some sponges are not net producers of detritus. Where all of the investigated encrusting species show a net production of detritus, three out of nine investigated massive sponges (all measured using the IN-EX method) do not. This may be especially true for open reef sponges, where competition for space is presumed lower as compared with cryptic sponges, and open reef sponges may invest in growing large, instead of rejuvenating their cell system.

8.3.2 Knowledge Gaps at the Ecosystem Scale

8.3.2.1 Interactions Between Sponge Communities and Other Reef Members

The main question here is: How do certain reef communities fuel sponge communities and how do sponge communities drive (the production and diversity of) reef communities? The main producers of (dissolved) organic matter on coral reefs are primary producers, such as corals, benthic algae, and phytoplankton (e.g., Wild et al. 2004b, 2010; Haas et al. 2010, 2013), but DOM may also be imported from the

pelagic domain (Nelson et al. 2011) or from terrestrial sources (Pawlik et al. 2016). Recent evidence indicates that production rates and degradability of DOM depend on the source: algae release comparatively more DOM per unit of primary production than corals (Haas et al. 2011), and algal-derived DOM is mineralized faster by microbes residing in the water column and in sediments than coral-DOM exudates (Haas et al. 2011; Nelson et al. 2013). It is virtually unknown how sponges process various types of DOM, but a recent study shows, for the first time, that Red Sea sponges do differentially process naturally sourced ^{13}C- and ^{15}N-enriched algal- and coral-DOM (Rix et al. 2016b). Algal-DOM assimilation and detritus production rates by two LMA sponge species and one HMA sponge were significantly higher compared with coral-DOM. But the DOM sources were also utilized differentially by the holobiont: algal-DOM was incorporated into bacteria-specific fatty acids at a higher rate, while coral-derived DOM was preferentially incorporated into sponge-specific fatty acids (Rix et al. 2016b). These first indications are essential in understanding how sponge communities selectively control the fluxes of one of the major food sources (i.e. DOM) that shape coral reefs. The biomass and species composition of the sponge community may shift in relation to the communities fueling it. To use the analogy of sponges as food web engines, the abundance and composition of coral and algal communities (as sources of DOM) may determine the abundance and composition of the sponge community processing the DOM into POM as a source of food that drives detritivores and, ultimately, higher trophic levels. In other words, not necessarily all sponge types (e.g., massive sponges) may eat DOM and/or produce detritus, which will significantly determine carbon and nitrogen fluxes on reefs. In turn, sponge communities drive the productivity and diversity of reef communities. But the extent to which this happens remains unknown at present. Whether sponge communities buffer against or facilitate community shifts on coral reefs will be discussed in Sect 8.4.

8.3.2.2 Reef Communities and Carbon and Nitrogen Fluxes in Space and Time

Top-down and bottom-up processes—Food web frameworks are a dynamic equilibrium between functional benthic and pelagic communities, driven by fluxes of particulate and dissolved food. As previously discussed, sponge communities may be controlled by reef communities through the intake of food (bottom-up processes), such as the release of different quantities and qualities of DOM or the availability of different sources of POM. In turn, products released by sponges will drive autotrophic (e.g., inorganic nutrient release) and heterotrophic (e.g., detritus) communities. However, reef communities may also drive sponge communities through predation (top-down processes). The scientific opinion on the influence of top-down factors has been discussed for Caribbean reef sponge communities (Pawlik et al. 2015a). While sponge predators could be clearly identified using gut content analyses (Randall and Hartman 1968; Meylan 1988), their effects on sponge communities were initially dismissed because the relative abundance of sponges in gut contents

was low, and known spongivorous fishes, mostly angelfishes, were found to be eating only small amounts of several sponge species (Randall and Hartman 1968). It was subsequently observed from manipulative experiments that not only were parrot fishes major sponge predators along with angelfishes, but a hierarchy of preferences for sponge prey existed among spongivorous fishes that resulted in the removal of preferred species from reef habitats (e.g., Pawlik et al. 1995; Dunlap and Pawlik 1996; Pawlik 2011). Additionally, the sponge species that were earlier identified as primary prey for spongivorous fishes (Randall and Hartman 1968) were discovered to be chemically undefended (Pawlik 2011). In this respect, top-down and bottom-up processes may be intertwined and change in space and time on reefs. For example, it was found that across a shallow to mesophotic depth gradient (10–76 m water depth), the sponge *Plakortis angulospiculatus* is less chemically defended but invests more energy into protein synthesis, with increasing depth (Slattery et al. 2016). These phenotypes were associated with the increased availability of food with depth, while predation pressure decreased with depth.

