José Luis Carballo · James J. Bell *Editors*

Climate Change, Ocean Acidification and Sponges

Impacts Across Multiple Levels of Organization

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Contents

Editors' Biography

Dr. José Luis Carballo is a senior researcher and professor of the postgraduate programme in marine biology at the Institute of Marine Sciences and Limnology at Universidad Nacional Autónoma de México. He received his doctorate in zoology from the University of Seville in 1994 obtaining the maximum distinction cum laude with the thesis 'Sponges from the Strait of Gibraltar' and after that obtained a postdoctoral research fellow on R & D (research and development) to work with natural products from marine sponges. He has published more than 120 scientific research papers, books and has successfully supervised to completion more than 40 postgraduate (MS and PhD thesis) and postdoctoral research fellows whose research focused mainly on the study of small and large patterns of sponge biodiversity and structure on the northeastern Pacific Ocean (México) and the factors influencing local and global biodiversity patterns, including habitat heterogeneity and sediment deposition. His current research interests focus mainly on coral reef sponges, and especially on boring sponges, on topics ranging from taxonomy, distribution, reproduction and dispersion to the influence of large and local environmental variables. He is also interested in the general broadscale variability in bioeroder communities and rates of erosion in Mexican Pacific coral reefs and to understand how climate change and ocean acidification will influence bioerosion distribution and abundance of boring sponges.

Associate Professor **James J. Bell** is a marine biologist in the School of Biological Sciences at Victoria University of Wellington, New Zealand, and is currently the marine biology programme director. James developed an early interest in marine biology through his love of the oceans where he grew up in Devon. He graduated from the University of Wales, Bangor, in 1998 with a first-class honours degree in marine biology and gained his PhD in 2001 from University College Cork in Ireland. He became intrigued by sponges during a research expedition to Lough Hyne Marine Nature Reserve in Southern Ireland, and his PhD research focused on the unusual sponge assemblages there. James moved to New Zealand to take up a lectureship at Victoria University in 2006. He is an internationally recognised sponge ecologist, whose current research is at the leading edge of sponge ecological research, particularly focusing on understanding the functional roles of sponges in marine systems, the ways in which human impacts influence these roles and the subsequent ecosystem consequences of declines or increases in sponge abundance. The research that James conducts is of global significance, increasing our understanding of how sponges respond and acclimate to environmental degradation and their potential to be ‘winners’ in response to future environmental change. James has published over 100 peer-reviewed journal articles and book chapters in leading international journals. He has led expeditions across the world to study sponges and has received funding from many sources to support his research. James makes an important contribution to the development of future marine scientists and leads a large postgraduate group working on sponges.

Chapter 1
Climate Change and Sponges: An Introduction

José Luis Carballo and James J. Bell

Abstract This chapter provides an introduction to our current understanding of the two most important features of climate change affecting marine sponges—ocean warming and ocean acidification. Of these two stressors, thermal stress associated with ocean warming is likely to have the greatest influence on the sponge assemblages through the induction of diseases and mortality by a decrease in the efficacy of defense mechanisms and development of pathogens. However, there is a considerable variability among species in their responses to increasing temperature, and some species have persisted during episodes of unusually high temperature. Conspicuous sublethal effects have also been described. Thermal stress can limit sponge reproductive capability and dispersal by causing the reabsorption of spermatic cysts and oocytes and by the disruption of the feedback mechanism that prevents the release of asexual propagules when ecological factors are unsuitable for propagule survival. Thermal stress also can affect sponge-feeding behavior by increasing or decreasing filtration rates and by decreasing choanocyte chamber density and size, causing shifts in the microbial communities of the host sponge, and can also increase the production of heat shock proteins, which leads to rapid upregulation of genes involved in cellular damage repair. The effects of ocean acidification on sponges are much less known, but recent studies have demonstrated the resistance of certain species to lowered pH conditions. It seems that this capacity to withstand OA lies in part in the ability of sponges to restructure their host-associated microbiomes mainly by acquiring new microbial components via horizontal transmission. The apparent resilience of some sponge species and the sensitivity of others highlight the need to understand the molecular basis of sponge responses to environmental stressors in order to determine if they will be able to adapt to rapidly changing ocean conditions. Future research focused on transcriptomic and

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metabolomic responses using genomic approaches will facilitate the assessment of molecular stress responses at different sponge life history stages.

Keywords Sponges • Climate change • Thermal stress • Ocean acidification

1.1 The Two Main Climate Change Factors: Impact of OW and OA

Shifts in climate regimes are a recurrent feature of the Earth's history (Zachos et al. 2001), but the peculiarity of modern-day changes is the unprecedented speed at which they are occurring and the undeniable human influence (Hansen et al. 2007), in particular being driven by burning fossil fuels, cement production, and changes in land use (IPCC 2007). These human activities are rapidly raising the atmospheric carbon dioxide concentration (CO_2) level at a rate that is unprecedented in at least the last 22,000 years (IPCC 2007; Joos and Spahni 2008).

It is predicted that by 2100, the CO_2 concentration will be in the range of 541–970 ppm (IPCC 2001), and much of this anthropogenically generated CO_2 will be absorbed by the oceans. The increase in atmospheric carbon dioxide concentration (CO_2) will have two immediate consequences: (1) it will rise Earth's atmospheric temperature (global warming, GB) and, particularly, global sea surface temperatures (SSTs) by up to 4 °C (IPCC 2007), and (2) it will dissolve in seawater forming carbonic acid (H_2CO_3), lowering the pH in a process known as ocean acidification (OA). In the last 200 years, the global ocean pH has dropped by 0.1 pH units (30% increase in acidity), and it is predicted to drop a further 0.3–0.5 units by 2100 (170% increase in acidity), which is more than 100 times as rapid as at any time over the past hundreds of the millennia (Meure et al. 2006).

Ocean warming and ocean acidification (pH, pCO_2, and calcium carbonate saturation) will impact marine organisms across all levels of biological organization, from cellular to ecosystem levels. Ocean warming will affect marine benthic ecosystems through epidemiologic diseases and mass mortalities of invertebrates, in particular bivalves, corals, and sponges (Harvell et al. 2002; Webster 2007), and also cause coral bleaching, species invasions, and shifts in species' latitudinal ranges (Doney et al. 2012). Ocean acidification, in contrast, affects calcifying marine invertebrates most severely, such as coralline algae (Kuffner et al. 2008), corals (Silverman et al. 2009), echinoderms, and mollusks (Michaelidis et al. 2005). This is because it decreases the availability of the carbonate ions required for skeletogenesis; abundance of particular group such as pteropod is expected to decline by half during this century due to increased atmospheric carbon dioxide levels (Orr et al. 2005). OA and particularly elevated CO_2 also affect animals by disrupting the acid-base balance of internal fluids, leading to narcotizing acidosis, and also by triggering physiological mechanisms that slow or stop metabolism (Knoll et al. 1996). Even more important, reductions in pH may interfere with ion exchange, depressing metabolism and leading to a narrower window of thermal tolerance (Portner et al. 2005). Organisms that produce $CaCO_3$ skeletons are particularly sensitive to hypercapnia, because carbonate biomineralization requires precise control of the acid-base balance (Fabry et al. 2008).

1.2 Marine Sponges: An Introduction

Marine sponges are the evolutionary oldest multicellular animals that still exist, with records from the Precambrian over 700 million years ago (Finks 1970), and a large and consistent phylogenomic dataset supports sponges as the sister group to all other animals (Simion et al. 2017).

Their long continued survival since then is closely linked to their simple level of organization characterized by a lack of organs and true tissues and to the adaptability of their body plan. In fact, they have been described as “dynamic multicellular systems” whose cells have the ability to change into others if they need it, similar to the stem cells in vertebrates (Bond 1992). This apparently simplistic body structure, coupled with a unique tolerance to symbiotic microorganisms, gives sponges an enormous versatility that greatly affects many aspects of their biology and allows for a great diversity of evolutionary solutions for environmental challenges. In fact, part of their evolutionary success is ascribed to their intricate association with a diverse community of microorganisms that occur both intercellularly in the sponge mesohyl and intracellularly (Thomas et al. 2016) and which can comprise 40–60% of total tissue volume in some species (Taylor et al. 2007). For this reason, sponges are described as “holobionts,” that is, a unit comprised of the sponge host and the consortium of bacteria, archaea, unicellular algae, fungi, and viruses that reside within it (Webster and Taylor 2012).

Sponges are widely distributed in marine systems and occur mainly in shallow waters of the continental shelf, but there are species that can be found at 7000 m depth (Hooper and Van Soest 2002). Sponges represent a significant component of benthic communities in the oceans with respect to diversity, abundance, and their potential to influence benthic or pelagic processes. Thanks to their highly efficient capability to pump water, over a half liter of water per second per kg dry mass (Weisz et al. 2008), and the link they provide between nutrient transfer in the open water column and the benthos, means they are important for benthic-pelagic coupling of particulate and dissolved carbon (Gili and Coma 1998; Kahn and Leys 2016).

The relationship of sponges with macro- and microbial communities can also facilitate high levels of benthic primary production and nutrient cycling, including dissolved carbon (Mohamed et al. 2010; De Goeij et al. 2008), nitrogenous compounds (Corredor et al. 1988; Jiménez and Ribes 2007), silicate (Reincke and Barthel 1997; Maldonado et al. 2010), and phosphate (Zhang et al. 2015). Because of this, sponges play a major role in the cycling of dissolved organic matter (DOM) on coral reefs via the “sponge loop” pathway (de Goeij et al. 2013; Rix et al. 2017).

It has also recently been suggested that calcifying bacterial symbionts of sponges may have been involved in the early evolution of the skeleton in the Precambrian metazoans and represent a relict mechanism involved in the evolution of skeletons in lower Metazoa bacteria-mediated skeletonization (Garate et al. 2017).

Sponges are also important habitat builders and can provide hard substrate and add complexity in otherwise sediment-dominated environments, thereby increasing abundance and biodiversity of the surrounding area (Dayton et al. 1974; McClintock et al. 2005). Some species have essential functions in binding unconsolidated substrate such as coral rubble and pebbles into stable surfaces (Wulff 1984). Sponges are also important bioeroders in coral reefs, coralline bottoms, and oyster beds, where they are able to excavate tunnels and galleries into calcium carbonate (Rützler 2002; Schönberg 2008; Carballo et al. 2013; Hernández-Ballesteros et al. 2013).

Because of their feeding habits, sponges can accumulate a wide range of pollutants from both the suspension and dissolved phases, and they are considered useful biomonitoring organisms and can provide convenient tools for characterizing the state of a marine ecosystem (Carballo et al. 1996; Carballo and Naranjo 2002). They are capable of accumulating metals (Zahn et al. 1981; Cebrian et al. 2006), organochlorinated compounds (Pérez et al. 2003), radionuclides (Patel et al. 1985), and combustion-derived PAHs in relation to petrogenic compounds (Batista et al. 2013). Recently *Theonella* sp. has been shown to possess a specific and unique bacterial system for element accumulation and mineralization of both arsenic and barium (Keren et al. 2017).

1.3 Direct Impacts of Climate Change on Sponges

Unable to escape from the alteration of their environment, sponges are particularly exposed to environmental factors, which control their survival, distribution, and physiological performance. Thus, the changes associated with climate change will have diverse consequences on sponge survival and fitness. Research into the effects of climate change on sponges initially focused on thermal sensitivities. Thus, the first study that associated a positive thermal anomaly with sponges was that by Vicente (1989), who suggested that higher water temperature was responsible for the mortality and extinction of sponges of the genera *Spongia* and *Hippospongia* in the Caribbean. No explanation of the causes of the mortality was given, but a decade later, in 1999, a massive mortality, also of *Spongia*, *Hippospongia*, and *Cacospongia*, *c*oincided with a sudden increase in seawater temperature, higher than normal in the Mediterranean Sea. In this case, it was hypothesized that the cause of that mortality could be due to an extensive attack by opportunistic protozoans and fungi on the sponges (Cerrano et al. 2000). Subsequent studies have attributed sponge mortality to abnormal temperatures as a result of the loss of symbionts and the subsequent establishment of alien microbial populations, including potential pathogens (Webster et al. 2008; Cebrián et al. 2011). However, unusually high temperature does affect all sponge species by the same way. For example, *Chondrilla* cf. *nucula* survived during an episode of unusually high temperature that caused severe coral bleaching in the Caribbean (Aronson et al. 2002). Furthermore, some encrusting boring sponges tend to spread faster into and over corals, increasing bioerosion and killing corals, during high temperature events (Rützler 2002). Interestingly, some of these excavating sponges harbor zooxanthellae in symbioses, which are much less affected by bleaching than corals (Fang et al. 2016).

Unusual increases in temperature not only cause sponge mortality but also affect physiological performance and reproductive capability and dispersal. Massaro et al. (2012) showed a significant reduction in filtration rate and lower choanocyte chamber density and size in *Rhopaloeides odorabile* at only 2 °C higher than the average ambient seawater temperature. However, this response is not ubiquitous as other species, such as *Halichondria panicea*, increased filtration rates at seawater temperatures 5.5 °C above the normal ambient temperature (Riisgard et al. 1993). Further studies of thermal stress and sponge-feeding ecology are necessary for determining the mechanisms for this selective behavior. Water temperatures may have important implications for population reproductive success where oogenesis and spermatogenesis and larval release are cued by minimum and maximum water temperatures (Ettinger-Epstein et al. 2007). Thus, thermal stress has been also associated with the reabsorption of spermatic cysts and oocytes in the sponge *Petrosia* sp. (Asa et al. 2000) and to the disruption of the feedback mechanism that prevents the release of propagules of *C. reniformis* when ecological factors do not favor their survival (Sugni et al. 2014). Surprisingly, *Rhopaloeides odorabile* larvae are remarkably able to withstand seawater temperatures up to 9 °C above normal, despite adults being susceptible (Webster et al. 2013).

It is important to also mention that unusually low seawater temperatures have also been associated with the mortality of sponges in temperate latitudes (Pérez et al. 2006) and to sublethal effects, such as slowing growth and causing contraction in size of some species (Fowler and Laffoley 1993).

On the other hand, not much is known about the effect of thermal stress on deep sea sponge populations, despite that mass mortalities of important deep-water populations of Geodia barrette were associated to an unusual increase of water temperature in a cold-water coral reef (Norwegian shelf) (Guihen et al. 2012). However, later studies determined that G. barrette has a high thermal tolerance, and a highly stable microbiome even at temperatures 5 °C above ambient, and that other ecological processes such as low oxygen concentrations, elevated nutrients levels and reduced salinity should be explored to provide insight into the cause:effect pathways of G. barrette mortality (Strand et al. 2017). The apparent resilience of some sponge species and the sensitivity of others highlight the need to understand the molecular basis of sponge responses to environmental stressors and to understand if they may be able to adapt to rapidly changing ocean conditions. This was investigated for the first time in the sponge *Suberites domuncula*, which expressed a polypeptide after heat treatment (Bachinski et al. 1997). Higher-than-normal temperatures also caused a significant increase in heat shock protein Hsp70 transcript levels in the Caribbean sponge *Xestospongia muta* (López-Legentil et al. 2008) and in Hsp40 and Hsp90 in *Rhopaloeides odorabile*, indicating the activation of a heat shock response system. Exposure to high temperatures also produces a rapid downregulation of many genes (actin-related protein, ferritin, calmodulin) and the induction of others involved in signal transduction and in the innate immunity pathways, which affects expression patterns of genes involved in cellular damage repair, apoptosis, signaling, and transcription (Pantile and Webster 2011). It is likely that differences in ecological and physiological features of different sponges, and even their different life stages, will reflect variations in thermal tolerance and resilience. *Haliclona tubifera* subjected to elevated temperature showed activation of various processes that interact to maintain cellular homeostasis. It seems that this species, which is normally located in shallow water, is exposed to variable temperatures and has a more robust response to temperature fluctuations compared to sponges found at deeper depths with colder and more stable temperatures (Guzmán and Conaco 2016).

Regarding OA, it has been shown that acidification decreases the diversity, biomass, and trophic complexity of benthic communities (Kroeker et al. 2013). However, both experimentally (Duckworth et al. 2012) and through field research of sponges across natural temperatures and pH ranges, such as those occurring in naturally acidified areas close to CO_2 seeps, have been demonstrated the resistance of certain sponges to low-pH conditions (Morrow et al. 2015). It seems that their capacity to withstand OA lies in their ability to restructure their host-associated microbiomes mainly by acquiring new microbial components via horizontal transmission (Goodwin et al. 2014). Species with greater microbial diversity may develop functional redundancy that could enable the holobiont to survive even if particular microbes are lost at low-pH conditions (Ribes et al. 2016). It has also been suggested that OA may provide a potential advantage for boring sponges, since OA accelerates bioerosion (Duckworth and Peterson 2013; Wisshak et al. 2014). Recent research has demonstrated increased bioerosion rates under experimentally elevated partial pressures of seawater carbon dioxide (pCO_2) with or without increased temperatures, which may lead to net erosion on coral reefs in the future (Wisshak et al. 2012). However, this may depend on the ability of sponges to survive and grow in the warmer and more acidic future environments and, fundamentally, on the energy reserves they have accumulated through the rest of the year (Fang et al. 2014). It is important to note that there has been relatively little research investigating about how ocean acidification affects the interaction between coral and boring sponges, which is important as OA weakens and chemically dissolves the coral skeletons, making boring easier (Stubler et al. 2014). As seawater pH decreases, many corals are likely unable to create new layers of calcium carbonate as efficiently resulting in net erosion rates on reefs.

More information of the potential effect of OA on sponges comes from the past. The overturning of anoxic deep oceans during the Permian-Triassic boundary occurred about 252 million years ago and introduced high concentrations of carbon dioxide into surface environments (Knoll et al. 1996), which is thought to be responsible for the extinction of marine organisms that produced calcareous hard parts, notably reef-building calcareous sponges (Knoll et al. 1996; Pörtner et al. 2004; Pruss and Bottjer 2005), but also the majority of siliceous sponge species (88–92%), including all hexactinellids and species with tetraxons (Liu et al. 2008). Low metabolic rate, the absence of a circulatory system, and gas-permeable surfaces may increase vulnerability in siliceous sponges (Knoll et al. 1996).

Most studies concerning the impact of climate change on sponges discuss independent effects of warming and ocean acidification, but it is also necessary to include synergies with other local effects, such as pollution, sedimentation, and other anthropogenic stressors. Understanding the connection between the different local effects and climate-related stressors will be also necessary in order to predict the consequences of future climate change on the survival of sponge populations. It is also important to predict the biological stress responses of sponges to climate change and ocean acidification in order to understand how sponges can modify their gene expression as a potential mechanism for surviving in the future.

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Chapter 2
Lessons from the Past: Sponges and the Geological Record

Lucy A. Muir, Joseph P. Botting, and Matilde S. Beresi

Abstract Sponges have been a major part of marine ecosystems, in both shallow and deep water, from the time of the earliest animal communities. The great shifts in climate that have occurred over the past 541 million years have affected all organisms, including sponges. Although patchy knowledge of the sponge fossil record hinders recognition of trends, some general patterns are apparent. Shallow-water siliceous sponges were severely affected by glacial intervals, whereas deeper-water siliceous sponges appear to have flourished during these times. Some groups of hypercalcified sponges (such as stromatoporoids) were abundant during times of global warming and high sea level, but other groups (archaeocyathans and sphinctozoans) had their acme during times of low sea level and relatively cool climate. Overall, sponge diversity appears to have been controlled more by sea level than by climate: large-scale sponge biotas occurred at times of high sea level, when there were large areas of shallow sea.

Keywords Porifera • Deep time • Greenhouse • Icehouse • Mass extinction

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2.1 Introduction

Sponges are a diverse phylum that has a long and complex history, and include a large number of extinct groups. At times in Earth history, they have been much more prominent than they are currently and at other times appear to have declined in relative importance. As some groups have thrived, others have diminished, in response to a complex suite of ecological and environmental changes. At the same time, the Earth itself has passed through enormous tectonic changes, combined with large-scale biogeochemical, sea-level and climate cycles, each of which feeds into the others. It is therefore difficult to identify clear patterns that summarise the response of sponges to climatic changes, since such changes are inextricably linked to other environmental fluctuations on global and local scales.

This paper provides a brief overview of the histories of different sponge groups in relation to major Earth changes and attempts to draw out generalisations regarding the response of sponges to changing climates with particular reference to mass extinction events.

2.2 The Sponge Fossil Record

The first unambiguous records of sponges (phylum Porifera) are in lower Cambrian rocks (535 million years old; Antcliffe et al. 2014; Fig. 2.1). Throughout the Phanerozoic (the part of the geological record with abundant animal fossils, the past 541 million years), sponges have been significant in marine ecosystems as both reef-forming taxa and as individuals. Three of the four present-day sponge classes (Demospongiae, Hexactinellida and Calcarea) are recognisable in the fossil record back to the Palaeozoic (Pisera 2006); the fourth, the Homoscleromorpha, have a questionable Carboniferous record and otherwise appear in the Mesozoic (Reid 2004). The earliest sponges, however, represent stem-group forms or extinct lineages, and their affinities are often obscure (Botting and Muir 2013; Botting and Zhang 2013; Botting et al. 2013).

The quality of the sponge fossil record is good for some groups but very intermittent for others. Keratosan sponges, which do not possess a mineralised skeleton, have a low preservation potential and hence a very sparse fossil record (Luo and Reitner 2014). Sponges with massive skeletons, such as stromatoporoids and lithistids, inevitably have a much better fossil record than sponges with skeletons composed of unfused spicules, such as modern lyssacinosan hexactinellids, heteroscleromorph demosponges and most early taxa. Sponges with unfused spicules must be buried alive or shortly after death to be preserved in an articulated state and without that preservation are rarely identifiable. Although disarticulated spicules are common in the fossil record, these are not generally useful for taxonomic work or assessment of diversity, since spicule morphology is extremely homoplasic. As a result, there is a strong bias against loose-spiculed sponges (particularly those

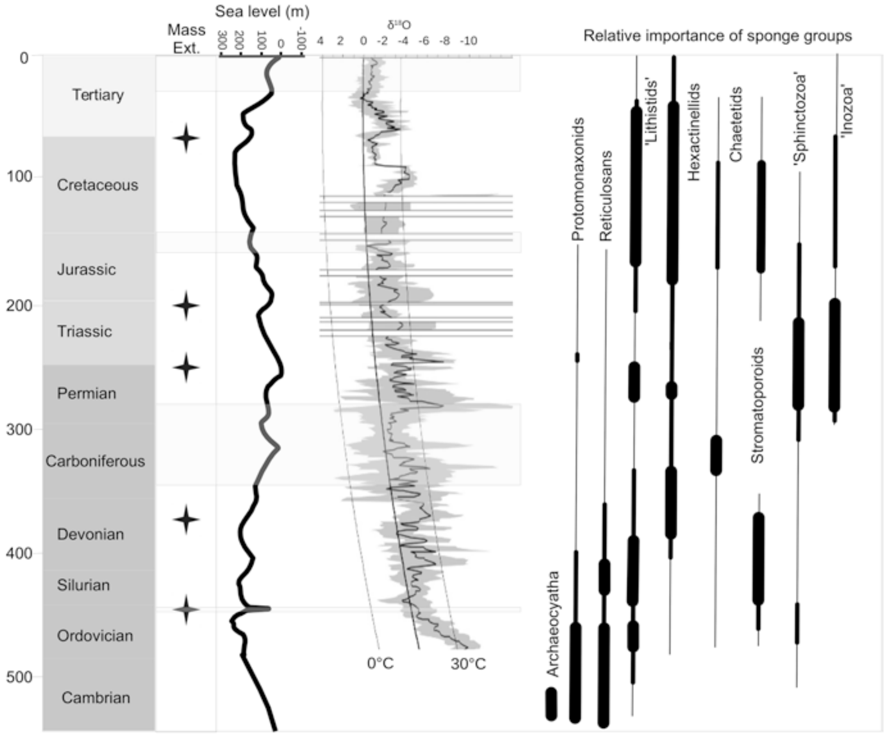

Fig. 2.1 Summary log of sea level, temperature (based on oxygen isotopes) and ranges of various sponge groups. *Thin lines* denote presence but at insignificant levels; *medium lines* represent significant presence; *thick lines* imply notable abundance (see text for more detail). *Crosses* mark major mass extinction events. *Pale grey boxes* represent global glaciation intervals. Sea-level curve based on Sneddon and Liu (2010); secular seawater temperature modified after Veizer and Prokoph (2015)

with small spicules) such as non-lithistid heteroscleromorphs, homoscleromorphs, lyssacinosan hexactinellids, non-hypercalcified calcareans and virtually all stem-group lineages, and this must be taken into account when considering the observed responses to environmental change.

2.2.1 Fossil Sponge Groups

Numerous groups of sponges, only some of which are familiar to neontologists, are preserved at least intermittently in the fossil record. There has been an expectation that most fossil lineages can be squeezed into extant classes if they share any features such as basic spicule symmetry (e.g. Finks et al. 2004), but this view is being undermined by the appreciation of extinct character combinations in the various

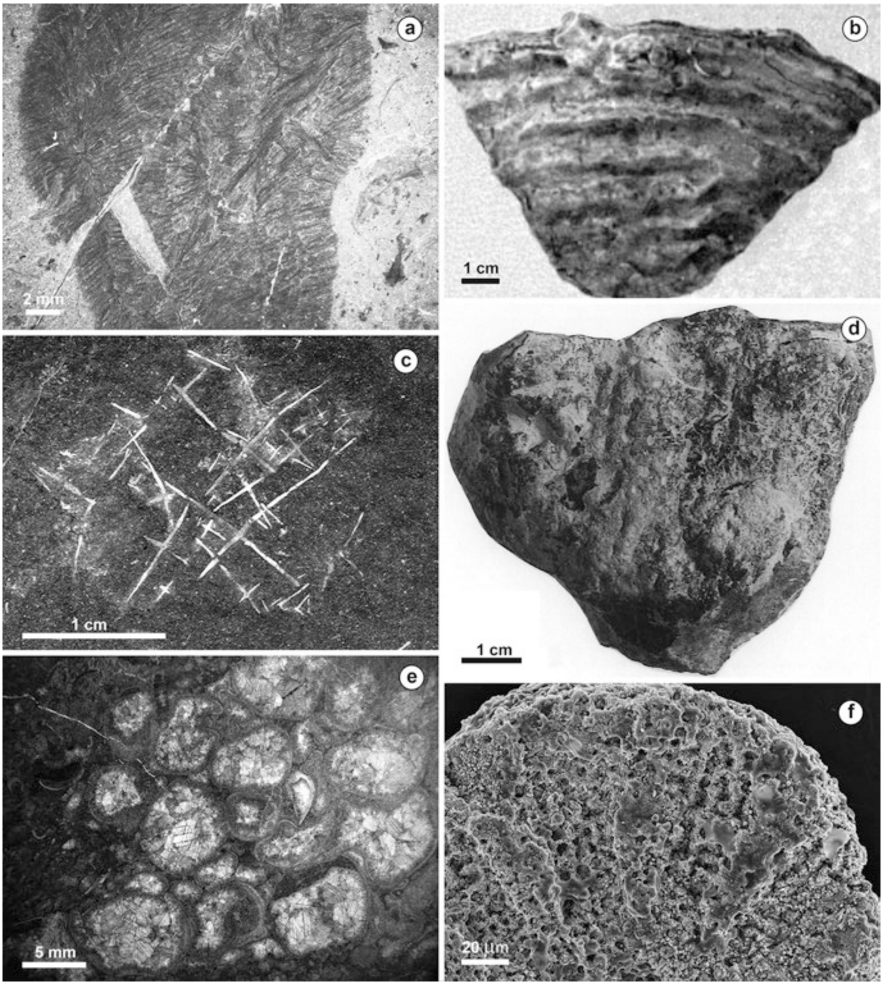

Fig. 2.2 Representative specimens of major sponge groups. (**a**) Protomonaxonid: *Wapkia elongata*, middle Cambrian, Burgess Shale, Canada (ROM53549, Royal Ontario Museum, Canada). (**b**) Lithistid demosponge: *Anthaspidellida annulata*, Middle Ordovician, Talacasto Gulch, Argentine Precordillera (CRICYT T-49, Centro Regional Investigaciones Cient. Tec., Mendoza, Argentina). (**c**) Reticulosan: *Protospongia* sp., middle Cambrian, San Juan Precordillera, Argentina (CRICYT TS-1, Centro Regional Investigaciones Científicas y Tecnológicas, Mendoza, Argentina). (**d**) Hexasterophoran hexactinellid: *Laocoetis* sp., Upper Jurassic (Oxfordian), Neuquén Basin, Argentina (IANIGLA-PI 926, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Argentina). (**e**) Sphinctozoan: *Corymbospongia* (thin section) upper Sanqushan Formation (upper Katian, Upper Ordovician), southeast China (NIGP 166033, Nanjing Institute of Geology and Palaeontology, China). (**f**) Lithistid demosponge: *Hindia* sp., showing the wall structure, Middle Ordovician, Huaco locality, Argentine Precordillera (IANIGLA-PI 3096, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales)

stem groups (see below). Only a simple outline of the major groups is provided here. Some major types of sponge in the fossil record, including a hexactinellid and lithistid demosponges, are illustrated in Fig. 2.2.

2.2.1.1 Archaeocyaths

Archaeocyaths are apparently sponge-like organisms with massive, calcitic skeletons that formed reefs. They are generally thought to be sponges (Kerner and Debrenne 2013), although this has been disputed (see Rowland 2001 for a history of research). Archaeocyaths appeared and rapidly became widespread during the early Cambrian, with a more limited distribution in the middle Cambrian, and had virtually disappeared by the late Cambrian, when they went extinct (Kerner and Debrenne 2013). Most records of archaeocyaths are from the palaeotropics (Kerner and Debrenne 2013), but they show a global distribution at low latitudes.

2.2.1.2 Heteractinids

With the exception of some problematic early taxa with a mosaic of characters including hexactines (Botting and Butterfield 2005), heteractinids are widely accepted to be stem-group calcareans. They are widespread (often as isolated spicules) but only locally common in Palaeozoic strata and are found particularly in Ordovician (Fig. 2.3a) and Silurian shallow-water deposits (e.g. Mehl and Reitner 1996; Carrera and Botting 2008). Unlike modern calcareans, their spicules were generally hexaradiate, often with two perpendicular rays (octactines), but were composed of calcite with a similar structure to that of modern spiculate Calcarea; in some cases, a secondary calcareous skeleton bound the spicules into a solid framework (Mehl and Reitner 1996).

2.2.1.3 Reticulosans

Reticulosans are a complex group of hexactinellid-like sponges with a thin wall of loose hexactines and derivatives (Fig. 2.2c; most of them, however, fall into the stem groups of Hexactinellida and Silicea (Botting and Butterfield 2005; Botting and Muir 2013). These sponges usually dominated Cambrian to Silurian offshore sponge communities, below storm wave base (Muir and Botting 2015), but declined dramatically thereafter. An exception is the Dictyospongiidae, a distinctive family in which the skeleton developed into a tough, woven structure that was able to survive shallow-water conditions, which thrived during the Devonian and Carboniferous in particular (Hall and Clarke 1898); these possessed some hexactinellid-like microscleres (Kling and Reif 1969) and probably fall into the late stem group of Hexactinellida.

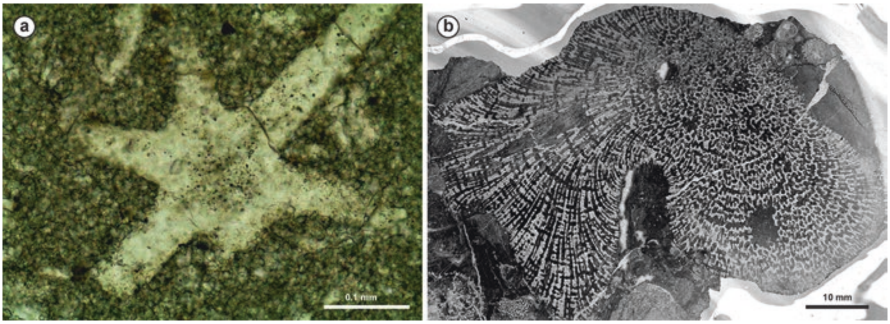

Fig. 2.3 Representative specimens of major sponge groups. (**a**) Heteractinid: hexaradiate spicule, Middle Ordovician, Talacasto Gulch, Argentine Precordillera (IANIGLA-PI 3021, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza). (**b**) Inozoan: *Irregulaspongia parva*, longitudinal section through a branched specimen exhibiting the upwardly oriented skeletal fibres, Upper Triassic (Norian), Taurus Mountains, southern Turkey (sample number BG6. Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany); reproduced with permission from Senowbari-Daryan and Link (2016)

Numerous lineages of Ordovician to Devonian sponges developed thick walls of hexactine-based spicules and have traditionally been assigned to the Hexactinellida (e.g. Brachiospongiidae, Pelicaspongiidae, Malumispongiidae; see Finks et al. 2004) but in many cases may have independent origins from reticulosans. Other early sponges with complex and unique architectures have been described (e.g. Rigby and Webby 1988; Rhebergen and Botting 2014). It remains very difficult to distinguish reticulosans and their independent offshoots from crown-group hexactinellids in the early part of the fossil record.

2.2.1.4 Protomonaxonids

Protomonaxonids were a major group of Cambrian sponges (e.g. Rigby and Collins 2004; Botting and Peel 2016) that declined rapidly thereafter (but were still important components of at least polar communities in the Early Ordovician; Botting 2016). Until recently, they were assigned to the demosponges on the basis of having siliceous monaxon spicules (Fig. 2.2a; Finks et al. 2004). However, they have since been shown to possess, in at least some cases, biminerallic spicules, which are inferred to have been composed of both silica and calcite (Botting et al. 2012), and to represent a deeper part of the poriferan evolutionary tree (Botting et al. 2013). Some members of the group survived until the Mesozoic (Keupp and Schweigert 2012; Brayard et al. 2017).

2.2.1.5 Stromatoporoids

Several groups of sponges have developed secondary, usually aragonitic basal skeletons. There appears to be a distinction between Mesozoic and Palaeozoic forms, and the two groups may be unrelated (Cook 2002) and should be treated separately. Palaeozoic stromatoporoids, which originated in the Ordovician, have unknown origins and may have been polyphyletic; Mesozoic taxa are probably related to demosponges (Cook 2002). Stromatoporoids were major reef-building organisms during the Late Ordovician to Devonian and during the Jurassic (Leinfelder et al. 2005; Nestor and Webby 2013), associated with various corals and other organisms.

2.2.1.6 Inozoans

Inozoans were a major polyphyletic group of reef-building, hypercalcified calcareans and demosponges that were particularly abundant during the Permian–Triassic interval (Rigby and Senowbari-Daryan 1995a; Pisera 2006). Inozoans (Fig. 2.3b) were non-chambered, usually cylindrical or clavate, and some Mesozoic examples possess spicules that clarify their affinities (Pisera 2006).

2.2.1.7 Chaetetids

Chaetetids are a problematic group of compound organisms that have been widely assigned to various animal and algal taxa but are now considered to be sponges (Senowbari-Daryan and Amirhassankhani 2013). They are also now understood to include various groups that have previously been classified as algae (Solenoporaceae; Riding 2004). Vacelet (1985) argued strongly for a demosponge origin, particularly relating to the basal skeleton of certain living tetractinellid demosponges such as *Spirastrella*.

2.2.1.8 Sphinctozoans

This term refers to chambered, hypercalcified sponges (Fig. 2.2e). The sphinctozoans are a diverse, disparate and long-ranging group that are certainly polyphyletic, including both demosponges and calcareans (Wood 1991; Senowbari-Daryan and García-Bellido 2002). Some taxa closely resemble certain archaeocyaths, and their first appearance is as early Cambrian heteractinid calcareans such as *Nucha* (Pickett and Jell 1983). The single living example, *Vaceletia*, is a demosponge (Vacelet 2002).

Chambered growth forms presumably evolved repeatedly due to the hydrodynamic advantages of a nearly enclosed, solid-walled chamber for feeding and the inability of such structures to be enlarged by accretion while maintaining the body form. Iterative growth of chambers is an inevitable solution, especially in compound organisms capable of reproduction by budding. Chambered growth has even evolved among hexactinellids (e.g. *Casearia* Quenstedt 1858). The growth style is also conducive to construction of frameworks, and sphinctozoans are common components of reefs, particularly in the Permian and Triassic (e.g. Ott et al. 1980; Wood 1991).

2.3 Climatic Changes in Geological Time

Over the past 540 million years, since the rise of animals, the Earth's climate has fluctuated between warmer (greenhouse) and cooler (icehouse) states as a result of long-term changes in continental arrangement, resulting in ocean–atmosphere dynamics, atmospheric composition and solar output (e.g. De Boer and Smith 1994; Zachos et al. 2001; McKenzie et al. 2014). The transition between these states is usually slow and gradual: an icehouse state is one in which there is permanent ice at the poles; under greenhouse conditions, ice at the poles is seasonal or absent. Within icehouse states ('ice ages'), there are short-term, smaller-scale changes (glacial and interglacial intervals) that are produced largely by orbital mechanics (e.g. Webb and Bartlein 1992 and references therein) and are predictable. The present day falls within a warm interval (interglacial) of an icehouse: the current glaciation began during the Oligocene, approximately 34 million years ago (Zachos et al. 2001).

Major climatic changes through the Phanerozoic are listed in Table 2.1, for comparison with poriferan ecological history as outlined in the next section. Climate changes have inevitably had major effects on the biota, but the rate of change is more critical than the magnitude. For example, the long-term changes associated with normal icehouse–greenhouse transitions (e.g. from the Late Devonian to the mid-Permian) result in gradual adaptation of the biosphere, with particular groups evolving to the new conditions better than others. When the transition is very abrupt, either entering an icehouse state (Late Ordovician; Harper et al. 2014) or a severe greenhouse (Permian–Triassic interval; Benton and Twitchett 2003), the result is typically a mass extinction.

Mass extinctions are intervals of global biodiversity loss that greatly exceed the normal rate of taxonomic overturn. They have operated at a wide range of scales, from barely worse than background losses to the end-Permian crisis in which approximately 81% of species became extinct (Stanley 2016). Although some, such as the end-Ordovician event, appear to have been directly caused by climatic changes, there are normally several major contributing factors that ultimately lead to ecological collapse. Most famously, a bolide impact at the end of the Cretaceous Period caused a major mass extinction that eliminated ammonites, various marine reptiles and non-avian dinosaurs (Schulte et al. 2010). (Other factors were also involved in the extinction event, as discussed in the section on the Cretaceous sponge record.) Due to the limited resolution of the fossil record, it can be very difficult to assess which environmental changes were implicated in specific changes to the biosphere, and on precisely what time scales. This applies especially to studying groups with an intermittent fossil record, such as in attempting to document the

Table 2.1 Selected major climatic changes and events during the Phanerozoic

Interval	Approximate time (Ma)	Climatic changes
Oligocene to recent	34–0	Cooling, leading to current Ice Age with abrupt glacial–interglacial cycles
Palaeocene–Eocene	55	Abrupt temperature peak related to methane clathrate release (Palaeocene–Eocene Thermal Maximum)
End-Cretaceous	65	Bolide impact with climatic side effects; mass extinction
Mid-Jurassic to Late Cretaceous	170–65	Gradual, prolonged warming; transition from icehouse to greenhouse conditions
Permian–Triassic transition	252	Gradual warming, with abrupt temperature peak at boundary; extreme mass extinction
Carboniferous	358–298	Gradual, long-term cooling
Late Devonian (Frasnian–Famennian)	372	Complex episode probably involving high temperatures and anoxic events; mass extinction
Late Ordovician	445	Abrupt, short-lived glaciation, then deglaciation, with mass extinction
Late Cambrian	490	Uncertain: either high-temperature peak or a glaciation (conflicting evidence)

Numerical ages are from the International Chronostratigraphic Chart 2016 (Cohen et al. 2013; latest version at http://www.stratigraphy.org/ICSchart/ChronostratChart2016-12.pdf)

ecological response of sponges. Bearing this in mind, the following is an outline of sponge evolution during major phases of climatic change during the Phanerozoic.

2.4 Sponge Diversity Patterns Through Time

Reconstructing diversity patterns of sponges through geological time is not straightforward. Different lineages have vastly different fossil preservation potential, due to differences in skeleton type and preferred habitat, and also show discordant appearance and extinction dates. Also, some time intervals (notably the Cambrian) are very rich in exceptionally preserved fossil biotas, which give a much clearer idea of the diversity of offshore spiculate sponges during these intervals. Each part of the fossil record therefore needs to be considered individually.

2.4.1 Precambrian

There are no convincing sponge fossils described from the Precambrian: all reports of putative sponge remains are not sponges (Antcliffe et al. 2014). The biomarker evidence for Precambrian sponges is also not convincing (Antcliffe 2013). The lack of Precambrian sponges is problematic, as both molecular-clock studies (e.g. Wörheide et al. 2012; Cunningham et al. 2017) and the diversity of sponges in the early Cambrian (e.g. Rigby and Collins 2004) suggest that poriferans originated well before the Cambrian and thus should have a Precambrian fossil record. An attempt to explain this lack by a taphonomic bias against siliceous remains in the late Precambrian (Sperling et al. 2010) is not feasible, as silica-rich rocks such as cherts are abundant in the late Precambrian due to high levels of dissolved silica in seawater (Muscente et al. 2015). Thus, at present we are unable to say anything about Precambrian sponge diversity. If present, sponges were apparently rare, obscure (perhaps due to very small size) or restricted to abnormal environments that have not been preserved. It is thus not possible to make inferences about the sponge response to 'Snowball Earth' episodes, even though some authors have tried (Corsetti 2015).

2.4.2 Cambrian

Cambrian climate studies are complex and reveal partly conflicting results. A transition from aragonite to calcite primary precipitation supports interpretations of steadily increasing sea level and temperature through the Cambrian (Miller et al. 2005), although this appears to conflict with the traditional understanding of a late Cambrian sea level lowstand (e.g. Hersi et al. 2002). During the Cambrian Explosion, global mean temperatures appear to have been relatively cool; extensive lower Cambrian evaporite deposits may not reflect high temperatures and can be consistent with cold climates (Frakes et al. 2005). Furthermore, there is some evidence of early Cambrian glaciation at high latitudes (Landing and MacGabhann 2010).

In general, the late Cambrian interval is regarded as having experienced greenhouse conditions, which may have been extreme (Frakes et al. 2005), but another work (Runkel et al. 2010) indicates ice at sea level in tropical regions. In the absence of evidence for extensive ice, previous discussions of the global lowstand in sea level at this time, combined with a carbon isotope shift typical of glaciation intervals, implicated tectonic or hydrological factors (Saltzman et al. 2000). Overall, a pronounced cold interval is looking increasingly reasonable for the late Cambrian, at least as part of a complex sequence of cooling and warming intervals (Elrick et al. 2011; Eoff 2014), with a major regression–transgression interval (Saltzman et al. 2004).

Cambrian sponge faunas show complex diversity patterns involving several major groups. In the early and to some extent middle Cambrian, archaeocyathan reefs were abundant and widespread in low latitudes (Debrenne and Courjault-Rade 1994). These reefs also housed a range of spiculate sponges that appear to have included very early, cavity-dwelling demosponges (Kobluk 1981; Rowland and Gangloff 1988). The entire community, however, appears to have been lost with the decline of the reefs in the middle Cambrian (Debrenne 1991). Due to the difficult nature of the material (often preserved as fragments or three-dimensional but amorphous bodies within limestones), interpretation of the cavity dwellers is often difficult. The carbonate reef environment also housed a variety of robust, thick-walled sponges such as the apparent calcarean *Nucha* (Pickett and Jell 1983) and the early anthaspidellid ‘lithistids’ *Jawonya* and *Wagima* (Kruse 1996).

A distinct community of sponges occupied relatively deep-water carbonate areas but have only been described as assemblages of complex, often problematic spicules (Zhang and Pratt 1994; Zhao and Li 2006). Many of these spicules cannot be assigned even to major groups but may include heteractinids. This assemblage of diverse, ornate spicule types also continued through the Ordovician (Webby and Trotter 1993, and below) in similar habitats, but most taxa have never been found articulated.

With the exception of archaeocyathans, which arose slightly earlier, the earliest articulated sponge faunas (e.g. Steiner et al. 1993; Yang and Zhao 2000; Xiao et al. 2005; Botting and Peel 2016) date from around 15 to 20 million years (Myr) after the base of the Cambrian, although records of isolated hexactine-type spicules have been described from the lowermost Cambrian (Antcliffe et al. 2014; Chang et al. 2017). There is also a diverse suite of exceptionally preserved Burgess Shale-type faunas in the early and middle Cambrian, with a typical diversity of between 20 and 50 species after long-term collecting (e.g. Rigby and Collins 2004; Rigby et al. 2010; Wu et al. 2014).

The sponges from Burgess Shale-type faunas are often referred to as primarily hexactinellids and demosponges but are dominantly reticulosans and protomonaxonids. Rare examples of true demosponges are also known (e.g. Beresi and Rigby 1994; Rigby and Collins 2004; Botting et al. 2013, 2015). These sponges constitute a significant portion of the species diversity and usually also individual abundance and biomass (Caron and Jackson 2008; Dornbos and Chen 2008; Wu et al. 2014; Botting and Peel 2016).

Late Cambrian sponge faunas, coincident with the major climate change interval, are extremely poorly known (Carrera and Botting 2008; Muir et al. 2013). There are no Burgess Shale-type faunas from this time period, so continuity of pre-existing lineages is in many cases uncertain. However, several of the major sponge families, and even genera, from these deposits are known to have survived into the Early Ordovician (Botting and Muir 2014; Botting et al. 2015; Botting 2016).

In shallow water, there is less direct evidence for survivorship of sponges. Few if any hypercalcified groups were present at this time, with the archaeocyaths declining abruptly in the middle Cambrian and finally going extinct in the early part of the late Cambrian. Lithistid demosponges, however, show progressive diversification into the Early Ordovician (Beresi and Rigby 1993; Carrera and Botting 2008; Muir et al. 2013), although their main diversification phase occurred later in the Ordovician as part of the Great Ordovician Biodiversification Event (see below). Nonetheless, some late Cambrian lithistids such as *Rankenella* contributed to small reefs, together with the calcimicrobe structure *Girvanella* (Kruse and Zhuravlev 2008). Late Cambrian sponges appear to have been slowly developing, without spectacular taxonomic overturn or extinction but with small-scale diversification among offshore taxa and the initial development of reef-building habits. However, this is probably partly a result of the poor record at this time, because some Early Ordovician spicule assemblages (Carrera and Maletz 2014) suggest that a major diversification including crown-group Hexactinellida had occurred before this point.

2.4.3 Ordovician

During the Ordovician Period, the climate was generally very warm in the early part and gradually became colder until the glacial event in the Late Ordovician (Trotter et al. 2008; Munnecke et al. 2010). An apparent warming interval within this trend (the Boda Event; Fortey and Cocks 2005) has also been interpreted as a phase of cooling (Cherns and Wheeley 2007) and remains somewhat ambiguous. Eustatic sea level was extremely high for most of the Ordovician (Miller et al. 2005), with broad shallow low-latitude epeiric seas and generally high levels of volcanicity (Stillman 1984). Climatic disruption came at the end of the period with glaciation in Gondwana producing the terminal Ordovician mass extinction (Sheehan 2001; Harper et al. 2014), the second most severe of the entire Phanerozoic (Krug and Patzkowsky 2015; Stanley 2016).

Sponges flourished during the Ordovician Period, perhaps more than at any other time. The Great Ordovician Biodiversification Event (GOBE) was a sustained rise in diversity, primarily through diversification of sessile filter-feeding organisms such as brachiopods and corals (Servais et al. 2010). Sponges diversified as part of the GOBE, but at present it is difficult to be certain of large-scale patterns because of overwhelming monographic bias: a single new fauna can change the entire global diversity curve (Botting and Muir 2008).

Overall, reef-forming sponges such as lithistids flourished in shallow water during the Ordovician (Beresi and Rigby 1993; Carrera and Botting 2008). These sponges appear to have been severely affected by the Late Ordovician extinction, although some of this was temporary with numerous Lazarus taxa (Muir et al. 2013). (Lazarus taxa are groups that vanish from the fossil record for a period of time, such as after a mass extinction, but reappear some time later; Fara 1991.) Stromatoporoid sponges were abundant and diverse in subtropical and tropical carbonate platform settings during the Late Ordovician (Nestor 1990).

Diverse Ordovician non-reef-forming siliceous sponge faunas have been found at palaeolatitudes from polar (Botting 2016) to tropical (Dawson 1888) settings, including persisting Cambrian lineages (Botting 2004, 2007a; Botting and Muir 2014). The Little Métis assemblage (Dawson 1888; Dawson and Hinde 1889) from Quebec has been reported to be late Cambrian in age but is more likely to be Early Ordovician (Conway Morris 1989): this fauna contains a diverse offshore assemblage of reticulosans and protomonaxonids with simple architectures. The temperate-palaeolatitude Afon Gam Biota of North Wales, UK (Botting et al. 2015), has yielded the most diverse assemblage of Early Ordovician sponges yet known (although most are as yet undescribed) and includes a wide range of typical Burgess Shale groups such as the Piraniidae, Hazeliidae, *Choia*, *Hintzespongia* and

Valospongia. Although there is obvious diversification among the reticulosans, most of these taxa closely resemble those seen in the middle Cambrian. Additional surviving protomonaxonid lineages known from the near-polar Fezouata biota (Botting 2007a, 2016) include the Leptomitidae and *Choiaella*. Overall, there is little evidence for any significant biodiversity loss among sponges inhabiting offshore environments through the late Cambrian and Early Ordovician, as many of the families and genera have been reported from younger rocks (e.g. Botting and Clarkson 2007b; Beresi et al. 2010).

In addition to surviving taxa, there was also substantial diversification of apparently new lineages, including characteristically modern groups (Kozur et al. 1996; Botting 2005; Carrera and Maletz 2014). Sponges appear to have dominated many Ordovician marine communities (Botting et al. 2015; Muir and Botting 2015). There has been little discussion of the distribution of various sponge groups during this interval. Muir and Botting (2015), in their study of a small area of Wales, found that thick-walled sponges (which tended to belong to newly evolved groups) lived in shallow, turbulent water; thin-walled sponges (which tended to belong to older lineages) occupied deeper water. In the deeper, quiet-water environments, protomonaxonids primarily occupied intermediate depths around or above storm wave base, and reticulosans dominated the deepest localities. Some aspects of modern deep-water communities may have been established by this time; for example, Botting et al. (2011) described a late Ordovician sponge-dominated community from relatively deep water with similarities to modern deep-water faunas.

The Late Ordovician extinction severely affected reef-forming taxa such as stromatoporoids (Nestor and Webby 2013). In contrast, deeper-water sponges may have been relatively unaffected, at least in some areas: the presence of diverse, abundant sponge faunas in mudstone in low latitudes immediately after the extinction (Li et al. 2015; Botting et al. 2017) implies that the diversity of deeper-water sponges was not seriously affected by the Ordovician extinction.

2.4.4 Silurian

This period was characterised by a warm but fluctuating climate with generally very high sea levels (Munnecke et al. 2010) and widespread shallow continental seas. However, there were numerous carbon isotope excursions and minor mass extinction events (primarily affecting planktonic organisms such as graptolites; Rickards 1978; Štorch 1995), suggesting extremely complex oceanographic changes on relatively small scales but without the major glaciations or long-term trends that characterise other time periods. Understanding of the detailed climate of this interval is at this stage rudimentary.

The Silurian sponge record is currently very incomplete (Muir et al. 2013), with relatively few diverse faunas yet described but numerous Lazarus taxa indicated by comparison of Ordovician with later Silurian faunas. The current record shows a steady increase in diversity over time, but the total numbers of species are so low that this is not likely to be meaningful.

During the Silurian Period, stromatoporoids (Nestor 1990) and lithistids (e.g. Rhebergen and Botting 2014) flourished in shallow, tropical/subtropical carbonate platform settings and were major components of Silurian patch reefs (e.g. Crowley 1973; Kano 1989; Li et al. 2002). As in several other periods, the late Silurian shows a strong association of microbial mud mounds with siliceous sponges (often lithistids), producing a distinctive reef ecology (Brunton and Dixon 1994).

The record of non-lithistid siliceous sponges from this interval is extremely poor, with most described faunas being composed of single species (summarised by Muir et al. 2013). Although there are reports of spicule assemblages (e.g. Beresi 2013), these are generally only identifiable at high taxonomic level and thus are not useful for studies of sponge taxonomy or diversity. There are no records at all of complete sponges from the lowest Silurian (Rhuddanian and Aeronian). This is probably not due to the effects of the end-Ordovician extinction event: several siliceous sponge families are known from the Upper Ordovician and the middle or upper Silurian but not from the lower Silurian (Muir et al. 2013). The few known assemblages from shallow siliciclastic environments indicate diversification of apparently new and distinctive body forms, as well as adaptations based on earlier reticulosan lineages, even in the early Silurian (Botting and Clarkson 2007b).

2.4.5 Devonian

The climate during the Early Devonian was warm, with cooling during the Middle Devonian and warming during the Late Devonian (Joachimski et al. 2009). The spreading of land plants during the Devonian had marked influences on CO_2 levels and climate and probably helped to maintain warm temperatures during this time (Le Hir et al. 2011). In the latest Devonian, rapid cooling led to a glaciation (Kaiser et al. 2011).

Devonian sponge faunas are poorly known overall. Described faunas include some textbook assemblages; most notably, the Chemung Formation of New York State records a huge nominal diversity of dictyosponges (Hall and Clarke 1898) from shallow-water sandstone deposits. Stromatoporoids (together with corals) formed small patch reefs during the Early Devonian (Joachimski et al. 2009). Stromatoporoids were major reef constituents in tropical to subtropical environments during the Middle and Late Devonian, forming mega-reefs with corals that could extend over great distances (Stock 1995; Joachimski et al. 2009). Stromatoporoid reefs vanished during the Late Devonian extinction (Joachimski et al. 2009). The diversity of deep-water siliceous sponges increased during the latest Devonian (McGhee 1996).

There was a mass extinction (the Frasnian–Famennian event) during the Late Devonian. The causes of the mass extinction are not yet fully understood, with factors as diverse as global warming (e.g. Thompson and Newton 1988), global cooling (e.g. Joachimski and Buggisch 2002), bolide impact (e.g. McGhee 1996) and oceanic anoxia (e.g. Joachimski and Buggisch 1993), or some combination of several factors (e.g. Buggisch 1991), having been suggested. For animals in general, reef dwellers and pelagic animals in the tropics were particularly badly affected by this mass extinction (Buggisch 1991; Joachimski and Buggisch 1993).

The Late Devonian extinction had different effects on different sponge groups. In heteractinids, astraeospongiids became extinct during the event, whereas wewokellid sponges began to diversify during this interval (see Rigby 1991). For siliceous sponges, there was an ecological transition from assemblages dominated by lithistids to those dominated by loose-spiculed siliceous sponges (hexactinellids and non-lithistid demosponges) during the event (Vishnevskaya et al. 2002). Among the demosponges, a large number of anthaspidellid genera became extinct (data in Finks and Rigby 2004). Palaeozoic stromatoporoids effectively became extinct at this time (Herbig and Weber 1996), with only a few surviving into the latest Devonian, when they also died out.

2.4.6 Carboniferous

There was a generally warm climate during the early Carboniferous, during which time limestone deposits were abundant in low latitudes (Bruckschen et al. 1999). The migration patterns of marine invertebrates and land plants towards poles suggest that both poles became warmer in the middle part of the early Carboniferous (Raymond et al. 1990), supported by more recent work (Scheffler et al. 2003) that shows a succession of long-term transgressive intervals in the early Carboniferous, interspersed with short glacial intervals. However, the late Carboniferous was marked by an increase in the extent and duration of glaciation in the Southern Hemisphere (Isbell et al. 2003); this change coincided with a trend towards increased aridity during the late Carboniferous and Permian (Roscher and Schneider 2006).

Many Carboniferous sponge faunas are impoverished, containing a few lithistids (orchoclads and rhizomorines) along with some monaxonid demosponges and less abundant sphinctozoid demosponges (e.g. reef carbonate facies of northern England; Rigby and Mundy 2000). A few genera, such as *Amblysiphonella*, have a wide geographic spread (García-Bellido et al. 2004). The genus *Hyalostelia* (formerly *Hyalonema*; Young and Young 1877; Reid 1968) is, however, very characteristic of the Carboniferous limestones and peri-deltaic sediments into the late Carboniferous (e.g. Howitt and Brunstrom 1966), and other siliceous sponges are also recorded from these habitats (Weller 1930). Lyssacinosid hexactinellid sponges are well known in Devonian and Carboniferous rocks in parts of North America, particularly as an extension of the Devonian dictyosponge fauna (occurrences worldwide were reviewed by Pisera 2006). Lower and upper Carboniferous hexactinellids and demosponges occur in several localities on the Iberian Peninsula (García-Bellido and Rigby 2004). An assemblage of hexactinellid and calcareous sponges from the upper Carboniferous was reported from northwestern China (Rigby et al. 1999); the lack of records from many other regions is likely to reflect a lack of study, rather than an absence of fossils.

Hypercalcified sponges began to show some dominance of reef communities during the Carboniferous. Chaetetids, in particular, were locally abundant shallow-water organisms in Pennsylvanian (upper Carboniferous) rocks (e.g. West and Kershaw 1991). Overall, chaetetids had their acme in the middle part of the Carboniferous and dominated some reefs (e.g. Stemmerik 1988; Almazán-Vázquez et al. 2007) but are generally scarce fossils outside this interval. Heteractinid sponges are moderately common in Carboniferous rocks of Europe and North America (Rigby and Nitecki 1975; Finks and Rigby 2003).

The first records of freshwater demosponges are from the late Carboniferous to Permian interval (Schindler et al. 2008), suggesting that this habitat was invaded at the same time that shallow marine siliceous sponges were generally declining in comparison with hypercalcified groups.

2.4.7 Permian

Gradual warming occurred during the Permian Period, following the late Carboniferous icehouse conditions (e.g. Parrish 1995), but this process was complex and fluctuating and tied to continental configuration and atmospheric circulation (Schneider et al. 2006). The period was also marked by increasing aridity due to the supercontinental configuration (Roscher and Schneider 2006). The gradual warming was followed by an abrupt temperature peak at the end of the period (Benton and Twitchett 2003), related to the Siberian Traps volcanism, which caused both short-term volcanic winters and long-term greenhouse effects (Saunders and Reichow 2009). The mass extinction at the Permian–Triassic boundary was caused by global warming resulting from massive methane releases and oceanic anoxia (e.g. Retallack and Krull 2006). The climate changes were linked to a runaway greenhouse climate and a period of major volcanism at the Permian–Triassic boundary (Benton and Twitchett 2003; Kidder and Worsley 2004).

Permian sponge faunas were dominated by hypercalcified groups, although siliceous sponges were still present and few major groups appear to have gone extinct. Sphinctozoan sponges were the most abundant group in reef facies along the equatorial belt: late Permian sphinctozoan assemblages are known from the eastern Oman mountains (Arabia), Sicily (Italy), Texas, Tunisia, eastern Russia and Hubei and Guangxi provinces of China (Weidlich and Senowbari-Daryan 1996). Additionally, inozoans were widely associated with reefal facies in the middle and late Permian (Rigby and Senowbari-Daryan 1995a). The continued success of these groups through the crisis intervals during the later part of the Permian is a striking pattern that has been suggested as having been due in part to endosymbiotic bacteria (Finks 2010).

Siliceous sponges, though not nearly as abundant as sphinctozoans, were reasonably diversified at this time (e.g. Finks 1960; Rigby and Senowbari-Daryan 1995a).

Demosponge assemblages are dominated by orchoclad and rhizomorine forms, and moderately diverse assemblages are recorded from numerous locations, often in association with sphinctozoans (e.g. Rigby 1984). In the upper Permian of the northern Guadalupe Mountains, New Mexico, USA (Rigby and Bell 2006), hypercalcified sponges, associated with lithistid and other demosponges and encrusting bryozoans and algae, dominated wave-resistant patch reefs in an open-marine setting. Similar assemblages have been reported from several other areas, such as Tunisia (Rigby and Senowbari-Daryan 1995b); this balance of sponge groups appears to have been consistent for shallow-water carbonate settings during the interval. For a review of further examples, see Pisera (2006). Cold but shallow-water late Permian faunas containing abundant sponges (together with brachiopods and bryozoans) were deposited in carbonate sequences of Spitsbergen, Greenland, the Canadian Arctic and the Urals (Davies et al. 1989; Ezaki et al. 1994).

The Permian–Triassic mass extinction was the most severe extinction event of the Phanerozoic (Stanley 2016). A figure for overall species extinction of 95% is frequently quoted (e.g. Benton and Twitchett 2003), but this number is the result of combining extinction figures for the middle and late Permian: a better estimate for species extinction during the end-Permian extinction is approximately 81% (Stanley 2016). Many groups of sponges were badly affected by the extinction, with groups such as the heteractinids and many families and genera of demosponges, hexactinellids and calcareans disappearing (Finks et al. 2004). However, other groups were not severely affected: both sphinctozoans and inozoans exhibited little change across the Permian–Triassic boundary (Finks and Rigby 2003; Finks 2010).

2.4.8 Triassic

The climate in the Triassic was overall somewhat variable (Preto et al. 2010), commencing with extremely warm (severe greenhouse conditions) during the Early Triassic (e.g. Sun et al. 2012) accompanied by probable anoxia in the deep ocean. These unfavourable conditions may have delayed recovery from the end-Permian extinction event (Grasby et al. 2016). The Middle Triassic was characterised by humid episodes (Preto et al. 2010); there was another humid episode associated with global warming in the early Late Triassic (Sun et al. 2016). There was apparently a long period of climatic stability in the Late Triassic (Preto et al. 2010), but at the end of the Triassic, warming conditions and associated oceanic anoxia resulted in another mass extinction (e.g. Schoepfer et al. 2016 and references therein).

For animals in general, recovery from the end-Permian extinction was slow, with complex ecosystems becoming established only after 8–9 Myr (Chen and Benton 2012); but see also Brayard et al. (2017). Although there is a marked absence of coral reefs in Lower Triassic strata, reefs formed by sphinctozoan sponges and other organisms were widespread in the Early Triassic (Brayard et al. 2011 and references therein). The Triassic demosponge faunas were markedly different from those of the Permian and were extremely limited worldwide (Finks and Rigby 2003). In contrast, sphinctozoan sponges survived the end-Permian crisis relatively well and were subsequently widely distributed in shallow water (Finks and Rigby 2003), including as reef framework constructors (Flügel 1981; Senowbari-Daryan et al. 1993). Records of Triassic hexactinellids are sparse (e.g. Pisera and Bodzioch 1991), but abundant hexactinosan and lyssacinosid hexactinellid sponges occur in deep-water reef mounds in the Upper Triassic of China (Wendt et al. 1989; Wu 1990).

The end-Triassic mass extinction had a severe effect on sphinctozoan sponges (although they remained significant reef builders in the Early Jurassic; Senowbari-Daryan and Stanley 1994) but a less marked effect on other calcareous reef-forming sponge groups (Kiessling et al. 2007). In general, siliceous organisms were less affected by the mass extinction than were calcareous organisms, and siliceous sponges dominated some environments during the Early Jurassic (Corsetti et al. 2015).

2.4.9 Jurassic

The Triassic warm climate appears to have continued into the Jurassic. Rees et al. (2000) suggested that in the Jurassic, low latitudes were seasonally dry and warm temperate, with hot tropical regions and warm, ice-free high-latitude regions. Sea level was generally rising during this period (Miller et al. 2005), leading to increases in the area of shallow sea.

During the Early Jurassic, siliceous sponges (demosponges and hexactinellids) flourished and were widespread in shallow water: this probably resulted from a combination of colonisation of vacant niches resulting from the lack of corals and increased silica availability (Corsetti et al. 2015). This situation lasted until carbonate production recovered after approximately 2 Myr (Delecat et al. 2011; Ritterbush et al. 2014, 2015).

Siliceous sponges (both lithistids and hexactinellids) were significant components of Jurassic reefs in some areas: during the early Late Jurassic, sponge reef facies extended over large distances (Leinfelder et al. 2002). Similar siliceous sponge assemblages occur in reef coral facies of the Upper Jurassic of the Neuquén Basin, western Argentina (Beresi 2003; Beresi et al. 2017). The later Mesozoic decline in reef-building siliceous sponges has been speculatively linked to silica limitation (Maldonado et al. 1999). Calcisponges occur in Upper Jurassic reefs in western and central Sicily (Senowbari-Daryan and Schäfer 1986) but were not as important in Jurassic ecosystems as they were in the Triassic. An Australian record of hexactinosans, which were also widespread in Europe during the Jurassic (Pisera 2006 and references therein), suggests that sponges were widespread at that time (Finks and Rigby 2003, p. 292).

During the Late Jurassic, stromatoporoids were significant components of low-latitude reefs in the south and intra-Tethys Ocean (present-day Southern Europe, the Middle East and Asia) but were only minor faunal elements in the north Tethys Ocean and North Atlantic areas (present-day Iberian Peninsula, France and

Germany; Leinfelder et al. 2005). Jurassic chaetetids appear to have favoured high-energy settings (Leinfelder et al. 2005). Lithistid demosponges flourished during the Late Jurassic (Pisera 2002). The later Mesozoic decline in siliceous reef-building sponges has been linked to silicon limitation (Maldonado et al. 1999).

2.4.10 Cretaceous

In general, there was an extreme greenhouse climate during the Cretaceous, with very high sea levels (Miller et al. 2005), particularly during the later part. In the middle part of the period, extensive volcanism combined with accumulation of organic matter associated with sea-level changes may have increased the acidity of the ocean surface (Arthur et al. 1985). Gradual cooling took place in the Late Cretaceous, which was a time of extreme sea-level changes with episodic flooding on the majority of continents (Miller et al. 2003).

Siliceous sponges are common in the Upper Cretaceous of Europe (Pisera 2006), particularly in the Cenomanian chalk facies. Sponges can be extremely well preserved within flint concretions, which have revealed an extremely diverse fauna (e.g. Reid 1962; Olszewska-Nejbert and Świerczewska-Gładysz 2011). Hexactinellids in particular are prolific; they appear to have been almost confined to calcareous facies at this time, with the hexactinosans and lychniscosans reaching their peak of development in the Cretaceous chalk deposits (Finks and Rigby 2003). The record of the less robust lyssacinosans is comparably poor in the Mesozoic, but under particular conditions, they were preserved; a diverse sponge fauna from Bornholm, Denmark consists mainly of lyssacinosan sponges with very modern characteristics (Brückner and Janussen 2005). Other examples include a diverse siliceous sponge fauna from the Caribbean region (Pisera et al. 2006).

Demosponges also peaked in diversity and abundance during the Cretaceous in Europe, although the record is dominated by lithistids (Pisera 2002). Several lithistid lineages, particularly rhizomorines and dicranocladines, dominated in the shallow seaways and continental margins of Europe (Rigby 1983; Świerczewska-Gładysz 2016). Lithistid sponge reefs started to decline in the Late Cretaceous and progressively disappeared through the early Paleogene (Rigby 1983). At the same time, a rich calcarean fauna (particularly sphinctozoans) dominated in the glauconitic greensand facies (Reid 1958). Stromatoporoids declined during the Cretaceous and became extinct at the Cretaceous–Tertiary boundary (Cook 2002).

The end-Cretaceous mass extinction is generally agreed to have been primarily caused by an asteroid impact (e.g. Schulte et al. 2010), although the full story is rather more complicated: large-scale volcanism and climatic changes also had effects, with many groups having been in decline prior to the bolide impact (MacLeod et al. 1997; Keller 2014). Although the records of many fossil groups before, during and after the extinction event have been studied in great detail (e.g. MacLeod et al. 1997), there is little information on the effect of the extinction on sponges.

2.4.11 Palaeogene and Neogene

Cenozoic (Palaeogene and Neogene) climate was marked by a gradual increase in temperature (from already high levels) culminating in the Palaeocene–Eocene Thermal Maximum at approximately 55 Ma, followed by a subsequent decline towards the present Ice Age (Zachos et al. 2008). Glaciation initiated in Antarctica long before the north polar region and may have commenced as early as the late Eocene (approximately 35 Ma; Barker et al. 2007) but is generally agreed to have begun by the Oligocene (e.g. Zachos et al. 2001). Arctic glaciation, and a more rapid global temperature shift towards metastable glacial–interglacial cycles, occurred around 3.15 Ma, associated with the closure of the Panama seaway (Bartoli et al. 2005).

The post-Cretaceous fossil sponge record is very limited and is most useful for the Palaeogene; as the climatic resolution increases, the fossil information declines. This may be related to a shift towards a modern style of sponge ecology, in which the shallow environments are dominated by nearly unpreservable demosponges, and the hexactinellids have retreated largely to the deep oceans. Some aspects of sponge ecology and distribution are visible, however, and these may be useful for interpreting the likely response of the modern sponge biosphere to contemporary changes.

There are only isolated records of Palaeocene sponges, such as lithistids from Ukraine (Pisera 2000) and a sphinctozoan from Denmark (Clausen 1982). Sponge reefs have been reported from Alabama, USA: these were hypothesised to have flourished opportunistically in the absence of corals after the end-Cretaceous mass extinction (Bryan 1991).

Most of the reported Cenozoic sponge records are from Eocene strata: several diverse and well-preserved assemblages are known (e.g. Pisera and Busquets 2002; Kelly and Buckeridge 2005; Finks et al. 2011). These sponges include numerous hexactinellids found in glauconitic sandstones, representing unusually shallow-water conditions (Kelly and Buckeridge 2005), and a combination of hexactinellids with lithistids that resemble Cretaceous taxa more than modern groups (Finks et al. 2011). The character of these assemblages is more reminiscent of Mesozoic faunas, including shallow-water siliceous spiculites in warm, shallow water (Gammon et al. 2000).

A suite of assemblages from the Eocene, Miocene and Pliocene (approximately 23–2.5 Ma) of the western Mediterranean region are as yet poorly studied but seem to continue a similar pattern, with Miocene and even Pliocene hexactinellids and other sponges exhibiting links to Cretaceous faunas (Matteucci and Russo 2011). The active tectonic context of these widespread deposits can be difficult to interpret, with deep-water sediments potentially uplifted in accretionary zones. It is therefore difficult to assess the significance of the hexactinellid-rich assemblages, which may not represent unusually shallow-water occurrences in all cases. The general pattern is of little faunal change through the Miocene, with the Pliocene faunas being either much reduced or just poorly known (Matteucci and Russo 2011). These faunas are predominantly composed of hexactinellids and lithistids with readily preservable skeletons; non-lithistid and aspiculate demosponges are effectively absent.

Among the dominant modern demosponge groups, the Cenozoic saw a dramatic increase in the prevalence of endolithic clionid borings (Perry and Bertling 2000). No clear trends were seen from the Oligocene onwards, and no preference for particular geographic regions or water depths (Perry and Bertling 2000). This suggests that their success was not tied to particular conditions and reflects non-climatological changes in global marine ecology. For the later part of the Cenozoic, however, other demosponge groups are represented as fossils only by rare examples (e.g. Rigby and Cunningham 2007) that are not informative as to general patterns. Some results can be obtained from well-preserved assemblages of isolated spicules, as has been achieved for the late Eocene (Łukowiak 2015) and Miocene (Pisera et al. 2006), but such studies are very few.

The most recent glacial–interglacial cycling interval is on too rapid a scale for useful comparison with the poor fossil record of sponges. Some studies comparing living with subfossil communities in the substrate (Wagoner et al. 1989) can offer indications of how rapidly sponge faunas adapt to changing environmental conditions, but these relate more to local and regional distribution than to long-term trends in sponge biodiversity dynamics. Unfortunately, there is currently little information regarding how sponges have responded to glacial–interglacial cycles.

2.5 Sponge Diversity Through Mass Extinctions

Mass extinctions are short (on geological timescales) time intervals during which extinction rates are significantly elevated above background levels. There are generally agreed to be five major mass extinctions, known as the 'Big Five', which occurred at the end of the Ordovician Period, during the Devonian Period (Frasnian–Famennian), at the end of the Permian Period, at the end of the Triassic Period and at the end of the Cretaceous Period (Raup and Sepkoski 1982), although there is still some debate over exactly which events should be called mass extinctions (Stanley 2016). The end-Cretaceous event, during which non-avian dinosaurs became extinct, is the best known in terms of popular science; however, it was not the largest event of the Big Five: in terms of percentage extinction, the end-Permian was most severe, followed by the end-Ordovician (e.g. Stanley 2016).

A summary of taxonomic survival of sponge genera and families between periods before and after mass extinctions is provided in Tables 2.2 and 2.3. These data are taken directly from the taxonomic summary of Finks et al. (2004, Table 2.1), which provides only presence/absence information during an interval of geological time. Thus, it is not possible to distinguish taxa going extinct early in a particular period from those dying out during a mass extinction at the end of that period. The results should therefore be considered a crude assessment, but nonetheless near to the best that is available, since the incompleteness of the fossil record of sponges makes significantly higher levels of precision somewhat spurious. Taxa that were

Table 2.2 Absolute numbers and percentages (in brackets) of sponge genera present in the geological interval before a mass extinction event and not present in the interval after the event

Event	Ordovician	Devonian	Permian	Triassic	Cretaceous
Hexactinellids	29 (80.6%)	62 (86.1%)	12 (100%)	27 (90%)	126 (84.6%)
Demosponges	70 (80.5%)	35 (79.5%)	108 (77.1%)	103 (93.6%)	183 (88.4%)
Calcareans	5 (71.4%)	3 (50%)	6 (66.7%)	5 (33.3%)	16 (39.0%)
Heteractinids	5 (100%)	5 (100%)	2 (100%)	–	–
Total	**109 (80.7%)**	**105 (82.7%)**	**128 (78.5%)**	**135 (87%)**	**325 (81.90%)**

Information from Table 2.1 of Finks et al. (2004)

Table 2.3 Absolute numbers and percentages (in brackets) of sponge families present in the geological interval before a mass extinction event and not present in the interval after the event

Event	Ordovician	Devonian	Permian	Triassic	Cretaceous
Hexactinellids	4 (19%)	5 (20.8%)	4 (33.3%)	6 (31.6%)	22 (47.8%)
Demosponges	5 (17.8%)	3 (13%)	28 (41.8%)	43 (76.7%)	36 (42.9%)
Calcareans	–	–	2 (28.6%)	–	2 (25%)
Heteractinids	–	1 (50%)	1 (100%)	–	–
Total	**9 (17%)**	**9 (17.6%)**	**35 (40.2%)**	**49 (56.9%)**	**60 (43.5%)**

Information from Table 2.1 of Finks et al. (2004)

undescribed or unnamed in 2004 are not, however, included in the analysis, and this does limit our analysis significantly. Note that these data are based on the traditional taxonomy applied by Finks et al. (2004), such that reticulosans are included within Hexactinellida, and protomonaxonids (a minor group even by the end of the Ordovician) are treated as demosponges. Hypercalcified taxa are all included under the generic heading of Calcarea, although this does not reflect the complex phylogenetic affiliations of some of the groups involved.

Siliceous sponges are known to have flourished after some mass extinctions, although the species now known are either not yet taxonomically described or represent abundant but undescribable fragments: this has been documented for the end-Ordovician (Li et al. 2015; Botting et al. 2017), Devonian (Vishnevskaya et al. 2002) and end-Triassic (Delecat et al. 2011; Ritterbush et al. 2014, 2015, 2016) events. In contrast, siliceous sponge abundance was severely affected by the end-Permian event (Liu et al. 2013; Botting et al. 2017), although diversity was already depressed following the late Carboniferous ice age. These differences between events are not readily visible in the data presented, because much of the taxonomic work has been conducted on lithistid demosponges and more robust, shallow-water hexactinellid-like sponges, both of which appear to have been badly affected by all extinctions. The more delicate (including offshore) sponges are so rarely preserved that we have little information about their temporal or spatial distribution, and many genera are known from single localities.

Botting et al. (2017) hypothesised that abundance of siliceous sponges may have aided in ecosystem recovery after the Ordovician, Devonian and Triassic events.

Siliceous sponges with unfused skeletons decompose after death to form spicule mats, which could have stabilised sediment and facilitated colonisation by other groups, as occurs in the modern deep sea (e.g. Bett and Rice 1992; Beazley et al. 2015) and the Antarctic Ocean (e.g. Gutt and Starmans 1998; Gutt et al. 2013).

Calcareous reef-forming sponges were severely affected by extinction events, similarly to other reef-forming taxa such as corals (Veron 2008), but calcareans generally appear to have been much less severely affected than shallow-water siliceous sponges. For example, stromatoporoids suffered a marked fall in diversity during the Late Ordovician and Devonian mass extinctions (Nestor 1990; Stock 1995). In contrast, hypercalcified demosponges were affected less than virtually any other taxonomic groups by the end-Permian event: Finks (2010) hypothesised that this resulted from these sponges incorporating photosymbiotes that provided the sponge with nutrition during the extinction event. Heteractinids are extremely susceptible to extinction events, with no genus known before any event surviving until afterwards; however, this must be considered an artefact of their general scarcity and gross incompleteness of their fossil record.

Overall, at the genus level, sponges show similar levels of extinction across each of the relevant period boundaries, but some unexpected trends emerge from the data. The fundamental pattern appears to be that shallow-water siliceous sponges were severely affected by both major glaciation intervals and also by greenhouse-related extinction events. Shallow-water hypercalcified sponges, in contrast, were more severely affected by glaciation intervals than by greenhouse intervals, even when the extinction levels across all taxa were higher. For siliceous sponges, the end-Permian and end-Triassic events were the most severe, but there are no consistent differences between the two classes, which appear to respond to crises in similar ways (at least, for the robust shallow-water taxa that dominate the fossil record). For sponges overall, and especially for demosponges, the end-Triassic extinction appears to have been the most cataclysmic.

2.6 Discussion

General interpretations of the response of sponges to climatic changes are severely hindered by the intermittent fossil record. There is a pronounced monographic bias, and some intervals have attracted a strong tradition of sponge researchers due to the abundance of fossils or the quality of material. For other intervals, almost nothing is known, and the absence of described sponge fossils must not be considered an indication of genuine rarity at that time. The Permian siliceous sponge faunas described by Finks (1960) are one example of extreme monographic bias. The recent discovery of around 100 species of latest Ordovician, post-extinction sponges (Li et al. 2015; Botting et al. 2017), when only a very few species had previously been described from that time interval (Rigby and Nitecki 1973), illustrates this clearly. A literal reading of the known fossil record for the latest Ordovician and earliest Silurian would show a diversity of approximately 15 species in the Late Ordovician (middle Ashgill of Carrera and Rigby 2004), a peak of approximately 100 species immediately after the extinction event in the latest Ordovician (Li et al. 2015; Botting et al. 2017) and a marked fall to 12 species during the early Silurian (Llandovery; Muir et al. 2013). This does not reflect the real pattern of sponge diversity but instead highlights the gaps in our knowledge resulting from lack of sponge preservation at certain intervals and lack of knowledge of the faunas that are preserved.

With these caveats, it is still possible to draw some generalisations from the observed patterns of high abundance and the differences between major groups represented in the assemblages. Among the most striking results is that shallow-water siliceous sponges appear to be severely affected by extreme cold intervals (e.g. Muir et al. 2013 for loss of shallow-water taxa through the end-Ordovician extinction), irrespective of whether a mass extinction occurred at the time. Siliceous sponges were not prominent in Permian deposits, having declined dramatically through the late Carboniferous icehouse; instead, they were replaced by various hypercalcified forms, which then thrived through the Permian and survived better than most groups into the Triassic. Hypercalcified sponges, therefore, appear to be better able to survive during even rapid and extreme global warming, perhaps due to the difficulties of secreting siliceous skeletons under those conditions.

In contrast, deep-water sponges appear to have been effectively immune to severe glacial intervals (Botting et al. 2017) but are too poorly known to assess their survival of unusually warm intervals. The survival of offshore taxa through long periods without a fossil record, and later reappearance (Keupp and Schweigert 2012; Brayard et al. 2017), also supports the concept of long-term survival of lineages in the deep oceans, despite hypothesised intervals of anoxia during mass extinctions.

More gradual changes in the climate, and prolonged warm and cold intervals, show few obvious patterns regarding sponge evolution and abundance. The richest shallow-water sponge faunas, including hypercalcified taxa, tend to have occurred during times of very high sea level (e.g. Early to Middle Ordovician, Late Jurassic, Cretaceous), but this may be related to habitat area as much as temperature. In particular, high sea levels result in widespread, shallow epeiric seas in continental interiors, where conditions are much more sheltered than on the continental shelves. These conditions can allow delicate sponges to colonise the continental regions much more successfully than under low sea level, as seen in the abundant hexactinellid faunas of the Cretaceous chalk deposits of Europe. It should be noted that the most specialised shallow-water demosponges, with small, unfused spicules and encrusting habits, have virtually no fossil record and cannot be assessed in this context.

In contrast to the above, some groups of hypercalcified sponges are particularly prominent in lower Cambrian rocks (archaeocyathans) and in Permian and Triassic strata (sphinctozoans and others): both these times were cool intervals with relatively low sea level, except for the extreme greenhouse conditions of the end-Permian (Miller et al. 2005). This pattern may reflect the robustness of these sponges under turbulent water conditions, allowing them to colonise wave-exposed habitats such as reefs on continental margins. The preferential survival of hypercalcified sponges (relative to other groups) after intervals with severe greenhouse conditions (Late Devonian, end-Permian) implies that this is not a preference for cold environments *per se*, but rather an ability to thrive under the global environmental conditions resulting from low sea level.

2.7 Conclusions

The geological history of sponges is difficult to generalise with regard to climatic changes, because of biases in the fossil record and uncertainties over identifying causal relationships. The clearest patterns relate to sea level rather than to temperature, with high sea level resulting in the widespread colonisation of shallow, sheltered seas by groups that might otherwise be most abundant in offshore to deep-water environments. At times of very low sea level, the dominant sponges in the fossil record are those with robust, usually hypercalcified skeletons, but this will be related partly to their high preservation potential. The history of nearshore heterosclero-morph demosponges, for example, is almost unknown.

Shallow-water sponges generally appear to have been severely affected by mass extinction events involving sudden cooling and are less prominent in icehouse intervals generally. However, shallow-water sponges often increased in abundance during extinctions related to extreme greenhouse conditions. Deep-water sponges are reasonably well known only in relation to the end-Ordovician icehouse-driven extinction, and in this case their abundance and diversity remained extraordinarily high or even increased.