Sponge loop fluxes revisited along a reef depth gradient—All fluxes estimated at reef scale usually assume homogeneous distribution of DOM along a depth gradient. These fluxes will, however, significantly change if the availability of DOM, in quantity and quality, varies along a depth gradient. To the best of our knowledge, there are few data available for dissolved organic carbon (DOC) concentrations along any shallow to mesophotic depth gradient on coral reefs. Two studies showed no DOC gradient along a reef depth gradient (Torréton et al. 1997; Nelson et al. 2011), but in the first publication (Indo-Pacific, French Polynesia and Fiji), the authors did not present the data that corroborated that claim, and the latter (Indo-Pacific, French Polynesia) only sampled to a maximum water depth of 20 m. Interestingly, when sampling mesophotic water depths (>30 m; Caribbean, Bahamas), a significant effect of depth was found, with higher DOC concentrations at shallow depths (<30 m) compared to mesophotic depths (>30 m) (Slattery and Lesser 2015). However, in contrast, data from St. Thomas (Caribbean) shows no significant differences from shallow to mesophotic depths (Slattery and Lesser 2015). Slattery and Lesser (2015) hypothesize that this is because St. Thomas is a shelf reef with a moderate slope. This results in greater downwelling irradiances (E_d) on horizontal surfaces as opposed to irradiances on the vertical surfaces of Bock Wall, Bahamas, where irradiances on walls can be as low as 25% of downwelling measurements in open water at equivalent depths (Falkowski et al. 1990). These differences result in greater cover of corals and macrophytes at mesophotic depths in St. Thomas (Locker et al. 2010; Smith et al. 2010) and therefore greater potential for DOC production at all depths. These depth-dependent changes in DOC in the Bahamas were paralleled by changes in DON (Lesser unpublished) as well as significant changes in the microbiome of the dominant sponge, *Xestospongia muta*, along the same shallow to mesophotic depth gradients (Morrow et al. 2016). Additionally, POC resources (both autotrophic and heterotrophic picoplankton and phytoplankton, including prochlorophytes and picoeukaryotes) for the Bahamas increased significantly with increasing depth (Lesser 2006). Comparing both POC and DOC concentrations for the Bahamas, a pattern is seen of increasing POC and

decreasing DOC as depth increases (Slattery and Lesser 2015). DOC may continue to decrease into the deeper mesophotic depths, and it was shown that on many coral reefs in the Caribbean, POC increases at least down to 92 m on reefs with steep vertical relief (Lesser 2006). The quantitative importance of sponge loop carbon fluxes is based on shallow reef data from Hatcher (1988, 1990), and therefore more studies that include depth-related DOM cycling are needed through the shallow to mesophotic depth range to determine its importance on reefs generally.

Seasonal and diurnal variation in DOM production and concentrations on reefs—To increase complexity, there is also the time aspect to consider. DOM concentrations on reefs significantly change throughout the year. For example, in the Red Sea, highest DOM concentrations and production rates are measured in spring and fall (Wild et al. 2009; Haas et al. 2010; Naumann et al. 2010). On Curaçao, significantly higher DOM concentrations are measured in spring (May/June) as compared with fall/winter (November/December) (Mueller et al. 2014b).

DOM production by primary producers is usually enhanced in light as compared with dark conditions (e.g., Brylinsky 1977; Crossland 1987; Ferrier-Pages et al. 1998, 2000; Naumann et al. 2010; Haas et al. 2010; Mueller et al. 2014b; Cherrier et al. 2015). On a 24-h daily cycle scale, elevated DOM concentrations would then be expected to occur on reefs during daytime as compared with nighttime. Again, the absolute lack of data hampers proper discussion here, but two studies reporting on diurnal DOM concentrations on reefs corroborate these assumptions (Van Duyl and Gast 2001; Tanaka et al. 2011). However, the first study consists of one day-night pair of measurements, and the latter (showing an increase of DOC concentrations during daytime and decrease during nighttime) was measured in stagnant water, a 1–6-h situation where seawater is trapped at spring tide on the reef flat of the sampling site. Counterintuitive, but interesting, are the results of elevated DOM production by cyanobacterial mats on reef sediments during *nighttime* (not daytime!). Also, these cyanobacterial mats constituted up to 79% of the estimated total release of DOC in the study area (Brocke et al. 2015). Clearly, the challenge in developing a new food web framework, including sponges as key ecosystem drivers, is to integrate all processes, assessed at ecosystem scale through space and time.

Particulate versus dissolved organic matter: POM undervalued?—Another potential source of error in the present estimation of sponge loop fluxes, in this case an underestimation, is related to the particulate fraction of the organic matter (Lesser and Slattery 2013). In the organic matter flux studied leading to the sponge loop fluxes, particulate organic carbon (POC) was not directly measured but based on heterotrophic bacterial counts using epifluorescent microscopy (using a single carbon equivalent conversion factor for bacterial cells) and a conversion factor of two for bacterial carbon to particulate organic carbon (De Goeij et al. 2008a; Mueller et al. 2014a). Alternatively, flow cytometry protocols to quantify plankton communities in seawater (Cucci et al. 1985; Lesser et al. 1992; Marie et al. 1997) provide detailed information on sponge consumption of picocyanobacteria, heterotrophic bacterioplankton, and picoeukaryotes in conjunction with known carbon and nitrogen conversion factors (e.g., Pile et al. 1996, 1997; Ribes et al. 1999; Yahel et al. 2003, 2007; Lesser 2006; McMurray et al. 2016). The overall particulate organic

matter intake rates by sponges may be underestimated as compared with DOM uptake rates, and their contribution to overall carbon fluxes on reefs may significantly increase over the full-depth range of reef ecosystems.

Carbon versus nitrogen: nitrogen undervalued?—While not as widely emphasized, De Goeij et al. (2013) also showed that sponges take up DON and similar to the net efflux of dissolved inorganic nitrogen (DIN) by sponges (Southwell et al. 2008b; Fiore et al. 2013) release significant amounts of nitrogen trapped in detritus. In fact, $^{13}C/^{15}N$ isotope tracer studies consistently show—for six out of six sponge species from tropical Caribbean and Red Sea, and cold-water deep-sea coral reefs, using both artificially (diatom lab cultures) and naturally sourced (coral mucus) DOM sources—that sponge-derived detritus has lower C/N ratios then the C/N ratios of the dissolved food they assimilate (De Goeij et al. 2013; Rix et al. 2016a). In other words, this implies that sponges add nitrogen in the conversion of DOM to detritus. This release of additional nitrogen subsidies for coral reefs is potentially important, since nitrogen is considered to be a limiting resource in oligotrophic tropical waters (e.g., Lapointe 1997; Larned 1998). The question is: From which sources do sponges derive their nitrogen before they assimilate it into biomass? Accumulating evidence points to a mysteriously missing nitrogen source in the energy budgets of sponges (Jiménez and Ribes 2007; Hadas et al. 2009; Hoffmann et al. 2009; De Goeij et al. 2013; Rix et al. 2016a). DOM in the open, oligotrophic waters of coral reefs has a high C/N ratio (>10: Ogawa and Tanoue 2003, De Goeij 2009, Tanaka et al. 2011), such that one would hypothesize that this carbon-rich DOM would be a good respiratory substrate and source of energy similar to the "junk food" diet that corals get from their symbiotic *Symbiodinium* sp. as translocated photosynthate (Lesser 2004). The POM fraction could be an underestimated source of nitrogen (see also previous discussion), relative to their abundance on the reef slope. Sponges may also acquire nitrogen from inorganic sources or through nitrogen fixation. However, the missing nitrogen does not have to be provided by sponges. An alternative explanation for the addition of nitrogen to sponge-derived detritus is that it comes from bacteria colonizing the detritus as occurs with "marine snow" (Azam and Malfatti 2007). The source of these bacteria is very likely to be from the sponge microbiome itself but could include bacteria from the surrounding seawater once the detritus is released. Taken together, there is a critical need to document the distribution of particulate and dissolved nitrogen (both organic and inorganic) pools to which sponges have access to develop a more complete model of sponge biogeochemical contributions to the trophic ecology of coral reefs.

8.3.2.3 Sponge Biomass Estimations on Coral Reefs

Key to determining fluxes of any element within a food web framework are proper estimates of the biomass and elemental composition (e.g., carbon and nitrogen) of each functional compartment. Biomass estimations of sponges on coral reefs require survey data taken by divers or through remotely operated cameras (for deep-sea areas) that provide sponge (1) identity and (2) quantification. The first of these is

often difficult, even at the most basic level, because other taxa of organisms (e.g., compound tunicates) can superficially resemble sponges. When clearly identifiable as a sponge, many sponges are difficult to identify at the species level, either because of limited taxonomic reference or because of morphological variation or cryptic speciation (Hooper and Levi 1994; Zea et al. 2014). Sponge identification to the species level is easiest on Caribbean coral reefs, because of the homogeneity of benthic taxa in the region due to the "mixing bowl" effect of surface currents that distribute propagules and genes widely within the region (López-Legentil and Pawlik 2009; Pawlik 2011; Zea et al. 2014). Sponge identification is more difficult on reefs in other tropical areas because basic taxonomic resources are often lacking and because of high levels of biodiversity and endemism (Hooper and Levi 1994). Therefore, global comparisons of sponge distributions are often limited to survey data that go no lower than the phylum level of sponge identification. Benthic surveys that include sponges generally use one of the four metrics: abundance (number of specimens per m^2 projected reef), percentage cover (per m^2 projected reef), volume (per m^2 projected reef), or biomass (in g wet weight, dry weight, or ash-free dry weight per m^2 projected reef). Percentage cover expresses the relative amount of substratum covered by sponge, regardless of tissue thickness. Moreover, reef area is usually projected as two-dimensional, whereas reefs are clearly not. Of these four metrics, abundance and percentage cover are the least informative, because sponges can become meters wide in three dimensions, as opposed to the mm-thin layer of living tissue that corals possess. Sponge volume (note: only when volume to dry weight and carbon/nitrogen content conversion factors are included) or biomass is by far the most accurate and useful measurement from an ecological perspective. These are also the most difficult to obtain, because of the variable morphology of most sponge species (Fig. 8.1), the complex system of channels and spaces inside them, the nearly impossible task to determine the biomass of excavating sponges, and the daunting task to determine biomass of cryptic sponges. Percentage cover is, unfortunately, the single most common community estimation used in reef ecological studies, although more and more scientists now implement two- to three-dimensional image software. In conclusion, as for biogeochemical cycles within benthic ecosystems, elemental composition (i.e., carbon, nitrogen, etc.) of a certain community (pelagic or benthic) is a prerequisite to calculate fluxes, and biomass calculations based on weight or volume are the best parameter to normalize flux rates.

8.3.2.4 Caribbean, Red Sea, and Indo-Pacific: How Distinct Are These Geographical Regions in Terms of Sponge Ecological Function on Coral Reefs?