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Chapter 3
Sponges as Proxies for Past Climate Change Events

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Abstract An understanding of past environmental conditions and the processes that govern change is essential in order to predict future climate changes. Historical environmental conditions can be reconstructed based on the composition of mineral skeletons of marine organisms. Some marine sponges, such as the hypercalcified ('sclerosponge') sponges, the desma-bearing ('lithistid') sponges and hexactinellid (glass) sponges, are estimated to live for hundreds to thousands of years. These sponges accrete elements in isotopic equilibrium with seawater, making them good potential Paleoclimate indicators. We review the literature on the use of sponges as proxies for climate change. The accuracy of sponge proxy data is highly dependent on the accuracy of dating methods, and multiple samples per specimen are recommended to confirm the reproducibility of results. δ^{13}Carbon values in shallow-water hypercalcified sponges appear to be a good proxy for atmospheric carbon dioxide concentrations, with good correlations between δ^{13}carbon measurements from sponge skeletons and atmospheric carbon dioxide concentrations. Results using δ^{18}oxygen values and strontium/calcium ratios as proxies for temperature are mixed, and results appear to be influenced by sponge species and region. δ^{30}Silicon values in siliceous sponge spicules from dated sediment cores appear to be a good proxy for long-term changes in ocean silicon concentrations. Quantification of zinc/silicon and germanium/silicon ratios in sponges also show potential as proxies for ocean silicon concentrations, but more research is needed in this area. In summary, research on a number of sponge proxies has shown promising results for use as Paleoclimate indicators. Application of these

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proxies generally produces climatic reconstructions that are in agreement with published results from other proxies. However, much more research is needed to further develop sponge proxies and to gain a better understanding of the processes that control both the incorporation of the proxy within the sponge and its concentration in the surrounding water.

Keywords Porifera • Paleoclimate • Proxy • Temperature • Carbon dioxide

3.1 Introduction

In order to predict future changes in our global climate, it is essential to have an understanding of past environmental conditions and the processes that govern change, over timescales of thousands of years. The world's oceans are a major sink for atmospheric carbon dioxide (CO_2) and land-derived nutrients and a moderator for global temperatures and atmospheric gases (Ragueneau et al. 2000). However, the breadth and magnitude of anthropogenic impacts on the marine environment are still not well understood, particularly in deeper regions. Over the past 30 years, considerable research has been conducted on attempting to reconstruct historical environmental conditions based on marine Paleoclimate proxy data from the mineral skeletons of marine organisms such as corals, diatoms, molluscs and sponges. During the growth phase of these organisms, trace minerals from the surrounding water are sequestered into the growing skeleton, potentially providing a historical marker of past environmental conditions over the life span of the organism. In addition, the time range of the Paleoclimate reconstruction can be extended beyond the life span of the organism by measuring the mineral concentrations in skeletons found within dated sediment cores.

Marine sponges, particularly hypercalcified sponges (previously known as 'sclerosponges'), the desma-bearing ('lithistid') sponges and some hexactinellid (glass) sponges, have been proposed to be good candidates for the study of climate change because they are present throughout the world's oceans, inhabit a very wide range of depths, can be very long-lived and generally appear to incorporate chemical elements in equilibrium with the surrounding seawater. These sponges form calcium carbonate or silica skeletons by the addition of incremental layers, in the manner similar to that of tree rings, thus potentially providing important Paleoclimate data. To date, the measurement of carbon, oxygen and silicon isotopes and trace elements in sponges shows potential to be useful proxies for reconstructing historical environmental conditions. The rationale behind the use of various environmental proxies and their potential application in sponges is given in this section. The results of research studies that have measured environmental proxies in sponges are presented in Sect. 3.4.

3.1.1 $\delta^{13}C$ as a Proxy for Historical Ocean CO_2 Concentrations

Global concentrations of CO_2 have been increasing since the industrial period in the early 1800s due to the burning of fossil fuels and trees. The accelerating global CO_2 production has major implications for marine ecosystems because oceans are a major sink for atmospheric CO_2 (Siegenthaler and Sarmiento 1993). One method of measuring the increase in anthropogenic CO_2 production is by quantifying the ^{13}carbon to ^{12}carbon ratio ($\delta^{13}C$), because the burning of fossil fuels and trees releases proportionally less $\delta^{13}C$ than what is naturally present in the atmosphere (the 'Suess effect') (Keeling 1979). Direct measurement of dissolved inorganic carbon in seawater ($\delta^{13}C_{DIC}$) provides little information on the long-term trends in the oceans because there is a lack of high-quality historical data, and spatial and seasonal variations in $\delta^{13}C_{DIC}$ are much larger than the annual increase (Siegenthaler and Sarmiento 1993; Fallon et al. 2003a). Instead, $\delta^{13}C$ measurements from the calcium carbonate skeletons of corals, molluscs and foraminifera are commonly used as proxies for determining historical $\delta^{13}C_{DIC}$ trends in oceans. However, $\delta^{13}C$ assimilation in these organisms has been shown to be affected by physiological factors and, consequently, may not be directly correlated to the $\delta^{13}C_{DIC}$ values of the surrounding water (Grossman 1987; McConnaughey 1989; Putten et al. 2000). The use of hypercalcified sponges as a proxy for $\delta^{13}C_{DIC}$ is advantageous over other commonly used organisms because hypercalcified sponges secrete $\delta^{13}C$ in isotopic equilibrium with water. Evidence supporting the isotopic equilibrium of $\delta^{13}C$ in hypercalcified sponges with their environment includes:

- A 1:1 correlation between $\delta^{13}C$ values in hypercalcified sponges and predicted equilibrium values (Druffel and Benavides 1986; Böhm et al. 1996).
- A lack of correlation between $\delta^{13}C$ and $\delta^{18}O$ concentrations in hypercalcified sponges[1] (Druffel and Benavides 1986; Böhm et al. 1996; Grottoli 2006).
- Similar trends between $\delta^{13}C$ measurements in hypercalcified sponges and atmospheric $\delta^{13}C$ (Böhm et al. 1996; Lazareth et al. 2000).

3.1.2 Proxies for Historical Sea Temperature

3.1.2.1 $\delta^{18}O$

Measurements of the ratio of ^{18}oxygen to ^{16}oxygen ($\delta^{18}O$) are often used for historical temperature reconstructions. As water vapour moves from warm areas to the pole, water molecules containing more of the heavier ^{18}O precipitates out first, resulting in increasing depletion of ^{18}O as the vapour moves towards the poles. Consequently, glacial ice contains low $\delta^{18}O$ values. During glacial periods ^{16}O is

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[1] A correlation between $\delta^{13}C$ and $\delta^{18}O$ is an indication that these isotopes are not accreted in isotopic equilibrium (Swart 1983).

trapped as ice, and the oceans have relatively high $\delta^{18}O$ values, while during warm periods the glacial ice melts, reducing the $\delta^{18}O$ values in the ocean (Riebeek 2005).

Direct measurements of $\delta^{18}O$ from polar ice cores have been found to produce reliable historical temperature reconstructions (Johnsen et al. 2001; Andersen et al. 2004). In warmer regions where there is no ice, measurements of $\delta^{18}O$ from the skeletons of corals, molluscs and foraminifera are commonly used as proxies for temperature reconstructions. However, like $\delta^{13}C$, $\delta^{18}O$ assimilation in these organisms has been shown to be affected by physiological factors and, consequently, may not be directly correlated to $\delta^{18}O$ values of the surrounding water (Weber and Woodhead 1972; Grossman 1987; McConnaughey 1989).

Hypercalcified sponges generally appear to accrete $\delta^{18}O$ in isotopic equilibrium with water (Swart et al. 1998a, b; Moore et al. 2000). However, $\delta^{18}O$ values in some specimens (Rosenheim et al. 2009; Grottoli et al. 2010) or for some transects within a specimen (Böhm et al. 2000) were found to be offset from the predicted equilibrium values by a relatively constant (unknown) factor. Consistently offset $\delta^{18}O$ values can still be good proxies for temperature reconstruction as long as the offset is taken into account (Rosenheim et al. 2009; Grottoli et al. 2010), but variations in $\delta^{18}O$ chronologies within a specimen are a cause for concern because they indicate that skeleton formation may be inhomogeneous (Böhm et al. 2000).

3.1.2.2 Trace Element to Calcium Ratios

Trace elements such as strontium (Sr), magnesium (Mg), barium (Ba), boron (B) and uranium (U) are incorporated in the skeleton of calcareous marine organisms at the same time as calcium carbonate. Research on corals and bivalves indicates that certain trace elements may be good proxies for historical temperature reconstructions (Shen and Boyle 1987; Beck et al. 1992; Mitsuguchi et al. 1996; Sinclair et al. 1998). For example, good correlations have been demonstrated between Sr/calcium (Ca) ratios in corals and water temperatures (Beck et al. 1992; McCulloch et al. 1994, 1999), and between Mg/Ca ratios in corals (Mitsuguchi et al. 1996; Watanabe et al. 2001) and bivalves (Klein et al. 1996) and water temperature.

Incorporation of trace elements in marine organisms is controlled by their concentration in seawater and their distribution coefficient between aragonite[2] and seawater (which is affected by temperature). The use of trace elements as a proxy for temperature is based on several assumptions:

- Temperature is the primary control of trace element accretion in marine organisms.
- Biological or 'vital' effects on the trace element accretion are negligible.
- The trace element to calcium ratio of seawater is constant over the reconstructed time period (Beck et al. 1992; de Villiers et al. 1995).

However, it has been shown that these assumptions are not always valid for certain species or locations (de Villiers et al. 1995; Cardinal et al. 2001; Cohen

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[2] A form of calcium carbonate found in marine organisms such as molluscs, corals and sponges.

et al. 2002; Kisakürek et al. 2008; Saenger et al. 2008), and some studies have demonstrated poor correlations between Sr/Ca and temperature (Rosenthal et al. 1997) or Mg/Ca and temperature (Schrag 1999; Fallon et al. 2003b; Reynaud et al. 2007). Likewise, the suitability of using Sr/Ca or Mg/Ca ratios in hypercalcified sponges for historical temperature reconstructions appears to be species specific (see Sect. 3.4.2.1).

3.1.3 Proxies for Historical Nutrient Concentrations

An understanding of the processes that control ocean productivity is essential to understanding the impacts of climate change, because productivity partly controls the partitioning of CO_2 between the atmosphere and the deep sea (Ragueneau et al. 2000). Phytoplankton take up carbon dioxide and other nutrients for growth. Upon dying, a proportion of phytoplankton sink to the seabed, effectively removing these nutrients (and particularly carbon) from the productivity cycle (Volk and Hoffert 2013). Quantification of historical carbon concentrations in the ocean is difficult because most carbon proxies are affected by remineralization and diagenetic[3] effects (Emerson and Hedges 1988). Quantification of isotopes of silicon, zinc and germanium in marine organisms have been proposed as potential proxies for historical nutrient concentrations in oceans.

3.1.3.1 δ^{30}Si

The uptake and biogeochemical cycling of silicon (Si) in the marine environment plays a major role in the global carbon cycle. This is because diatoms, which are responsible for up to 45% of the ocean's productivity (Mann 1999), are the primary driver of biogeochemical cycling of Si in the marine environment (Ragueneau et al. 2000; Yool and Tyrrell 2003). Increased productivity of biogenic silica in surface waters is mainly sustained by the upwelling of silicic acid ($Si(OH)_4$) from deeper waters, while sinking and dissolution of diatom skeletons to deeper waters results in a loss of Si from productive surface waters (Ragueneau et al. 2000).

The concentration of Si in deep waters is governed by ocean productivity, ocean circulation (particularly the mixing of surface waters with deep waters), tectonics and silicate weathering (Reynolds et al. 2006). Quantifying changes in $Si(OH)_4$ in deep waters will increase our understanding of the relationship between the sequestering of Si, carbon (C) and other nutrients, and the reduction in atmospheric pCO_2 (Hendry et al. 2010).

The fractionation of biogenic Si by marine organisms such as diatoms and siliceous sponges can be used to estimate the $Si(OH)_4$ concentrations in seawater. These organisms preferentially consume more of the lighter isotopes (^{28}Si and ^{29}Si)

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[3] A chemical, physical or biological change to sediment.

than ^{30}Si, resulting in negative δ^{30}Si values (de la Rocha et al. 1997). The vast majority of studies on Si concentration in the marine environment have used diatoms as a proxy indicator species (Leng et al. 2009). However, diatoms only reflect the Si concentration of surface waters and have been shown to have species-specific Si fractionation (Sutton et al. 2013).

Hexactinellids and demosponges show good potential for using δ^{30}Si measurements to estimate the deposition rate of biogenic Si to the seafloor. δ^{30}Si values in these sponges are correlated with $Si(OH)_4$ concentrations in seawater, and δ^{30}Si values are independent of temperature, salinity or pH (Hendry et al. 2010; Wille et al. 2010). Reproducibility of δ^{30}Si values within a sponge, and between different species of sponges collected from the same site are also good (Hendry et al. 2010, 2011; Wille et al. 2010), indicating that measurements of δ^{30}Si in sponges are robust and that there are no apparent species-specific effects.

3.1.3.2 Trace Element to Silicon Ratios

Two novel methods for estimating historical productivity are the measurement of zinc (Zn)/Si ratio and germanium (Ge)/Si ratio in siliceous sponges. Ellwood et al. (2004) proposed that the Zn/Si ratio may be a useful proxy for tracking changes in historical particulate organic carbon (POC) concentrations near the seafloor. Sponges appear to acquire Zn through consumption of particulate organic matter in direct proportion to the amount of POC 'raining down' from surface waters (Ellwood et al. 2004). Measurement of Zn/Si ratio in live deep-sea hexactinellids and in loose spicules from mixed demosponge species within sediment cores were found to have a strong linear correlation to POC in the surface sediment from nearby cores, and were unaffected by temperature or pressure (Ellwood et al. 2004, 2005). Zn/Si ratios in sponges are advantageous over other proxies for POC (e.g. authigenic barium) because Zn is locked into the silica matrix and, therefore, is unaffected by remineralization and diagenesis, either in the water column or in the sediment (Ellwood et al. 2004, 2005).

Germanium (Ge) has also been proposed to be a potential proxy for productivity (Ellwood et al. 2006) because the cycling of inorganic Ge in the ocean closely matches the distribution of Si (Froelich and Andreae 1981; Froelich et al. 1989). This implies that the processes that control Si in the ocean also control Ge (Froelich and Andreae 1981; Froelich et al. 1989). Siliceous sponges appear to accumulate Ge in direct proportion to seawater Ge concentrations (Ellwood et al. 2006).

3.2 Sponge Species Used for Paleoclimate Research

Several types of marine sponges have potential as Paleoclimate indicators including hypercalcified sponges, desma-bearing sponges and several long-lived glass sponges (class Hexactinellida) (Fig. 3.1). Despite their diverse taxonomic spread, these sponges have several features in common:

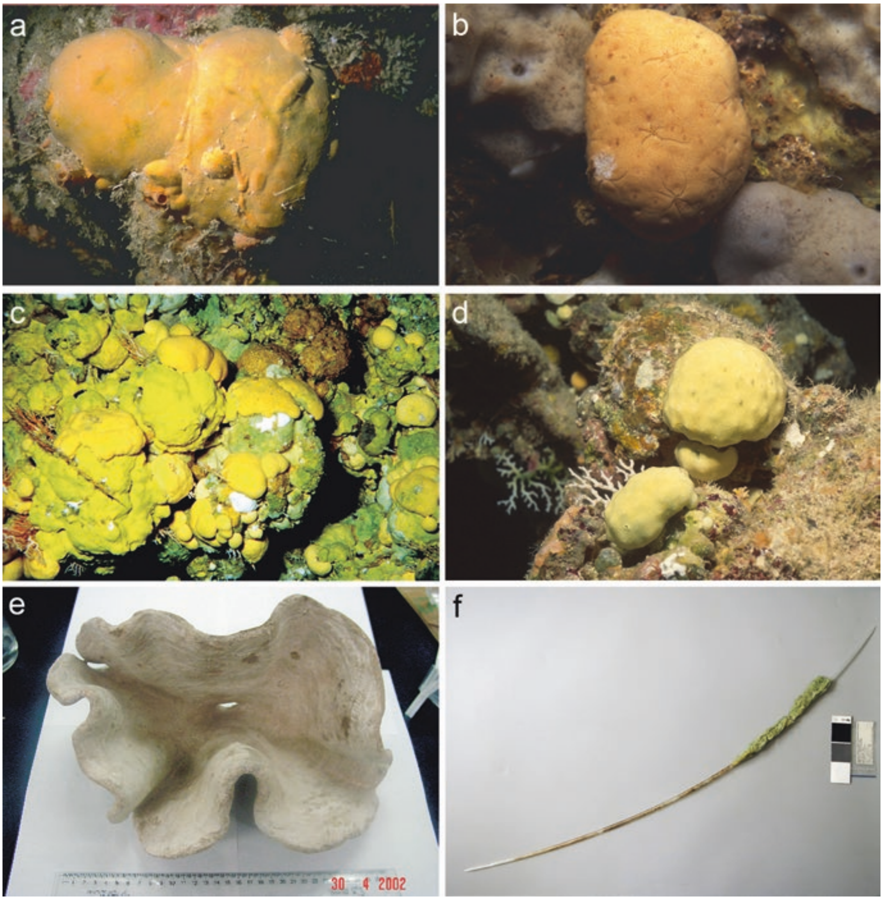

Fig. 3.1 (**a**) The hypercalcified sponge *Ceratoporella nicholsoni* from Jamaica. The sponge is approximately 10 × 20 cm (Photo: P. Willenz, with permission). (**b**) The hypercalcified sponge *Astroclera willeyana* in a cave in Cebu, Philippines (Photo: G. Wörheide, with permission, www.geobiology.eu). (**c**, **d**) The hypercalcified sponge *Acanthochaetetes wellsi* in a cave in Palau, Micronesia (Photos: Coral Reef Research Foundation, with permission). (**e**) The desma-bearing sponge, *Corallistes undulatus* (Reproduced from Ellwood and Kelly (2003) with permission from NIWA). (**f**) The hexactinellid glass sponge *Monorhaphis chuni* (Photo: NIWA, with permission)

- They are generally very long-lived (hundreds to thousands of years).
- They grow by the progressive, chronological addition of material to the outermost surface of their skeleton.
- Chemical signatures within their skeleton reflect the chemical composition of their environment.

3.2.1 Hypercalcified Sponges

The hypercalcified sponges, or ‘sclerosponges’ as they were previously known, are a polyphyletic group of tropical sponges once clustered in the class Sclerospongiae, but which are now distributed amongst various unrelated taxonomic orders (Vacelet 1985; Chombard et al. 1997). These sponges are characterized by the possession of an inert calcium carbonate (aragonite or calcite) base with a living tissue veneer on the surface. Many also have silica spicules in conjunction with the calcium carbonate base (Hartman and Goreau 1970; Willenz and Hartman 1989; Wood 1990a). These sponges are thought to be relicts of fossil reef-building sponges (stromatoporoids, chaetetids, sphinctozoans and inozoans) (Hartman and Goreau 1970; Wood 1990b).

The most common species of hypercalcified sponges used as Paleoclimate indicators are *Ceratoporella nicholsoni* (Hickson, 1911) (Agelasida, Astroscleridae) from the Caribbean; *Astrosclera willeyana* Lister, 1900 (Agelasida, Astroscleridae), from the South Pacific and eastern Africa; and *Acanthochaetetes wellsi* Hartman & Goreau, 1975 (Clionaida, Acanthochaetetidae), from the west Pacific.

Biomineralization in hypercalcified sponges occurs through a variety of methods:

- *Ceratoporella nicholsoni* (Fig. 3.1a) constructs tubes of aragonite (pseudocalices) that are perpendicular to the surface and contain the living tissue (0.5–1 mm) (Willenz and Hartman 1989; Swart et al. 2002). Biomineralization occurs extracellularly via a secretory pinacoderm[4] that exudes a thin mucus or fluid-filled layer (Wood 1990a). Aragonite is deposited simultaneously at the top of the pseudocalicle walls and at the bottom of the pseudocalicles, below the living tissue (Hartman and Goreau 1972; Willenz and Hartman 1999). Pseudocalices are then slowly infilled, resulting in aragonite of mixed ages (Fig. 3.2a). The time difference between the construction of the wall material and complete infilling is around 5 years (Böhm et al. 1996).
- *Astrosclera willeyana* (Fig. 3.1b) has a similar pseudocalices growth habit to *C. nicholsoni*, but the skeleton has an intracellular origin. The living tissue is around 5 mm thick and comprises three zones: the ectosome, choanosome and zone of epitaxial backfill. In the ectosome, aragonite spherules are formed intracellularly (Fig. 3.2b) and are then transported to their position at the top of the choanosome, where they gradually grow larger and fuse together by epitaxial growth, though there is still space amongst the spherules (Wood 1990a; Wörheide 1998). At the base of the pseudocalices, the soft tissue is gradually rejected and the remaining space slowly filled up by epitaxial growth (Fig. 3.2c) (Wörheide 1998).
- *Acanthochaetetes wellsi* (Fig. 3.1c, d) has a high-Mg calcite basal skeleton covered by a thin veneer of living tissue. The basal skeleton is constructed of bundles of elongated crystals (Fig. 3.2e) that are formed extracellularly via a secretory pinacoderm (Wood 1990a; Reitner and Gautret 1996). Biomineralization

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[4] The outermost layer of cells in a sponge.

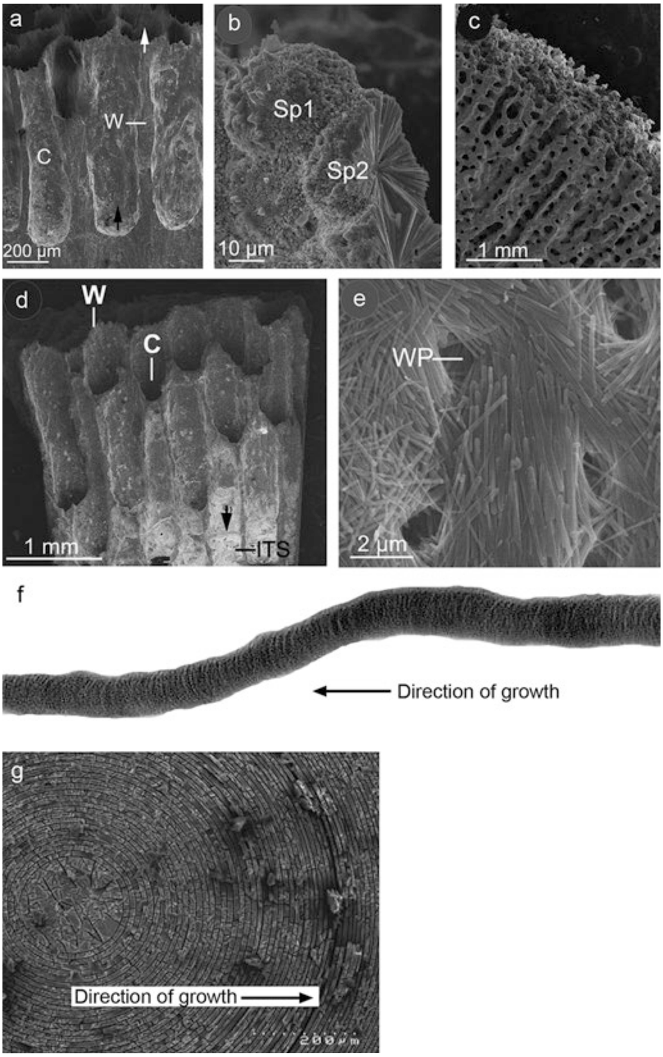

Fig. 3.2 (**a**) Scanning electron micrographs (SEM) of a longitudinal section of *Ceratoporella nicholsoni* skeleton showing the pseudocalices (C). Growth zones are located at the tip of the walls (W) (*white arrow*) and at the bottom of the pseudocalicles (*black arrow*). (**b**) SEM of *Astroclera willeyana* showing the intracellularly formed spherulites (Sp1 and Sp2) released from the soft tissue growing at the surface of the basal skeleton during the secondary extracellular growth. (**c**) SEM of the basal skeleton of *A. willeyana*. (**d**) SEM of the pseudocalices of *Acanthochaetetes wellsi*. The vertical pseudocalices are subdivided by horizontal tabulae (*black arrow*). ITS = inter-tabular space. (**e**) SEM of the lamellar microstructure in the wall of a pseudocalices from *A. wellsi*. Elongated fibres are tangentially organized around wall perforations (WP) (**f**) X-radiograph of a longitudinal section of *Corallistes undulatus* showing the growth bands. (**g**) SEM of a cross section of a spicule from *Monorhaphis chuni* showing the concentric layers of silicon (Figure **a**–**e** is reproduced from Gilis et al. (2013) with permission from Elsevier. Figure **f**–**g** is reproduced from Ellwood and Kelly (2003) with permission from NIWA)

occurs mainly at the top of the calices (Reitner and Gautret 1996). In contrast to *C. nicholsoni* and *A. willeyana*, *A. wellsi* constructs horizontal partitions between the pseudocalices (Fig. 3.2d) and there is little to no secondary infilling of the spaces (Hartman and Goreau 1975; Wood 1990a).

3.2.2 Desma-Bearing Demosponges

Other types of sponges that show good potential as Paleoclimate indicators include the heavily siliceous, desma-bearing demosponges or 'lithistid' Demospongiae, as they were previously known. These sponges are also now known to be polyphyletic, forming an artificial group of deep-sea sponges once clustered in the order Lithistida, but which are now distributed amongst various taxonomic orders (Vacelet 1985; Chombard et al. 1997; Pisera and Lévi 2002; Kelly 2007). Present-day, desma-bearing demosponges are largely confined to deep, silicon-rich environments, which is likely to be due to their high silicon requirements (Uriz 2006).

Desma-bearing demosponges have hypersilified skeletons that are made up of articulated siliceous spicules, which confer a rigid, stony texture to the sponge. The geometry of the spicules is controlled by an organic, proteinaceous axial filament. Silica granules are deposited onto the axial filament, encasing it. Enlargement of the spicule occurs by the deposition of more silica granules in approximately regular concentric layers. The final shape of the spicule is controlled by a membrane, called silicalemma, which governs the shape of secondary branches and spicule ornamentation (Pisera 2003). The formation of spicules in desma-bearing demosponges differs from other demosponges in that the axial filament is very short, or sometimes invisible, while the axial filament in other demosponges is quite distinct and extends to the tips of the spicule (Pisera 2003).

Research on the desma-bearing demosponge, *Corallistes undulatus* Lévi & Lévi, 1983 (Tetractinellida, Corallistidae) (Fig. 3.1e), suggests that it may be a useful Paleoclimate indicator. This species appears to deposit successive layers of siliceous desma spicules to its exterior surface (Ellwood et al. 2007) (Fig. 3.2f).

3.2.3 Hexactinellids

Hexactinellids are long-lived, silicon-rich sponges that are mainly confined to deep, silicon-rich environments (Uriz 2006). The unusual fishing rod-shaped hexactinellid, *Monorhaphis chuni* Schulze, 1904 (Amphidiscosida, Monorhaphididae) (Fig. 3.1f), has the potential to provide useful Paleoclimate data. This species forms a huge basal spicule that can reach 3 m in length and up to 11 mm in diameter (Jochum et al. 2012). These basal spicules are composed almost entirely of silicon dioxide and are formed by the deposition of successive layers of silicon dioxide around the outside of the spicule that are separated by a silicatein protein matrix (Müller et al. 2008) (Fig. 3.2g).

3.3 Estimating the Age and Growth of Sponges

Precise knowledge of the age of extracted isotopic or elemental material is necessary for the interpretation of environmental proxy data from sponges. Average population growth rates cannot be used because growth rates can vary by an order of magnitude amongst species and by up to 50% between specimens of the same species collected from the same location (Willenz and Hartman 1999; Grottoli et al. 2010).

Growth rings in sponge proxy species do not generally correspond to annual or other periodic increments (Swart et al. 2002), with the possible exception of *C. undulatus*, which has concentric bands of light and dark material that appear to be deposited annually[5] (Ellwood and Kelly 2003; Ellwood et al. 2007).

Consequently, dating of sponges relies on in situ staining methods, tracer chronologies of $\delta^{13}C$, lead (Pb) or radiocarbon (^{14}C), or radiometric dating of ^{234}uranium (U) or ^{32}silicon (Si). Quantification of these isotopes allows the chronological sponge proxy data to be anchored to known dates such as the occurrence of nuclear weapon testing in the Pacific, the peak usage of leaded petrol or the decay rate of radioactive isotopes. The age and growth rate of the sponge can then be back-calculated assuming:

- Growth of the sponge was constant over the life span of the sponge.
- Growth was linear along the axis that the material was sampled.
- Sponges accrete the tracer isotope at a constant ratio throughout their growth period.

3.3.1 *In Situ Staining*

Growth rates of hypercalcified sponges have been estimated using in situ staining methods. Sponges are stained using fluorescent dyes such as calcein or calcein-Na_2 (Willenz and Hartman 1985; Wörheide 1998) or strongly pigmented dyes such as Alizarin Red (Dunstan and Sacco 1982; Grottoli et al. 2010). Sponges are either injected with the dye in situ (Wörheide 1998), encased with a plastic bag filled with the dye in situ (Willenz and Hartman 1985), or are removed, stained and then glued back in place (Grottoli et al. 2010). The sponges then need to be left to grow for 1–2 years before the growth rate can be measured due to the very slow growth of most hypercalcified sponges (Fig. 3.3a, b).

In situ staining experiments have recorded growth rates of 0.1–0.29 mm/year for *C. nicholsoni* (Dunstan and Sacco 1982; Willenz and Hartman 1985; Rosenheim et al. 2004), 0.8–1.6 mm/year for *A. wellsi* (Grottoli et al. 2010) and 0.23–1.6 mm/year for *A. willeyana* (Wörheide 1998; Grottoli et al. 2010) (Table 3.1).

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[5] Measurement of the number of light and dark density bands (137–144 pairs ±~10%) corresponds well to the estimated age of the sponge (135–160 years) by ^{32}Si dating.

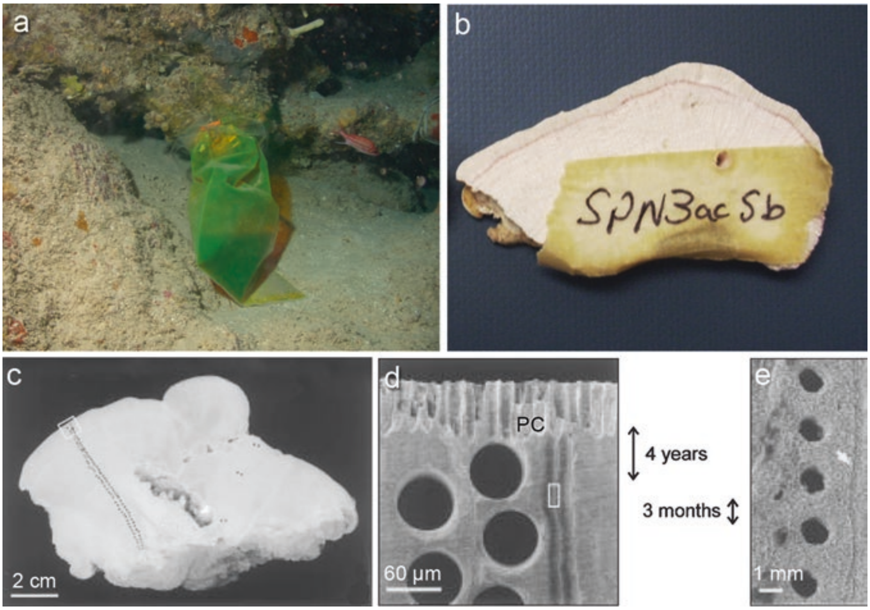

Fig. 3.3 (**a**) *Ceratoporella nicholsoni* being stained with calcein in situ (Photo: P. Willenz, with permission). (**b**) Cross section of *Acanthochaetetes wellsi* 1 year after staining (Photo: A. Grottoli, with permission). (**c**) Longitudinal section of *C. nicholsoni* showing the microdrilled samples along the major growth axis. (**d**) SEM of the surface of the longitudinal section of *C. nicholsoni* showing the microdrilled samples (*large circles*) and the laser ablation inductively coupled plasma mass spectrometry craters (*dark tracks* to the right of the *circles*) (PC = pseudocalices). (**e**) SEM of the framed view in (**b**) showing the laser ablation craters (Figure **c**–**e** is reproduced from Lazareth et al. (2000) according to the copyright policies of the Geological Society of America)

3.3.2 δ^{13}Carbon Dating

The large decrease in δ^{13}C due to the burning of fossil fuels is apparent in the skeletons of shallow-water hypercalcified sponges. Consequently, δ^{13}C can be used to validate the age and growth of sponges by anchoring the large decrease in δ^{13}C to the start of the industrial period (early nineteenth century) (Böhm et al. 1996). Concentrations of δ^{13}C along a transect towards the centre of the sponge skeleton are measured using microdrilling and a mass spectrometer or laser ablation inductively coupled plasma mass spectrometry (Fig. 3.3c–e). Growth rates of hypercalcified sponges estimated from δ^{13}C data are 0.22–0.23 mm/year for *C. nicholsoni* (Lazareth et al. 2000; Swart et al. 2002), which correlate well with in situ growth measurements (Table 3.1).

Table 3.1 Growth rate of sponges used in Paleoclimate studies estimated by various methods

Sponge group	Species	Method	Average growth rate (mm/year)	Reference
Hypercalcified	*A. wellsi*	Staining	0.8–1.6	Grottoli et al. (2010)
Hypercalcified	*A. wellsi*	Width increase	1.3	Hughes and Thayer (2001)
Hypercalcified	*A. wellsi*	$\Delta^{14}C$	1.4	Grottoli (2006)
Hypercalcified	*A. willeyana*	Staining	0.23	Wörheide (1998)
Hypercalcified	*A. willeyana*	Staining	1.6	Grottoli et al. (2010)
Hypercalcified	*A. willeyana*	$\Delta^{14}C$	1–1.2	Fallon and Guilderson (2005)
Hypercalcified	*A. willeyana*	$^{234}U/^{230}Th$	0.4–0.7	Moore et al. (2000)
Hypercalcified	*C. nicholsoni*	Staining	0.23	Willenz and Hartman (1985)
Hypercalcified	*C. nicholsoni*	Staining	0.17–0.29	Willenz and Hartman (1999)
Hypercalcified	*C. nicholsoni*	Staining	0.18	Rosenheim et al. (2004)
Hypercalcified	*C. nicholsoni*	Staining	0.1–0.2	Dunstan and Sacco (1982)
Hypercalcified	*C. nicholsoni*	$\delta^{13}C$	0.22	Swart et al. (2002)
Hypercalcified	*C. nicholsoni*	$\delta^{13}C$	0.23	Lazareth et al. (2000)
Hypercalcified	*C. nicholsoni*	Pb	0.22	Swart et al. (2002)
Hypercalcified	*C. nicholsoni*	Pb	0.22	Benavides and Druffel (1986)
Hypercalcified	*C. nicholsoni*	Pb	0.23	Lazareth et al. (2000)
Hypercalcified	*C. nicholsoni*	Pb	0.25	Druffel and Benavides (1986)
Hypercalcified	*C. nicholsoni*	$\Delta^{14}C$	0.22	Böhm et al. (1996)
Hypercalcified	*C. nicholsoni*	$\Delta^{14}C$	0.25	Druffel and Benavides (1986)
Hypercalcified	*C. nicholsoni*	$\Delta^{14}C$	0.27	Benavides and Druffel (1986)
Hypercalcified	*C. nicholsoni*	$^{234}U/^{230}Th$	0.17	Swart et al. (2002)
Hypercalcified	*C. nicholsoni*	$^{234}U/^{230}Th$	0.19	Haase-Schramm et al. (2003)
Hypercalcified	*C. nicholsoni*	$^{234}U/^{230}Th$	0.15–0.17	Rosenheim et al. (2005b)
Hypercalcified	*C. nicholsoni*	$^{234}U/^{230}Th$	0.23–0.43	Haase-Schramm et al. (2003)
Desma bearing	*C. undulatus*	^{32}Si	1.1–1.3	Ellwood et al. (2007)
Glass	*R. racovitzae*	$\Delta^{14}C$	2.9	Fallon et al. (2010)

3.3.3 Lead Dating

The concentration of Pb in the atmosphere increased threefold between 1930 and 1970 due to the combustion of leaded petrol and industrial outputs (Murozumi et al. 1969; Lazareth et al. 2000). Atmospheric Pb concentrations reached a peak in 1971; thereafter, concentrations decreased with the decrease in the use of lead alkyl additives in petrol (Shen and Boyle 1987). This peak in Pb concentration is also apparent in shallow-water hypercalcified sponges (Lazareth et al. 2000; Swart et al. 2002; Rosenheim et al. 2005a), enabling the back-calculation of the age and growth rate of sponges. The Pb chronology in a hypercalcified sponge is typically matched to the Pb chronology in a coral from the same location, to determine the precise year of maximum Pb at that location. This is because corals have annual growth rings, which allow them to be dated more accurately than hypercalcified sponges (Fallon and Guilderson 2005). Growth rates of hypercalcified sponges aged using Pb range from 0.22 to 0.23 mm/year for *C. nicholsoni* (Benavides and Druffel 1986; Lazareth et al. 2000; Swart et al. 2002) (Table 3.1).

3.3.4 Radiocarbon ($\Delta^{14}C$) Dating

Nuclear weapon testing that was conducted in the Pacific between 1954 and 1962 resulted in the widespread enrichment of bomb radiocarbon in the environment. Peak atmospheric values of $\Delta^{14}C$ occurred between 1963 and 1965, but peak surface seawater $\Delta^{14}C$ values did not occur until the early 1970s because there is approximately a decade lag before $\Delta^{14}C$ seawater attains isotopic equilibrium with atmospheric values (Fallon and Guilderson 2005). $\Delta^{14}C$ values of surface ocean waters began to rise in the early 1950s, reaching a maximum in the early 1970s (Fallon et al. 2003a; Fallon and Guilderson 2005). Similar to Pb, maximum $\Delta^{14}C$ values present in shallow-water sponges can be anchored to coral-validated dates to calculate the age and average growth rate of the sponge.

Growth rates of hypercalcified sponges aged using $\Delta^{14}C$ range from 0.22 to 0.27 mm/year for *C. nicholsoni* (Benavides and Druffel 1986; Böhm et al. 1996) and 1.0–1.2 mm/year for *A. willeyana* from the Pacific (Fallon and Guilderson 2005) (Table 3.1).

Sponges that live in deep waters where the effects of bomb carbon are not apparent do no show a peak in $\Delta^{14}C$ (Ellwood et al. 2007). However, the decay of natural radiocarbon can also be used to estimate the age and growth of sponges that live in deep waters (Fallon et al. 2010).

3.3.5 ^{234}Uranium/^{230}Thorium Dating

The ratio of ^{234}U/^{230}Th can be used to estimate the age and growth of sponges. ^{234}U is naturally present in water, but ^{230}Th is insoluble, and consequently, its dissolved concentration is low. ^{234}U, which has a half-life of 245,500 years, decays to ^{230}Th, which is also radioactive with a half-life of 75,000 years (Audi et al. 2003). As a result, ^{230}Th does not accumulate indefinitely but eventually reaches secular equilibrium with ^{234}U, which is when the production of ^{230}Th from ^{234}U decay equals the decay rate of ^{230}Th (Edwards et al. 1987).

Growth rates of hypercalcified sponges aged using ^{234}U/^{230}Th dating range from 0.15 to 0.43 mm/year for *C. nicholsoni* (Swart et al. 2002; Haase-Schramm et al. 2003; Rosenheim et al. 2005b, 2007) and 0.4–0.7 mm/year for *A. willeyana* (Moore et al. 2000) (Table 3.1).

3.3.6 ^{32}Silicon Dating

The indirect measurement of the radioactive isotope ^{32}silicon (^{32}Si) can also be used to date sponges (Fifield and Morgenstern 2009). ^{32}Si is cosmically generated in the atmosphere and enters the oceans via rain and snow, where it is incorporated into silica as the sponge grows (Lal et al. 1970; Ellwood and Kelly 2003). Direct detection of ^{32}Si in sponge silica is difficult due to the very low energy emissions of the atomic particles. However, ^{32}Si decays into ^{32}phosphorus (^{32}P), which is easier to detect than ^{32}Si because it emits high-energy atomic particles (Lal et al. 1970; Ellwood and Kelly 2003; Ellwood et al. 2007).

^{32}Si measurements of a *C. undulatus* specimen estimated an average growth rate of 1.1–1.3 mm/year and an overall age of 135–160 years (Ellwood et al. 2007). ^{32}Si values from the sponge were similar to ^{32}Si seawater values of the South Pacific for the same depth (Somayajulu et al. 1973), adding support for the accuracy of the dating method (Ellwood et al. 2007).

3.3.7 Comparison of Dating Methods

The accuracy of historical reconstructions from sponge proxy data is highly dependent on the dating accuracy. Dating of the same specimen by various methods generally shows relatively good agreement amongst methods. For example, estimated growth rates of a *C. nicholsoni* specimen were 0.22 mm/year, using δ^{13}C and Pb chronologies, and 0.17 mm/year for ^{234}U/^{230}Th dating (Swart et al. 2002). However, it should be noted that large error terms are still possible between

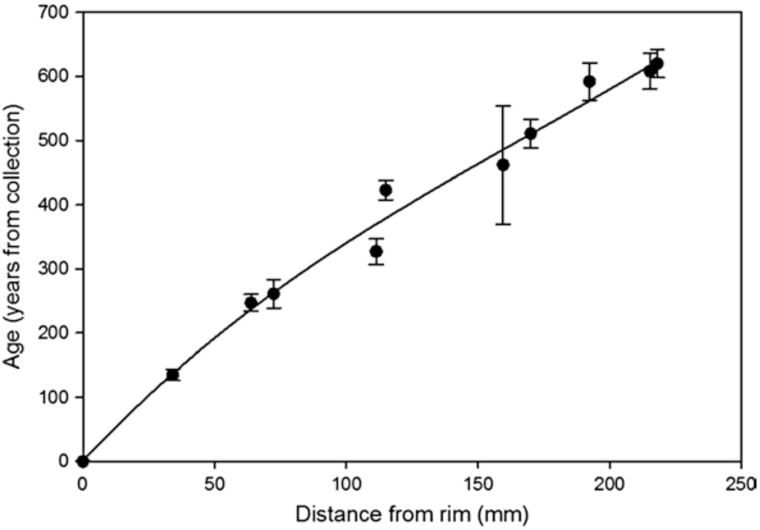

Fig. 3.4 Age of a *C. nicholsoni* specimen estimated by ^{234}U/^{230}Th dating (data from Haase-Schramm et al. 2003). Error bars represent double standard errors from the mean. Note the unusually large standard error around 160 mm

samples from a single specimen. For example, Haase-Schramm et al. (2003) found that the majority of samples taken from a *C. nicholsoni* specimen had a statistical uncertainty of ±20 years or ±5% (two standard errors), with the exception of one sample, which had an uncertainty of ±92 years or ±20% (Fig. 3.4). These results highlight the need to take multiple samples to confirm the reproducibility of age estimates.