Sponge biomass—The distribution of open reef sponges (i.e., excluding all cryptic sponges) on shallow-water coral reefs (<30 m water depth) exhibits distinct global patterns. Benthic surveys across 69 Caribbean reef sites, conducted at depths below the influence of high flow generated by surge and storms, reported a range of open reef sponge cover per project m^2 reef of 2.2–74.4%, with a mean of 15.9% (Loh and

Pawlik 2014; Loh et al. 2015). Among common Caribbean non-cryptic sponge species, all morphologies were represented (e.g., barrel, tube, vase, branch, mound) (Pawlik et al. 2015a). The percentage cover of open reef sponges is very low across most of the Indo-Pacific, including reefs in the Red Sea, Eastern Indian Ocean, Oceania, and Western Pacific. Benthic surveys from reefs in these areas seldom mention sponges at all, and if they do, they indicate that shallow open reef sponge cover is minimal or less than 1% (Benayahu and Loya 1981; McClanahan et al. 2009; Vroom et al. 2010; Stuhldreier et al. 2015; Freeman and Easson 2016). Open reef sponge cover on outer reefs of the Great Barrier Reef is also low (1.1–1.4% for Myrmidon) but higher for inner reefs (0.7–6.8% for Davies) (Reichelt et al. 1986). For Indo-Pacific coral reefs, among the highest open reef sponge cover data are for Wakatobi, Indonesia, in the "Coral Triangle," with values ranging from 25 to 45% (Bell and Smith 2004), while other areas in the Coral Triangle have reported values of <10% open reef sponge cover (Chou et al. 2010). In addition to the geographical pattern indicated above, a depth-related pattern, in which the percentage cover of sponges changes as depth increases into the mesophotic depths in both regions, is intensely debated (Slattery and Lesser 2015; Pawlik et al. 2015a, b). The only few available data (Lesser and Slattery 2011; Slattery and Lesser 2012) show increasing percent cover and species diversity of sponges with increasing depth into the mesophotic zone, but more data are needed to confirm the broad generality of these patterns. One major group of sponges that might provide answers in this discussion is the generally overlooked group of encrusting sponges. They reside in cryptic habitats on shallow reefs but appear on the open reefs with increasing water depths.

No sponge loop in the Indo-Pacific? Cryptic sponges are generally overlooked…—There seems to be a clear difference in abundance and cover of open reef sponges between Caribbean and non-Caribbean tropical shallow reefs, with consistently higher open reef sponge cover on Caribbean reefs (discussed in Pawlik et al. 2016). However, moving down the reef slope, sponge cover was not found significantly different at the depth range 60–90 m water depth between two Caribbean and four Indo-Pacific mesophotic coral reefs (Slattery and Lesser 2012). But, the Indo-Pacific sponge biomass at those depths was significantly lower than in the Caribbean areas, since cover was dominated by encrusting sponges (Indo-Pacific) as opposed to massive growth forms (Caribbean) (Slattery and Lesser 2012). These encrusting sponges usually dominate the cover of cryptic reef habitats on shallow reefs. The Indo-Pacific suffers a general lack of data on cryptic sponge cover and biomass. However, throughout the Berau area, East Kalimantan, Indonesia (21 cavities within different reef types) (De Goeij and van Duyl 2007), cryptic sponge cover was roughly (only by sight) estimated at 15–30% of total cryptic surface area (including sediment floor; de Goeij, personal comment), which is in line with estimations from the Red Sea (11–24%) (Wunsch et al. 2000; Richter et al. 2001) and Caribbean (19–27%) (Jackson and Winston 1982; Scheffers 2005; Van Duyl et al. 2006) reef ecosystems. Carbon fluxes through cryptic communities were found to be lower, but within the same order of magnitude, than those found on Caribbean reefs (De Goeij and van Duyl 2007). These (predominantly dissolved organic) carbon fluxes are hypothetically, but most likely, due to an active sponge

loop in these Indo-Pacific areas, although data must be acquired to confirm this hypothesis. Hutchings (1974) implied that the biomass of cryptic reef communities is equal to, or exceeds, that of open reef community biomass. No scientist to date has provided evidence to corroborate or refute this claim. This clearly stresses the need to quantify the biomass of this highly overlooked cryptic sponge community (note: which also includes the excavating sponge biomass). Sponge biomass estimates of Indo-Pacific regions, in general, are one of the most important data sets to obtain in order to quantify sponges as key players in coral reef food webs.

Extent of sponge photoautotrophy on Caribbean reefs—Sponges in the chiefly photoautotrophic category have been described as largely restricted to Indo-Pacific regions, with no similarly foliose phototrophic species known for the Caribbean. Studies of photoautotrophy of Caribbean sponges do show net growth under high light levels for some sponge species in the Caribbean with photoautotrophic symbionts, but not to the extent described for foliose Indo-Pacific sponge species (Erwin and Thacker 2008; Freeman and Thacker 2011). Work by Wilkinson and Cheshire (1990) originally described the Caribbean basin as favoring heterotrophic sponges due to a greater abundance and utilization of planktonic food, whereas the Indo-Pacific, specifically the Great Barrier Reef (GBR), appeared to favor photoautotrophic sponges due to enhanced light transparency under more oligotrophic conditions. However, the amount of particulate organic matter (POM) on Pacific coral reefs (e.g., Charpy et al. 2012) is comparable to that of the Caribbean (Lesser 2006; Lesser and Slattery 2013) and is actively grazed by a range of suspension feeders including sponges in both geographical areas (Ribes et al. 2003, 2005; Lesser 2006; Houlbreque et al. 2006). Additionally, the underwater light environment does not differ significantly between regions as both irradiances of photosynthetically active radiation (PAR, 400–700 nm) and downwelling attenuation coefficients (K_d m^{-1}) on Caribbean reefs are similar (Lesser 2000, Lesser et al. 2010, Lesser unpublished) to those of offshore reefs of the GBR (Wilkinson 1983; Wilkinson and Trott 1985). This suggests that particulate food and light may not be a strong determinant of the number or distribution of photoautotrophic sponges between the two regions. However, DOM and inorganic nutrients could be determinants distinguishing the geographical regions. DOC concentrations and uptake rates by cryptic communities were found significantly lower on the Indo-Pacific reefs of the Berau area (East Kalimantan, Indonesia) as compared with Curaçao reefs (Caribbean) (De Goeij and Van Duyl 2007). On the other hand, preliminary data showed no difference between DOC and DON concentrations between shallow reefs in the Pacific (Great Barrier Reef and Hawaii) and Caribbean (Curaçao) (Lesser, unpublished). In those areas inorganic nutrient concentrations, specifically dissolved inorganic species of nitrogen, were also not found to be significantly different between regions, which all would be considered as oligotrophic (i.e. consistently below 1 μmol L^{-1} nitrate) from an oceanographic perspective (O'Neil and Capone 2008). However, the aforementioned difference between the abundant, non-foliose sponge fauna of the Caribbean, with many sponge morphologies represented, and the scarce, phototrophic and foliose sponge fauna of most Indo-Pacific coral reefs suggests that the evolutionary constraints on the communities of sponges in these two regions have

been different (Pawlik et al. 2015a, 2016). More data are needed to test the hypothesis that the photoautotrophic condition of sponges in the Pacific versus the Caribbean is different and to determine the factors that drive any differences in the sponge fauna.

To conclude Sect. 8.3, it is obvious that critical knowledge gaps exist at both the organismal and the ecosystem level that hamper our understanding of sponge physiology in general and their function within reef ecosystems. As long as these knowledge gaps are not filled, scientific discussion of the proposed key role of sponges in their ecosystem will continue but will not necessarily progress toward a better understanding. Therefore, in Sect. 8.4, an attempt will be made to present a new food web framework, including sponge-driven resource cycling. This will be the foundation (of the discussion) to predict future scenarios of reef development.

8.4 Sponges Drive and Modulate the Food Web of Reef Ecosystems in a Warming Ocean

8.4.1 Coral Reefs in a Changing World

The worldwide decline of coral reefs has been attributed to a variety of natural and anthropogenic stressors in the Anthropocene (Jackson et al. 2001, Gardner et al. 2003, Hughes et al. 2003, Waters et al. 2016, and see Cramer et al. 2012 for evidence that this decline can be traced back to the nineteenth century). The consequences of climate change to coral reefs appear to be significant. Specifically, increasing seawater temperatures (SWT) have resulted in an almost annual incidence of coral bleaching in recent years (Donner et al. 2005), with 2015 the warmest year on record to date (NOAA 2016). Additionally, ocean acidification (OA) is also directly related to the net increase in atmospheric CO_2 from fossil fuel combustion (Kleypas et al. 1999; Caldeira and Wickett 2003). This has already resulted in a reduction of 0.1 pH units, equivalent to a 30% increase in acidification over preindustrial era levels, and the greatest rate of change in oceanic pH since the Pleistocene (Wootton et al. 2008; Pörtner et al. 2014). Furthermore, models constructed on a "business-as-usual" scenario for greenhouse gas emissions indicate further declines of 0.3–0.4 pH units by the year 2100 (Caldeira and Wickett 2005; Field et al. 2014). However, these predictions are based on *oceanic* conditions, and there is now ample evidence that watershed inputs, metabolic activities (i.e., respiration), and oceanographic processes in *coastal* environments can increase ocean acidity in specific habitats (e.g., upwelling regions (Feely et al. 2008), volcanic seeps (Fabricius et al. 2011), comparative sampling across 15 sites spanning from polar to tropical shallow benthic ecosystems (Hofmann et al. 2011), marine caves (Crook et al. 2013; Slattery et al. 2013)) and over diel and tidal temporal scales (e.g., Price et al. 2012; Slattery et al. 2013; Smith et al. 2013). On coral reefs, pCO_2 has increased ~3.5 times faster than in the open ocean over the past 20 years, likely due to a combination of local

and global stressors (Cyronak et al. 2014). In addition, as climate change causes the onset of alterations in the community structure and food web of reef ecosystems, there is evidence accumulating that certain biological pathways are triggered, such as the sponge loop (De Goeij et al. 2013; Pawlik et al. 2016) and the microbial loop (Rohwer et al. 2010; Haas et al. 2016), which may shift reef ecosystems faster than their original stressors (SWT and OA leading to coral bleaching and dissolution of calcifying organisms). Unfortunately, these biological pathways receive much less attention at present, which seriously hampers our ability to predict future changes within reef ecosystems. The role sponges play in future reef ecosystem dynamics will be discussed on the basis of a new sponge-driven food web framework for coral reef ecosystems.