Given the slow growth rate of hypercalcified sponges, in situ staining is best used for estimating short-term growth rates (years), while indirect methods such as radiometric dating are more suitable for estimating long-term growth rates (decades to centuries) (Willenz and Hartman 1999). However, radiometric dating methods are reliant on the measurement of very low concentrations of isotopes, and therefore, samples are vulnerable to contamination.

Furthermore, the choice of method will depend upon the location and depth the sponge was collected from. δ^{13}C, Pb and bomb Δ^{14}C dating methods are unlikely to be suitable for deep-water sponges because they rely on anchoring sponge chronological data to atmospheric concentrations of these isotopes. The transport of these isotopes to the ocean floor is largely determined by the rate of vertical transport of water masses, which results in deep-water concentrations lagging by decades to centuries behind atmospheric concentrations (Siegenthaler and Sarmiento 1993).

3.4 Using Sponges to Reconstruct Past Environmental Conditions

3.4.1 *$\Delta^{13}C$ as a Proxy for Historical Ocean CO_2 Concentrations*

$\delta^{13}C$ chronologies in hypercalcified sponges can be used to estimate the magnitude and timing of anthropogenic CO_2 penetration to oceanic waters. Böhm et al. (2002) recorded one of the longest $\delta^{13}C$ chronologies from a hypercalcified sponge (*C. nicholsoni*), spanning around 600 years from 1380 to 1996. $\delta^{13}C$ measurements from this shallow-water Jamaican sponge were highly correlated with atmospheric pCO_2 data. The $\delta^{13}C$ hypercalcified sponge chronology clearly illustrates the pre-industrial and post-industrial periods. During the pre-industrial period (1380–1850), $\delta^{13}C$ values were stable (4.9–5.05‰), and fluctuations appeared to be controlled by climatic variations, such as the Little Ice Age, which corresponded to an increase of 0.1‰ in $\delta^{13}C$ between 1550 and 1800. Post-1850, there has been an accelerating decline in $\delta^{13}C$, with a total decrease of 1‰. The major decline post-1850 is attributed to the increased burning of fossil fuels and deforestation (Böhm et al. 2002). This decline is also evident in $\delta^{13}C$ hypercalcified sponge chronologies from other locations (Druffel and Benavides 1986; Böhm et al. 1996; Wörheide 1998; Moore et al. 2000), though the timing and magnitude of the decrease varies with location (Table 3.2).

Modelling calculations based on the $\delta^{13}C$ sponge data estimated a pre-industrial CO_2 concentration of 280 parts per million by volume (Druffel and Benavides 1986), which is in direct agreement with measurements of air occluded in Antarctic ice cores (Neftel et al. 1985). Furthermore, trends in $\delta^{13}C$ chronologies in hypercalcified sponges closely match atmospheric CO_2 trends (Lazareth et al. 2000; Böhm et al. 2002). Together, these results suggest that $\delta^{13}C$ in hypercalcified sponges from shallow waters (<30 m) reflects the global atmospheric signal, and that hypercalcified sponges are good proxies for determining the timing and magnitude of the ingress of anthropogenic CO_2 into oceanic regions (Swart et al. 1998b). However, it should be noted that $\delta^{13}C_{DIC}$ concentrations in seawater can vary locally due to regional changes in water mass mixing, changes in water mass source and photosynthetic processes (Ravelo and Hillaire-Marcel 2007).

$\delta^{13}C_{DIC}$ concentrations in deep-water sponges may also be useful for estimating the time and depth of anthropogenic $\delta^{13}C$ penetration into deep oceanic regions. The penetration of $\delta^{13}C_{DIC}$ in deep subsurface waters is largely determined by the rate of vertical transport of water masses. This is because the time for surface waters to reach equilibrium with the atmosphere (~1 year) is much shorter than the contact time of most surface waters with the atmosphere, which results in $\delta^{13}C_{DIC}$ lagging behind atmospheric levels (Siegenthaler and Sarmiento 1993). Hypercalcified sponges live in a range of locations and depths (5–1000 m). $\delta^{13}C$ values of shallow-water sponges are likely to be in isotopic equilibrium with the atmosphere, whereas

Table 3.2 Estimated start of the ingress of anthropogenic CO_2 to the oceans based on $\delta^{13}C$ measurements in hypercalcified sponges

Species	Collection location and depth	Sponge chronology dates	$\delta^{13}C$ start (‰ ± 2σ)	$\delta^{13}C$ end (‰ ± 2σ)	Start of Suess effect[a]	Reference
A. wellsi	Vanuatu, 10 m	1955–1999	3.6	2.7	–	Fallon et al. (2003a)
A. willeyana	Great Barrier Reef, <30 m	1550–1990	4.7	4.0	~1870	Wörheide (1998)
A. willeyana	Solomon Is., 17 m	1895–1995	4.7	4.1	–	Moore et al. (2000)
A. willeyana	Bunaken Is., Indonesia, 20 m	1910–1995	4.2	3.7	–	Moore et al. (2000)
A. willeyana	Kapoposang, Indonesia, 20 m	1910–1995	4.2	3.7	–	Moore et al. (2000)
A. willeyana	Kapota, Indonesia, 10 m	1910–1995	4.3	3.6	–	Moore et al. (2000)
C. nicholsoni	Jamaica, 20 m	1380–1996	4.9	3.8	~1850	Böhm et al. (2002)
C. nicholsoni	Jamaica, 125 m	1380–1996	4.9	3.8	~1850	Böhm et al. (2002)
C. nicholsoni	Bahamas, 30 m	1750–1985	4.95	4.15	~1830	Lazareth et al. (2000)
C. nicholsoni	Jamaica, 25 m	1790–1990	4.9 ± 0.1	4 ± 0.05	~1790	Böhm et al. (1996)
C. nicholsoni	Jamaica, 84 m	–	4.9	4	–	Böhm et al. (1996)
C. nicholsoni	Jamaica, 26 m	1830–1972	4.8	4.3	~1900	Druffel and Benavides (1986)

[a] Sponges that were born near or after the start of the industrial period were not included in this assessment

$\delta^{13}C$ values of deep-water sponges are likely to be in isotopic disequilibrium with local atmospheric conditions (Böhm et al. 2002). Consequently, hypercalcified sponges can potentially be used to measure regional variations in the timing, magnitude and depth of anthropogenic CO_2 penetration to different water bodies (Böhm et al. 1996; Moore et al. 2000). However, this has not been tested as the majority of hypercalcified sponges analysed for $\delta^{13}C$ have been shallow-water specimens (<30 m) that are likely to represent local atmospheric conditions (Table 3.2). The two sponges that were collected from below the mixed layer (84 and 125 m) showed very minor differences in their $\delta^{13}C$ profiles to their shallow-water conspecifics (Böhm et al. 1996, 2002).

3.4.2 *Proxies for Historical Sea Temperatures*

3.4.2.1 δ^{18}O as a Proxy for Historical Sea Temperatures

Research on using δ^{18}O chronologies from hypercalcified sponges to reconstruct temperatures have produced mixed results. δ^{18}O *C. nicholsoni* chronologies showed relatively good correlations to low-resolution temperature data over the past century (Swart et al. 1998b; Moore et al. 2000), and δ^{18}O chronologies from *A. wellsi* and *A. willeyana* from Saipan showed good correlation to high-resolution (~monthly) in situ temperature measurements (Grottoli et al. 2010). δ^{18}O hypercalcified sponge chronologies from multiple specimens of *A. wellsi* and *A. willeyana* from Saipan were found to have good reproducibility, providing additional support for using δ^{18}O values for temperature reconstructions (Grottoli et al. 2010). However, in the same study, δ^{18}O chronologies from multiple specimens of *A. wellsi* collected from Palau showed lower reproducibility (Grottoli et al. 2010). Similarly, poor reproducibility in δ^{18}O values within *C. nicholsoni* specimens has been demonstrated (Haase-Schramm et al. 2003), which question the accuracy of temperature reconstructions that are often only based on one or two specimens per location.

A lack of correlation between δ^{18}O values in hypercalcified sponges and in situ temperatures (Grottoli 2006; Rosenheim et al. 2009; Grottoli et al. 2010) or regional atlas temperate data (Moore et al. 2000) has also been demonstrated for some specimens. This lack of correlation may be due to sampling errors (see below), salinity-driven variations (Grottoli 2006; Grottoli et al. 2010) or inaccurate temperature data (Moore et al. 2000). For example, Moore et al. (2000) found no correlation between δ^{18}O hypercalcified sponge and sea surface temperature (SST) data for *A. willeyana* from Indonesia but found that subsurface temperatures and winds provided a better correlation for the observed δ^{18}O data. In another study, Grottoli (2006) found that δ^{18}O data from *A. wellsi* from Palau reflected salinity variations rather than temperature variations. The δ^{18}O chronology was found to be inversely correlated to the Southern Oscillation Index, which caused the water in the region to become more saline during El Niños and less saline during La Niñas (Fig. 3.5).

The desired temporal resolution of the study needs to be taken into account when choosing a study species. The faster-growing *A. wellsi* and *A. willeyana* appear to be better suited for studying interannual to interdecadal temperature variability, while the longer-lived, slower-growing *C. nicholsoni* is better suited for studying longer-term variability. High-resolution (~monthly) δ^{18}O measurements from multiple specimens of the faster-growing *A. wellsi* and *A. willeyana* showed good seasonal correlations with in situ temperature measurements taken over 2 years, indicating that δ^{18}O values from these two species are good proxies for subannual temperature reconstructions (Grottoli et al. 2010). However, δ^{18}O measurements from the much slower-growing *C. nicholsoni* did not correlate to seasonal temperature variations (Rosenheim et al. 2009). This lack of correlation was attributed to the mechanical homogenization of closely spaced samples that occurred during micro-milling. Subannual samples from faster-growing species are less prone to homogenization because the samples can be spaced further apart.

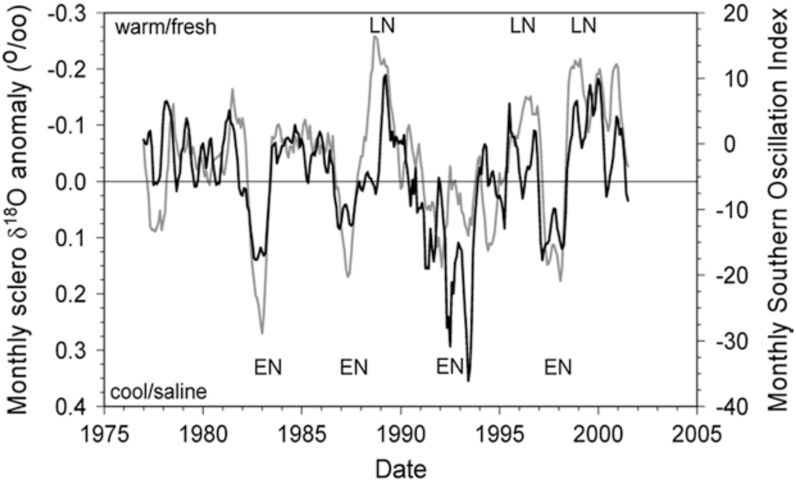

Fig. 3.5 Inverse correlation between monthly δ^{18}O anomaly data from *A. wellsi* (*black line*) and monthly Southern Oscillation Index (*grey line*). El Niños (EN) and La Niñas (LN) events are indicated at the bottom and top of the figure, respectively. Note that the δ^{18}O scale is reversed (Reproduced from Grottoli (2006) with permission from A. Grottoli)

These findings have important implications for the use of sclerosponges as proxies of Paleoclimate because they emphasize the need for a precise yearly chronology so that proxy data can be compared with climatic variables.

3.4.2.2 Trace Elements

Validation of the relationships between trace elements and temperature in hypercalcified sponges appears to be complicated by the different growth forms of the different species (Sect. 3.2). The gradual infilling of aragonite in the pseudocalices of *C. nicholsoni* and *A. willeyana* results in a ‘blurring’ of trace element signals over this period. It has been demonstrated that the Sr/Ca and Mg/Ca ratios in *A. willeyana* were lower at the surface than in the epitaxial backfill zone just below the living tissue layer (Allison et al. 2012). As a result of the gradual infilling that occurs in *C. nicholsoni* and *A. willeyana*, the calibration of trace element measurements taken within the living zone with in situ temperature measurements is questionable because the precise age of the sampled material is unknown.

Strontium/Calcium

The suitability of using Sr/Ca ratios in hypercalcified sponges for temperature reconstructions appears to depend on the sponge species. Sr/Ca ratios in the Jamaican sponge, *C. nicholsoni*, were found to be reproducible and well correlated with low-resolution, long-term temperature records (Haase-Schramm et al. 2003). Higher-resolution sampling has also demonstrated that Sr/Ca ratios in *C. nicholsoni* display approximately annual cycle patterns (Swart et al. 2002; Rosenheim et al. 2004, 2005a) that were well correlated to in situ temperature measurements (Rosenheim et al. 2004, 2005a). However, Sr/Ca ratios in the Pacific species, *A. willeyana* and *A. wellsi*, were not well correlated to SSTs (Fallon et al. 2005; Grottoli et al. 2010), and there were significant differences in the Sr/Ca ratios between the two species collected from the same location, which suggests a species-specific biological effect (Grottoli et al. 2010). In *A. willeyana*, temperature was found to only explaining 20–25% of the variance in Sr/Ca. This lack of correlation was attributed to the gradual infilling of pseudocalices (Fallon et al. 2005). However, it should be noted that gradual infilling also occurs in *C. nicholsoni*, which showed good correlation between Sr/Ca and temperature on an intra-annual scale (Rosenheim et al. 2004). In *A. wellsi*, which has no secondary infilling, it is hypothesized that the high Mg content (21 mol%) of the species interferes with Sr uptake (Grottoli et al. 2010).

Sr/Ca ratios in hypercalcified sponges have two potential advantages over $\delta^{18}O$ as a proxy for temperature: (1) they appear to be more sensitive to temperature changes than $\delta^{18}O$ (Swart et al. 2002); and (2) they are primarily affected by changes in temperature, while $\delta^{18}O$ is affected by changes in both salinity and temperature. Thus, in areas of high salinity fluctuations, $\delta^{18}O$ will also reflect changes in salinity (Grottoli 2006; Grottoli et al. 2010). Rosenheim et al. (2005b) used the difference in temperature estimates from Sr/Ca ratios and $\delta^{18}O$ to estimate the change in salinity (0.35–0.5 psu) that occurred in the Caribbean over the last century. However, there is still much that we don't understand about the accretion of Sr/Ca in hypercalcified sponges, and Sr/Ca does not appear to be a good proxy for temperature in *A. willeyana* and *A. wellsi*.

Magnesium/Calcium

Preliminary research on Mg/Ca ratios in hypercalcified sponges show that Mg/Ca ratios in *C. nicholsoni* were weakly (but significantly) correlated to Sr/Ca in *C. nicholsoni* ($r^2 = 0.21$, $p < 0.05$) (Swart et al. 2002; Rosenheim et al. 2005a) and *A. willeyana* ($r^2 = 0.42–0.87$) (Fallon et al. 2005; Allison et al. 2012). However, cyclic patterns in Mg/Ca were found to be inferior to Sr/Ca ratios (Swart et al. 2002). Mg/Ca ratios were not correlated to SST in *A. willeyana* (Fallon et al. 2005).

3.4.3 Proxies for Historical Nutrient Concentrations

3.4.3.1 δ^{30}Si

δ^{30}Si data from loose sponge spicules within dated sediment down-cores can be used for reconstructing historical $Si(OH)_4$ concentrations. The use of down-core data is reliant on the accuracy of the sediment dating (which can have large uncertainties due to poor preservation of benthic foraminifera and other datable carbonates). Down-core data also assumes that the $Si(OH)_4$ concentration of the water was constant over the time period sampled, and the sponge spicules are the same age as the surrounding sediment (Hendry et al. 2010).

There have only been a couple of studies on the application of $\delta^{30}Si$ data from hexactinellids and demosponges as a proxy for historical Si concentrations. $\delta^{30}Si$ values of sponge spicules from the Atlantic sector of the Southern Ocean during the Last Glacial Maximum (LGM) (20–25 ka) were found to be not significantly different from $\delta^{30}Si$ values of present-day, deep-sea sponges (Ellwood et al. 2010; Hendry et al. 2010). In contrast, sponge spicules from the Pacific sector of the Southern Ocean showed a more variable pattern and were often 1–2% lower than the corresponding Atlantic values, which suggests that Pacific waters, at these times, were more enriched with Si (Ellwood et al. 2010). Similarly, $\delta^{30}Si$ values of sponge spicules indicate that Si concentrations in the Pacific were found to be higher during the LGM and deglacial period than present day (Rousseau et al. 2016). The differing $\delta^{30}Si$ results for various Southern Ocean sites highlight the need for good spatial replication when using proxy data from down-cores.

3.4.3.2 Zinc/Silicon and Germanium/Silicon

Two novel proxies for estimating historical productivity are Zn/Si and Ge/Si in siliceous sponges. Measurement of Zn/Si ratios in live deep-sea hexactinellids and in loose spicules from mixed hexactinellid and demosponge species were found to

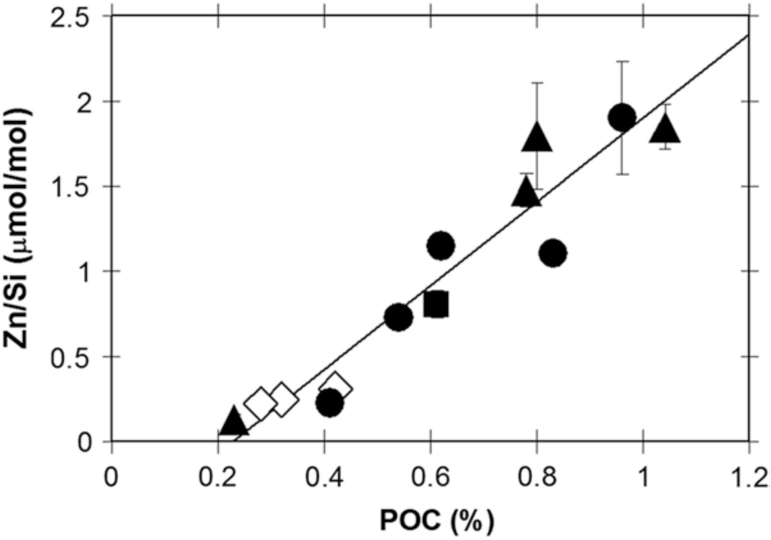

Fig. 3.6 Zn/Si ratios of sponge spicules versus surficial sediment POC. *Filled symbols* represent live sponges, while *open symbols* represent sponge spicules recovered from sediment cores. Samples were collected from the Ross Sea (*triangles*), Chatham Rise (*circles* and *squares*) and Campbell Plateau (*diamonds*) (Reproduced from Ellwood et al. (2004) according to the copyright policies of Wiley)

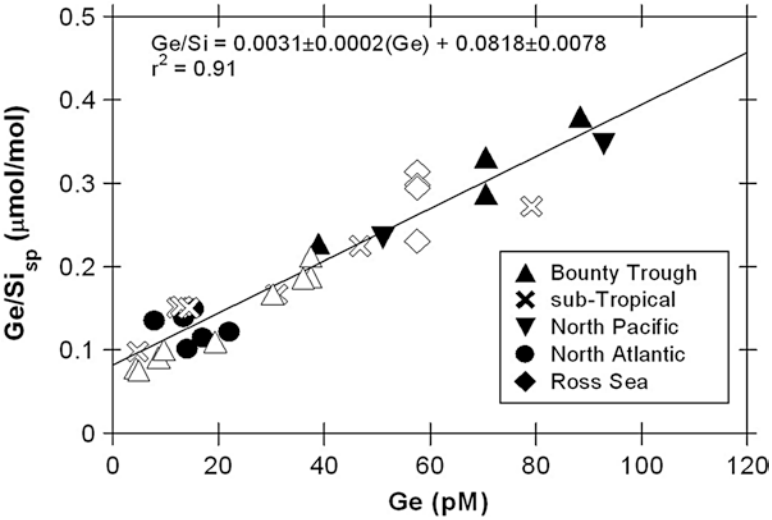

Fig. 3.7 Germanium content of sponge spicules (Ge/Si$_{sp}$) from live sponges (*open symbols*) and sediment-bound spicules (*closed symbols*) versus Ge (and Si) concentrations of seawater. Dissolved Ge concentrations were estimated from existing Si data (NIWA, GEOSECS and WOCE datasets) using a Ge/Si ratio of 0.7 µmol/mol (Froelich et al. 1989) (Reproduced from Ellwood et al. (2006) with permission from Elsevier)

have a strong linear correlation to POC in the surface sediment for nearby cores (r^2 = 0.89–0.93) (Fig. 3.6) (Ellwood et al. 2004, 2005). However, Hendry and Andersen (2013) demonstrated that there were differences in the uptake and fractionation of Zn between hexactinellids and demosponges, and that Zn/Si ratios in demosponges were less suitable than hexactinellids as a proxy for historical carbon concentrations. Zn fractionation in hexactinellids was similar to deep-water Zn fractionation values, and Zn/Si ratios were weakly positively correlated to dissolved organic carbon (DOC) concentrations of the seawater ($r^2 = 0.68$, $p = 0.03$). In contrast, demosponges showed both heavier and lighter Zn fractionation values than seawater and a poor, non-significant relationship between DOC and Zn/Si ratios.

Ge/Si ratios in siliceous sponges have been suggested to be a proxy for Si and, thus, nutrient concentrations in marine environments (Ellwood et al. 2006). Ge/Si ratios in various hexactinellids and demosponges from New Zealand and Antarctica were positively correlated with Ge concentrations in seawater between 0 and 100 pmol/L ($r^2 = 0.91$) (Ellwood et al. 2006) (Fig. 3.7). Currently, the mechanism(s) that controls Ge uptake in sponges is unknown. Temperature, pressure and sponge species appear to have little effect on Ge incorporation (Ellwood et al. 2006). The use of Ge/Si ratios in sponges as a proxy for Si assumes that the Ge/Si ratio of seawater remains constant. However, research has shown that Ge in the ocean can also be lost via sediment diagenesis, which can lead to a decoupling of Ge and Si (Hammond et al. 2000, 2004; King et al. 2000; McManus et al. 2003).

Much more research is required on these two proxies before their value for predicting historical nutrient concentrations can be assessed.

3.5 Conclusions

Research on the use of sponges as proxies for past climatic change events is still in its infancy, with the vast majority of studies conducted within the last 20 years. Early research focused on the quantification of stable isotopes in hypercalcified sponges, but this limits climate reconstructions to the life span of the sponge (<1000 years). Subsequent research has focused on the quantification of trace elements in spicules within dated sediment cores, which greatly extends the potential range of climate reconstructions. The main findings highlighted in this review are summarized below:

- The accuracy of hypercalcified sponge proxy data is reliant on the accuracy of dating methods. All dating assumes that growth is constant over the life of the sponge, growth is linear along the sample axis, and the tracer isotope is incorporated at a constant ratio over the life span of the sponge.
- Concentrations of proxies in deep-sea sponges do not necessarily accurately reflect surface conditions directly above them, only the water surrounding them. The concentration of the proxy at depth is dependent on the movement of water masses, dispersal and factors that may affect the integrity of proxy in the water column, e.g. dissolution.
- Hypercalcified sponges secrete $\delta^{13}C$ in isotopic equilibrium with seawater. $\delta^{13}C$ values in shallow-water hypercalcified sponges appear to be a good proxy for atmospheric CO_2 concentrations, with $\delta^{13}C$ values showing a high correlation to atmospheric pCO_2 data over the last 600 years.
- Hypercalcified sponges generally secrete $\delta^{18}O$ in isotopic equilibrium with seawater. Results using $\delta^{18}O$ as a proxy for temperature are mixed. Some studies have shown good correlations with temperature but other studies have not. Changes in salinity may mask any temperature effects, because salinity has been found to be the major determinant of $\delta^{18}O$ sponge values at some locations. Reproducibility of $\delta^{18}O$ results in some studies has been poor.
- Gradual infilling of skeletons of *C. nicholsoni* and *A. willeyana* results in skeletal material of mixed ages that is likely to ‘blur’ trace element signals, thus limiting the resolution of trace element analysis in these two species. High-resolution analysis of *C. nicholsoni* is also currently technology-limited because of the extremely slow growth of this species.
- Sr/Ca ratios are potentially a good proxy for temperature in *C. nicholsoni* but not for *A. willeyana* or *A. wellsi*. One of the benefits of Sr/Ca ratios over $\delta^{18}O$ is that Sr/Ca ratios are not affected by salinity changes, only temperature.
- Mg/Ca ratios in hypercalcified sponges are unlikely to be a suitable proxy for temperature with low Mg/Ca ratios in hypercalcified sponges and poor correlations with temperature data.
- $\delta^{30}Si$ values in siliceous sponge spicules appear to be a good proxy for $Si(OH)_4$ concentrations in water. Measurements were reproducible within a sponge and

there were no species-specific differences. δ^{30}Si values in spicules from down-cores are potentially a good proxy for long-term changes in Si concentrations.
- Zn/Si and Ge/Si in sponges are potential proxies for Si concentrations but more research is still needed in this area.

In summary, research on a number of sponge proxies has shown promising results for use as Paleoclimate indicators. Application of these proxies generally produces climatic reconstructions that are in agreement with other published studies. However, much more research is needed to further develop these proxies and to gain a better understanding of the processes that control both the incorporation of the proxy within the sponge and its concentration in the surrounding water.

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Chapter 4
Molecular Responses of Sponges to Climate Change

Jose Maria Aguilar-Camacho and Grace P. McCormack

Abstract We live in a time of concern regarding predicted environmental damage due to climate change, i.e. sea temperature increase and a reduction in ocean pH. Such changes will have severe consequences for at least some marine organisms. Developments in molecular and genomic techniques allow for genome-wide comparisons of genes and proteins that may be impacted by such changes with knock-on consequences for cell and organism function. Understanding of impacts at the molecular level is important to understand how organisms will respond to changes and to develop conservation strategies accordingly. Despite sponges having a very simple body plan, they possess gene diversity and genome complexity that mirrors other metazoa. The cellular stress response and adaptation of sponges to increased temperature and low pH are varied and diverse with many genes implicated and their expression patterns complex. Survival thresholds differ between species in their tolerance to temperature increase and lowering of ocean pH. The expression patterns of a variety of genes have been investigated particularly with regard to change in temperature but in few sponge species. Likewise genome and transcriptome data exists for few species, and even fewer studies focus on applying these approaches to stress response. Despite the requirement for more studies in this area, existing data suggests that some sponge species will be severely impacted if climate change predictions hold, while other species will adapt and thrive.

Keywords Sponges • Climate change • Gene expression • Genomics • Epigenetics

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4.1 Introduction

Sponges (phylum Porifera) are important elements of bottom communities globally, both in marine and freshwater habitats (Bell 2008). They form a large portion of the biomass on coral reefs in sensitive habitats, in deep-sea environments, and also are common members of intertidal and subtidal communities. Essentially nonmotile as adults, these animals are filter feeders drawing in significant volumes of surrounding water from which to select organic material and dissolved nutrients, e.g. a 1 kg sponge can reportedly filter 24,000 L of seawater per day (Vogel 1977). Instead of the digestive, osmoregulatory and excretory organs that are found in most other animal phyla, sponges have evolved a unique aquiferous system through which they obtain food, release waste and obtain oxygen. Inside the majority of sponges is a maze of canals and small chambers connected by the mesohyl (a matrix of cells, collagen, spicule skeleton and where present symbionts/associated microorganisms). The canals are lined with choanocytes, which, via the beating of their flagella, draw in water through pores on the sponge surface (called ostia). This water travels through incurrent canals to the chambers and out via larger excurrent canals and oscula (Bergquist 1978; Leys and Hill 2012). As such almost the entire internal sponge body is also exposed to the external aqueous environment (Fig. 4.1a, b). This factor in addition to the fact that sponges do not move very much makes them potentially very vulnerable to any changes in their immediate environment.

Patterns of gene expression when integrated with organismal functional performance under normal and stressed situations can inform conservation strategies as

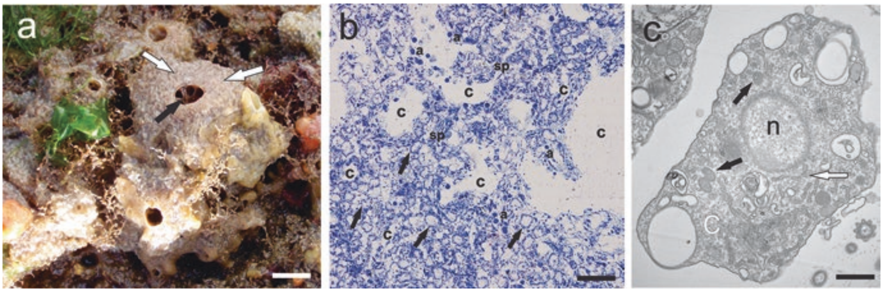

Fig. 4.1 (**a**) Photograph of a living specimen of *Haliclona indistincta* growing over flat boulders (*arrows* showing the incurrent (*white*) and excurrent (*black*) canals and obvious oscula). Water from the aqueous environment circulates deep within this sponge which has many such canals throughout. (**b**) A semi-thin section of *H. viscosa* using transmission electron microscopy (TEM) and stained with toluidine blue showing the canals penetrating to the centre of the sponge and very close to the cells: canals (c) choanocyte chambers (*black arrows*), spicules (sp) and amoebocytes (a). (**c**) A TEM micrograph of an amoebocyte from *H. simulans* showing the nucleus (n) which contains the sponge genome and where transcription occurs (mRNA being made from DNA); rough endoplasmic reticulum with ribosomes along it (*white arrow*), which is the site of translation (protein being made from mRNA); cytoplasm (c) where proteins are further modified; and mitochondria with their own small genomes involved in energy production primarily (*black arrow*). Scale (*a*) 5 mm, (*b*) 400 µm (*c*) 500 nm

part of the emerging field of conservation physiology (Evans and Hofmann 2012; Cooke et al. 2013). Nearly all cells will respond to environmental stress by inducing certain proteins that function in preventing and repairing damage in the cellular stress response, while others try to maintain homeostasis in the face of a change in an environmental variable (Kültz 2005). Many of the genes that are involved in the response to environmental stress are shared between distantly related organisms (e.g. heat-shock proteins), meaning that a universal set of biomarkers may be used to explore reactions across a wide set of organisms in a particular environment even though the levels of expression and the thresholds at which they are induced may differ (Evans and Hofmann 2012). Furthermore, the same set of genes can be induced as a result of different stressors and so can be used to explore an organisms' response to different physiological challenges (Kültz 2005). In most eukaryotes, including sponges, environmental stress induces expression of a number of genes most notably the acute-phase genes and heat-shock proteins. The former is reportedly triggered by lower-level stressors and is mediated by signalling molecules towards cell-specific responses, while the heat-shock response involves a range of genes (Hsp 70, Hsp 90, Hsp 50–60 and Hsp 20–30) to varying levels of environmental stress in efforts to maintain homeostasis (Koziol et al. 1997). This family of proteins is involved in protein folding/unfolding, minimizing the aggregation of non-native proteins and in targeting non-native proteins for removal (Feder and Hofmann 1999; López-Legentil et al. 2008). Hsps are useful as bioindicators because an increase in their gene expression is evident in response to stress, and as elucidated below, their expression changes in response to different kinds of stress. Apoptosis (programmed cell death) is also implicated in the stress response often followed by the death of the sponge (Wiens et al. 2000). Proteins involved in the cell death pathway include stress-activated protein kinases, caspases, BCl2 and tumour necrosis factor (Wiens et al. 2003; Pozzolini et al. 2016).

Despite their relatively simple body plan, sponges contain much of the genetic machinery present in higher animals and have a diversity of cell types that carry out various functions required for survival, growth and reproduction (Bergquist 1978; Riesgo et al. 2014a). Sponges have varying life spans, and while some species show 'boom-and-bust' patterns of rapid growth followed by a large degree of die off, others appear to be very long-lived (McCormack GP, Personal Observation; Wulff 2006). Therefore, sponges need mechanisms to adapt and survive environmental stress, and their responses to challenges introduced due to climate change such as increase in temperature and ocean acidification may vary depending on life history strategy and stage. What the molecular mechanisms are, how patterns of gene expression vary according to environmental challenge and how well sponges can adapt to environmental changes associated with climate change and ocean acidification are only now being investigated. Given that researchers have developed ways to maintain some species in aquaria and have also developed unique primmorph cultures from dissociated sponges means that sponges have become useful experimental animals (Custodio et al. 1998; Schippers et al. 2012; Fang et al. 2013). For many years before genomes and transcriptomes were available, genes could be isolated by cloning, and their activity studied using western and northern blots and gel electrophoresis (see Glossary). More recently, quantitative polymerase chain reaction (qPCR) and genome and transcriptome techniques are available, and the fields of epigenetics and epigenomics are being developed. These methods are extremely valuable for studying acclimatory mechanisms, and how they have been applied to members of the Porifera are discussed in more detail below.

4.2 Gene Expression in Sponges

Isolating specific genes and investigating how they are expressed (switched on/off, producing high/low amounts of mRNA/protein) across organisms and tissues have been important for determining the evolutionary origin, function and importance of proteins. Most sponge genes are found in the genome of the sponge located in the cell nucleus with additional genes (involved in energy production primarily) located in the mitochondria (Fig. 4.1c). When cells are active (e.g. sclerocytes), the DNA of particular genes in the genome (e.g. silicateins) is transcribed to mRNA (i.e. expressed). The mRNA moves out of the nucleus to the ribosomes in the cytoplasm where the information they contain is translated into proteins (Fig. 4.2). Sponges have fewer cell types than other animals, but differentiated cells will produce different mRNAs and at differing amounts, e.g. sclerocytes would be expected to have some genes active that are different to those expressed by spherulous cells. A certain number of genes, e.g. housekeeping genes, which are those involved in basic cellular metabolism, are active/expressed in all cells. There are many studies published from the 1990s onwards describing the cloning and genetic characterization of genes from marine and freshwater sponges that had been previously found in other metazoa (e.g. polyubiquitin, integrin and receptor tyrosine kinase in *Geodia cydonium*, Pfeifer et al. 1993, Wimmer et al. 1999; longevity gene SDLAGL in *Suberites domuncula*, Schröder et al. 2000a).

To investigate patterns of expression of particular genes, first it involves obtaining cDNA of the targeted gene from extracted RNA using a specific commercial kit or via RT-PCR (see Glossary). Western or northern blots are then used to determine

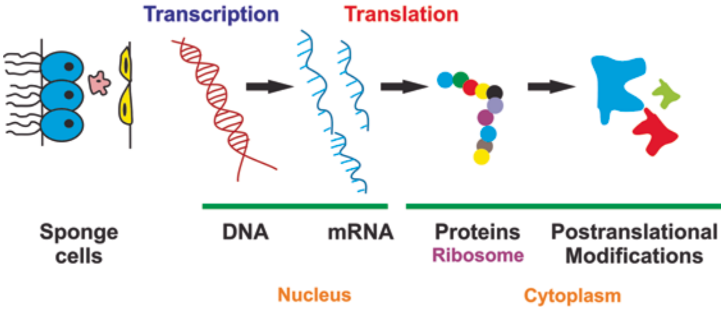

Fig. 4.2 A schematic representation of gene expression in sponges

to what degree a particular gene is active (e.g. Pfeifer et al. 1993). Another approach involves in situ hybridization where probes are applied directly to the tissue of the species to determine where the gene is expressed and at what level of expression (e.g. Adell et al. 2003). This approach can be applied to whole-mounted embryos or larvae, for example, or to complete specimens of small organisms or sections of larger ones (e.g. Larroux et al. 2006). Tissue is normally mounted on a microscope slide and stained with fluorescently labelled probes. More recently quantitative real-time PCR (see Glossary) is being applied to detect the copy number of specific mRNAs as a way to detect differential levels of expression (e.g. López-Legentil et al. 2008). High numbers of a particular mRNA would indicate that the gene in question is highly expressed and cause high levels of fluorescence, while lower fluorescence would indicate a lower number of copies of mRNA, which in turn indicates a lower level of expression. Thus animals under different environmental conditions can be compared to investigate how expression levels of particular genes change under different conditions. Finally, the entire set of expressed genes (the transcriptome) can be sequenced from sponges held under different environmental regimes, e.g. temperature, and compared to explore how gene expression varies (e.g. Guzman and Conaco 2016).

Many such studies have focused on expression patterns of developmental genes, e.g. EmH-3, a homeobox-containing gene in *Ephydatia muelleri* (Richelle-Maurer and Van de Vyver 1999), embryological body formation axis genes (Wnt and TG-Fβ) and hedgehog proteins at different life stages of *Amphimedon queenslandica* (Adamska et al. 2007a, b). Many other genes have been investigated in this latter sponge, e.g. sensory proteins such as delta and notch and postsynaptic scaffold genes (Sakarya et al. 2007; Richards et al. 2008), immunity genes such as toll like, interleukin receptor and NF-κB (Gauthier and Degnan 2008; Gauthier et al. 2010) and regulatory transcription factors related to embryo development (Homeobox genes) such as ANTP, *Pax*, POU, LIM-HD, Sox, NR, Fox, T-Box, Mef2 and Ets (Larroux et al. 2006). Recent studies also include differential expression in sponges with and without symbiont partners to help determine genes associated with the symbiotic state (e.g. Steindler et al. 2007; Riesgo et al. 2014b). Such studies are relevant to understanding climate change effects on sponges given the presence of photosynthetic symbionts in many sponge species which can vary in their response to changes in temperature in some situations offering potential benefit to the sponge (Bell et al. 2013). Furthermore, a large literature is accumulating on the genes associated with collagen and skeleton formation in sponges (e.g. Pozzolini et al. 2004; Voigt et al. 2014; Germer et al. 2015). The pressure of climate change on calcium-based organisms on coral reefs may increase the competitiveness of siliceous-based organisms (Bell et al. 2013; Vicente et al. 2015). However, there is likely to be some impact of increased temperature and reduced pH on metabolic pathways and biomineralization of all species; thus studies of biomineralization genes are also of interest here. Sponges need to sense their environment to cope with stress; therefore expression patterns of sensory and signalling proteins are also potentially very important in assessing sponge responses to changing environments.

Sponges are exposed to different kinds of environmental challenges such as changes in temperature, salinity, pH, organic matter and other pollutants (Wulff 2006; Webster et al. 2013; Vicente et al. 2015). Most published works on sponges have focused on expression of common genes related to stress response including the expression of the heat-shock protein, Hsp70. This protein is a large multigene protein that is found in several compartments of the cell and whose main function is to fold the peptides newly produced by the ribosomes (Mayer and Bukau 2005). An increase in activity of Hsp70 is detected when the cells response to disturbance is to fold more proteins that are required for the relevant response (Pratt and Toft 2003). Hsp70 has been reported to be a very good biomarker for environmental stress as the approaches used to study it require very little tissue and are therefore non-destructive (Koziol et al. 1996; Krasko et al. 1997; López-Legentil et al. 2008). This protein forms a complex with DNAJ-like proteins, which also respond to environmental stress and which may thus also be used as a biomarker and together are indicative of the presence of a heat-stress protection mechanism in sponges.

4.2.1 *Response to Temperature*

Given the predicted rise in seawater temperatures described in many studies (e.g. Bell et al. 2013), identifying indicators of thermal stress in coastal organisms is important as is developing an understanding of how well or poorly marine sponges will cope with rising temperatures. To this end there is a need to identify genes that have altered expression under thermal stress and investigate what the impacts of such changes in expression are. One of the first genes to be shown to be involved in adaptation to temperature stress in sponges was Hsp70 described above. Koziol et al. (1997) found that there was an 18- and 3-fold increase in the expression of Hsp70 and DNAJ-like protein, respectively, in *G. cydonium* when the temperature was raised by 7 °C. These authors showed DNAJ-like expression but not Hsp70 expression in untreated animals. A time-dependent increase in hsp70 expression was noted by Efremova et al. (2002) for Baikalian sponges exposed to temperature increases 10–16 °C above ambient, while increases in temperatures of a few degrees also resulted in increased expression of Hsp70 in *Xestospongia muta* (López-Legentil et al. 2008), while individuals maintained at lower temperatures showed no change in Hsp70 expression. This latter study also suggested that not all individuals respond in the same way to temperature increase given that there was variability in the expression levels between individuals undergoing the same treatment. These authors suggest that an increase in chaperone protein activity can assist the sponge in coping with minor stress, while larger degrees of stress may cause the metabolic defence system to collapse (López-Legentil et al. 2008).