8.4.2 *A New Food Web Framework, Including Sponges as Key Ecosystem Drivers*

To predict future changes in community biomass and structure on coral reef ecosystems, we need to redevelop the existing food web framework, since the old models, lacking sponge-driven energy and nutrient cycling, are incomplete. Figure 8.2 represents the proposed new food web framework, for the first time including sponges as key ecosystems engineers. The proposed framework consists of *fueling* communities, sponge holobiont *engine* communities as well as the non-sponge-associated bacterial *engine* communities, and *driven* communities. In the resulting framework model, changes in food input (arrows, Fig. 8.2) modify the biomass and composition of benthic and pelagic reef communities (boxes, Fig. 8.2) along a depth gradient from source to sink and vice versa. In other words: How much food is produced by different functional members of the fueling community, how much is processed by which functional groups of sponges and bacteria, and how is it used to drive reef productivity and diversity? Different scenarios of food input and reef community development (i.e., the biomass and composition of each community) can then be tested using this framework, in order to predict how reef ecosystems change in the future. But, with this proposed framework, we can already start to hypothesize the role of sponges on future reefs.

8.4.3 *The Battle for DOM: Sponge Loop Versus Microbial Loop*

Under oligotrophic conditions, sponges supply resources in several forms of carbon and nitrogen to the reef ecosystem. Additionally, by converting the largest source of carbon and nitrogen (DOM), which in its original state would be lost from the ecosystem, into a readily available form (detritus or sponge biomass), sponges now

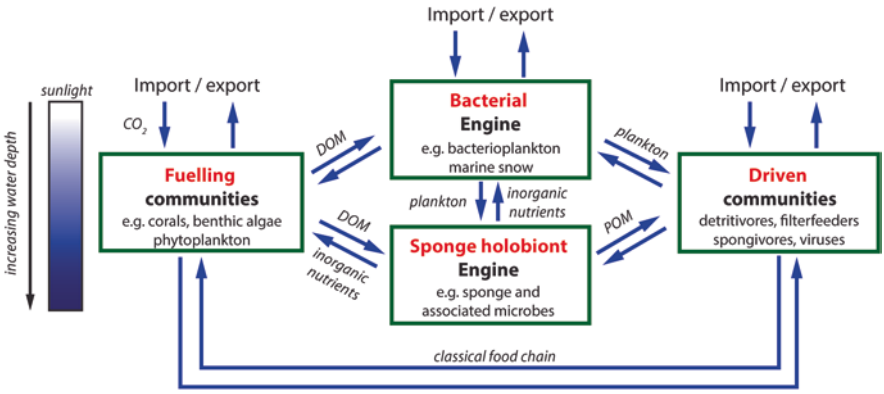

Fig. 8.2 Concept of sponge-driven food web framework along a depth gradient, indicating the direction and size of energy and nutrient fluxes (*arrows*) as well as the biomass and composition of benthic and pelagic reef communities (*boxes*). A simplified overview of predicted dominant pathways for a tropical coral reef ecosystem is given in *italics*. *DOM* dissolved organic matter, *POM* particulate organic matter

appear to be an important ecosystem engineer on reefs. Under the present-day and future scenario of higher nutrient input conditions (e.g., through land or air input; Fig. 8.3), the very fast and efficient sponge loop will retain and recycle those extra nutrients within the originally oligotrophic ecosystem. Effects will be enhanced because of the oligotrophy of the systems. This may catalyze reef destruction by nutrient-induced community shifts, a hypothesis that was first proposed by De Goeij et al. (2013) (Fig. 8.3a). Pawlik et al. (2016) expanded upon the key role of sponges under changing reef conditions to explain the lack of resilience of Caribbean reefs relative to those in other tropical areas, a hypothesis referred to as the "vicious circle" (Fig. 8.3a). At the same time, it has recently been proposed that microbes follow a DOM-related path of reef degradation: A "microbialization" of coral reefs is suggested to occur in response to an increased algal biomass on coral reefs as a result of coral degradation (Haas et al. 2016). Under oligotrophic conditions, DOM recycling within the water column is mediated through the microbial loop. However, as algal biomass on reefs increases on reefs worldwide, it triggers a positive feedback loop (DDAM, dissolved organic carbon, disease, algae, microorganisms), whereby DOC release by algae leads to increases in microbial abundances including potentially pathogenic species. This, in turn, maintains the competitive dominance of algal communities on reefs (Rohwer et al. 2010; Haas et al. 2016) (Fig. 8.3b). Interesting questions arise as to how these newly described biological pathways interact. Do sponges (including their microbiome) and non-sponge-associated microbes compete for DOM? Do sponges *buffer against* the microbialization of reefs? Or does the interaction of the sponge loop and microbial loop increase fluxes through each pathway? Do sponges *facilitate* the microbialization of reefs?

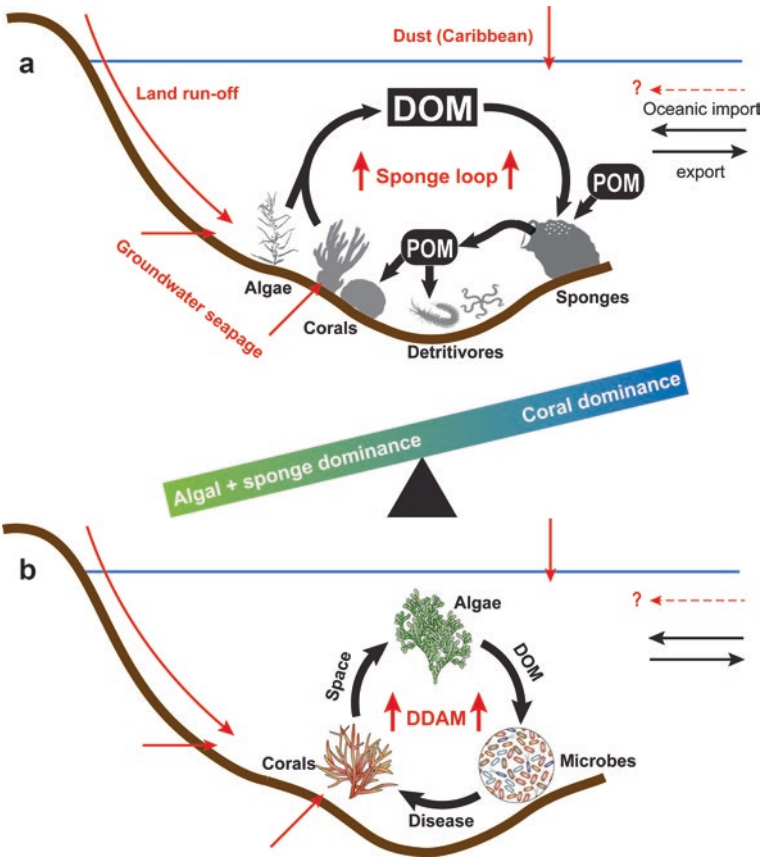

Fig. 8.3 The hypothetical role of the sponge loop (**a**) and the microbial loop (**b**) in catalyzing reef community shifts through enhanced anthropogenic input (indicated by *red arrows*). (**a**) Dissolved organic matter (DOM) is released by algae and corals and converted to particulate organic matter (POM) that fuels local detritivore communities. Anthropogenic inputs, such as carbon and nitrogen influxes through land runoff, groundwater seepage, airborne nutrients (e.g., African desert dust into the Caribbean basin), and additional inflow of nutrients from the surrounding ocean, will increase fluxes through the sponge loop (including the biomass of algae, DOM concentrations in the seawater, sponge biomass, and sponge-derived detritus and inorganic nutrients). This figure is modified from Pawlik et al. (2016). (**b**) A simplified representation of the DDAM (DOC, disease, algae, microorganism) model (after Garren 2016). On degraded reefs algae become more dominant and release more and better quality DOM than corals that is subsequently increasing microbial production, including potential coral pathogens. This, in turn, increases coral diseases and will further enhance the shift from coral toward algal dominance on reef ecosystems. Both biological pathways will hypothetically catalyze the shift toward algae- and sponge-dominated reef system

Before we can study both processes, we need to approach the microbialization theory, as with every new theory, with a healthy level of skepticism to understand it better.

8.4.3.1 How Strong Is the Relationship Between DOC, Microbial Abundances, and Algae?

The two primary data sets used to support DDAM are a negative relationship between DOC and benthic algal cover and an increase in microbial abundance with increasing percentage of benthic algal cover (Haas et al. 2016). These two functional relationships, analyzed using regression analyses, show significant relationships with linear correlation coefficients (r) that range from −0.17 to −0.34 for DOC and 0.22 to 0.36 for microbial abundance, and both should be considered as very weak relationships (87–97% of the variation is *not* explained by these processes). In addition, published values for DOC need to be discussed. Firstly, DOC concentrations presented are very low (an average around 40–50 μmol L^{-1} in each geographical region as presented in Fig. 2a of Haas et al. 2016) and within a narrow range (28–80 μmol L^{-1}) compared to published data. For example, DOC concentrations measured in coral reef waters in 40 stations in two distinct geographical areas averaged 84/124 μmol L^{-1} (Caribbean, Curaçao Summer-Fall/Winter-Spring) and 71 μmol L^{-1} (Indo-Pacific, East Kalimantan, Indonesia) and ranged between 42 and 160 μmol L^{-1} (De Goeij and van Duyl 2007; De Goeij et al. 2008a). Atkinson and Falter (2003) published an average reef water DOC concentration of 100 μmol L^{-1} and a range of 9–290 μmol L^{-1}.

Nonetheless, the DDAM theory triggers many interesting new insights on how previously largely neglected players, such as microbes and sponges, drive the food web of coral reefs in a changing world (Fig. 8.3). Some considerations are presented in the next subchapter:

8.4.3.2 Sponge Loop and Microbial Loop: Friend or Foe in Processing DOM?

Sponges graze on microbes: buffers DDAM in the future?—Sponges are efficient grazers of microbes, both bacterio- and phytoplankton (e.g., Reiswig 1971; Pile et al. 1996; Ribes et al. 1999; Lesser 2006; Yahel et al. 2007; McMurray et al. 2016). At lower removal efficiencies, sponges can also filter viruses (Hadas et al. 2006). In the presence of active cryptic sponge communities, in situ bacterial abundances decreased significantly (28–38%) (De Goeij and van Duyl 2007). Also, while studies to date have shown that sponges efficiently retain different groups of bacterioplankton in proportion to their abundance in the water column (e.g., Lesser 2006), other evidence continues to accumulate showing that bacteria can also be *selectively* taken up by sponges (Ribes et al. 1999; Yahel et al. 2006; McMurray et al. 2016), including pathogenic bacteria (Maldonado et al. 2010). In theory, sponges should thus be able to decrease the number of microbes in the water column (pelagic or attached to marine snow) and decrease the activity of DDAM on reefs (Figs. 8.2 and 8.3b). Sponges could also directly compete over DOM as food source with non-sponge-associated microbes (Figs. 8.2 and 8.3). In contrast, sponge-associated microbes may benefit from their associated role, which could lead to an increase of certain types (encrusting? HMA?) of sponges on reefs. Interestingly, this interaction of associated microbes

and their filter-feeding hosts has been suggested as being part of the microbial loop (Graham et al. 2014) but in fact is part of the (holobiont) sponge loop.