This pattern was clearly shown by Pantile and Webster (2011) who investigated changes in expression of six genes in response to an increase in temperature of 4 and 5 °C above ambient (27 °C) in *Rhopaloeides odorabile.* Their work confirms that the molecular mechanisms to adapt to some thermal stress are evident (such as up to 4 °C above ambient), but there is a limit to the temperature at which the protective functions of the heat-shock system can outweigh the damage caused. At 31 °C five proteins were significantly downregulated in comparison to the controls (held at ambient temperature). While the sponges survived the experiment and expression levels for genes involved in signalling (CaM) and removal of degraded proteins (UbC) recovered 24 h after temperature levels returned to normal, genes involved in cytoskeleton formation (arp2/3), oxidation (ferritin) and molecular chaperone (Hsp90) did not recover. The reduction of expression in these genes in response to an increase in temperature of 4 °C suggests that the sponge shuts down/reduces some cellular activity and perhaps indicates some permanent or longer-term physiological damage (Pantile and Webster 2011). Whether or not all of the genes would have eventually recovered to normal expression at ambient temperature remains to be seen but if so would indicate some adaptability of this species to recover from significant heat stress.

In the above study, a further increase in temperature of 1 °C (to 32 °C) resulted in all sponge clones showing signs of necrosis and subsequent death after 3 days (Pantile and Webster 2011). At this temperature, expression levels of the signal transducer gene, CaM, dropped significantly after a single day. While the patterns of expression of Arp2/3, ferritin and Hsp90 also showed a significant drop in expression after 1 day, expression of these genes increased again by day 3. Hsp40 and UbC all showed significant increase in expression by day 3. According to Pantile and Webster (2011), the perhaps surprising increase in expression of some of these genes by day 3 indicates further induction of the heat-shock system, activation and upregulation of systems to neutralize reactive oxygen species and to degrade damaged and unfolded proteins. But at 32 °C the physiological damage must be too great for the protective systems to overcome and the sponges all died. In Bolinao, Philippines, seawater temperature varies from 25 to 32 °C, and the shallow water sponge *Haliclona tubifera* is exposed to regular widely fluctuating temperatures. According to Guzman and Conaco (2016) who applied a comparative transcriptomics approach, thermal stress at 34 °C resulted in much greater changes in gene expression than sponges held at 32 °C, the latter temperature within the natural temperature range, if the extreme. In this latter sponge, genes that were downregulated were those involved in housekeeping or first line of defence, while stress-induced genes were upregulated.

As mentioned by Webster et al. (2013), seawater temperatures at the Great Barrier Reef have occasionally already exceeded 30 °C. If water temperatures increase by a further 1.8–4 °C (IPCC 2007), this would bring temperatures to a point at which adult *R. odorabile* could not physiologically adapt, an eventuality that may hold for many more sponges. Indeed *X. muta* is indicated to have a stricter thermal limit than *R. odorabile* with individuals suffering mortality after being held in tanks 2 °C above the control temperature of 28 °C (López-Legentil et al. 2008). In the study of Guzman and Conaco (2016), experiments were carried out over 12 h on sponge pieces, and it was not reported whether any of the sponge pieces survived afterwards.

Further work by Webster et al. (2013) investigated differences in stress response between adults and larvae of the same species, *R. odorabile.* Such work is of fundamental importance given the different environments utilized by different life history stages of sponges and thus potentially different impacts of temperature increase on each stage. Both life history stages are obviously of importance in the continued survival of a species, so it is important to assess mechanisms of survival/adaptability in both. Using RT-qPCR (see Glossary) to measure differential gene expression, a whole suite of genes were investigated including those involved in cytoskeleton/skeleton arrangement, signal transduction, protein folding and heat shock, protein synthesis and degradation, oxidative stress and detoxification. Their research and others indicate that the sponge larvae of *R. odorabile* are more tolerant to thermal stress than the adults (Whalan et al. 2008; Webster et al. 2013) with the adult sponges displaying signs of necrosis after 3 days of exposure to 5 °C above ambient but larvae surviving temperatures up to 9 °C above ambient.

As the authors noted, larvae move from benthic to pelagic habitats experiencing a natural change of temperature. Thus larvae may have additional and different mechanisms in place to adapt to changing temperatures compared to adults, which remain on the benthos (Webster et al. 2013). In larvae, at 32 °C after 24 h, all of the genes showed some increase in their expression levels, but at 34–36 °C the heat shock (Hsp70, Hsp90) and the cell death pathway genes (Alg 2 1) were highly expressed. While larvae will survive temperature increases predicted (1–4 °C over the next 100 years), the fitness of the adult stage of some sponge species will clearly be negatively impacted (Webster et al. 2013). There is a need for information from more species and scenarios to fully understand the molecular and cellular mechanisms affected by temperature increases and subsequent likely impact on different habitats where sponges play a role. Higher temperatures will also cause a further impact to many sponges due to the relationship between them and their symbionts given that up to 40% of the biomass of some sponges may comprise of bacteria (Lesser et al. 2016). Cebrian et al. (2011) showed mortality in *Ircinia* in the Mediterranean in response to the higher temperatures evident in 2008 and 2009 due to mortality of their cyanobacterial symbionts. Differential responses of the sponge holobiont at adult and larval stages have also been described (Webster et al. 2008, 2011) and will be discussed further in Chaps. 5, 6 and 9.

4.2.2 Changes in pH

Animals form inorganic skeletons through biomineralization, a process that involves a number of different chemical reactions (Marin et al. 1996). Marine sponges have a wide variety of skeletons made predominantly of biogenic silica, calcium carbonate, collagen fibres and/or chitin (Ehrlich et al. 2013; Wang et al. 2012), and both the mechanisms to generate the skeletons and the genes/proteins involved vary significantly. It is well accepted that increased acidification of our oceans due to higher atmospheric CO_2 will have a significant effect on organisms with calcium-based skeletons (e.g. O’Donnell et al. 2010). Less is known about the impact of ocean acidification on species with silica-based skeletons.

Most published studies on biomineralization in sponges to date have focused on the chemical composition and mechanical properties of the spicules (Sundar et al. 2003; Sethmann et al. 2006); the identification, expression and evolution of the genes responsible for biomineralization (Krasko et al. 2000; Mohri et al. 2008; Ehrlich et al. 2013; Riesgo et al. 2015); biotechnological applications of the proteins and skeleton as new sources of biomaterials (Shkryl et al. 2016; Gardères et al. 2016); and variability in skeletal arrangement and spicule morphology with silica concentration (Maldonado et al. 1999, 2012). In the context of climate change, there are very few studies on its potential effects on the sponge skeleton, and none of these have applied gene expression approaches. Yet gene expression analyses are very important to help understand the genetic response of targeted species in response to climate change variables that impact the biomineralization process (Kaniewska et al. 2012). As might be expected, sponges that produce high Mg calcite and/or aragonite will be most vulnerable to ocean acidification because of the dissolution of the carbonates (Smith et al. 2013). Furthermore, saturation levels of CO_2 are predicted to be higher in temperate shallow waters than in deeper habitats, indicating that shallow water sponges with calcareous skeletons are more susceptible than those living in deeper habitats. Vicente et al. (2015) investigated the effects of high pCO_2 and warmer temperatures in silica uptake and spicule length of *Mycale grandis* and found a decrease in silica uptake and spicule length under high pCO_2 conditions. While the cause behind the impact was not determined, it is possible that the lower pH denatured the proteins responsible for spicule production.

Several proteins have been identified in sponges that are responsible for skeleton construction, and their function may be negatively impacted as conditions move away from ambient. For siliceous sponges they include silicateins, silinthaphins, galectin, BMP, short-chain collagen and others (Cha et al. 1999; Wang et al. 2014; Nakayama et al. 2015). In contrast, skeleton formation in calcareous sponges is due to their possession of two (one intracellular and one extracellular) specific α-carbonic anhydrases (Müller et al. 2012; Voigt et al. 2014). Coralline sponges (sclerosponges), in addition to siliceous spicules, have a calcareous basal skeleton made of intracellular spherulites, and the protein responsible for the formation of these structures has been identified as astrosclerin (Jackson et al. 2007, 2011; Germer et al. 2015). Recent studies have demonstrated that even bacteria are responsible for the calcification of the sponge skeleton in certain species such as *Hemimycale* (Uriz et al. 2012). O'Donnell et al. (2010) and Stumpp et al. (2011) both showed a reduction in expression of genes involved in the biomineralization process in echinoderm larvae under pH stress. It is likely that skeleton formation would slow down as mechanisms for survival are activated, an effect that may also occur in sponges. However, in a range of experiments investigating bioerosion, with progressively lower pH and higher temperatures in clionaid sponges, individual sponges not only survived experiments up to eight weeks but also showed an increase in biomass indicating that these sponges can physiologically adapt to lower pH and maintain the biomineralization processes (Fang et al. 2013).

Reducing pH does induce the stress response in some sponges (e.g. *G. cydonium;* Koziol et al. 1997). This latter study showed an increase in Hsp70 expression via western blots in one of the first studies of cloning and expression of functional genes in sponges. However, variability clearly exists in the ability of different species to survive with decreasing pH. While clionaid sponges may benefit from reduced pH due to ocean acidification, Goodwin et al. (2014) showed that sponge cover and species composition reduced with lower pH treatments. Four species (*Phorbas tenacior*, *Petrosia ficiformis*, *Chondrilla nucula* and *Hemimycale columella*) were very vulnerable to reduced pH, only surviving in sites with normal pH, while *Crambe crambe* was able to survive at pH of 6.6 (Goodwin et al. 2014), and reduced pH had no discernible impact on spicule form in those that survived at lower pH concentrations. What metabolic processes are impacted by reduced pH or what mechanisms help some sponge species to survive in lower pH environments have yet to be determined, and more gene expression profile studies are needed in relation to the ability of sponges to adapt to ocean acidification specifically.

Gene expression profiling has been very informative for other animal species, and lessons could be learnt here on what might be expected from sponges. In addition to biomineralization genes being downregulated in response to pH, O'Donnell et al. (2010) and Stumpp et al. (2011) showed that genes involved in ion regulation and acid-balance pathways showed an increase in expression in echinoderm larvae. Wells et al. (2012) showed that pH was also implicated in regulating potassium channels in *A. queenslandica*, and it may be likely that cell signalling would increase in individuals under pH stress. Kaniewska et al. (2012) described major physiological impacts resulting from lower pH in the coral *Acropora millepora* resulting in metabolic suppression, oxidative stress, apoptosis and symbiont loss, while genes involved in membrane transport were upregulated. Moya et al. (2012) also showed a decrease in the expression of metabolic genes and secreted carbonic anhydrases as pH was lowered in early stages of *A. millepora* using transcriptomic approaches, while they found no differences in the expression of the ion transporter genes. Rocker et al. (2015), however, found no significant changes in 19 out of 20 metabolism and calcification genes in the same coral species under high pCO_2 and warmer temperatures using RT-qPCR. Such variation in results from the same species using different approaches and the lack of studies on sponges cries out for more work to be done and a consistency of approach across researchers to allow comparisons to be made and general patterns drawn. The recent development of a panel of reference genes for stress response using a qPCR approach for coral by Shimpi et al. (2016) may help to standardize approaches.

4.2.3 Other Impacts

In addition to environmental challenges as a result of climate change such as increased temperatures and lower pH, sponges must acclimate to other factors implicated in environmental change such as changes in salinity, exposure to sedimentation and pollutants [e.g. Evans and Hofmann (2012)]. López-Legentil et al. (2008)

suggested that an increase in salinity may cause temporary stress to *X. muta* but that after a period of time, the sponges appeared to adapt to the change and Hsp70 expression levels were seen to drop suggesting that the sponges had adjusted and recovered. Koziol et al. (1996) found no change in Hsp70 expression in *G. cydonium* under different ionic conditions, while Böhm et al. (2000) showed an increase in expression of the stress-activated protein kinase (SPAK) p38 in the tissue and cells of *S. domuncula* under different salinity concentrations using western blot assay. These studies again suggest variability amongst sponge species in adapting to environmental stress.

Sponges can be used as indicators of toxic metals because the metals accumulate in the tissues of some species with varied impacts from reduced survival, induction of gemmule formation to simple accumulation of the metal. Wagner et al. (1998) investigated the response of *S. domuncula* to cadmium using expression of a metazoan apoptosis marker (the MA-3 gene), which increased on the addition of the metal. Hsp70, GRP78, metallothionein expression and DNA damage also increased in this sponge in response to higher loads of zinc and cadmium (Müller et al. 1998; Schröder et al. 1999b, 2000b). While exposure to cadmium did not result in the death of the sponge, it accumulated in the tissue and induced apoptosis, which in turn lead to gemmule formation. *Halichondria panicea* was also shown to accumulate this metal, as well as copper, zinc and chromium (Olesen and Weeks 1994; Hansen et al. 1995). In comparison, Cebrian et al. (2006) found that copper accumulation did not occur in *Chondrosia reniformis* exposed to an environment with moderately high levels of copper pollution. In this case there was also no change in expression of heat-shock protein or sponge growth or shape. These authors however did detect a negative impact on sponge physiology leading to a lower survival rate. A lack of hsp70 induction in response to copper was also shown by Efremova et al. (2002) in sponges from Lake Baikal, while Hsp70 induction was seen for exposure to lead and zinc.

Some sponge species are able to accumulate other heavy metals and contaminants in their tissue such as plumb, aluminium, titanium, PHAs and PCBs as well as copper, cadmium and zinc (Cebrian et al. 2007; Gentric et al. 2016; Batista et al. 2013), and metallothionein is used as a common biomarker for accumulation of such heavy metals in sponges and other filter-feeding organisms (Berthet et al. 2005; Amiard et al. 2006; Aly et al. 2014). When polychlorinated biphenyls (PCB77, PCB118 and PCB153) accumulated in the tissue of *S. domuncula*, the heat-shock system was activated with Hsp73 consistently expressed at high levels in all samples tested, while Hsp75 was expressed at low levels (Schröder et al. 1999a). Two stress-activated protein kinases (PKAS), which are signalling molecules, were reported in *S. domuncula* in response to TBT (tributyltin) exposure by Fafanđel et al. (2003) who suggested that this indicates the presence of a mechanism that promotes apoptosis in sponges that are under oxidative stress. Châtel et al. (2011) described activation in ERK (extracellular signal-regulated kinase) and p38 (involved in cell differentiation and apoptosis) and increase in expression of cyclin D1 (involved in regulation of cell cycle) in the presence of TBT, hydrogen peroxide and water-accommodated fraction (WAF) of diesel oil in the same sponge species. An increase in apoptosis activity was determined based on the high levels of DNA fragmentation and caspase activity.

In these studies apoptosis seems to feature in the stress response quite significantly and is advocated by Wagner et al. (1998) as a biomarker for environmental stress in sponges. Apoptosis is a complicated process involved in cell death, which is necessary to prevent overgrowth of tissues as new cells are being generated and to get rid of unwanted cells. Sponge cells are thought to have unlimited proliferation capacity (Koziol et al. 1998). However, apoptosis can occur in response to physiological necessity to get rid of infected cells or those that are no longer necessary when the sponge undergoes metamorphosis and gemmule formation or has exhausted a need for a particular cell type (Wiens and Müller 2006). It can also be used to remove cells that have been damaged due to exposure to a damaging environmental variable (e.g. Wagner et al. 1998). The process is complicated, involves a whole range of mechanisms including signalling pathways that must be regulated and has been detected in sponges by DNA fragmentation assays, by caspase activity and by the expression of particular apoptosis-related genes (Wiens et al. 2000, 2003).

4.3 Genomics and Epigenetics

With the advent of affordable high-throughput whole genome and transcriptome sequencing, a new avenue opens up for investigations of comparative gene expression, e.g. in response to environmental change. Being able to identify genes with known functions in other metazoa as well as those specific to the Porifera, and being able to determine changes in expression of many thousands of genes simultaneously in response to particular sets of conditions, allows a picture to emerge of how sponges respond to their environment (Evans and Hofmann 2012). Given the many studies utilizing these approaches in recent years for sponges and other organisms, many standardized pipelines and analysis software now exist that can be applied to climate change investigations.

4.3.1 Genomics

There are still very few sponge genomes available (summarized in Table 4.1), but efforts of GIGA (Global Invertebrate Genome Alliance) will undoubtedly lead to additional sponge genomes and established protocols and expertise to facilitate their application to sponge adaptation (giga-cos.org). The first sponge genome sequenced was that of *A. queenslandica* with an initial assembly of 30,060 predicted protein-coding loci (Srivastava et al. 2010). This number increased to 40,122 after deep transcriptome sequencing of this species under different life stages (Fernandez-Valverde et al. 2015). The genome contains a large number of genes related to cell cycling and growth (i.e. p53, cyclin-dependent kinases, Myc), apoptosis (i.e. Bcl-2, caspases, APAF1, TNRF), cell-matrix adhesion (i.e. collagens, integrins, cadherins), developmental signalling and gene regulation pathways (i.e. Sox, Fkh, Wnt, TG-Fβ), allorecognition and innate immunity (toll-like receptors, MDA-5-like RNA helicases, aggregation factors) and specialization of cell types (laminin-like domains, GPCRs, Dlgs) (Srivastava et al. 2010) in addition to universal genes involved in the stress response. The genome of the homoscleromorph *Oscarella carmela* (Nichols et al. 2012) and the genomes of the calcareous sponges *Sycon ciliatum* and *Leucosolenia complicata* have since also been released (Fortunato et al. 2012, 2014a, b) as have genomes from two additional demosponges, *Stylissa carteri* and *Xestospongia testudinaria*, from the Red Sea (Ryu et al. 2016). The availability of these genomes allows the identification of homologs of stress response genes across the entire phylum for further investigation.

4.3.2 Transcriptomics

Transcriptomes have been generated for a larger number of species also allowing investigations of differential gene expression in these species (Table 4.1), but almost all of the work to date in this field involves different life history stages rather than response to environmental change. Knowledge of the data that exists and optimization of the technology required however pave the way for planning valuable experiments in the area. Conaco et al. (2012), Pérez-Porro et al. (2013) and Qiu et al. (2015) studied differential gene expression of developmental genes from *A. queenslandica*, *Crella elegans* and *Mycale phyllophila*, respectively, under different life stages. Riesgo et al. (2014b) studied the differential gene expression of the bioeroding sponge *Cliona varians* in relationship with its *Symbiodinium* symbiont in three different experimental cases (normal, aposymbiotic and reinfected). Many transcriptomes have been sequenced to identify metazoan genes in sponges and to compare patterns of evolution across phyla (Riesgo et al. 2014a; Schenkelaars et al. 2015, 2016; Alié et al. 2015; Pozzolini et al. 2016), as well as to provide additional data for phylogenomic studies (Whelan et al. 2015) and biomineralization (Germer et al. 2015). Guzman and Conaco (2016a) sequenced the transcriptome of *Haliclona amboinensis* and *H. tubifera* from the coast of the Philippines identifying genes related to the stress response such as Hsp90, Hsp70, death effector domain, glutathione S-transferase, thioredoxin, caspase domains and death domains. These authors (Guzman and Conaco 2016) went on to generate transcriptome data from *H. tubifera* held at different temperatures and were able to analyse 1584 genes that showed differential expression across temperature treatments including an assessment of the functional groups impacted by temperature. The transcriptomes of three additional *Haliclona* species (*H. oculata*, *H. simulans* and *H. indistincta*) have been sequenced by the authors to investigate environmental plasticity of the skeleton in the Haplosclerida. Many EST (expressed sequence tags) libraries are also available for many sponges now and can be found in the public databases such as GenBank (www.ncbi.nlm.nih.gov/ncest).

Table 4.1 List of sponge genomes and transcriptomes available

Genomes			
Species	Class	Contigs (DNA) or proteins assembled	Reference
Amphimedon queenslandica	Demospongiae	40,122 proteins	Fernandez-Valverde et al. (2015)[a]
Oscarella carmela	Homoscleromorpha	67,767 contigs	Nichols et al. (2012)[a]
Xestospongia testudinaria	Demospongiae	22,327 proteins	Ryu et al. (2016)[a]
Stylissa carteri	Demospongiae	26,967 proteins	Ryu et al. (2016)[a]
Sycon ciliatum	Calcareous	50,731 proteins	Fortunato et al. (2014a, b)[a]
Leucosolenia complicata	Calcareous	92,106 proteins	Fortunato et al. (2014a, b)[a]
Transcriptomes			
Species	Class	Contigs (DNA) or proteins assembled	Reference
Ephydatia muelleri	Demospongiae	85,751 contigs 28,154 proteins	Peña et al (2016)[a]
Haliclona amboinensis	Demospongiae	44,693 contigs 20,280 proteins	Guzman and Conaco (2016a)[a]
Haliclona tubifera	Demospongiae	50,067 contigs 18,000 proteins	Guzman and Conaco (2016a)[a]
Oscarella sp.	Homoscleromorpha	172,354 contigs	Hemmrich and Bosch (2008)[a]
Aphrocallistes vastus	Hexactinellid	46,897 contigs 28,243 proteins	Riesgo et al. (2014a)
Spongilla lacustris	Demospongiae	70,220 contigs 15,025 proteins	Riesgo et al. (2014a)
Petrosia ficiformis	Demospongiae	49,507 contigs 20,152 proteins	Riesgo et al. (2014a)
Pseudospongosorites suberitoides	Demospongiae	20,925 contigs 11,536 proteins	Riesgo et al. (2014a)
Ircinia fasciculata	Demospongiae	34,868 contigs 16,898 proteins	Riesgo et al. (2014a)
Chondrilla nucula	Demospongiae	56,696 contigs 21,229 proteins	Riesgo et al. (2014a)
Sycon coactum	Calcareous	41,571 contigs 19,062 proteins	Riesgo et al. (2014a)
Corticium candelabrum	Homoscleromorpha	141,629 contigs 41,146 proteins	Riesgo et al. (2014a)
Cliona varians	Demospongiae	292,108 contigs	Riesgo et al. (2014b)
Mycale phyllophila	Demospongiae	76,640 contigs 12,142 proteins	Qiu et al. (2015)
Crella elegans	Demospongiae	203,078 contigs	Pérez-Porro et al. (2013)

(continued)

Table 4.1 (continued)

Transcriptomes			
Species	Class	Contigs (DNA) or proteins assembled	Reference
Latrunculia apicalis	Demospongiae	76,210 contigs	Whelan et al. (2015)
Kirkpatrickia variolosa	Demospongiae	100,231 contigs	Whelan et al. (2015)
Hyalonema populiferum	Hexactinellid	58,839 contigs	Whelan et al. (2015)
Rosella fibulata	Hexactinellid	40,103 contigs	Whelan et al. (2015)
Sympagella unix	Hexactinellid	85,237 contigs	Whelan et al. (2015)
Chondrosia reniformis	Demospongiae	19,678 contigs	Pozzolini et al. (2016)
Ephydatia fluviatilis	Demospongiae	17,149 proteins	Alié et al. (2015)
Xestospongia muta	Demospongiae	35,219 contigs	Fiore et al. (2015)
Cinachyrella sp.	Demospongiae	34,147 contigs	Smith et al. (2013)
Halisarca dujardini	Demospongiae	138,992 contigs	Borisenko et al. 2016)
Vaceletia sp.	Demospongiae	Unknown	Germer et al. (2015)
Oscarella carmela	Homoscleromorpha	Unknown	Schenkelaars et al. (2015, 2016)
Oopsacas minuta	Hexactinellid	Unknown	Schenkelaars et al. (2015, 2016)
Microciona prolifera	Demospongiae	Unknown	Gaiti et al. (2015)
Haliclona oculata	Demospongiae	Unpublished data	Unpublished data
Haliclona indistincta	Demospongiae	Unpublished data	Unpublished data
Haliclona simulans	Demospongiae	Unpublished data	Unpublished data

[a]The genomes and transcriptomes of these species are available in the COMPAGEN website (Hemmrich and Bosch 2008)

As comparative genomics/transcriptomics in Porifera is still in its infancy, these data have not yet been used to explore the range of genes whose expression is/might be affected by climate change and other stressful situations. However, establishing the gene families present and active in different species under normal life history stages and environments will pave the way for exploring how these patterns change under stress. Despite the costs of data generation reducing wholesale, the main obstacle to widespread use of such approaches is the bioinformatics expertise and hardware necessary to be able to handle and interpret the data.

4.3.3 Epigenetics

The response of organisms to environmental change can occur through both genetic and non-genetic processes. Adaptation often refers to Darwinian evolution where changes to a phenotype from one generation to the next are via natural selection, and most often refers to changes in the DNA of an individual becoming fixed in the population if it confers an advantage. However acclimatization, which is a phenotypic response to variation in an environment, doesn't always involve a genetic change meaning that modification of gene expression does not necessarily involve changes in DNA structure or sequence (van Oppen et al. 2015). The term "epigenetics" can refer to a change in gene expression directly in response to environmental and/or development triggers or to the "transgenerational heritability" of mechanisms that get passed down through generations and affect the phenotype or fitness of the population (Mirouze and Paszkowski 2011; Verhoeven et al. 2016). Research and development in the area of transgenerational acclimatization has become popular because it is possible to select candidates through experimental manipulation, which are better able to survive various stresses (Boyko and Kovalchuk 2011; van Oppen et al. 2015). A glimpse at some epigenetic patterns in sponges was discussed by Webster et al. (2013) in relation to differences in physiological adaptations of larvae and adults and how this was reflected in their tolerance to temperature increases. Similar physiological flexibility may be found in sponges that occupy a broad ecological niche, perhaps leaving them more tolerant to climate change.

Changes in regulation/expression of a particular gene can be altered by enzymatic and RNA-based mechanisms (Gibney and Nolan 2010). Despite some preliminary work in both of these mechanisms existing for Porifera (e.g. Conaco et al. 2012; Levin et al. 2016; Riesgo et al. 2014b), applications of these approaches to investigate acclimatization of sponges to climate change or other stressors have not yet occurred, and so again lessons can be learnt from studies on other organisms. During methylation, DNA is modified by a methyl group being added to the fifth carbon of cytosine, which in turn can modify expression of the genes impacted (Angers et al. 2010; Deaton and Bird 2011). In the coral *A. millepora*, genes involved in basic biological functions (i.e. cellular and nucleic acid metabolism) tend to be strongly methylated, while genes responsible for functions that are dynamically regulated (i.e. development, cell signalling pathways) tend to be sparsely methylated (Dixon et al. 2014). DNA methylation patterns between coral colonies from native and transplanted locations highlighted 321 genes with differential gene expression that were all indicated to have low DNA methylation. These genes are more likely to display environmentally driven variation in expression and could be targets for further studies on coral acclimatization. Indeed it is possible that sponges will show the same DNA methylation patterns, and those with low methylation may suggest themselves as targets for further study on sponge adaptation to environmental change.

Normalized CpG content (CpG O/E) is a well-established evolutionary signal of DNA methylation with low values indicating strong methylation, while high values indicate weak methylation (Roberts and Gavery 2012; Dixon et al. 2014). CpG O/E content can be identified using transcriptomic and genomic data but is more precise with bisulfite genomic data (Grunau et al. 2001). Currently, several bisulfite genomes (see Glossary) have been sequenced from invertebrates and the CpG O/E content identified (Zemach et al. 2010) but none yet from sponges. Sarda et al. (2012) identified and compared the CpG O/E content of four invertebrate species: sea anemone (*Nematostella vectensis*), sea squirt (*Ciona intestinalis*), honeybee

(*Apis mellifera*) and silkworm (*Bombyx mori*) confirming the same pattern as above; highly methylated genes were more conserved than sparsely methylated or non-methylated genes and were often housekeeping genes. This implies that strong methylation leads to more stable gene expression, while weak methylation facilitates flexible expression in the coral genome and may therefore also indicate genes that may adapt more easily to climate change effects and those that will not. Dimond and Roberts (2016) confirmed this pattern regarding genes with low methylation, using transcriptome data from six coral species under different life stages, finding similar patterns of methylation across the species and to those above. Highly methylated genes, however, were more variable across species but generally corresponded to DNA metabolism and protein metabolism. More relevant to the focus of this chapter, Dixon et al. (2016) also evaluated CpG O/E content for 24,320 genes expressed in response to environmental stress for *A. millepora* and found that the most highly expressed genes under stressful conditions tended to have intermediate rather than high levels of methylation. Highly expressed genes were, on average, strongly methylated and were less likely to be differentially expressed across developmental stages and environmental regimes.

DNA in eukaryotes is packaged into a compact structure called chromatin that includes eight histone molecules (two each of H2A, H2B, H3 and H4) and a histone linker (H1) that binds to the DNA between the nucleosomes (Cedar and Bergman 2009). The histones have residues called “tails” protruding from the nucleosomes that are subjected to post-translational modification (PTM), i.e. modification to the protein (Henikoff and Shilatifard 2011; Huang et al. 2015). Several enzymes are responsible for histone PTM some of which are able to change the structure of the chromatin arrangement, which in turn can affect expression or repression of a particular gene (Grunstein 1997). Current knowledge on histone modifications in sponges have been focused on genome-wide mapping and expression patterns of the elements regulating this process (i.e. H3 PTM, distal enhancers, PCR2) at different life stages of *A. queenslandica* (Gaiti et al. 2017). Furthermore, the detection, expression and manipulation of the proteins involved in nucleosome remodeling and the deacetylase complex (NuRD) has been investigated in the freshwater sponge *E. muelleri* (Cramer et al. 2017). Given the dearth of studies in this area, it is likely to be sometime before sufficient understanding exists on chromatin biochemistry in sponges to allow its application for specific gene expression studies in the context of climate change.

RNA-based mechanisms involve a number of different types of RNA molecules that function in gene regulation. Long non-coding RNAs (lncRNA) are molecules >200 nucleotides in length that are non-conservative, evolving faster than sRNAs or functional genes (Mercer et al. 2009). In humans and plants, lncRNAs are implicated in RNA maturation and transcriptional gene silencing through regulation of the chromatin structure (Gupta et al. 2010). For example, lincRNA-p21 acts as a transcriptional repressor in the canonical p53 pathway in human cells triggering apoptosis as a stress cue (Huarte et al. 2010). In sponges studies on lncRNAs are currently limited to their identification and expression. Again, *A. queenslandica* life stages have been a focus of research in this regard with 2935 lncRNAs identified and classified according to their genomic location (Gaiti et al. 2015). The authors suggest that the expression of lncRNAs varies throughout the life history stages of this sponge and correlated their expression with morphogenetic and developmental events. This pattern was confirmed by Bråte et al. (2015) in the calcareous sponge *S. ciliatum* also using a transcriptomic approach where certain transcripts were upregulated during specific life history stages. More work will need to be carried out to investigate if expression of these RNAs is altered during acclimatization and evaluate their utility as biomarkers of environmental stress.

MicroRNAs (miRNAs) are single-stranded RNA molecules greater than 22 nt, which bind to target mRNA suppressing the translation of the genes involved (Krol et al. 2010; Volinia et al. 2006). As above, studies of miRNAs in sponges have been focused on their identification and expression and largely during life history stages. Grimson et al. (2008) identified eight miRNAs in *A. queenslandica*, six of which were highly expressed in adult specimens and two were only expressed at the embryo stage. No similarity was found between these transcripts and miRNAs from other metazoa; however, homologs of the enzymes responsible for the biosynthesis of the miRNAs in humans were identified in this sponge (Grimson et al. 2008). miRNAs have subsequently been identified in a range of demosponges, homoscleromorphs and calcareous species though miRNA presence/absence and the similarity of miRNAs between species appear to be variable across sponges, raising questions about the extent of their independent evolution (Wheeler et al. 2009; Robinson et al. 2013; Sperling et al. 2010; Liew et al. 2016). Robinson (2015) investigated differential expression of miRNAs on disassociated cells, cell aggregations of varying densities, on different parts of the sponge, between juveniles and gemmules and between eight species overall. Results from these experiments revealed that miRNA expression is likely related to cell cycle and differentiation and survival mechanisms because low miRNA expression levels were found where the tissue was dissociated (cell aggregations or cell suspensions) or in stand-by conditions (gemmules). The decrease in the expression of the miRNAs witnessed may also be related to cellular inactivation and apoptotic tendency making miRNA expression a good candidate for studies related to stress response in sponges. However a lot of work needs to be done initially on the homology of these RNAs to enable comparison across taxa.

4.4 Conclusions

There is clear evidence that sponges possess mechanisms to respond and adapt to various stressors in the environment. Heat-shock proteins prove to be useful indicators of stress in sponges as would be expected, but many other genes are implicated in the stress response. Some genes are involved in maintaining homeostasis in the face of adverse environmental conditions, while others are involved in limiting damage. At the same time, there are a myriad of genes involved in specific functions whose expression is up- or downregulated as the sponge undergoes stressful time. In addition factors implicated in epigenetic mechanisms affecting gene expression have also been identified in sponges. Currently, however, there are too few studies to enable us to unravel the complexity of responses. At the same time, it appears that sponge species vary in their capacity to survive increases in environmental challenges such as increase in temperature and decrease in pH with some sponges having very broad niche requirements and others having stricter thresholds for environmental factors. Only few sponge species have been targets of focused research in the area of climate change adaptability, *R. odorabile, X. muta, G. cydonium, S. domuncula* and *A. queenslandica* being the source of most of the current information with regard to gene expression and genomics approaches. More data is necessary utilising these techniques to develop the field of conservation physiology for Porifera but also for the complete range of habitats they inhabit.

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Glossary

Bisulfite Sequence Determination of the patterns of DNA methylation (CpG islands) of the genome of an organism using bisulfite treatment.

cDNA (complimentary DNA) cDNA is DNA that is produced from mRNA of cells or tissues and therefore consists of the genes that are being expressed at that time in a particular tissue or specimen.

EST Determination of short sequences of cDNA (mRNA) in a biological sample in a particular time. A portion of the genes expressed is available by this approach, but not entire genes or the entire transcriptome.

Genome Sequence Determination of the sequence of the entire DNA from a particular organism.

mRNA (messenger RNA) mRNA represents all of the genes that are active in a cell at a particular time and will vary between differentiated cells due to the different functions of the cell.

PCR (polymerase chain reaction) a method where a targeted portion of an organisms' DNA is copied in an eppendorf tube creating billions of copies that can then be used in downstream processes such as being sequenced.

qPCR/QRT-PCR (quantitative realtime PCR) A further development of the PCR technique where fluorescence is used to detect the amount of mRNA copies present in cells or tissues.

RT-PCR (reverse transcriptase PCR) a method where the mRNA of an organism is turned back into DNA as it is being copied. The method uses reverse transcriptase, an enzyme that 'reverse transcribes' RNA back to DNA.

Transcriptome Sequence Determination of the DNA sequence of the entire mRNA from a particular organism, i.e. a sequence from all genes that are active in the tissue at that time.

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Chapter 5
Molecular and Functional Ecology of Sponges and Their Microbial Symbionts

Malcolm S. Hill and Oriol Sacristán-Soriano

Abstract Sponge-microbe symbiotic interactions are important features of modern marine ecosystems. It is likely that these ancient partnerships are as old as the phylum Porifera. Powerful new tools have exposed remarkable microbial diversity within sponge tissues. We are now able to study the composition and structure of the microbial communities at unprecedented levels of resolution. We also recognize that the partnership cannot be disaggregated and should be considered as an integrated holobiont. New hypotheses (e.g., the sponge loop hypothesis) have opened exciting avenues for future experimental work that link holobiont performance from micro- to macro-perspectives. This type of research has taken on added significance given that our planet is experiencing accelerating rates of ocean warming and ocean acidification. It is essential that we examine how sponges respond to environmental stressors that are increasing in intensity and frequency. This review focuses on the molecular and functional ecology of sponge-based microbial symbioses. We discuss the coevolutionary processes that operate to generate partner specificity or to maintain promiscuous partnerships and consider reciprocal selective forces that shape the material exchanges that occur between the partners. We focus attention on the functional ecological role the holobiont plays in marine habitats. The role that the symbionts play in host physiology, and ultimately in the function of sponges on marine ecosystems, is also discussed. We stand to gain important basic information about symbiotic interactions through the detailed study of sponge-microbe interactions, but important practical lessons will be afforded to resource managers who are looking for strategies to protect aquatic habitats worldwide.

Keywords Symbiosis • Bacteria • Holobiont • Porifera • Coevolution

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5.1 Introduction

Symbiotic interactions between sponges and microbes date back to the Precambrian era and represent one of the keys to the evolutionary success of the Porifera (Wilkinson 1984; Jackson et al. 2010; Uriz et al. 2012). Our understanding of the ecological and evolutionary consequences of sponge-microbe relationships is emerging, and several reports and recent comprehensive reviews have evaluated the scope of work that has been done while highlighting the work that remains to be done (Taylor et al. 2007a, b; Hentschel et al. 2012; Thacker and Freeman 2012; Webster and Taylor 2012; Webster and Thomas 2016; Thomas et al. 2016; Sacristán-Soriano and Becerro 2016). This chapter, rather than iterate upon these contributions, presents distinctive perspectives on the molecular and functional ecology of the microbial symbionts that reside in sponges, the specificity of partners, and interspecific interdependencies specifically within the context of climate change. Since the first report of bacteria living in the tissues of sponges, biologists have made important strides in understanding the nature of the association. With new tools, we are entering a period that will allow even greater understanding of these important symbioses. However, we are also entering a period of significant environmental challenges. Ocean habitats are changing due to human-induced modification to Earth's atmosphere. The consequences of these changes are not fully understood, and it is more important than ever that we continue to explore interspecific associations involving sponge hosts.

This chapter will explore sponge microbial symbioses from five interrelated perspectives. The first perspective focuses on microbial and host diversity. From this vantage point, we will examine the types of microbes that have been discovered in sponges and how that diversity is distributed among extant sponge taxa. The second perspective focuses on host-symbiont interactions at molecular and chemical levels. We will examine what is known about the genetic and cellular means of communication between partners and look for evidence of genomic interactions. We will also examine how the metabolic characteristics of the symbionts (individually and collectively) interact with the physiological capabilities of the host to create an "extended phenotype" of the holobiont. The third perspective explores how the actions of the holobiont influence whole community processes. Given the importance of sponges in many benthic habitats around the world, we examine how the integration of host and symbiont behaviors infiltrates different levels in marine food webs. The fourth perspective focuses on symbiont community structure as an independent line of inquiry. Are sponge symbiont ecological communities purely neutral, weakly niche structured, or strongly niche structured? Sponge symbiont communities may provide important opportunities to compare the relative importance of niche structuring and species-specific interactions in shaping ecological communities. While of fundamental intellectual interest, the answer to this question is also important for predicting how symbiont communities might respond to human-induced changes to marine ecosystems. The final perspective will examine sponge-microbe associations through the lens of climate change. We will examine recent data that investigate ocean acidification and thermal stressors on symbiotic systems involving sponges. While necessarily incomplete due to the scope of the topic, the ultimate goal of this chapter is to investigate the relationship between community structure and community function in the symbiotic assemblages associated with sponges and to point toward future work in these systems.

5.2 The Partners: A Holobiont Perspective

5.2.1 Defining Terms: "Symbiosis"

Symbiosis is a term often used in ordinary scientific language, but generates confusion unless semantic intent is identified and ascribed (see Saffo 1992). One of the challenges of a term as flexible as "symbiosis" is that it includes ecological interactions of high and low levels of intimacy, with different outcomes for the partners, and that can span temporal and spatial scales that range across orders of magnitude (e.g., subcellular to biome level and seconds to decades). de Bary's (1879) original sense for the word was outcome neutral—it only required the living together ("zusammenlebens") of two dissimilarly named organisms. Thus, mutualism (both partners benefit, +,+), parasitism (one partner benefits and the other is harmed, +,−), inquilinism (neither partner may benefit from the association, 0,0), and commensalism (one partner benefits while the other is unaffected, +,0) could be included under the umbrella term symbiosis. More often, however, symbiosis is used to indicate positive outcomes, usually for both partners, which distinguish the term from parasitism. If we focus only on "positive" associations, however, the term becomes static in that the ecological outcomes for both partners are assumed to be constant.

Throughout this chapter, we adopt a definition of symbiosis that includes intimate ecological interactions, and as in the manner of de Bary, our definition allows for flexibility in sign of the interaction (i.e., a positive interaction might change to neutral or even negative depending upon context). We also use the convention of naming the host as the larger of the interacting species. Finally, we apply an explicit evolutionary perspective so that we may employ the greatest diversity of comparative tools (e.g., phylogenetic, physiological, ecological). In this context, sponges offer an extraordinary opportunity to learn about the forces that shape interspecific interactions between multicellular hosts and microbial partners.

5.2.2 Everything Is Everywhere: Probably More so for Sponges

For symbionts looking for potential hosts, sponges represent a diverse and ancient group to colonize. A substantial diversity of potential host partners can be found in marine and freshwater ecosystems. As of early 2016, 8730 valid sponge species have been identified, with many other extant species yet to be validated (World Porifera Database: http://www.marinespecies.org/porifera/porifera.php?p=stats). These modern-day descendants of the earliest multicellular metazoans have an evolutionary history that extends for more than 500 million years (Hooper and van Soest 2000). The four poriferan classes include the Demospongiae (7287 valid species), Calcarea (720 valid species), Hexactinellida (618 valid species), and Homoscleromorpha (104 valid species). Recent progress in demosponge systematics (see Morrow and Cárdenas 2015) has identified 22 orders within the three subclasses (Verongimorpha, Keratosa, and Heteroscleromorpha). The new demosponge classification scheme provides a framework to test ideas about the evolution of symbiotic interactions because comparisons of various symbiont strategies among and within families become possible. For example, despite the diversity of potential hosts, we have a limited understanding of the features of sponge biology that make one host a preferred habitat for dense populations of microbes while other potential hosts are minimally infected by bacteria (e.g., Gloeckner et al. 2014; Poppell et al. 2014).

Sponge-microbe symbiotic partnerships are ubiquitous in marine and freshwater habitats from the poles to the tropics (Vacelet and Donadey 1977; Wilkinson 1978a, b, c; Taylor et al. 2007a, b, 2013; Thomas et al. 2016). Intra- and intercellular associations can co-occur in the same host, and these interactions range from persistent to facultative. Next generation sequencing has revealed impressive bacterial diversity that had previously been hidden from view (e.g., Caporaso et al. 2011; Thomas et al. 2016). Given that the host represents habitat for the symbionts, it is perhaps unsurprising that the composition of the microbiota is often specific to the host (i.e., not a random sampling from the environment) and that some degree of specialization is observed (e.g., Ochman et al. 2010; Sipkema et al. 2015; Steinert et al. 2016). The reciprocal nature of the selective forces that act on the host and symbiont partners is one of the more fascinating aspects of this type of ecological interaction. The host may provide selective nutrients to favor growth of one type of microbe, or it might produce discriminating antimicrobials ("the potter's wheel" of Bevins and Salzman 2011). Microbial symbionts can also exert selective pressure on hosts and can direct host evolution to increase the likelihood of continued occupation of a particular host (e.g., the well-known sharing of amino acid biosynthesis pathways between the aphid and *Buchnera* (The International Aphid Genomics Consortium 2010)). Recent work has called into question the degree of specialization among hosts and symbionts (Taylor et al. 2013), and this represents an active area of research, which we discuss in more detail later.

A thorough exploration of the uneven taxonomic distribution of symbioses across the poriferan phylogeny would be fruitful. Not all types of symbioses are found in all sponge groups. For example, *Symbiodinium* species can be found in the vast majority of cnidarian hosts on tropical reefs, but the distribution of this dinoflagellate in sponges is limited primarily to the members of the Clionaidae (Schönberg and Loh 2005; Schönberg and Suwa 2007; Hill et al. 2011; Hill and Hill 2012; Hill 2014). One of the most notable aspects of sponge-microbe symbioses involves differences in density of bacteria among sponge hosts. Some sponge species harbor extraordinarily dense communities of microbes, and these sponges are referred to as high microbial abundance (HMA) sponges (Fig. 5.1; Hentschel et al. 2006; Taylor et al. 2007a; Schmitt et al. 2012; Gloeckner et al. 2014; Poppell et al. 2014). Other sponge hosts harbor bacterial communities at very low levels (low microbial abundance sponges (LMA)). Some of the differences between LMA and HMA sponges will be discussed later, but evidence indicates that the ecological structure of HMA and LMA communities appears to differ in terms of species richness and evenness (e.g., Poppell et al. 2014). Furthermore, HMA symbiont communities appear to play a role in nitrogen cycling on coral reefs (Fiore et al. 2010), but microbial communities play important nutrient cycling roles *in hospite* in a number of settings regardless of HMA or LMA status (e.g., Schläppy et al. 2010; Thacker and Freeman 2012).

The characteristics of hosts that permit residency of high or low concentrations of bacteria, or the preferences of the symbionts to colonize particular hosts at high or low abundances, are poorly understood but offer a promising line of inquiry. For example, Gloeckner et al. (2014) found 29 HMA and 28 LMA species in sponges from the Caribbean, Mediterranean, and Red Sea waters. The taxonomic distribution of HMA and LMA sponges indicated some degree of convergence in that symbiont status was independent of the evolutionary history of the host. All of the sponges in the Verongida were HMA species, and all sponges in the Poecilosclerida were LMA. However, several orders contained sponge taxa that were either LMA or HMA, often in the same family (e.g., *Spheciospongia* (HMA) and *Cliona* (LMA); *Svenzea* (HMA) and *Scopalina* (LMA)). Poppell et al. (2014) found that the community characteristics (e.g., species richness, evenness) differed between HMA and LMA sponges.

The underlying cause of this pattern is unknown, but it is clear that much additional work is required to determine which factors create conditions favoring HMA or LMA symbioses (e.g., Blanquer et al. 2013).

While the density of the symbiont communities is an important factor to consider, equally, perhaps more, important is the diversity of microbes that associate with sponges, and there has been considerable effort focused on this aspect of the symbiosis (Hentschel et al. 2002, 2012; Usher et al. 2004; Hill et al. 2006; Webster et al. 2010; Erwin et al. 2012a, b; Schmitt et al. 2012; Simister et al. 2012a, b, c; Thacker and Freeman 2012; Fan et al. 2012; Gloeckner et al. 2013; Schöttner et al. 2013; Taylor et al. 2013; Easson and Thacker 2014; Moitinho-Silva et al. 2014; Reveillaud et al. 2014). The advent of deep-sequencing technologies has opened opportunities to study the microbial biosphere far beyond the detection limit of conventional molecular approaches. We are now able to establish whether bacteria are specific to particular hosts or are distributed in other habitats throughout the environment. A number of studies have described the existence of sponge-specific 16S ribosomal RNA (rRNA) gene sequence clusters, but 77 of the 173 previously described "sponge-specific" clusters have been detected in seawater or other nonsponge samples, albeit generally at extremely low abundances (Taylor et al. 2013). For example, the candidate phylum "*Poribacteria*" (so named because it was presumed to be restricted to sponge habitats) was recently detected in >11% of seawa-

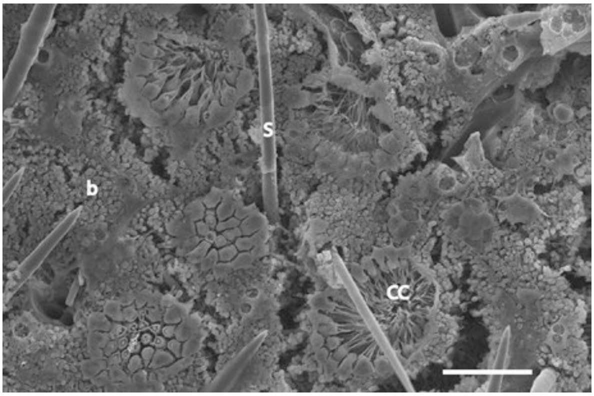

Fig. 5.1 Scanning electron micrograph of freeze-fractured tissue from the HMA sponge, *Calyx podatypa*. Choanocyte chambers (*CC*) and spicules (*S*) of the host sponge are obvious. The dense extracellular microbial community (*b*) can be seen throughout internal regions of the mesohyl. Scale bar = 20 μm (Image taken by E. Poppell)

ter samples and nearly 32% of sediment samples. These data highlight how little we understand about the mode of transmission between generations of sponge (Sipkema et al. 2015) or the degree of the intimacy between partners in sponge-microbe associations.

The most recent survey uncovered "exceptional microbial diversity" in sponges compared to microbial communities associated with sediment and water samples (Thomas et al. 2016). This was the most comprehensive analysis of symbiont microbial communities in sponges and involved a survey of 81 species of poriferan host sampled from habitats in the Mediterranean, Red Sea, Atlantic, Indian Ocean, and Pacific (Thomas et al. 2016). Multiple individuals were sampled from each species of sponge host (from 3 to 133 individuals per host), which allowed for intraspecific as well as interspecific comparisons of microbial community structure. This extensive survey used the Earth Microbiome Project's procedures and focused on the V4 region of the 16S rRNA gene. While this study did not consider the intrahost microbial load (see below), the authors did use network analyses to infer important ecological interactions among symbiont compartments. Representatives from each of the three domains of life (Archaea, Bacteria, and Eukarya) have been observed as sponge symbionts. Attempts to estimate the potential diversity of prokaryotes in sponges are difficult given that a unified classification system and nomenclatural framework for all bacteria and archaea do not exist (Yarza et al. 2014). Nonetheless, many of the major prokaryotic groups were identified (over 40 phyla), though sponges seem to have a tendency toward harboring *Proteobacteria*, especially *Gammaproteobacteria* and *Alphaproteobacteria* (Thomas et al. 2016). Richness of the symbiont communities varies widely among hosts, with estimates of anywhere from 50 to over 3000 distinct symbionts per host (Thomas et al. 2016). In aggregate, Thomas et al. (2016) estimated 40,000 operational taxonomic units (i.e., putative microbial species) in the 81 sponge species they examined. Given that this number of hosts represents almost 1% of the total global diversity of sponges, the phylum Porifera is undoubtedly a major source of unique microbial diversity.

One of the intriguing findings of Thomas et al. (2016) was the substantial variability that exists among sponge hosts in terms of the core and variable microbial communities. Hentschel et al. (2002) were the first to call attention to the possibility that the sponge microbiome might consist of core, variable, and species-specific components (Schmitt et al. 2012). Polónia et al. (2016) found that the biotope could explain over 50% of the variation in archaeal and bacterial communities and that two congeneric sponge species hosted communities of distinct biodiversities. Thomas et al. (2016) found that the core microbiome for a given species includes a relatively small number of generalist microbes (from 7 to 20 OTUs) and some of these are truly cosmopolitan (found in several species of host sponge). The majority of OTUs in a given species, however, seem to be unique to that host species. This level of specificity indicates that community assembly (through ecological interactions or evolutionary specialization) is occurring in sponge-microbe associations. Reconciling these data with the realization that the bacteria can persist in non-sponge habitats (e.g., Taylor et al. 2013) should be a goal of future research.

Thomas et al. (2016) did not consider the density of microbes that were harbored by a particular host species. The ecological behavior of particular microbiomes might differ depending on the nature of resource limitation, quorum sensing, or any of a number of other density-dependent factors that differentiate HMA from LMA microbiomes. In fact, the effects of nutrient limitation might change interactions from competitive to mutualistic (e.g., Le Chevanton et al. 2016). Thus, the networks that were constructed by Thomas et al. (2016), with predicted interspecific interactions, will likely require much more detailed work to determine how members of the core microbiome interact with one another. Furthermore, differences in community structure appear to define HMA and LMA sponges (Weisz et al. 2007; Erwin et al. 2011; Schmitt et al. 2012; Giles et al. 2013; Moitinho-Silva et al. 2014; Poppell et al. 2014). Moitinho-Silva et al. (2014) examined the microbiota associated with the HMA sponge *Xestospongia testudinaria* and the LMA sponge *Stylissa carteri*. While both sponges harbored specific microbiota, the latter was found to harbor a microbiome more similar to that found in seawater (24% of the sequences examined matched those found in seawater), while the former shared only about 6% of its sequences with seawater. Poppell et al. (2014) found that the microbiomes in HMA sponges were more diverse and even, while LMA sponge microbial communities were dominated by one or a few OTUs. The ecological processes that would generate those patterns are decidedly different, which indicates that density is an important factor in any consideration of the interspecific interactions that shape the microbiome.

5.3 Partner Interactions and Host-Symbiont Phenotypic Synergisms

We are entering an exciting era of research in sponge symbiosis that involves a paradigm shift in the way biologists approach the concept of "phenotype." We now recognize that any multicellular organism must be considered a metaorganism or holobiont and that we must adopt a holistic perspective on ecological performance that accounts for the host and its associated symbionts (Bosch and McFall-Ngai 2011; McFall-Ngai et al. 2013). Gene expression must now be considered from the perspective of multiple genomes (the hologenome) of the holobiont (Webster and Thomas 2016). The balance between health and disease, proper development and nutrition, of most host organisms relies on the activities of members of complex microbial symbiont communities (e.g., Mazmanian et al. 2008). The synergistic products of holobiont activities shape the functional ecology, and ultimately the reciprocal evolution, of all members of the consortium (Hill 2014). Thus, holobiont characteristics affect fitness of all participants, and the evolutionary consequences of this phenomenon are just now being considered (Kau et al. 2011; Hacquard et al. 2015).

Identifying the specific forms of interaction that occur between a host and a symbiont at a physiological, cellular, and genetic level is a major objective of current research. New tools are opening lines of research that had been impossible in the past, and new insights into genetic integration, trophic interrelationships, and secondary metabolite production are elucidating ways that sponge hosts and their associated microbial communities are linked together in complex networks. Clear evidence is emerging that host sponges and their microbial communities are involved in highly intimate, ancient relationships and that these interactions have far-reaching effects on marine communities (Thomas et al. 2016; Webster and Thomas 2016).

5.3.1 Genomic Interactions Among Partners

Genomic adaptations for symbiotic lifestyles provide compelling evidence for the degree of intimacy and length of time partners have been interacting. Evidence for metabolic interchange is accumulating (e.g., Fiore et al. 2015). Compelling evidence for the selective forces that shape evolutionary outcomes for sponge symbionts comes from two recent studies (Gao et al. 2014a; Burgsdorf et al. 2015) that evaluated genome structure for the cyanobacterial "*Candidatus* Synechococcus spongiarum" group (Erwin and Thacker 2008; see also Liu et al. 2011). Gao et al. (2014b) examined sponge-symbiont strain SH4 obtained from the Red Sea sponge *Carteriospongia foliascens*. When compared to free-living cyanobacterial strains, they found that SH4 had a reduced genome size, a lack of methionine precursor biosynthesis genes, and appeared to have lost genes involved in cell wall formation. Intriguingly, Gao et al. (2014b) also found in the SH4 genome (1) an enrichment of eukaryotic-type domains that appear to be involved in sponge-symbiont interaction and (2) the loss of genes that encode low-molecular-weight peptides of photosystem II. These last two observations are significant in that the former may represent a strategy to avoid digestion by the sponge and the latter indicates that photosynthetic efficiency of SH4 may rely on host participation. They hypothesized that the genome streamlining of the sponge symbiont was a product of adapting to low-light environments of the "sponge's mild intercellular environment" (Gao et al. 2014a).

Burgsdorf et al. (2015) expanded the coverage of the diverse clade VI group of cyanobacteria by examining the genomes of three additional lineages of cyanobacteria collected from *Theonella swinhoei*, *Ircinia variabilis*, and *Aplysina aerophoba*. All four of the symbiont genomes that were compared appeared to be specialized for living in sponge hosts. For example, each of the four lineages examined had elevated numbers of DNA modification and recombination genes, but reduced numbers of genes and genetic pathways involved in inorganic ion transport and metabolism, antioxidant enzymes, cell wall biogenesis, and signal transduction (Burgsdorf et al. 2015). The loss of low-weight peptides of photosystem II was observed in all four lineages. An intriguing observation was the large degree of variability within the "*Candidatus* Synechococcus spongiarum" group often related to immune system features and siderophore-mediated metal transport. The former is likely important in mediating the interactions between host and symbiont and might afford some level of protection from the phagocytotic capabilities of the host. The latter may represent a mechanism the host can employ to control the growth of phototrophic symbiont populations (e.g., limiting availability of metals used in processes such as electron transport).

Work with the heterotrophic microbial (Bacteria and Archaea) populations has also pointed to genomic coupling between sponges and their symbionts. Hallam et al. (2006) showed that the *Cenarchaeum symbiosum* genome was distinct from those of other Archaea, shared many core metabolic features with free-living planktonic relatives, but also had some signature sequences that may be involved in genetic interactions between host and symbiont. Using single-cell genomics, Kamke et al. (2013); see also Siegl et al. (2011), examined individual cells representing three distinct phylogenetic groups within *Poribacteria* to explore the metabolic potential of this important group of sponge symbionts. The genomes contained genes and pathways likely involved in carbohydrate metabolism, uronic acid degradation, and sulfatases, which indicates that the symbiont may be involved in the breakdown of the proteoglycan host matrix. Thomas et al. (2010) found genomic signatures in sponge bacteria that pointed to host-symbiont interaction. These included mechanisms to protect against foreign DNA, vitamin-linked metabolic interactions between the host and symbiont, nutrient transport and utilization pathways, and ankyrin and tetratricopeptide repeat-mediated protein interactions. Nguyen et al. (2014) also found that ankyrin repeats might be important targets of host-symbiont genomic interface when they identified ankyrin repeats from an uncultured putative sponge symbiont that modulated phagocytotic behavior of heterotrophs (see below).

5.3.2 Trophic Interactions Among Partners

Linking the exceptional pumping and filtering characteristics of sponges (Fig. 5.2; Vogel 1977; Reiswig 1971a, b, 1974, 1975, 1981; Riisgård et al. 1993; Pile et al. 1996, 1997; Turon et al. 1997; Lynch and Phlips 2000) with the microbiome is an important step toward understanding sponge metabolic processes. Many, if not most, of the cells in a sponge can capture material phagocytotically (Fig. 5.2; information from Simpson 1984). Particles of the largest-size classes (>50 μm in diameter or with a diameter larger than the incurrent pores) that cannot enter the aquiferous system can be phagocytosed by exopinacocytes on the surface of the sponge (see 1 in Fig. 5.2). Particles with a diameter greater than the choanocyte collar (>2 μm depending on species) can be digested in one of four ways. Roaming archaeocytes can move through the canals to phagocytose particles that stick to the channel walls (see 2 in Fig. 5.2). Particles can pass through holes in the canal system where they are ingested by archaeocytes (aka amebocytes) in the mesohyl (3 in Fig. 5.2). Endopinacocytes can phagocytose particles. These pinacocyte cells can then migrate into the mesohyl and undergo “cellular transformations” to become archaeocytes, or they can pass their contents to roaming archaeocytes (4 in Fig. 5.2). Prey items can pass through openings in the choanocyte chamber where they are phagocytosed by archaeocytes within the mesohyl (5 in Fig. 5.2). Finally, the smallest prey items (<2 μm) are phagocytosed by choanocytes.

Capture may occur within the collar as well as at the interface between two cells. Choanocytes pass their captured particles to archaeocytes (6 in Fig. 5.2). At each of these stages, dissolved organic matter (DOM) can pass into the sponge though the precise mechanism of this transfer is poorly understood but likely involves pinocytosis and adsorptive processes.

Reiswig (1971a, b) conducted some of the first work to understand how sponges feed by examining incurrent (i.e., ambient) and excurrent water samples from sponges in Jamaica. While Reiswig could not identify the major source of food for sponges using the tools available to him, others (e.g., Pile 1997; Pile et al. 1997; Turon et al. 1997) used flow cytometry to determine that sponges feed on nanoplankton and picoplankton. But the role of the microbial symbionts (phototrophic and heterotrophic) in processing other material in the water column remains obscure (Hentschel et al. 2003, 2006). A diverse range of microbially mediated processes undoubtedly affect the processing of carbon, nitrogen, and other elements necessary for sponge growth. For example, Reiswig (1981) provided evidence that the HMA sponge *Aplysina fistularis* required DOM to meet its carbon and energy needs—particulate organic matter (POM; like pico- and nanoplankton) could not sate the sponge’s energetic needs. This was among the first pieces of evidence that a sponge’s microbial community influenced the trophic status of its host. Refining Reiswig 1981 study, two studies highlight some of the ways that the microbiome influences host feeding. Yahel et al. (2003) demonstrated that dissolved organic carbon (DOC) provided the majority of carbon taken up by the HMA sponge *Theonella swinhoei*. Subsequently, Diaz et al. (2004) showed that nitrifying bacteria harbored by another

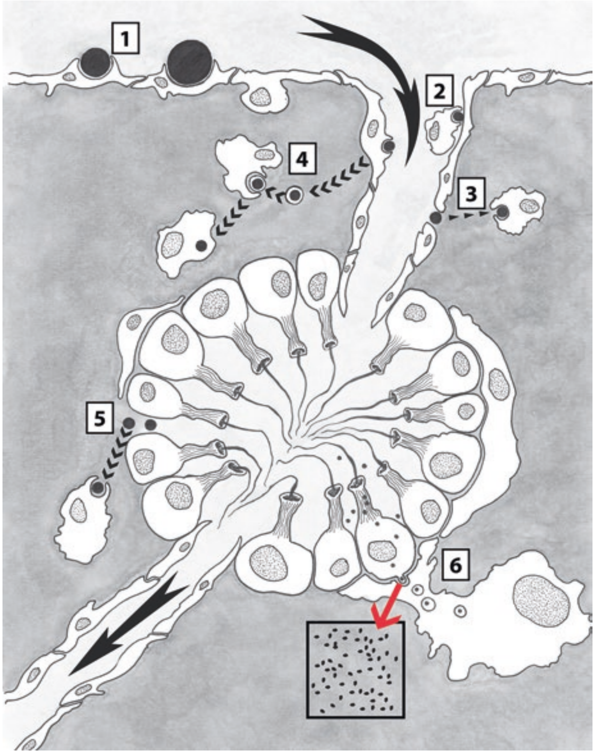

Fig. 5.2 Schematic representation of various phagocytotic pathways of POM (i.e., prey) and potential DOM capture in sponges (see also Simpson 1984). The pathways by which bacteria enter the mesohyl and gain residency within the host sponge remain obscure. One possibility involves symbiont escape from endomembranous compartments in sponge cells after phagocytotic capture (*red arrow* and inset *black box*). Drawing courtesy of S. Friday

HMA sponge (i.e., *Chondrilla*) oxidize the host-generated ammonia and the nitrate released from the sponge can be used to support primary productivity on a reef (see also Hoffmann et al. 2009; Radax et al. 2012a). This opens significant possibilities to study the integration of host and symbiont populations in terms of movement of material and energy between partners.

Stable isotopes of C ($^{13}C/^{12}C$) and N ($^{15}N/^{14}N$) offer the ability to trace movement of material through food webs (e.g., Fogel and Cifuentes 1993; Turner et al. 2010; Layman et al. 2012) and, in the case of sponges, through the microbiome (e.g., Weisz et al. 2010; Van Duyl et al. 2011; Radax et al. 2012b; Fiore et al. 2013a, b, 2015; Simister et al. 2013). Weisz (2006) was among the first to apply this technology to sponges, and in one of the largest comparisons to date (nearly 50 sponge species; Fig. 5.3), he showed that each occupied a distinct isotopic niche space (INS). This provided clear evidence that different species of sponge perform very different roles in terms of processing material from the water column. In fact, despite the fact that all sponges are bacterivorous filter feeders (capturing POM >0.1 μm from seawater

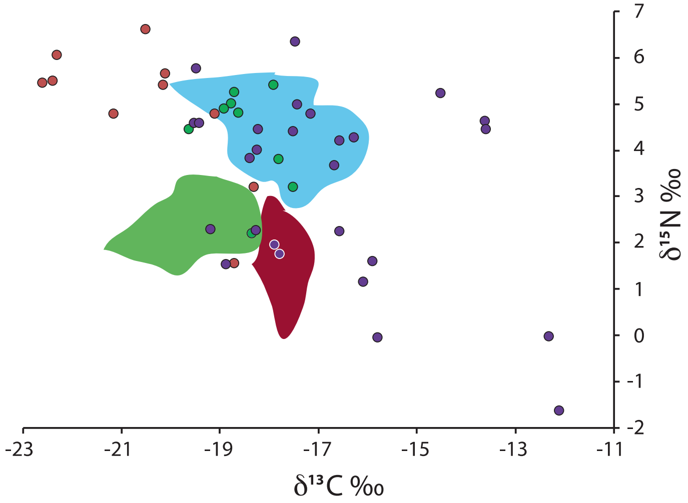

Fig. 5.3 Average stable isotope values for Atlantic, Caribbean, and Indo-Pacific sponges. Points represent data from Weisz (2006) for 48 sponges from the Florida Keys (*purple*), North Carolina (*red*), and Papua New Guinea (*green*). Clouds represent estimates of Freeman et al. (2014) clusters of isotope niche space (i.e., convex hulls) obtained from sponges collected in the Miskito Cays, Honduras. The *green cloud* is an HMA cluster of three sponges with high and low chlorophyll content, and the *red cloud* contains two HMA sponges with high chlorophyll content. The *blue cloud* represents a broad assortment of high chlorophyll content HMA sponges ($n = 2$), low chlorophyll content HMA ($n = 3$), and LMA ($n = 9$) sponges

(Riisgård and Larsen 2010)), it is clear that different species, even sympatric sponges coexisting in close proximity on the same reef, appear to occupy distinctive niches based on the characteristics of their feeding behavior—that is, these sponges appear to exist in different levels within a food web (Fig. 5.3). Freeman et al. (2014) compared INS for sponges from the Miskito Cays, Honduras. It is important to note that the Weisz (2006) and Freeman et al. (2014) datasets overlap in species composition and thus provide an opportunity to evaluate the potential influence of environmental drivers on isotopic signatures. For example, differences in δ^{15}N for *Aplysina* and *Ectyoplasia* are minor between Weisz et al. (2007) and Freeman et al. (2014), while sponges like *Ircinia campana* and *Callyspongia* differ more significantly. It is also important to note that all habitats in each of these studies contained both HMA and LMA sponges.

It is likely that the metabolic properties of the microbiome directly influence the trophic behavior of the host sponge in terms of INS (Weisz et al. 2007; Freeman et al. 2014). Weisz (2006) proposed that "the strong association between low δ^{15}N tissue values and the presence of abundant microbes in sponges suggest that internal microbial activity can exert significant control on the N isotopic composition of HMA sponges." Viewing sponge behavior through their INS raises important questions. The first is: why do sponges have such disparate INS within and among species? In reality, we know very little about the metabolic processes that operate within a sponge, nor the nuances of a sponge's heterotrophic feeding. Our ignorance of the role that microbial symbionts play in those processes is deeper. Do patterns exist in what niche space is available to sponges, and if so, what role do microbial symbionts play in expanding (or contracting) INS? Are some transformations improbable given the metabolic pathways available to microbial communities (e.g., combinations of lighter C and N ($\delta^{13}C < -19$; $\delta^{15}N < 1$))? Freeman et al. (2014) have pointed out that variation in biogeochemical cycling of C and N observed among species is complex and suggested some level of niche partitioning may be made possible by the microbial symbionts. They suggest that variation in INS may be driven more by the presence or absence of particular microbial taxa than by overall symbiont or photosymbiont abundance (see also Freeman et al. 2013) while recognizing that symbionts within HMA species increase the metabolic capacity of the holobiont. They argue that the presence or absence of productive photosymbiont taxa has a large effect on the INS available to host sponges (see also Weisz et al. 2010).

Despite recognizing their importance, the reality is that we know relatively little about the energetic transformations that occur within individual sponges, though that situation is improving (e.g., Yahel et al. 2005; Duckworth et al. 2006; Weisz et al. 2008; Hanson et al. 2009; Topçu et al. 2010; Radax et al. 2012b). We are learning that sponges demonstrate some selectivity for particular prey items. For example, Perea-Blázquez et al. (2013) found that retention efficiencies changed for three species of sponge in response to picoplanktonic species composition and abundance in temperate habitats around New Zealand. In this study, sponges appeared to obtain 20–40 times more C from heterotrophic bacteria than from the consumption of cyanobacteria like *Synechococcus* or *Prochlorococcus*. However, the sponges studied appeared to have fixed feeding strategies that did not respond to changes in ambient bacterioplankton concentrations (Perea-Blázquez et al. 2013). In contrast, Topçu et al. (2010) found that the Mediterranean *Spongia officinalis* had similar levels of capture efficiency for the major picoplanktonic groups, but lower efficiencies for the nanoplankton.

Despite the abundance of picoplankton, *S. officinalis* appeared to convert a larger percentage of nanoeukaryotic cells into sponge biomass as indicated by $\delta^{13}C$ INS. As in Weisz (2006), Topçu et al. (2010) argued that the low $\delta^{15}N$ signature was due to microbial symbionts (see also Freeman et al. 2014).

But what precise role do the symbionts play in holobiont trophic behavior? It is clear that a variety of experimental approaches are required including pulse-chase analyses. Using stable isotope tracers, Weisz et al. (2010) were able to demonstrate movement of C between *Symbiodinium* and *Cliona*, but the story with N was more subtle and complex. Are some metabolic processes linked among the members of the microbiome such that only some chemical transformations are possible (e.g., rules of community function deriving from rules of community assembly)? This is an area of research that deserves greater attention. We clearly have much to learn about sponge trophic ecology to understand how the host and microbial symbiont communities interact.

5.3.3 Natural Products: Another Level of Host-Symbiont Integration

Natural product chemistry is an area where clear phenotypic synergisms can be identified because large amounts of data are becoming more widely available (e.g., Hill 2004; Müller et al. 2004; Sipkema et al. 2005; Proksch et al. 2010; Sacristán-Soriano et al. 2012). Although Porifera has been the preferred phylum of the marine natural product community for the last 50 years (Blunt et al. 2015), the origin of many compounds remains controversial (König et al. 2006; Wang 2006; Hentschel et al. 2012). Many sponge-derived metabolites are suspected to be produced by bacteria, since they resemble bacterial compounds or belong to substance-type characteristic for these microorganisms. Vacelet (1975) was among the first to implicate bacteria in the origin of sponge natural products given the huge numbers of bacteria that inhabited sponge tissues. The classical strategy to isolate the putative microbial producer was to apply culture-dependent methods (Piel 2004 and references therein). However, the complexity and the difficulties in cultivation of associated microbial communities represented new challenges to explore secondary metabolite production.

Culture-independent methods have opened new paths to identify the true producer of sponge-derived compounds. In situ localization of a compound would indicate the origin of production, as is the case of the sponge *Dysidea herbacea* and its associated cyanobacterium *Oscillatoria spongeliae* that accumulates brominated and chlorinated metabolites (Unson and Faulkner 1993; Unson et al. 1994). Other examples of a suggested bacterial origin of sponge-derived compounds have been described in the sponge *Theonella swinhoei* (Bewley et al. 1996; Schmidt et al. 2000). Additional studies on other species reported instead a localization of natural products in sponge cells, suggesting a sponge origin (Uriz et al. 1996; Turon et al. 2000). However, localization studies have a major problem that the presence of a compound in a cell type does not undoubtedly prove the location of biosynthesis since organisms producing bioactive compounds frequently excrete them in the surrounding environment (Méndez and Salas 2001). Thus, one cell type could produce the metabolite that may be accumulated in a second.

Several researchers have attempted to use observational studies to link secondary metabolite production to the microbial consortia. Recent work in *Aplysina* using DNA-based molecular approaches highlights close associations between some bacterial phylotypes and major brominated compounds sharing spatial variation patterns (Sacristán-Soriano et al. 2011a, b). These correlative studies are promising and require further exploration given that the microorganisms could be directly producing or halogenating such compounds (van Pée et al. 2006) or contributing to their catabolism (Ahn et al. 2003). These results underline the complex control of the production of secondary metabolites with a potential environmental modulation. Experimentally modifying the concentrations of natural products or the abundance of endobiotic bacteria through alterations of environmental parameters might reveal their true association and infer functional relationships. Several studies successfully attempted to culture specimens of different sponge species to monitor both bacterial communities and chemical profiles, mimicking wild conditions (Klöppel et al. 2008; Mohamed et al. 2008) or altering a particular environmental factor (Friedrich et al. 2001; Klöppel et al. 2008; Sacristán-Soriano et al. 2016). All of those studies concluded major stability of chemical fingerprints and prevalence of microbial assemblages upon culture. Where some degree of variability in associated bacteria was detected, those changes were not linked with compound abundances. So, the possible involvement of symbionts in secondary metabolism could not be drawn using the molecular tools available to date.

The application of cutting-edge molecular techniques has transformed the field of sponge symbiosis. Next-generation sequencing offers the ability to uncover the diversity of the sponge microbiome (Webster et al. 2010). Besides the use of the 16S rRNA gene as a phylogenetic marker to characterize associated microbial communities, other genes have been selected to disclose putative functions from sponge symbionts, for example, secondary metabolite biosynthetic gene clusters. Different molecular approaches (e.g., gene-derived PCR amplicons, metagenomics, single-cell genomics) have led to the identification of several polyketide synthases (PKS) and non-ribosomal peptide synthetases (NRPS) in microbes from marine sponges, both of which represent prominent enzyme classes that are responsible for the synthesis of bioactive compounds (Schirmer et al. 2005; Piel 2009; Siegl and Hentschel 2010; Hochmuth et al. 2010; Hardoim and Costa 2014). Other target markers are those genes that encode for halogenase enzymes, which are responsible for the halogenation process of secondary metabolites. Bayer et al. (2013) identified three different halogenase gene clusters present in three symbiotic bacterial phyla from *A. aerophoba*. Culture-dependent methods also allowed detection of halogenase genes but with the limitations of the culture of sponge symbionts (Öztürk et al. 2013).

The ecological and metabolic significance of the expressed natural product biosynthetic genes still remains unclear. Once those gene clusters have been identified, the heterologous expression of the biosynthetic genes in culturable bacteria may prove the function of these genes in their original host, assess their role in symbiont physiology, and determine host-microbe integration. This knowledge will help to address a major challenge of human population growth, to make the marine drugs discovered marketable (see Indraningrat et al. 2016).

5.3.4 Establishing Residency: Phagotrophic Escape?

While many bacteria are consumed by the sponge, many are not and persist in the mesohyl indefinitely. The pathways by which bacteria enter the mesohyl and gain residency within the host sponge remain obscure. Nguyen et al. (2014) found eukaryotic-like, ankyrin repeat proteins in an uncultured gammaproteobacterial sponge symbiont that modulated the phagocytosis behavior of amoebal cells. Specifically, when *Escherichia coli* expressed the four symbiont-derived genes, the bacteria accumulated in a phagosome of the amoeba. Furthermore, phagosome development was disturbed in a way that reduced vacuole acidification because lysosomal fusion was blocked. The authors postulated that this might be an escape mechanism by which potential symbionts could make their way into the mesohyl of the sponge after phagocytosis (see red arrow in Fig. 5.2). If this is a strategy employed by extracellular symbionts, then the pathways that are usurped for exocytosis post-capture require elucidation. Hill and Hill (2012) proposed that *Symbiodinium* employ a mimicry strategy to avoid detection by the host. Their arrested phagosome hypothesis suggested that translocation of photosynthates might mimic digesting prey, thus providing a mechanism to avoid digestion by the host. The molecular mechanisms by which such arrest occurs are unknown, but might involve pathways similar to the one proposed by Nguyen et al. (2014). If the process of transfer into the mesohyl involves transport via endomembranous compartments, it is possible that vertically transmitted bacterial symbionts engage similar genetic pathways to gain entry to eggs or sperm (e.g., Sciscioli et al. 1994; Usher et al. 2001). The ontogenetic changes in symbiont communities (from larvae to adult) also deserve attention. For many sponge species, larvae are nonfeeding during the planktonic larval stage. Broadcast spawning species would have to pass symbionts to the larvae through the eggs, while brooders could transmit bacteria from mother to larvae (Kaye 1991). At metamorphosis, however, the sponge will shift from nonfeeding to filter feeding, which would potentially precipitate a rapid mixing of environmental populations of bacteria with resident symbionts. We require detailed study of the transition from one life stage to another in the context of the composition, structure, and stability of symbiotic communities in sponges and how the host distinguishes food from symbiont.

5.4 Community-Wide Consequences of Holobiont Behavior

Consideration of the holobiont is of paramount importance when one examines ecosystem-level metabolic processes involving sponges. Sponges are abundant and integral members of many marine communities from the poles to the tropics (e.g., Díaz and Rützler 2001; McClintock et al. 2005; Ribes et al. 2012). On Caribbean reefs, sponges occupy about the same amount of benthic cover as corals, but provide more biomass to these habitats. While the amount of sponge biomass matters, it is the behavior of sponges that can have profound effects on the entire community. Sponges are becoming the dominant faunal component of many reefs (McMurray et al. 2010; Colvard and Edmunds 2011; Bell et al. 2013), and their ecological significance to these communities is well established (Wulff 1997, 2006, 2008a, b, 2012; Hill 1998). However, biologists are beginning to focus attention on the role sponges play in creating bioavailable material for the entire ecosystem through their trophic behavior.

As efficient filterers that spend the majority of their days capturing prey items and processing and modifying large volumes of water (Fig. 5.2), sponges provide a locus for the movement of autochthonous and allochthonous carbon and nitrogen (among other nutrients) through marine communities. Sponge-mediated benthic:pelagic coupling influences properties of marine habitats in profound ways (Reiswig 1971a, b, 1974, 1981; Corredor et al. 1988; Riisgård et al. 1993; Pile et al. 1996, 1997; Diaz and Ward 1997; Savarese et al. 1997; Turon et al. 1997; Ribes et al. 1999; Lynch and Phlips 2000; Yahel et al. 2003; Lesser 2006; Peterson et al. 2006; Perea-Blázquez et al. 2012; Lesser and Slattery 2013). Sponges appear to contribute to the population dynamics of phytoplankton and benthic algae (e.g., Peterson et al. 2006; Lesser 2006; Lesser and Slattery 2013), sponges are dominant competitors for space (Rützler 1970; Hill 1998), and sponges serve as prey and habitat for other organisms (Westinga and Hoetjes 1981; Duffy 1996; Hill 1998; Ávila et al. 2007; Azzini et al. 2008; Ramsby et al. 2012). Thus, in marine habitats, sponges perform ecosystem services with far-reaching effects on community structure. These keystone ecological outcomes are made possible by the ability of sponges to convert POM and DOM into sponge biomass (Reiswig 1981; Pile et al. 1996, 1997; Pile 1997; Yahel et al. 2003, 2005; Hadas et al. 2009 Maldonado et al. 2012). Modes of action in converting matter from one form to another involve synergistic and interactive properties of the symbiont and host compartments (e.g., Erwin and Thacker 2007; Southwell et al. 2008; Gibson 2011), and teasing apart the contributions of microbial symbionts (e.g., HMA vs. LMA strategies) remains an important goal (e.g., Reiswig 1981; Weisz et al. 2008).

5.4.1 Sponge Loops and Detrital Linkages

The oligotrophic waters of tropical coral reefs support some of the most diverse and productive ecosystems on the planet. This enigmatic situation, known as Darwin's paradox, may have an explanation via the recently proposed sponge loop hypothesis (SLH—de Goeij et al. 2013). The "sponge loop" considers the trophic behavior of sponges as efficient filter feeders and the rapid cell turnover found in sponges, to posit a detrital-based component to coral reef food webs. That is, sponges represent sinks for POM and DOM, produce POM of their own through release of spent sponge cells, and mediate biogeochemical fluxes through their consumption and release of nutrients (e.g., nitrates, nitrites, phosphates, etc.; Bell 2008; Southwell et al. 2008; Fiore et al. 2010; Maldonado et al. 2012; Zhang et al. 2015). This bottom-up hypothesis provides a mechanism by which a large proportion of POM is released by sponges and then enters the food web through detritivorous benthic reef fauna. For example, Silveira et al. (2015) demonstrated that the SLH may help explain changes in fish biomass on coral reefs. According to the SLH, the loop begins with DOM, principally DOC, that is released by autotrophic organisms (e.g., seaweeds and *Symbiodinium*-bearing corals), taken up by the sponge, and converted to biomass through holobiont metabolic processes.

Thus, the SLH predicts that sponges perform vital roles in retaining biomass in these marine habitats. de Goeij et al. (2013) suggested that the conversion of DOC to POC by all the sponges on a reef is on par with the daily gross primary production of the entire reef ecosystem. The imagined steps in the trophic chain, that is, movement of sponge material through detritivores into higher trophic levels, are still hypothetical, and empirical work demonstrating these linkages is required.

While the SLH is an important contribution, several questions remain. What role do symbionts play in the SLH? Symbionts contribute to the sponge's diet. For example, Erwin and Thacker (2008) demonstrated that cyanobacterial symbionts contribute significantly to the energetic budgets of two Caribbean sponges, and Weisz et al. (2010) demonstrated that carbon is translocated from *Symbiodinium* to *Cliona varians*. Autotrophic contributions are easier to follow than the subtle chemical and energetic transformations that involve heterotrophic bacteria and archaea. Nitrogen translocation, or at least manipulation of the N profiles of the host sponge, has been more difficult to assess (Zhang et al. 2013). Weisz et al. (2010) found little evidence that N was transferred to *Symbiodinium* populations via phagotrophic capture of N-labeled bacteria in *C. varians*. Freeman and Thacker (2011) showed that the translocation pathways may be species specific. They found that symbionts transfer C but not N to *Neopetrosia subtriangularis*, N but not C to *Aplysina fulva*, and both C and N to *A. cauliformis*. While it is highly likely that the non-photosynthetic component of the microbial community plays important metabolic roles in determining the fraction of a sponge's diet that is comprised of DOM versus POM, the reasons for the types of discrepancies among species observed by Freeman and Thacker (2011) remain obscure. It is clear that many sponge-based anabolic and catabolic processes that shape the conversion of DOM/DOC to POM/POC are poorly understood, and this represents an important area of future research.

Some have questioned whether the bioavailability of DOC is broad enough to support the trophic cascades implied by the SLH (e.g., Pawlik et al. 2015). Labile DOM includes organic compounds that are present in systems from hours to days (e.g., sugars, lipids). Semi-labile and semi-refractory DOM are turned over on time scales of years and decades, but refractory DOM can last 104 years. Refractory DOM is the most ubiquitous fraction of DOM in the world's oceans and is not subject to cellular metabolism (Osterholz et al. 2015) though microbial community structure influences DOM composition (Kujawinski et al. 2016). The question sponge biologists are now facing is whether and how much the microbial symbiont communities affect the consumption and production of labile and refractory DOM. There are abundant opportunities to contrast HMA and LMA sponges to determine the extent of contributions of symbiont communities to holobiont behavior. It is likely that different sponge species, especially those with different symbiont communities, consume DOM and POM differently (e.g., Freeman and Thacker 2011). A common perception among sponge biologists is that HMA sponges pump at slower rates compared to LMA species and that HMA sponges obtain most of the dietary carbon from DOC, while LMA sponges, as true heterotrophs, use POC to fuel growth. This simplified view of HMA/LMA consumptive behavior is likely false in that feeding behavior is likely species specific and context dependent (see e.g., Topçu et al. 2010; Freeman and Thacker 2011; Perea-Blázquez et al. 2013). The HMA/LMA distinction is also likely a false dichotomy (Gloeckner et al. 2014; Poppell et al. 2014). For a few sponge species, an intermediate microbial load is harbored by the host sponge (Gloeckner et al. 2014). Mueller et al. (2014)

also provided data indicating that LMA sponges use DOC in a manner similar to HMA sponges. What is becoming clear is that trait-mediated ecosystem impacts caused by sponge feeding behavior (e.g., McMurray et al. 2014) must take into consideration characteristics of the holobiont. In the coral literature, an emerging perspective is that partner identity *and* density matter in determining holobiont performance (e.g., Cunning and Baker 2014). Thus, while density of microbial communities is important (e.g., Poppell et al. 2014), species richness—more importantly the type of species in the community—likely influences the trophic characteristics of the holobiont's extended phenotype.