Sponge biomass increases: buffers DDAM in the future?—The abovementioned interaction between the sponge and microbial loop becomes stronger when the biomass of sponges on reefs increases (Figs. 8.2 and 8.3), assuming most sponges effectively graze on microbes and feed on DOM. In the Caribbean, there is increasing evidence that sponges are becoming a dominant component of some coral reef communities (McMurray et al. 2010; Colvard and Edmunds 2011) following the continuing decline in coral cover (Gardner et al. 2003). In fact, several Caribbean coral reefs have been increasingly referred to as "sponge reefs" (León and Bjorndal 2002; Norström et al. 2009). Historically, sponges have been a dominant taxon for millennia after global extinction events (Bell et al. 2013). Given recent environmental changes affecting coral reefs, such as increased seawater temperature and ocean acidification, the current observations and predictions that sponge densities will increase as coral reefs respond to global climate change is well justified (Bell et al. 2013). But it is not that simple.

Sponge biomass decreases: less buffer against DDAM in the future?—Several studies (described above) indicate an increase of sponge biomass on future reefs, but these data are scarce and do not include the biomass and function of cryptic and excavating sponges. These sponges are specifically dependent on the 3D structure of the reef matrix. The decrease in calcifying corals (due to, e.g., competition with algae, ocean acidification, and warming) and (initial) increase in excavating sponges (increased food availability), but also the effect of increasing numbers of intense storm events predicted for future reefs, will lead to severe losses of reef 3D complexity. This will consequently lead to a severe loss of (both excavating and encrusting) sponges from the ecosystem. Their filter capacity will be lost, which could lead to an increase of reef microbialization.

Sponges release inorganic nutrients: facilitates DDAM in the future?—Sponges also increase the concentration of reef water inorganic nutrients and locally increase the productivity of bacterioplankton (Scheffers et al. 2005). That means that with increasing sponge biomass on reefs, the increased availability of inorganic nutrients may trigger a positive feedback to both algal and microbial growth. Sponges can thus also have a synergistic effect on reef degradation by upregulating DDAM (Fig. 8.3). Both microbes (Haas et al. 2011; Nelson et al. 2013) and sponges (Rix et al. 2016b) would benefit from DOM released by algae as compared with corals. The sponge loop and DDAM could therefore trigger a positive feedback loop, catalyzing the shift from coral-dominating reef ecosystems to algae- and sponge-dominated ecosystems (Fig. 8.3). And what about sponge detritus?

Sponges release detritus: buffers or facilitates DDAM, depending on production rates and nutritional quality—A recent study showed that the sponge *Halisarca caerulea* slows down cell proliferation after a wound infliction (Alexander et al. 2015b). Consequently, detritus production but also the quality of the sponge-derived detritus was found to decrease and takes at least a week to recover to "normal" values (Alexander 2015). We need to study different functional and morphological

types of sponges (see Sect. 8.3) to understand the generality of such processes to extrapolate fluxes to reef scale. Also, we need to establish whether sponge detritus increases the productivity and diversity of microbial and faunal communities (Fig. 8.2), being an important potential food source. The consequences of large-scale changes in detritus production by sponges and its availability to other reef communities could be important for future scenarios of reef ecosystem development. Sponge health may be an important determinant to understand these scenarios. Also predicted loss of 3D complexity (see above) may significantly decrease detritus production on reefs, since detritus production by massive sponges has not yet been established. A complicating factor to include detritus in any future scenario of future reef development is the missing baseline data on sponge detritus production in the past. The production rates and nutritional quality of sponge detritus could have already been affected by physical disturbances that compromise sponge physiological states, such as predation (Ayling 1983; Pawlik et al. 2015a) and storms (Wulff 2006, 2010), as well as changes in seawater composition (Imsiecke et al. 1996; Kuhns et al. 1997). For example, increasing frequencies and intensities of tropical cyclones predicted for the future (Knutson et al. 2010) would result in sponges becoming damaged more frequently, and, consequently, they will produce less detritus. In contrast, less predation due to declines in spongivorous fishes by overfishing (Burke and Maidens 2006; Paddack et al. 2009) may have already caused increases in the abundance of sponge detritus at present and may have shifted the reef community structure to fuel microbial detritivores and upregulate DDAM (Figs. 8.2 and 8.3).

8.5 Conclusions

In this chapter, we have tried to formulate the challenges and knowledge gaps that currently exist in order to understand and integrate the ecological functions sponges provide to their ecosystem. Many challenges, both at the organism and the ecosystem level, are in front of us, and not all will be easily assessed. Most challenges are still in an early stage, theoretical form, and we tried to shed light on as many different viewpoints (but surely not *all*) that we are aware of. In this early phase, many theories will be falsified in order for them to progress and develop. But what we do know is that sponges need to be recognized as key ecosystem engineers in the coral reef food web and in particular under present and future scenarios of environmental change.

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