5.5 Structure of Microbial Communities

Sponges offer ecologists incredible opportunities to test emerging ideas about community structure. This phylum has the opportunity to contribute to broader ecological issues as suggested in the analyses of the publication impact in sponge chemical and microbial ecology (Sacristán-Soriano and Becerro 2016). As with systems like gut microbiota, sponge microbial communities are island-like in that they occupy clearly delimited habitats. There is also an influx and efflux of microbes associated with the host, though the mechanisms that govern movement between host occupancy and the environment are obscure. At the simplest level, island biogeography theory may be a useful heuristic to determine whether a dynamic and equilibrial microbial species richness exists within sponges. In this regard, HMA sponges are probably the most appropriate study organisms. Nonetheless, understanding metacommunity dynamics is essential for sponge symbioses, and this is a wide-open area of study. We know very little about the effects of dispersal among connected communities. Furthermore, competition-colonization models may explain the coexistence of superior and inferior competitors as the result of trade-offs in colonization and competitive ability. Superior competitors may have a high probability of taking over a particular host, but may have reduced capacities for moving among hosts. On the other hand, superior colonizers may be inferior competitors despite their ability to more easily move between sponges. Dynamics such as these may explain the core, variable, and species-specific components that have been identified in sponge symbiont communities (Schmitt et al. 2012).

5.5.1 Neutral or Not: Networks and Rules of Community Assembly

Of the major processes (e.g., ecological drift, selection, dispersal, and mutation/speciation) that govern the assembly of ecological communities, our goal should be to determine under which conditions each has the strongest influence on sponge holobiont systems. While ecologists are largely agreed that neutral theory has provided valuable null models for community ecology (e.g., Gotelli and McGill 2006), particularly for species-rich systems, which sponge microbial communities may represent, there is much debate about the importance of interspecific interactions. Indeed, a central debate right now is over the relative significance of stochastic ("ecologically neutral") processes versus deterministic selection by specific environmental factors, which is especially important when considering the development of the host (e.g., Stegen et al. 2012; Yan et al. 2012). While selection is deterministic and drift stochastic (and speciation and dispersal can contribute to both deterministic and stochastic processes—Zhou et al. 2014), we do not know the relative contributions these processes make to sponge microbial communities. Indeed, we do not know the effect of these processes, in most cases, on any microbial community. Sponges offer the opportunity to couple spatiotemporal data on microbial symbiont communities from different sponge (i.e., environmental) habitats with metrics and null models of within and between community phylogenetic composition. If community assembly is controlled predominantly by stochastic processes, we would expect a high degree of site-to-site variation in composition regardless of respective niches in that habitat (Hubbell 2001; Purves and Turnbull 2010; Rosindell et al. 2012). Deterministic processes, on the other hand, would likely generate similar communities in similar hosts and would imply some rules for community assembly (Diamond 1975; Gotelli and McCabe 2002).

Debates about which ecological process dominates the development and maintenance of microbial communities continue (e.g., Erwin et al. 2012b, Fan et al. 2012). For example, Zhou et al. (2013) found that microbial communities in bioreactors were mainly shaped by stochastic processes, while Wang et al. (2013) argued that many aquatic bacterial communities were dominated by deterministic processes. The holobiont perspective adds another layer of complexity given that reciprocal evolutionary responses (i.e., coevolution) can further modify the nature of the interaction. If sponges are like biological fermenters (Hentschel et al. 2006), we might expect stochastic processes to dominate. However, the relative contributions of deterministic and stochastic processes to the assembly of microbial communities may vary across hosts. The relative importance of these processes may also shift within a specific host, especially when environmental disturbances occur (Ferrenberg et al. 2013; Zhou et al. 2014). The influence of host physiology is another factor that complicates aspects of community assembly in sponge symbiont microbiota given that environmental stressors and host performance influence the microbes' environment (Benson et al. 2010; Wong and Rawls 2012; Bolnick et al. 2014).

Questions about rules of assembly of complex microbial communities through space and time may be especially tractable using sponge models (e.g., Liu et al. 2012). In this regard, the use of ecological networks makes it possible to analyze and partition the effects of community properties and their effect on the stability of an ecosystem. Thomas et al. (2016) began to estimate the positive and negative effects, both direct and indirect, that species within sponge microbial communities might have on each other. Their approach is promising and demonstrates how large datasets can be employed to tease apart interspecific interactions. For example, the role of ecosystem complexity on community stability is an area of exploration that may benefit from the symbioses we see in sponges. Network structure may reduce the spread of indirect effects and thus enhance ecosystem stability. Sponges afford many important tests of ecological theory in this time of climate change-related environmental stress and disturbance.

Given that the sponge host develops from larvae and sponges have broad biogeographic distributions, we need to know if taxonomic composition and phylogenetic diversity change through community turnover on temporal (seasonal, life history) and spatial (disturbed vs. undisturbed habitats) scales (e.g., Easson and Thacker 2014; Luter et al. 2015). Several studies have shown that bacterial symbionts exhibit high levels of temporal stability in community composition despite large fluctuations in temperature (Erwin et al. 2012a, b). Other sponges that occur across sharp environmental gradients (e.g., subtidal and intertidal *Hymeniacidon heliophila*) have symbiont communities that differ in overall diversity, structure, and composition, and this appears to be driven by abiotic features of the different habitats (Weigel and Erwin 2015).

Processes that drive interindividual variation, if this is a major feature of sponge symbioses, are poorly understood, and this is an area that deserves greater attention. Burns et al. (2016) found that during host development, the fit of microbial communities to a neutral model of assembly decreased in later developmental stages, which points to deterministic factors such as microbe-microbe interactions, active dispersal, and selection by the host as driving the ultimate shape of the microbial community. If the evolutionary history of the symbiont communities matters, more closely related taxa are likely to have more similar habitat associations, which would be apparent in testing for phylogenetic signal. As has been found in subsurface microbial communities (Stegen et al. 2012), we should examine whether sponge microbial symbiont communities composed of ecologically similar taxa coexist to a greater degree than expected by chance (see Thomas et al. 2016).

5.5.2 *Horizontal or Vertical, High or Low?*

What features of HMA and LMA sponges are responsible for the obvious differences we see in microbial densities among species? One possibility is that HMA sponges actively recruit high densities of microbes. Conversely, HMA sponges may lack a particular type of immunological response, which LMA sponges have, that prevents clearing of resident microbes from their tissues once the symbiont establishes residency. Another possibility is that LMA sponges encourage recruitment of a competitive bacterial taxon that excludes other microbes from colonizing the host. Each of these hypotheses points to the key fact that we have very limited understanding of ecological, evolutionary, physiological, and developmental factors that produce the patterns we see among sponge hosts. Kaye (1991) provided the first clear evidence that brooding sponges had mechanisms to inoculate larvae with microbial consortia.

More recently, Schmitt et al. (2008; see also Lee et al. 2009, 2011) compared the microbial communities found in adult and reproductive material from five species of sponge. They identified 28 microbial clusters that co-occurred in the adult and larval tissue, which they deemed as strong candidates for vertically transmitted symbionts.

However, the lack of co-speciation between host and symbiont, and the clear evidence for some degree of horizontal transmission of symbionts between generations (Schmitt et al. 2008), indicates that we still have an incomplete understanding of the mechanism(s) by which sponge-symbiont associations develop. If sponge symbiont communities are influenced by competition-colonization trade-offs among their members, then we may be able to make some predictions about community structure in HMA and LMA sponges. For example, Orrock and Watling (2010) showed that the size of communities in a metacommunity framework dictated whether community dynamics were niche structured or neutral. Large communities, perhaps analogous to HMA sponges, would be expected to fit classic competition-colonization models where niche-based interactions (i.e., competitive hierarchies) drive overall outcomes (Orrock and Watling 2010). Small communities, like the symbiont communities found in LMA sponges, might be expected to experience greater levels of ecological drift because competitive ability between microbial species would be effectively neutralized given the infrequency of interactions and the lack of a correlation of species abundance to competitive ability. An interesting consequence of Orrock and Watling (2010) model is that poor competitors with good colonizing capabilities may find refuges in small communities, so sponge "specialists" might appear even if those species are merely a part of the larger metacommunity.

5.6 Sponge Symbioses in a Changing Ocean

The world's oceans are changing, though attention to this issue has lagged behind that for land-based change (Allison and Bassett 2015; Bennett et al. 2017). Part of the reason for this is that the effects of climate change on marine systems are invisible to many humans (Weber 2013). Nonetheless, compelling evidence indicates that human activities are modifying the physical characteristics of the atmosphere and the oceans (IPCC 2013, 2014). The biological consequences of these changes are difficult to predict, but scientists are united in their concern that the rapidity of change will have spreading detrimental effects on marine communities. Subtle shifts in currents, temperature regimes, primary productivity, pH of the water, etc., all lead to modifications of the interspecific interactions that have shaped ecosystems for millennia (Bell et al. 2013).

With a holobiont perspective, it is now recognized that we must understand how these changing conditions will affect not just the host but the plethora of organisms that reside within and on that host (e.g., Selvin et al. 2009; Cárdenas et al. 2014). The reasons for adopting this perspective are practical. Conservation of marine habitats and their organisms relies on healthy specimens, healthy organisms have healthy symbiont communities (Mazmanian et al. 2008), and healthy individuals contribute to robust marine benthic communities. In fact, theory indicates that if sponge symbiont communities are more strongly niche structured, which some evidence indicates they may be (Thomas et al. 2016), then they will be more stable than neutral communities in a static environment. These communities will, however, show more pronounced, predictable, and directional responses to environmental change.

Strongly niche-structured communities will also more tightly regulate the biogeochemical functioning of the ecosystem (Beare et al. 1995; Hector and Bagchi 2007), but they are more sensitive, in terms of biogeochemical functioning, to the loss of a particular species. Thus, a holobiont perspective is required as we think of ways to protect marine environments from the consequences of climate change: the unpredictable outcomes of climate-related modifications to the holobionts that reside in marine environments are cause for great concern.

5.6.1 Heat and pH

Early work explored the disruptive effects of stressful temperatures on the structure of sponge-associated microbial communities (Lemoine et al. 2007; Webster et al. 2008a) or on host responses to stress (López-Legentil et al. 2008). Despite some evidence indicating thermal tolerance (Schönberg et al. 2008; Webster et al. 2011; Duckworth et al. 2012; Luter et al. 2012; Simister et al. 2012c), small changes in temperature have been shown to cause shifts in the composition and behavior of sponges and their microbial communities (Lemoine et al. 2007; Webster et al. 2008a; Pantile and Webster 2011; Massaro et al. 2012; Simister et al. 2012a; Fan et al. 2013; but see Pita et al. 2013). Webster et al. (2008a) demonstrated a clear shift in community composition through the loss of symbiont species for the tropical sponge *Rhopaloeides odorabile* when temperatures reached those that induce coral bleaching. The loss of the symbionts from *R. odorabile* had several undesirable effects including the establishment of alien microbial populations that included potential pathogens and significant changes in sponge feeding behavior (Massaro et al. 2012). Most recently, Bennett et al. (2017) demonstrated that temperature and pH have complicated effects on sponges that harbor distinct symbiont communities, and these effects depend upon the developmental stage of the host.

The effects of warmer water extend to intracellular eukaryotic sponge symbionts. A mass bleaching event involving clionaid sponges, coincident with a mass coral bleaching event, was observed in the Florida Keys in 2015 (Fig. 5.4; Hill et al. 2016). Events like the 2015 sponge bleaching raise significant concern about the future health of marine sponges and the broader effects that destabilizing symbiont communities might have on the health of the entire ecosystem. Specifically, if the sponge loop relies on holobiont performance and if symbiont communities are disturbed by stressful environmental conditions, we may see unwanted and far-reaching changes to coral reef and other marine ecosystems. A more complete understanding of sponge impacts on coral reef biogeochemistry is important given that coastal eutrophication, climate warming, and overfishing create conditions detrimental to corals while favoring increases (Zea 1994; Rützler 2004) or, in some instances, decreases (Butler et al. 1995) in sponge abundance. The challenge now facing the scientific community is to develop tools that allow for nuanced examination of the subtle shifts in microbial

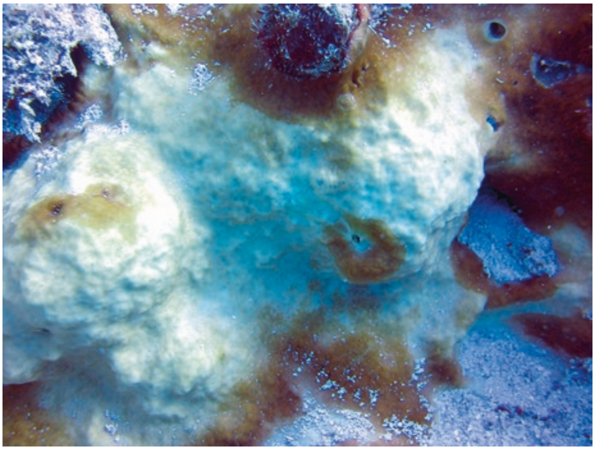

Fig. 5.4 Bleached *Cliona varians* from the Florida Keys observed during a mass bleaching event involving sponges in October, 2015 (Hill et al. 2016). Notice the unbleached circular region around the osculum located to the right of center of the image. This pattern was not uncommon; more extensive bleaching was observed in regions of the sponge some distance from an osculum, while resident *Symbiodinium* often remained in clearly delineated circular patches around oscula. Photo courtesy of C. Walter

community function and physiology and to correlate those changes with host behavior and host gene expression (e.g., Webster et al. 2013; Bennett et al. 2017).

Ocean acidification (OA) is another growing threat in marine habitats caused by human-induced changes to the atmosphere (Gattuso et al. 2015). Among sponges, the Calcarea may face challenges building calcitic skeletons under future OA projections. The majority of focus, however, has been on the effects of shifting pH (and temperature) on bioeroding sponges (Wisshak et al. 2012, 2013; Stubler et al. 2014). The chemical etching component of clionaid bioerosion was elevated under several OA scenarios (Wisshak et al. 2012; Bell et al. 2013). If clionaids experience faster growth with concomitant increases in bioerosion when temperatures and OA increase, then we can expect further declines in the development of coral reef habitats.

Stressors like temperature and ocean pH do not act in isolation (Bennett et al. 2017). Lesser et al. (2016) recently found that the microbiome of *Xestospongia muta* responded to OA and elevated seawater temperature, but did so in complicated, interactive, and indirect ways. They found that the microbiome (*sensu lato*) was generally resistant to temperature and OA stress. These results support those found in Bennett et al. (2017) where interactive effects of ocean warming and OA occurred and were species specific. Indeed, the fact that the sponges that relied on phototrophic symbionts were less susceptible to elevated $p\mathrm{CO}_2$ and temperature stress than those sponges that relied heavily on heterotrophic feeding deserves much greater attention (Bennett et al. 2017).

However, Lesser et al. (2016) demonstrated a decline in the productivity of symbiotic cyanobacteria, the effects of which manifested themselves to the entire microbiome through changes in nutrient translocation dynamics between symbiont and host. Lesser et al.'s (2016) observation that the stability, if not the species composition, of the microbiome was affected most by OA is important. This has not been a major line of inquiry and indicates that we need more research in this area.

5.6.2 Disease

Mass mortality events, and the incidence of unhealthy sponge hosts, appear to have increased in frequency, and disease events are positively correlated with anomalously high seawater temperatures (Olson et al. 2006; Webster 2007; Webster et al. 2008b; Angermeier et al. 2011; Uriz et al. 2016). In one of the better studied systems, a mass mortality event involving sponges from the Mediterranean affected over 90% of the *Ircinia fasciculata* observed in some localities during the warmest months of the year (Maldonado et al. 2010; Cebrian et al. 2011). Other die-offs of *Ircinia* populations have been recorded from the Adriatic and Ionian Seas (Stabili et al. 2012; Di Camillo et al. 2013). The causative agent is unknown, with some authors believing the disease is caused by a twisted rod bacterium, *Vibrio rotiferianus*, or thermally stressed cyanobacteria (Maldonado et al. 2010; Cebrian et al. 2011; Stabili et al. 2012). Interestingly, Blanquer et al. (2016) recently suggested that sponge disease was caused by a shift in the relative abundance of bacterial OTUs, which lead to community dysfunction (see also, Uriz et al. 2016). Thus, disease in this case would not be caused by the presence of a single pathogen, but rather a subtle shift in the microbiome may have resulted in host sickness, which is reminiscent of the balance between health and disease for hosts in gut symbioses relying on the activities of members of the entire microbial symbiont community (e.g., Mazmanian et al. 2008). Indeed, Gao et al. (2015) recently demonstrated shifts of prokaryotic communities between healthy and disease-like sponge tissues. Thus, Koch's postulates may not apply to some climate change-instigated diseases of the future, and results like those described above highlight the concerns that many have about a warming ocean that is experiencing shifts in general chemistry (e.g., Luter et al. 2010; Olson et al. 2014; Sweet et al. 2015). Stable microbial communities have been built, evolutionarily speaking, upon rates of material flux and strengths of interspecific interactions, and climate change-mediated fluctuations in environmental conditions may move sponge holobionts away from "equilibrial" conditions that support the health of the host.

5.7 Conclusions

It is well documented that the environment is changing due to our alteration of the earth's atmosphere and the world's oceans. Marine biologists face the daunting task of estimating and predicting the consequences, in terms of the structure and function of marine ecosystems, of those environmental changes. Given their essential ecological roles, we must increase attention on the effects that climate change will have on sponges and their microbial symbionts. Several recent studies highlight how urgent the problem has become given clear evidence that sponges are responding to environmental stressors that are becoming more frequent and more intense. The scale and scope of future studies must extend from the most nuanced aspects of integrated gene interactions to community-wide ramifications of holobiont behavior. Fortunately, we have entered a technological period where powerful tools are opening lines of investigation that previously have been difficult or impossible to pursue. The timing could not be any more propitious. If we can provide resource managers with guidelines about expected responses of sponge communities, we may be able to craft policies that protect marine habitats to a greater extent than is the case currently.

Furthermore, the sponge holobiont may provide a perspective on the way that symbiotic interactions can be harnessed to help address major challenges of human population growth (e.g., the manufacture of new drugs, sustainable production of energy, conservation of marine environments). The holobiont perspective of symbioses advocated here and by many authors promises to shed light on important questions of broad interest to the scientific community.

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Chapter 6
Impacts of Short-Term Large-Scale Climatic Variation on Sponge Assemblages

James J. Bell, Megan Shaffer, Holly Bennett, Emily McGrath, Charli Mortimer, Alberto Rovellini, Joseph Marlow, Andrew Biggerstaff, and José Luis Carballo

Abstract There are large-scale processes that are impacting marine communities across the world at a range of temporal scales. In this chapter, we consider the potential impacts of short-term, large-scale, climate processes on sponges with a major focus on temperature variation. We examined available case studies from across the world to assess the physiological and ecological impacts of such temperature anomalies. Sponges show a number of responses to temperature including changes to respiration rates and heat-shock protein production, and temperature can also alter symbiont function. At the ecological level, temperature influences sponge reproduction, feeding and growth and therefore has the potential to influence population dynamics and wider ecosystem function. Responses of sponges were variable when comparing the impacts of short-term temperature increases between different geographic regions, with reports of both tolerance and population declines. However, within tropical systems, there are increasing reports of higher tolerance of sponges to increases in temperature compared to corals and of sponges showing subsequent increases in abundance where coral populations have declined. However, there are still very few studies that have focused on understanding the mechanisms of acclimation to temperature stress, which should be a focus of future research.

Keywords Porifera • Temperature • El Niño • La Niña • ENSO • Physiology • Climate oscillation

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6.1 Introduction

Global scale events causing short-term climatic variation impact marine organisms across all levels of biological organisation and have been particularly noticed in tropical environments. While the consequences of these larger-scale impacts on corals have received considerable attention (e.g. Hughes et al. 2003; Kleypas et al. 2015), far less is known about their likely impacts on sponge assemblages. Long-term ecological data are critical for assessing the effects of climatic variation since such events are often irregular and difficult to accurately predict. Despite the importance of such data, this information is generally scarce. Good quality data are only now emerging from studies at suitable spatial and temporal scales to assess the possible effects of large-scale climatic variation on sponges. Furthermore, a number of studies are available that describe long-term monitoring data, which can be correlated with large-scale and quasi-natural climatic variations (e.g. the El Niño-Southern Oscillation (ENSO)). The objectives of this chapter are (1) to explore the potential consequences of large-scale climatic variation on sponges, particularly by focusing on the physiological and ecological effects of temperature, and (2) to examine case studies from across different geographical regions that describe how sponge populations and assemblages have been influenced by extreme temperature effects. There is an important distinction to be made between the way in which the more gradual impacts of increased sea surface temperature, associated more specifically with increased carbon dioxide levels, and the effects of short-term thermal anomalies will impact on sponges, and here we predominately focus on the latter.

6.2 Climatic Oscillations

There are several large cyclical ocean-scale climatic events across the world, although the best known and most relevant for the marine environment are those associated with the El Niño-Southern Oscillation (ENSO), mostly because the impacts of ENSO events have been devastating in the past and felt worldwide. The ENSO is an irregularly periodic variation in winds and sea surface temperatures over the tropical eastern Pacific Ocean, which can strongly influence global tropical and subtropical environments. Importantly, their effects vary in intensity and in some years have had devastating impacts on marine life. "El Niño" is the warm phase of the ENSO and is associated with a band of warm ocean water that develops in the central and east-central equatorial Pacific (between approximately the International Date Line and 120°W), including off the Pacific coast of South America. El Niño is accompanied by high air pressure in the western Pacific and low air pressure in the eastern Pacific. The cool phase of the ENSO is called "La Niña" with below-average sea surface temperatures in the eastern Pacific, higher air pressures in the eastern Pacific and lower air pressures in the western Pacific. The ENSO cycle, both El Niño and La Niña, causes global changes in temperature, rainfall and cloud cover. The El Niño and La Niña periods can last several months each and typically occur every few years. In recent decades, the El Niño events have become more common, while La Niña events have reduced in frequency.

In addition to the well-known ENSO events, there are also Arctic Oscillation (AO) and Antarctic Oscillation (ANO), which can also result in large-scale climatic variations. The negative impacts of these have been associated with both cold and warm water events, which are often linked with the extent of summer sea ice. Decreases in the extent of polar summer sea ice are generally associated with the positive AO phase and both positive and negative ANO phases depending upon the relevant Antarctic region. The AO is also related to the North Atlantic Oscillation (NAO), which is primarily an atmospheric phenomenon in the North Atlantic Ocean where there are fluctuations in the difference of atmospheric pressure at sea level between the Icelandic Low and the Azores High. There have been few studies that have looked directly at correlations between NAO variation and sponge assemblages, but NAO periods can also be associated with increased temperature and primary productivity (Ottersen et al. 2001), potentially increasing food supply to sponges.

6.2.1 Recent ENSO Events

There have been a number of strong ENSO events recorded in the last 30 years, and although the 1997–1998 ENSO has been considered to be the most extensive to date (McPhaden 1999a), initial reports suggest that the current 2014–2016 event may be far stronger and have even greater negative impacts on marine organisms (Normile 2016). During the 1997–1998 ENSO event record, high seawater temperatures were recorded (McPhaden 1999b) and were felt globally, compared to other ENSO events where impacts had been more regional. The evolution of ocean temperature anomalies in the Southern Hemisphere began a few months earlier than the envelope of prior ENSO events and had exceptional amplitude, lasting for approximately 18 months. This current event followed a similar pattern in terms of the timing of its maximum development and thus was similar in magnitude and duration to the previous strong events in 1982–1983 and 1986–1987, but the 1997–1998 event was much more dramatic globally. More recently, while the 2014–2016 El Niño has had major impacts on coral reefs worldwide, it is still not considered to be as strong as the 1997–1998 event. In particular, coral bleaching events were far more extensive in the 1997–1998 event, with widespread mortality associated with this bleaching (Wilkinson and Hodgson 1999).

6.2.2 Environmental Changes During ENSO Events

ENSO events are not only characterised by changes in temperature but also in patterns of rainfall and cloud cover (e.g. Rasmusson and Carpenter 1982, 1983; Ropelewski and Halpert 1986; Nicholson and Kim 1997), which can have secondary impacts on marine organisms. For example, increased rainfall may cause flooding and increased land erosion, resulting in greater terrestrially derived sediment reaching coastal waters. Such sediment has the potential to smother sponges, interfere with sponge filtering and increase water turbidity, all of which can have negative impacts on sponges (Bell et al. 2015). Furthermore, increased rainfall into coastal communities and flooding have the potential to result in localised reductions in salinity. Declines in salinity are known to influence sponges in a number of ways, including reductions in growth, abundance and reproductive output. For example, Roberts et al. (Roberts et al. 2006) reported a decline in growth, reproductive status and symbiotic algae (using chl *a* concentration as a proxy) across a decreasing salinity gradient for temperate reef sponge *Cymbastela concentrica*.

Reducing cloud cover has the potential to result in increased damaging ultraviolet B radiation reaching the earth's surface, and while this UVB is rapidly absorbed with depth in coastal regions, intertidal sponges might be susceptible. The one study available that examines the impact of UVB on sponges found that for temperate and tropical sponges, *Tethya bergquistae* and *Aaptos* sp., respectively, there was no effect of short-term exposure to UVB on respiration rates at environmentally relevant levels of 60 μW cm^{-2} (Murray 2009).

6.3 Physiological Effects of Temperature Stress on Sponges

Due to the fundamental effect of temperature on biological processes, organisms live in environments where average temperatures facilitate their optimal physiological performance (Hoegh-Guldberg and Bruno 2010). Shifts from optimum temperatures are likely to compromise biological processes, resulting in reduced organism fitness with subsequent implications for population survival and species persistence (Pörtner and Farrell 2008; Pörtner 2008; Hoegh-Guldberg and Bruno 2010; Byrne and Przeslawski 2013). The simple body plan of sponges should make them particularly vulnerable to environmental change as just one cell layer separates a sponge from the external environment; therefore, cellular processes are likely to be highly influenced by ambient water temperature. There are a number of key physiological processes that are influenced by temperature, and here we focus on respiration, stress protein production, photosymbiont responses and secondary metabolite production (summarised in Table 6.1); details on other physiological and molecular level responses including gene expression (of both sponges and symbionts) can be found in other chapters of this volume.

6.3.1 Respiration

Temperature is known to exert strong control over sponge metabolic rates, with respiration rates increasing in many species during summer as temperatures increase. For example, respiration rates of both the phototrophic sponge *Phyllospongia lamellosa* and the heterotrophic sponge *Ianthella basta* were significantly higher (25–40% higher) in summer compared to respiration rates for both species during winter (Cheshire et al. 1997). Similar results have been demonstrated for the phototrophic

Table 6.1 The effect of increasing seawater temperature on sponge physiological and ecological processes

Physiological processes	Effect	Ecological processes	Effect
Symbiont response 1) Cyanobacteria 2) Zooxanthellae	1) Decrease 2) Decrease	Feeding/pumping	Decrease
Respiration	Increase	Growth	Increase
Heat-shock proteins	Increase	Reproduction	Increase and decrease
Gene expression	Change	Mortality	Increase
Metabolism	Increase	Dispersal	Decrease
Secondary metabolites	Change	Morphology	Change
		Disease	Increase
		Competitive ability	Increase
		Bioerosion	No effect to slight decrease
		Regeneration	Increase

sponge *Cymbastela concentrica*, which also has a higher respiration rate in summer than in winter and spring (Cheshire et al. 1995). Oxygen consumption and filtration rates measured in the sponge *Axinella polypoides* at 16 °C increased significantly following a short-term exposure (~30 min) to experimentally induced temperature 8 °C above ambient (24 °C). Following the initial increase in these rates, long-term depression in both processes was observed, despite temperatures being returned to 16 °C. These findings demonstrate that even short-term exposure to temperatures above a sponge's thermal threshold can have a long-lasting effect on sponge physiology (Zocchi et al. 2003). The authors proposed that these long-lasting physiological effects are likely responsible for mass mortalities of sponges following sudden increases (2–4 °C) in seawater temperature in the Mediterranean (Cerrano et al. 2000; Zocchi et al. 2003). In contrast, the slower increases in temperature that are experienced seasonally which stimulate metabolic rates and activity are unlikely to have long-term negative effects such as the metabolic depression and reduced pumping or mortality (Zocchi et al. 2003). Furthermore, as energy is invested to support increased metabolic demand in response to temperature stress, other important processes such as protein synthesis and crucial energetic processes, including skeletal and tissue growth, and reproduction are likely to be compromised in favour of maintaining basic biological functioning (Fabry et al. 2008; Pörtner and Farrell 2008).

6.3.2 *Stress Proteins*

Many studies have demonstrated that sponges have strict thermal optima, with experimentally induced temperature extremes disrupting sponge functioning causing reductions in overall performance and ultimately sponge mortality. The expression of stress proteins, particularly heat-shock proteins (HSPs), has been measured in a number of studies to determine the level of cellular stress a sponge experiences when exposed to temperature anomalies, with most studies demonstrating increased heat-shock protein expression in sponges exposed to temperatures above their thermal threshold (Bachinski et al. 1997; Krasko et al. 1997; López-Legentil et al. 2008; Pantile and Webster 2011). For example, the Caribbean sponge *Xestospongia muta* exhibits high heat-shock protein expression and mortality when exposed to 30 °C (López-Legentil et al. 2008). The Great Barrier Reef sponge *Rhopaloeides odorabile* has a thermal threshold of 32 °C, with increased expression of heat-shock proteins and mortality within 3 days of exposure to 32 °C (Webster et al. 2008; Pantile and Webster 2011; Massaro et al. 2012). When exposed to temperatures above its thermal threshold, *R. odorabile* also exhibits a breakdown in host-symbiont molecular interactions (Fan et al. 2013) and a reduction in feeding efficiency (Massaro et al. 2012).

6.3.3 Photosymbionts

As with reef-building corals, some sponges are reliant upon photosynthetic symbionts to meet energy requirements (Wilkinson 1987; Vicente 1990; Cheshire and Wilkinson 1991), although sponges generally harbour cyanobacterial symbionts. A widely reported impact to reef-building corals as a result of elevated temperatures is coral bleaching. While there have been no mass sponge bleaching events recorded to date, smaller-scale sponge bleaching (Fig. 6.1), in response to elevated temperatures, has been reported on coral reefs globally (Vicente 1990; Fromont and Garson

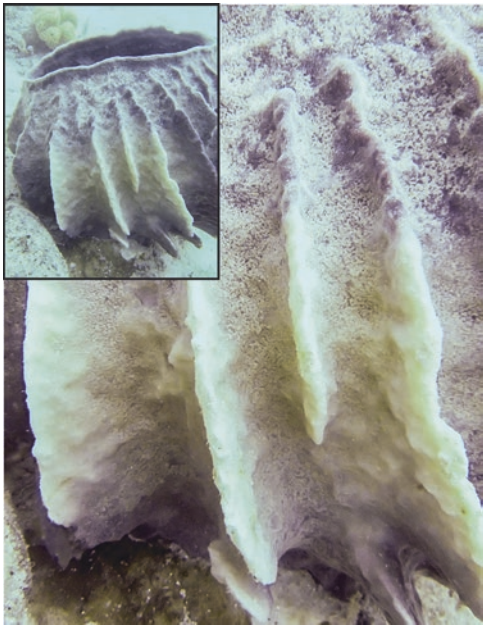


Fig. 6.1 Examples of bleached *Xestospongia testudinaria* from the Wakatobi Marine National Park, Indonesia

1999; López-Legentil et al. 2008; McMurray et al. 2011). The percentage of sponges within a population and the geographic area reported to have bleached during these episodes is low, and in most of these examples, bleaching does not eventuate in sponge mortality. Regardless, phototrophic sponge species are likely to be more susceptible to temperature anomalies due to their reliance upon carbon transfer from associated photosynthetic symbionts (Blanquer et al. 2016). An example of this was reported from the Mediterranean, where mass mortalities of the phototrophic sponge *Ircinia fasciculata* coincided with abnormally high temperatures (Cebrian et al. 2011; see below for more details). While no bleaching was reported for *I. fasciculata*, experimentally induced temperatures similar to those experienced during the anomaly demonstrated a reduction in measured photosynthetic parameters confirming a breakdown in this symbiosis to be the root cause of mortalities (Cebrian et al. 2011). Similarly, phototrophic cyanobacterial symbiont productivity declined in *Xestospongia muta* that were experimentally exposed to future climate change temperature and ocean acidification levels (~31.5 °C, 800 ppm CO_2; IPCC 2007). While there was no evidence of bleaching, the quantum yields of cyanobacterial photosystem II fluorescence declined, as did holobiont carbohydrate levels, suggesting a reduction in energy transfer from the sponge-symbiont to the host under such conditions (Lesser et al. 2016).

6.3.4 Secondary Metabolites

In nature, secondary metabolites play an important role in a variety of biological processes, but the majority of sponge research has centred on antibiotic, antifouling and toxic antipredator compounds (Proksch 1994). Changes in temperature can influence the production levels of these metabolites, and numerous studies have found higher concentrations of bioactive compounds during warmer summer months (e.g. Duckworth and Battershill 2003; Page et al. 2005a; Abdo et al. 2007). These increases have been proposed to be in response to the need for increased antifouling or anticompetitor compounds during these months as predators are more active (Turon et al. 1996; Duckworth and Battershill 2001). Metabolite concentration and composition change has also been associated with disease outbreaks, which are temperature related. For example, the tissue of *Xestospongia muta* infected with sponge orange band disease has significantly lower concentrations of the main secondary metabolites tetrahydrans than in healthy tissue (Angermeier et al. 2011). However, not all sponge species show a relationship between temperature and secondary metabolite production. Given that secondary metabolites can be responsible for deterring predation and fouling, Duckworth et al. (2012) tested the hypothesis that these compounds would increase under conditions of predicted future temperature and acidification stress. They found that elevated temperature and ocean acidification had no impact on secondary metabolite concentrations in the six coral reef sponges examined. These contrasting studies highlight how little is known about the potential for temperature stress to influence metabolite production.

6.4 Ecological Effects of Temperature Stress on Sponges

There are a number of important ways in which temperature can affect the ecology of sponges (see Table 6.1 for an overview). Given a number of aspects of sponge ecology are covered in other chapters (including disease and bioerosion), here we focus on feeding, reproduction, growth and mortality events (for the latter, see case study section). Other ecological effects of temperature anomalies on sponges include influences on regeneration rates, external and internal morphological variation and competitive ability. There is very little to no data on these parameters, so these are not covered here (however, see Henry and Hart 2005; Morley et al. 2016).

6.4.1 Reproduction

Large-scale temperature events and climate change associated increases in temperature have the potential to influence reproduction in sponges over both short and long time scales. Sponges use a variety of both sexual and asexual strategies to reproduce, as summarised in a recent review by Maldonado and Riesgo (2008). In general, sponges are either gonochoristic or hermaphroditic and either release their eggs (e.g. oviparity) or brood their larvae internally (e.g. viviparity). In addition, sponges can reproduce asexually by budding, fragmentation or gemmulation.

There have been multiple studies examining how reproduction is influenced by environmental variability, with the majority focusing on reproductive response to temperature. Both increased and decreased water temperatures are thought to potentially trigger sexual and asexual reproduction. In some sponges, gamete production and budding coincides with warmer temperatures (e.g. *Spongia ceylonensis*, Chung et al. 2010; *Xestospongia* spp., Fromont and Bergquist 1994; *C. reniformis*, Riesgo and Maldonado 2008; *Halichondria panicea*, Witte et al. 1994; *Geodia cydonium*, Mercurio et al. 2007; *Tethya citrina*, Cardone et al. 2008). However, the opposite has been reported in other sponges, where greater gamete production and budding occur at lower temperatures (e.g. *Axinella damicornis* and *Raspaciona aculeata*, Riesgo and Maldonado 2008; *Halisarca dujardini*, Ereskovsky 2000; *Mycale contarenii*, Corriero et al. 1998).

Large-scale temperature events resulting from El Niño will likely have short-term consequences for reproduction. In some sponges, rapid increases in temperature are thought to be a potential stressor, triggering an increase in asexual reproduction. For example, Cardone et al. (2008) induced budding in *Tethya citrina* by simply increasing the temperature by 7 °C. In the Ionian Sea, *T. citrina* was found to bud continuously throughout the year, and the growth rate of newly produced sponge “post-buds” was positively related to temperature (Cardone et al. 2010), suggesting that clones may be more successful in warming temperatures. Altering the proportion of sexual and asexual events through temperature changes may influence the fitness of individuals within a population and affect the genetic

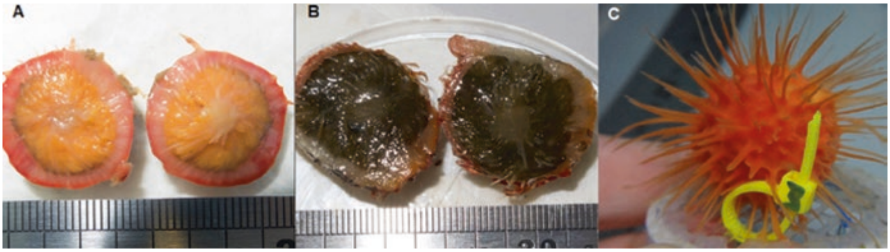


Fig. 6.2 Condition of *Tethya bergquistae* following exposure to elevated temperatures. Photo A: cross section of healthy sponge (kept at 13.5 °C for 2 weeks); B: cross section of thermally stressed sponge with extensive internal necrosis (kept at 18.0 °C for 2 weeks); C: reproductive buds produced in some specimens kept at higher temperatures (kept at 18 °C and 20 °C for 2 weeks). Pictures courtesy of Tracy Bates

composition of a population, having implications for overall population functioning and fitness. In another example from New Zealand, Bates (2015) found that *Tethya bergquistae* rapidly produced asexual buds when exposed to temperatures projected for 2100, while control sponges produced no such buds (Fig. 6.2).

In addition to temperature, reproduction can be affected by other short-term environmental changes resulting from El Niño, including fluxes of nutrient availability and changes in sediment, light and salinity levels. Phytoplankton blooms associated with El Niño events result in more food for sponges, allowing additional energy for increased reproduction. A positive relationship between embryo production and nutrient level has been recorded in multiple species of sponges (Elvin 1976; Witte 1996; Di Camillo et al. 2012). Increases in sediment, in contrast, generally decreases reproductive output. For example, fewer gametes were observed after the addition of sediment to *Cymbastella concentrica* over a 2-month period (Roberts et al. 2006). Light can trigger spawning and larval release in some sponges (Amano 1986, 1988; Lindquist et al. 1997), and sponges experiencing decreases in light have been shown to have a lower production of oocytes and spermatocytes (Roberts et al. 2006). Salinity also appears to influence reproduction, as both Roberts et al. (2006) and Witte et al. (1994) found a decline in reproductive status with decreasing salinities.

Temperature anomalies have the potential to affect larval dispersal in sponges. Both increases and decreases in temperature have been shown to reduce larval dispersal capabilities of certain sponges. For instance, Whalan et al. (2008) found that increases of 5–8 °C from ambient temperature reduced the duration of the planktonic phase of *Rhopaloeides odorabile* larvae from 54 h to 18 h, with metamorphosis occurring much sooner in larvae experiencing elevated temperatures. With temperature increases greater than 12 °C from ambient, *R. odorabile* larvae were no longer functional. Maldonado and Young (1996) observed the effects of colder water on larvae and found that dispersal was inhibited in larvae of four Caribbean demosponges, *Tedania ignis*, *Haliclona tubifera*, *Sigmadocia caerulea* and *Halichondria magniconulosa.* These larvae exhibited decreased swimming speeds and shortened periods of the free-swimming phase in decreased temperature. Temperature anomalies can therefore result in highly divided populations as larvae cannot as easily disperse between populations.

Extreme climatic events associated with high rainfall events in combination with increased sea surface temperature (SST) have also been shown to influence sponge reproduction. For example, Wahab et al. (2014) reported depressed sexual productivity in a population of *C. foliascens* with a reduced proportion of reproductive females and a lower female reproductive output index in response to both increased rainfall and SST. Reproductive output was depressed at low SST (23 °C), while peak sperm release occurred at temperatures above 25 °C, and the peak larval release occurred during the annual temperature maxima (28 °C). A twofold increase in maximum larval production, assessed using a population sexual productivity index (PoSPi), in *C. foliascens* was observed in the second reproductive cycle these authors monitored, following a depressed PoSPi in the first cycle. This reduction in PoSPi in the first reproductive cycle was associated with elevated SST and rainfall, coinciding with one of the strongest La Niña events on record.

Climate change associated with increases in temperature may also have long-term consequences for sponge reproduction, mainly influencing the timing of reproductive cycles. Many sexual events in sponges are seasonal and triggered by warming or cooling temperatures (Witte et al. 1994; Lindquist et al. 1997; Ereskovsky 2000; Mercurio et al. 2007; Riesgo and Maldonado 2008; Chung et al. 2010; Wahab et al. 2014). With changes in global temperatures, there is the potential for these events to shift in terms of both seasonality and frequency, although the consequences of such shifts is unknown, but could cause mismatches between sponge larvae and predators or food.

Temperature anomalies also have the potential to have sublethal effects on the populations during reproduction. For example, the sexual reproduction of the viviparous hermaphrodite sponge, *Petrosia* sp., was severely impacted by a thermal stress event in the Gulf of Thailand. A severe coral bleaching event during April to May 1998 coincided with the disappearance of spermatic cysts and oocytes in all samples between May and October 1998, and embryos and larvae were not found between May and November 1998 (Asa et al. 2000).

6.4.2 Feeding

Temperature anomalies might also affect feeding behaviour and efficiency of marine sponges. Temperature determines water viscosity and as a result may directly impact pumping rates of sponges. Indirect effects potentially include alterations in metabolism and nutrient availability, for instance, due to stratification and poor upwelling. Contrasting evidence exists about the effect of temperature on clearance rates of sponges. Changes in pumping rates as a result of increased temperature were not observed in natural conditions for *Dysidea avara* (Ribes and Coma 1999). However, an increase in temperature from 6 °C to 12 °C caused a significant increase (up to four times) in the mean filtration rate of *Halichondria panicea* under laboratory conditions (Riisgård et al. 1993). According to the authors, such increases cannot be explained simply by reduced viscosity, and acute effects might be due to constriction/dilation of the pumping cavities under different temperature regimes. The energetic cost of passive pumping is thought to be rather limited for sponges (Maldonado et al. 2012), with the metabolic cost of filter feeding below 4% of the whole metabolism for a range of marine invertebrate filter feeders (Riisgård and Larsen 1995). However, based on in situ measurements of filtration and metabolic rates of *Aphrocallistes vastu*s, Leys et al. (2011) proposed that sponges actively pump water at a relatively high metabolic cost, about 28% of the global cost of respiration. This significant metabolic expenditure for active filtration in addition to passive water inflow means that sponge feeding reflects metabolic rates and thus can be influenced by temperature. Sponges in temperate climates are not food limited during the warm months of summer because the pico- and nanoplankton communities are rather stable in abundance throughout the year. However, temperature does cause an increase in the metabolic rates of temperate sponges, thus limiting their growth and ultimately hampering their fitness (Coma and Ribes 2003; Coma et al. 2009). Negative effects of extremely high temperature have also been observed for tropical species. When exposed to increasing temperature, the Great Barrier Reef sponge *Rhopaloeides odorabile* showed significantly reduced pumping rates at 31 °C, with this being the threshold for normal feeding behaviour. A further increase in temperature resulted in extended necrosis of the sponge tissues and a dramatically reduced pumping rates and feeding efficiency (Massaro 2009). While the response of sponge feeding to thermal anomalies is probably species specific, future increased sea surface temperature is likely to reduce the ability of sponges to actively pump water. Stratification of the water column and reduced upwelling due to high sea surface temperature will likely mean lower carbon particles availability for sponges and other filter feeders.

6.4.3 Growth

Significant positive correlations have been seen between sponge growth rates and the ambient water temperature from observational studies worldwide, although there are no specific studies examining growth rates in responses to short-term thermal anomalies. This positive correlation has been reported based on in situ measurements of the branching sponge *Haliclona oculata* in the Netherlands (Koopmans and Wijffels 2008), the encrusting sponge *Halichondria panicea* in Germany (Barthel 1986) and the massive sponge *Corticium candelabrum* in Spain (De Caralt et al. 2008). The positive correlation between growth rate and inter-seasonal variation in temperature was also observed for experimental explants of *Mycale hentscheli* in New Zealand during aquaculture trials (Page et al. 2005b). Furthermore, for studies that did not directly measure temperature, sponge growth rates have been shown to be significantly greater in summer seasons for *Xestospongia muta* (McMurray et al. 2008), *Callyspongia armigera*, *Iotrochota birotulata*, *Niphates erecta*, *Amphimedon compressa*, *Aplysina cauliformis*, *Aplysina fulva* and *Ptilocaulis walpersii* (Leong and Pawlik 2010) with these studies all conducted in Florida. Duckworth et al. (2012) compared the growth rates of six species of Caribbean sponges (*Aiolochroia crassa*, *Aplysina cauliformis*, *Aplysina fistularis*, *Ectyoplasia ferox*, *Iotrochota birotulata* and *Smenospongia conulosa*) in aquaria at the present-day summer maxima (28 °C) and the predicted temperature increase by 2100 (31 °C). These authors found no significant effect of the temperature increase on the growth rate of any of these sponges, indicating that they will be relatively unaffected by predicted rises in SST compared to other benthic species such as corals.

6.5 Other Large-Scale Climatic Events

In addition to the potential for the environmental changes described above to occur as a result of large-scale climatic variation and particularly changes in response to temperature, there is also the potential for other large-scale, much shorter-term (days to weeks) disturbance events, particularly storms and cyclones, which can have devastating impacts on shallow-water benthic communities, including sponges. Furthermore, many studies have predicted that climate change will result in an increase in the intensity and frequency of storms and cyclones (Eldin and Donguy 1983; Philander 1983; Revell and Goutler 1986; Emanuel 1987; Knutson et al. 2010). Large-scale disturbance events have the ability to alter benthic structure and functioning over both short- and long-term time scales. Increased wave action often results in significant damage to organisms that play a key role in reef structure, like corals and sponges. Mass mortalities of such organisms are often reported following extreme storms and cyclones (Harmelin-Viven 1994; Van Woesik et al. 1995; Cahoon 2006).

Environmental conditions are often dramatically changed following a large storm event, with numerous studies reporting changes in sediment, salinity and light levels after storms. As a result, disturbance events indirectly impact all levels of benthic communities and often change community dynamics. For example, primary production has been shown to generally increase after a storm, which can result in a shift in the trophic composition of the benthic community. Changes in the abundance of certain reef organisms following a storm can also alter biological interactions like competition and predation. There have been multiple studies examining how cyclones/hurricanes in particular affect sponge assemblages. Some hurricane events have caused minimal to no damage in sponges (e.g. Hurricane Gilbert in 1988 in Cozumel, Fenner 1991), while others have caused mass mortalities, resulting in “sponge cemeteries” (e.g. Hurricane Emily in 2005 in Cozumel, Alvarez-Filip and Gil 2006). The fate of sponge populations after a hurricane is generally species and location specific and often depends on multiple factors including storm intensity, storm frequency, location (inshore vs. offshore) and other pre-storm characteristics of the reef (i.e. age of reef, community structure, site topography, organism morphology).

One of the earliest reports of the impacts of hurricanes on sponges was by Woodley et al. (1981), who examined the effects of 1980s Hurricane Allen on Jamaican coral reefs. A third of all the sponges surveyed showed signs of damage. When examining the morphologies of the damaged sponges, it became evident that morphology plays a key role in survival during extreme storm events. These authors found that nearly half of the ropelike morphological forms were broken at the base. Furthermore, massive and tougher sponges (e.g. *Ircinia* spp.) appeared unaffected, while soft, more crumbly sponges, such as *Neofibularia nolitangere*, showed significant signs of damage. The relationship between morphology and damage was also been reported by Wulff (1994a), who found a loss of half the biomass of the three dominant sponge species (*Iotrochota birotulata*, *Amphimedon rubens*, *Aplysina fulva*) in Panama reefs following Hurricane Joan in 1988. Differences in mortality rates between these species were attributed to the differences in macro- and micromorphological characteristics (i.e. the proportion of spicules to spongin). Sponges containing narrower branches suffered greater losses than those containing thicker, more robust branches (Wulff 1994a). In 1992, Hurricane Andrew resulted in the loss of 75–100% coverage of sponges in Florida, with encrusting sponges exhibiting less damage than erect or sprawling forms (Blair et al. 1994).

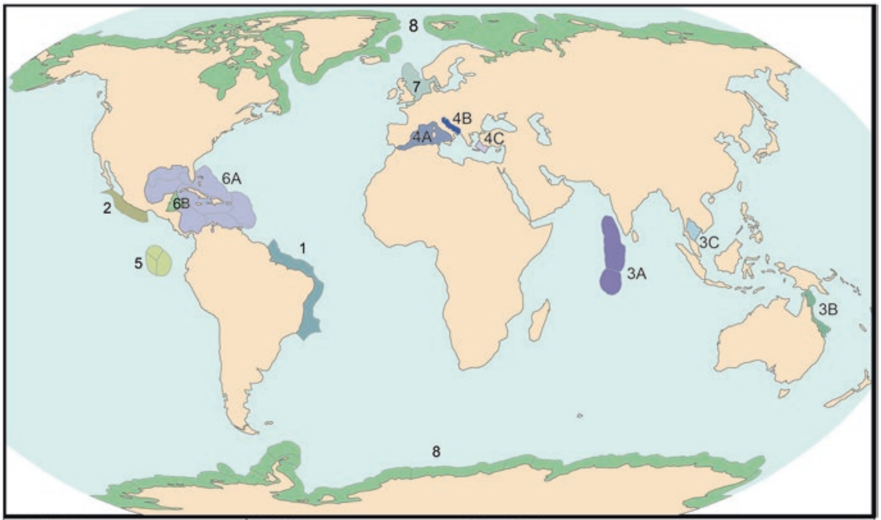
The location of sponge assemblages also appears to play a role in the extent of damage following a hurricane. Sites in protected areas experience reduced wave action, and sponges are often reported as having less damage and mortality than those in exposed areas. For example, during Hurricane Hugo in 1989, Witman (1992) found decreased cover of the sponge *Ectyoplasia ferox* in exposed areas due to dislodgement on the Virgin Islands, while Bell and Hall (1994) observed a high occurrence of detached non-resident sponges in South Carolina. Shallower protected areas had a greater number of patches of sponges in comparison to those in exposed areas following the hurricane. Similarly, Blair et al. (1994) found a greater loss of the sponge assemblage in offshore reefs versus inshore reefs, which served as a buffer to the increased wave action.

While there are many reports of significant damage and mass mortalities following extreme disturbance events, there are also numerous reports of resilience in sponge assemblages. Stevely et al. (2010) found that while there was a slight decrease in sponge abundance in Florida following Hurricane Wilma in 2005, in general, long-lived sponges tended to be more resistant and continued to dominate post-storm, suggesting that sponges have the ability to recover quickly. Similarly, Schönberg and Burgess (2013) found a high survival rate of bioeroding sponges following Cyclone Yasi in the Great Barrier Reef (GBR), and Fenner (1991) found that Hurricane Gilbert in 1988 resulted in only minor damage to sponge populations in Cozumel, with the only visible disturbance to sponges being a thin layer of sand covering the sponges. Sponges are thought to be fairly resilient to environmental changes caused by extreme disturbance events, and increases in sediment following a storm may be better tolerated by sponges than other reef organisms, as there have been many reports of sponges tolerating and even thriving in highly sedimented environments (Bell et al. 2015).

6.6 Impacts of Large-Scale Climatic Impacts of Sponges: Case Studies (Fig. 6.3)

6.6.1 *Atlantic Coral Reefs: Brazil*

There have been a number of recent studies describing the influence of ENSO events, particularly El Niño on coral reef communities, including sponges in Brazil (Figs. 6.3 and 6.4). The 1997–1998 ENSO event had different effects throughout the



LOCATION	CAUSE	RESPONSE
1. BRAZIL	1997-98 El Niño	Sponge resilience, some sponge mortality
2. EASTERN PACIFIC (MEXICO)	2001-06	Interannual variability correlated with ENSO events
3. INDO-PACIFIC		
A. CENTRAL INDIAN OCEAN	1997-98 El Niño	Possible sponge resilience and increased abundance
B. GREAT BARRIER REEF	1997-98, 2002-03 El Niños	Sponge resilience with subsequent increased abundance of bioeroding sponges
	2010-11 La Niña	Reduced reproductive output
C. GULF OF THAILAND	1997-98 El Niño	Reduced reproductive output of *Petrosia*
4. MEDITERRANEAN	Heat waves from:	
A. NORTHWESTERN BASIN	1999, 2003, 2008, 2009	No sponge resilience, mass mortality of sponges
B. ADRIATIC	1983, 2009, 2011	Limited sponge resilience, mass mortality of sponges
C. KOS ISLAND (GREECE)	SST warming between 1981-2013	Increase in abundance of some massive, submassive and encrusting sponge species
5. GALAPAGOS	1982-83 El Niño	Sponge resilience, no mortality of sponges
	1997-98 El Niño	Sponge resilience, no mortality of sponges, increase in sponge abundance & diversity
6. CARIBBEAN	Various temperature anomalies from 1990-2010	*Xestospongia* bleaching
A. CARIBBEAN WIDE	1987 unknown temperature event	Mortality of sponges
B. BELIZE	1998-99 La Niña	Mass coral bleaching and large increase in *Chondrilla* cf. *nucula*
7. NORTHEASTERN ATLANTIC	2006 heat wave	Mortality of sponges
8. POLAR	No information	

Fig. 6.3 Summary of studies where temperature has impacted sponge assemblages including information on the event causing the impact and consequences of the event. Map adapted from Spalding et al. (2007)

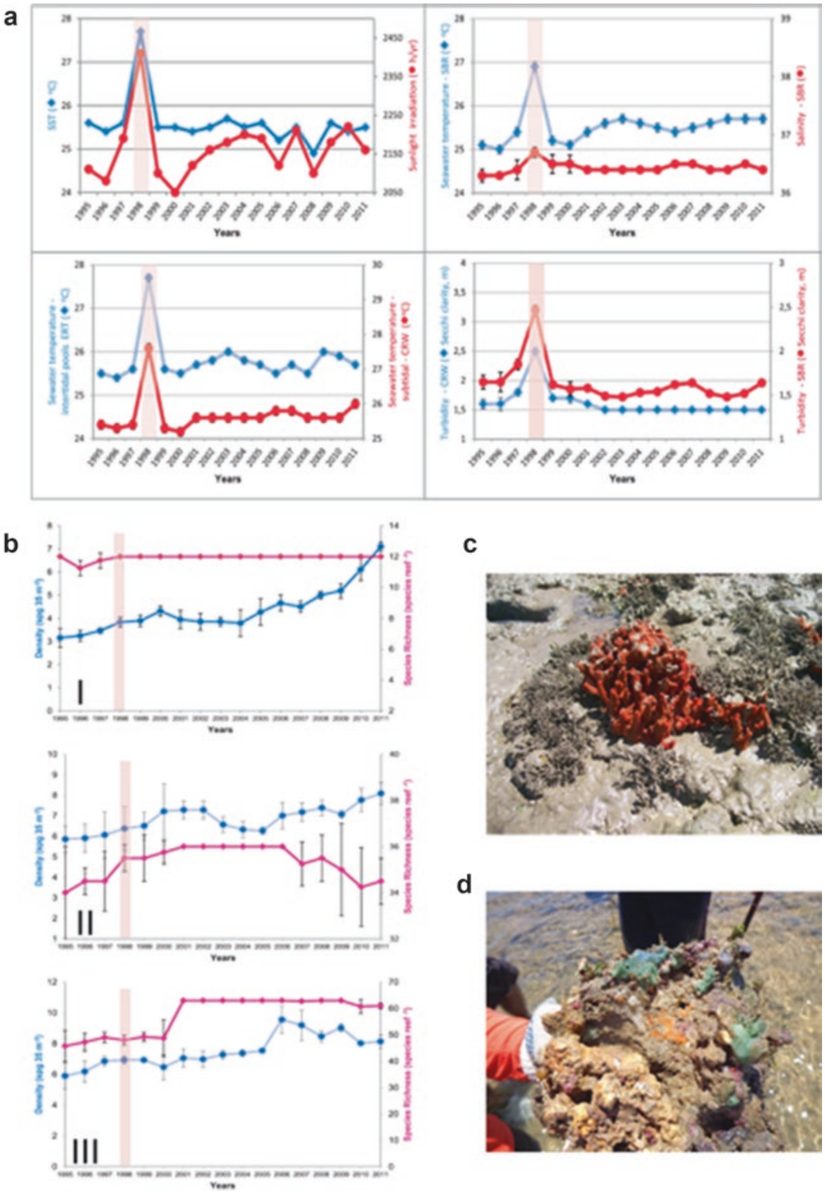


Fig. 6.4 (**a**) Summary of wide-scale and locally measured environmental variables recorded from the studied reefs throughout the sampling period in Bahia in Brazil, demonstrating changes in ambient conditions during the 1997–1998 El Niño period. (**b**) Changes in sponge abundance and richness (mean ± SE) of the sponge assemblage recorded over a 17-year period (1995–2011) including the severe 1997–1998 El Niño (I) reef tops, (II) walls and (III) shallow banks. (**c** and **d**) Examples of sponges that increased in abundance (**c**) *Tedania ignis* and (**d**) *Haliclona manglaris*, *H. caerulea* and a small patch of *Cliona celata* (complex). Redrawn with permission from Kelmo et al. (2014)

Brazilian region, with increased rainfall and flooding experienced in the southernmost and central states, while the northeastern states experienced devastating droughts because of abnormally reduced rainfall in the region (Rodrigues et al. 2011). The coral reefs from northern Bahia in Brazil have evolved under high temperature and turbidity conditions compared to other Atlantic coral reefs, resulting in a relatively low diversity coral assemblage. In 1995 a long-term monitoring programme was established along the northern coast of the state of Bahia in order to observe temporal and spatial patterns of biodiversity and community structure, including sponges. This monitoring is still continuing and therefore encompassed the 1997–1998 El Niño period.

There have been two studies describing the changes in sponge assemblages as a result of the 1997–1998 ENSO event. The first study (Kelmo et al. 2013) described the sponge assemblages from three contrasting subtidal reef habitats (reef tops, walls and shallow banks) at four sites each year between 1995 and 2011. The observations based on both univariate and multivariate analyses found sponges to be resilient to the event as there was no significant difference in sponge assemblage composition between immediately pre- and post-ENSO years for any of the habitats (Fig. 6.4). Perhaps most importantly, this was in stark contrast to the responses of other organisms including corals, echinoderms, bryozoans, and ascidians, which all suffered mass mortalities as a result of the ENSO event. Interestingly, although the sponge abundance was not different between the years preceding the ENSO event and immediately after, there has been a subsequent increase in sponge abundance since the event, particularly in bioeroding species, presumably due to increased space available and dead substrate to colonise. In a later study by the same authors, Kelmo et al. (2014) examined the response of emergent intertidal reef fauna, including sponges to the same event, with the expectation that these species would be more tolerant to extreme temperature events as they are likely to experience wider temperature fluctuations on a regular basis. In a similar way to the subtidal fauna, sponges were unaffected by the temperature rise, which caused mass mortality in other taxa. Furthermore, sponges once again increased in abundance following the event, however, in these lower diversity environments, so did the abundance of corals.

6.6.2 East Pacific Ocean: Mexico

ENSO events have had a long-lasting impact history on coral reefs in the eastern Pacific. During the last three decades, high (El Niño) and low (La Niña) sea temperatures associated with ENSO have caused bleaching and coral mortality in many areas (Toth et al. 2012). Along with triggering coral bleaching and subsequent mass mortality, ENSO events have also resulted in changes in composition and abundance of invertebrates (Hernández et al. 2010) and vertebrates on coral reefs (Glynn et al. 2014).

ENSO events have also been shown to correlate with variation in sponge assemblages in the eastern Pacific Ocean. Carballo et al. (2008) examined the temporal variability in shallow-water (5 m) sponge assemblages on a rocky coast located off

Venados Island in the centre of the bay of Mazatlán (México) over a 5-year period. In addition to correlating their data to local environmental drivers, these authors also correlated the variability they observed with two indices for global climate variability. The first was the Southern Oscillation Index (SOI), where sustained negative values of the SOI indicate El Niño episodes. Negative SOI values are usually characterised by sustained warming of the central and eastern tropical Pacific Ocean and increased convection or cloudiness in the central tropical Pacific Ocean. In contrast, positive SOI values are associated with La Niña episodes, where the waters in the central and eastern tropical Pacific Ocean become cooler. La Niña events are also associated with stronger than normal (easterly) trade winds across the Pacific Ocean. The second index was the Multivariate ENSO Index (MEI), which is based on six main variables measured over the tropical Pacific: sea-level pressure (P), zonal (U) and meridional (V) components of the surface wind, sea surface temperature (S), surface air temperature (A) and total cloudiness fraction of the sky (C). MEI integrates more information than other indices for the overall monitoring of the ENSO phenomenon and worldwide correlations with surface temperatures and rainfall and reflects the nature of the coupled ocean atmosphere system better than either component separately.

The study by Carballo et al. (2008) found low abundance of sponge species (from 0.1 to 0.5 sponges m^{-2}) but high total number of species per sampling event (between 14 and 21). The sponge assemblages were highly variable and dynamic, and although a consistent short-term pattern was found in most of the years sampled, there was considerable interannual variability. Local winds were thought to play a key role in explaining the short-term intra-annual patterns. During the rainy season and during the transition between the dry and rainy seasons, the winds coming from the southwest increased the net sediment movement, which appears to negatively influence the sponge assemblages. The interannual variability in the sponge assemblages also correlated positively with wind speed (88% of the variance observed) and sediment deposition (69% of the variance observed) but even more strongly with the SOI and MEI (82% and 88% of the observed variance for MEI and SOI, respectively). Similarly, Ávila et al. (2011) reported high sponge biomass washed ashore in the bay of Mazatlán between spring and summer. These authors found a strong correlation between sponge deposition and changes in wind direction, wave patterns and high levels of sediment resuspension, all indicating a high-energy system. These results suggest that sponge assemblages in this region (and likely other components of the benthic fauna) are controlled by different factors at a range of temporal scales but mostly by relatively large-scale process.

6.6.3 Indo-Pacific

The 1997–1998 ENSO event and the associated widespread bleaching and mortality of scleractinian corals constituted one of the most severe large-scale coral reef disturbances in recent history (Spalding et al. 1998). Some of the worst hit regions during this event were the reefs within the Maldives-Chagos region of the north-western Indian Ocean with up to 90% coral mortality (Sheppard 1999; McClanahan 2000). Unfortunately, prior to this event, coral reef monitoring was primarily focused on changes in the abundance of reef-building corals, and as a consequence, we know very little of the impact on other important benthic taxa such as sponges. Studies in the region comparing the benthic composition at the same sites pre- and post-El Niño are hampered by this lack of baseline data. For example, a study by McClanahan (2000) found that sponges occupied approximately 2% of the benthos in the Maldives and Chagos 1 year post-El Niño but could only assume that this was an increase on pre-1997 levels as there were no reliable pre-event data. The inevitable increase in dead substrate and coral rubble following such mass mortalities also provides a habitat for bioeroding endolithic sponges. In the Chagos (in 2001), widespread rubble was found to have a sponge infestation rate of 81% (Sheppard et al. 2002), although again there were no baseline data for bioeroding sponge abundance pre-coral mortality, but it seems likely that the increase in coral rubble resulted in an increase in the abundance of these sponges.

The most studied reef system within the Indo-Pacific is the Australian GBR, which has had a number of temperature-related disturbance events in recent years. Despite this, there is still a paucity of information on the impact of these events on GBR sponges. The exception to this is bioeroding sponges; the GBR suffered two major bleaching events in 1998 and in 2002, resulting in reduced coral cover but an increase in bioeroding sponge abundance of 150% (Schönberg and Ortiz 2008). Increases appear to be dominated by certain resilient species, notably *Aka mucosa* on the upper reef flats and the photosymbiont-containing species *Cliona orientalis* and *Cliona caesia* on the lower reef flats and slope. However, not all sponges on the GBR are expected to benefit from large-scale temperature events. There is evidence that the reproductive output of a common reef sponge, *Carteriospongia foliascens*, is reduced during climactic anomalies. Wahab et al. (2014) charted the larval supply of this sponge over two reproductive cycles, the first of which coincided with a strong La Niña event that brought a 933% increase in monthly rainfall and a 2.1 °C increase in mean monthly temperature. The reproductive output of *C. foliascens* was found to be twice as high during the second cycle than under La Niña conditions (see above). Another common sponge on the GBR, *Rhopaloeides odorabile*, has been the subject of numerous studies that demonstrate an upper thermal tolerance for adult sponges of 31–32 °C (Webster et al. 2008; Pantile and Webster 2011; Massaro et al. 2012). This threshold is ecologically relevant as inshore waters periodically exceed 30 °C on the GBR (AIMS 2016) at which temperature some species of scleractinian corals also bleach (Berkelman and Willis 1999). Interestingly, the larvae of this species are much more thermally tolerant than the adults, being able to withstand temperatures up to 36 °C, although the ecological significance of this resilience is unknown.

6.6.4 Mediterranean (NW Basin)

The Mediterranean Sea is a semi-enclosed basin, which means it's likely to react faster to global climate change than open oceans (Bethoux and Gentili 1999; Lejeusne et al. 2010). An increasing trend in the mean SST has been recorded since 1980 in the Mediterranean Sea (Nykjaer 2009). Normally, SST and the temperature of the first 40 m of the water column show 3- to 6-year oscillations in the Mediterranean (Coma et al. 2009). However, an increase of 0.07 °C/yr. in the temperature of the upper water layer has been reported for a large part of the basin in the last few decades (Rivetti et al. 2014). In addition to this, there have been exceptional warm water events that have impacted the whole basin. These events have occurred as a consequence of heatwaves hitting Europe during the summer months rather than specific ENSO events. The summer of 2003 was the hottest ever recorded in Europe since 1500 (Luterbacher et al. 2004), and the heatwave had catastrophic effects on both terrestrial and marine ecosystems. The primary effect that these phenomena had on water basins was the stratification of the water column. If the stratification happens in early summer, surface water warms up even faster due to poor mixing, and this in turn results in a more pronounced layering (Coma et al. 2009). Increased temperatures and water stratification have been associated with large-scale mortality events of marine organisms (Walther et al. 2012), particularly for sessile benthic invertebrates that cannot move or migrate (Garrabou et al. 2009).

During the last few decades, the Mediterranean shallow-water benthic communities have experienced significant changes in taxa composition and distribution related to climatic change. Benthic communities of the north-western basin of the Mediterranean have been extensively studied, and mass mortality events of increasing frequency have been reported in the last few decades. The most catastrophic events recorded were those in 1999, 2003, 2008 and 2009. In 1999 a temperature anomaly was recorded in the NW Mediterranean, with temperatures of 23–24 °C down to 40 m deep for over a month (Perez et al. 2000). At least 28 species of benthic macroinvertebrates were decimated from Elba Island (Italy) to the Bay of Marseille (France). Mortality rates for gorgonians reached 100% in some sites (Cerrano et al. 2000). Among the sponges, the most heavily impacted were commercial species of the genera *Spongia* and *Hippospongia* (Perez et al. 2000). Sponge mortality was recorded in the upper 40 m of the water column, coinciding with the lower limit of the temperature anomaly. This event was the most dramatic ever recorded in the Mediterranean, being comparable to mass mortalities in other biogeographic regions such as the Caribbean in terms of number of species involved and geographic scale (Perez et al. 2000). In the 2003 summer heatwave, there was an even larger-scale mortality event of benthic organisms across 25 taxa (9 of which were sponge species) from the Gulf of Naples to the Balearic Islands. This mortality event coincided with a positive water temperature anomaly between 1 and 10 m depth at multiple locations across the whole Mediterranean (Garrabou et al. 2009). The depth range of the sponge mortality was between 15 and 30 m deep. More recent mass mortalities of sponges were recorded in 2008 and 2009. In these events, the most heavily affected species was *Ircinia fasciculata*, a phototrophic species (Cebrian et al. 2011). Cebrian et al. linked the increase in temperature to a drop in the phototrophic efficiency of *I. fasciculata*, probably due to a disruption of the symbiosis between the sponge and the cyanobacteria it harbours. According to the same study, the heatwave did not affect a second sponge species, *Sarcotragus spinosulum*, which harbours only heterotrophic bacteria.

The Northern Adriatic is the most highly productive basin in the Mediterranean resulting from high nutrient input into its semi-closed, shallow basin (Ott 1992). It is thought that the specialised environmental conditions are responsible for a high number of endemic species with the region holding 49% of the diversity in the Mediterranean. An increase in frequency of climatic anomalies in the summer is thought to have driven an increase in mass mortalities in this region (Di Camillo and Cerrano 2015). Extended summers of warm seawater temperatures and calm conditions prevent mixing and enhance water stratification, limiting food availability and resulting in extreme temperatures for benthic organisms (Walther et al. 2012; Di Camillo and Cerrano 2015).

In September 1983 in the Gulf of Trieste, all sponges were reported to have died in the first 2–3 days of a mass mortality event that affected an area of several hundred square kilometres (Stachowitsch 1984). The direct cause of sponge mortality was coating via mucus threads related to severe and rapid oxygen deficiency. One component of this oxygen deficiency was noted to be the development of an extremely strong thermocline caused by a hot summer in 1983 and low storm activity that prevented mixing that reduces stratification (Stachowitsch 1984). Thermal anomalies recorded in the Mediterranean basin in the summer of 2009 yielded numerous reports of extensive sponge mortality in the Northern Adriatic. During this event, 30% of the sponge assemblage was affected, represented mainly by three species of horny sponge: *Sarcotragus spinosulus*, *Ircinia variabilis* and *Spongia officinalis* (Gaino et al. 1992). In this case, the sponges were affected by an outbreak of sponge disease thought to be triggered by prolonged high seawater temperatures and calm sea conditions (Di Camillo et al. 2013). The onset of disease coincided with a peak in sea surface temperatures of over 27 °C in August, 2–3° higher than the average expected values. High temperatures were maintained throughout September until mid-October, when the temperature dropped to 20 °C and no further damaged sponges were observed.

A long-term study (25 years between 1987/1988 and 2012/2013) in the Ligurian Sea found significant changes in sponge populations over this period, with some sponges increasing in abundance and other species declining (Bertolino et al. 2016). For example, there were significant declines in the coverage of *Chondrosia reniformis*, *Phorbas tenacior*, *Acanthella acuta*, *Ircinia* spp., *Dysidea avara* and *Petrosia ficiformis*, and overall sponge coverage was significantly lower by 2012/2013. In contrast, some species also increased in abundance, including *Axinella* spp. and *Agelas oroides*, while other species abundance remained similar over the study period (*Cliona viridis* and a complex of red encrusting sponges). This demonstrates the contrasting impact large-scale climate can have on different sponge species.

In the same area of the Adriatic, another big mass mortality event was recorded in 2011 (Di Camillo and Cerrano 2015). Despite being unaffected by the mass mortality in 2009, during this event, the sponge *Chondrosia reniformis* was the most affected species, reducing in coverage by over 70% and almost completely disappearing from the study area. In this case, the authors noted that wave height and seawater temperature were not considered to be extreme enough to trigger mass mortality, suggesting that other environmental factors may also have played a role (Di Camillo and Cerrano 2015).

In the Aegean Isle of Kos, an increase in abundance by one order of magnitude of encrusting sponges has been reported for many sponges over a 30-year study. Over this period, water has warmed by several degrees, which has led to the invasion of herbivorous fish species that have decimated the algal beds allowing sponges to proliferate. The sponges in this location appear to be very tolerant to the water warming recorded in recent decades. Interestingly, once again not all sponges have increased in abundance, and many species have remained stable such as populations of the most common boring species, *C. viridis*, present in "beta" stage (Bianchi et al. 2014).

6.6.5 Galapagos Islands

The ecosystems of the coastal regions surrounding the Galapagos Islands have been some of the most affected by El Niño climatic fluctuations (Glynn et al. 2000). As the Galapagos Islands are situated very close to the equator, during non-El Niño periods, the islands experience a large amount of deep-water upwelling as the equatorial undercurrent which travels west to east intercepts the Galapagos Islands. This upwelling moves cool nutrient-rich waters from deeper to shallower environments within the photic zone. As this occurs, these nutrients reach shallower zones and fuel photosynthesis of phytoplankton, creating very dense phytoplankton populations. This cool water upwelling, along with the trade winds that blow west to east, creates an offshore surface current and assists in maintaining the shallow coastal environments at a fairly constant cool temperature (20–28 °C location and season dependent) (Dunbar et al. 1994). The high abundance of phytoplankton, nutrient-rich water and consistent cool temperature have been defined as the cause of the historical abundance and diversity of corals (Glynn and Wellington 1983), allowing the Galapagos Islands to become a hotspot for marine biodiversity. During El Niño events, the equatorial undercurrent and the trade winds are drastically reduced in strength. This allows water temperatures in shallow reef zones to rapidly increase (2–3 °C, Glynn et al. 2000) and heavily reduces the nutrient content and phytoplankton abundance. These combined effects have caused mass coral mortalities on the reefs of the Galapagos Islands through a dual effect of rapid increases in temperatures, leading to coral bleaching and a reduced feeding efficiency on phytoplankton. Coral mortality following the 1982–1983 El Niño event was estimated between 95% and complete coral mortality (Glynn and D'Croz 1990; Glynn et al.

2000). This led to knock on trophic impacts, reducing reef fish abundance, which utilise coral reefs as a habitat, and drastic reductions in the predators of these species such as penguins (Boersema et al. 2013) and fur seal (Aurioles and Trillmich 2008). Furthermore, reductions in coral reef-inhabiting fish species, specifically species that predate on sea urchins, such as triggerfish and hogfish (Dee et al. 2012), have been attributed to the large increases in urchin barrens and reduced benthic cover of macroalgae (Edgar et al. 2010). This reduction in macroalgae had severe implications for the local marine iguana populations (Nelson et al. 2004). However, despite all of these declines in the abundance of benthic reef species caused by El Niño periods, some species such as bioeroders appear unaffected and are even increasing in abundance as a result. Specifically sponge bioeroders of the genus *Cliona* spp. have been documented as having very high abundances post-El Niño mass coral mortality events (Scott et al. 1988). In addition to this, two species of encrusting sponge *Mycale (Carmia)* sp. and *Aplysilla* sp. were reported to be highly conspicuous post the 1998–1999 El Niño event (Witman and Smith 2003). Furthermore, from 1999–2000, the study also reported a threefold increase in the species diversity of sponges. With no major coral or macroalgae recovery observed between the 1982–1983 and 1998–1999 El Niño events or for 15 years post the 1998–1999 El Niño event (Edgar et al. 2010), there appears to be little hope for any drastic reversal of these benthic mass mortalities. This inference is even further compounded by predictions that with global climate change, El Niño events will occur more frequently (Timmermann et al. 1999). This may have major implications for sponge taxa of the reef systems surrounding the Galapagos Islands. Their apparent relative tolerance to these changing environmental conditions compared to other sessile reef invertebrates suggests the potential for these reefs to remain dominated by sponges (Bell et al. 2013).

6.6.6 Caribbean

The Caribbean has experienced a number of major thermal anomalies since the 1980s, which has resulted in bleaching of both corals and sponges. A major temperature-associated bleaching event beginning in the summer of 1987 and intensifying during the autumn was a Caribbean-wide phenomenon affecting a wide range of benthic invertebrates, including sponges. Affected species included *Chondrilla nucula*, *Anthosigmella varians*, *Cliona aprica*, *Spheciospongia* sp., *S. vesparium*, *Xestospongia muta*, *Agelas* sp., *Mycale laevis* and *Aplysilla* sp. (Williams and Bunkley-Williams 1988; Zea and Duque Tobón 1989).

A sponge that has received considerable attention likely due to its conspicuous nature and recognised ecological importance is the giant barrel sponge *Xestospongia muta*. This Caribbean species is considered the most important habitat-forming reef organism in this region due to its large size and ability to pump vast quantities of water, as well as its productivity due to the *Synechococcus*/*Prochlorococcus* clade of photosynthetic cyanobacterial symbionts that it harbours (Steindler et al. 2005). Two types of bleaching have been described for *X. muta*: the more common cyclical bleaching, from which the sponges are able to recover, and fatal bleaching, which affects <1% of the population and is often associated with "sponge orange band (SOB) disease", the latter of which typically results in sponge death (Cowart et al. 2006; López-Legentil et al. 2008). Both types of large-scale bleaching events have been reported throughout the Caribbean, including Cuba and Mexico (Gammill and Fenner 2005), Belize and the Florida Keys (Gammill and Fenner 2005; McMurray et al. 2011), Puerto Rico (Vicente 1990), Curacao (Nagelkerken et al. 2000), the Bahamas (Dennis and Wicklund 1993), and the US Virgin Islands (Angermeier et al. 2011). Although a number of these studies have linked such bleaching to increased seawater temperatures, more recent work by McMurray et al. (2011) suggests that high temperatures alone do not explain bleaching variability seen regardless of season. The authors suggest that bleaching is a complex response triggered by light availability and thermal sensitivity of *Synechococcus* symbionts (López-Legentil et al. 2008; McMurray et al. 2011).

It is worth noting that other mass sponge mortality events have been reported in Caribbean, although not specifically the result of extreme temperature events. For example, Wulff (2013) reported two large-scale mortality events in Belize in 2006 and 2011, and while the cause of the 2011 event was linked to a major plankton bloom, the cause of the mortality event in 2006 was unexplained. Sponge abundance decreased substantially, by 49% by 2007 and 71% by 2012. In a further example, widespread sponge mortality occurred in the Florida Keys between 1991 and 1995, and it was thought to be a result of successive blooms of the picoplanktonic cyanobacterium *Synechococcus* sp., although the exact mechanism of mortality remains unknown (Stevely et al. 2010).

Finally, on reefs in the central sector of the Belizean shelf lagoon, positive thermal anomalies during the La Niña phase of the ENSO cycle in 1998 resulted in very extensive bleaching-related mass mortality of scleractinian corals, some of the highest recorded in the Caribbean to date, with nearly 100% of the coral colonies completely killed by early 1999. The collapse of coral populations in Belize in 1998–1999 opened extensive areas that were colonised by *Chondrilla* cf. *nucula*, which grew rapidly (Aronson et al. 2002). The study suggested that this sponge is primarily opportunistic and was taking advantage of the space opened by coral mortality after mass mortality event provoked by extreme climatic events. Importantly, these authors also suggested that the presence of the sponge would inhibit the recovery of the reef as it reduces the space available to coral recruits.

6.6.7 Polar and Temperate Environments

Recorded incidents of mass mortality or detrimental impacts on sponges as a result of large-scale temperature events seem particularly rare in temperate and polar regions. There have been no reports from polar regions to our knowledge and only one report from a temperate region. In September 2006, researchers studying the seasonal growth rate of *Haliclona oculata* in the Oosterschelde estuary in Holland documented complete mortality of all monitored individuals. This was surprising considering that for the 8 years prior to the study, *Haliclona oculata* had been the most stable species present at the site. Researchers tentatively attributed the mortality event to unseasonable high seawater temperatures (23 °C) that were approximately 3 °C above the average normal temperature for the summer months. A lack of understanding of how extremes of temperature may affect Antarctic sponges is particularly worrisome considering the high thermal stability of the area; consequently, Antarctic species could be expected to exhibit limited tolerance to changes in temperature and may be future losers under climate change scenarios. This has been examined for some Antarctic invertebrates but not for sponges (Peck et al. 2014).

6.7 Cold-Water Event Impacts on Sponges

The majority of literature addressing detrimental effects of thermal anomalies on benthic communities has focused on warming events (see Lesser 2011 for a review). However, for coral reefs in marginal habitats, cold-water events can have equally severe consequences, particularly in shallow-water habitats. The bulk of existing literature has focused on the effects of these events on corals (Hoegh-Guldberg et al. 2005; Lirman et al. 2011), and only one has addressed cold-water effects on sponges (Colella et al. 2012).

As a result of extremely negative values of the North Atlantic Oscillation index, there was an unusual cold-water event in the Florida Keys in January 2010, resulting in water temperatures in some areas reaching a low of 4–12 °C, which is up to 20° lower than average recorded temperatures. In addition to causing extreme coral mortality and loss of coral cover in this area (Lirman et al. 2011), this event resulted in a significant decrease in live cover of other benthic invertebrates including sponges (Colella et al. 2012). Total sponge cover declined an average (±SE) of 3.8 ± 1.4%—2.3 ± 1.2% in many areas (Colella et al. 2012). Similarly, following prolonged exposure to cold-water masses, shallow coral reefs and seagrass communities in Morrocoy, Venezuela, suffered mass die-offs of many benthic species. Mortality in the sponge assemblages, however, varied widely; some species were completely eradicated, some reduced and some remained completely unaffected (Laboy-Nieves et al. 2001). There are a few anecdotal reports of species die-offs due to cold-water events in other parts of the world. The North-East Atlantic sponge *Celtodoryx girardae* was documented as having a mass mortality event during the winter of 2003 (Perez et al. 2006), although the exact impact of an extreme cold-water event is difficult to ascertain.

During January 2010 cold-water event in the Florida Keys, sponges were observed to bleach, demonstrating a loss of colour attributed to symbiotic cyanobacteria loss and correlated to high temperatures. This response was similar to coral bleaching and coral-symbiont disruption reported following cold-water events (Hoegh-Guldberg et al. 2005; Kemp et al. 2011). This suggests that sponges may also exhibit physiological stress in response to prolonged or severe exposure to low temperatures that affects the sponge-symbiont relationship and similar to what has been reported in response to increased seawater temperatures (Fromont and Garson 1999; Celliers and Schleyer 2002; McMurray et al. 2011). Although coral mortality following this event was catastrophic, sponges in the Caribbean have been documented to dominate the benthos in abundance following events deleterious for coral populations (Aronson et al. 2002).

The general lack of representation of sponges in most monitoring programmes (Wulff 2001) makes it difficult to determine the extent of sponge ranges and therefore their thermal tolerance. Fowler and Laffoley (1993), as part of the UK Nature Conservancy Council marine monitoring programme at Lundy Island and Isles of Scilly in southwest England, found that some sponges at the northern limits of their distribution showed apparent shrinkage in years known to be abnormally cold. Furthermore, the authors reported sponge degeneration and mortality associated with winter years when seawater temperatures were very low (Fowler and Laffoley 1993). In contrast, a survey of temperate hard-bottom reefs of coastal Georgia, USA, found nine species that had previously been considered to be tropical sponges (Freeman et al. 2007). These large extensions of previously known ranges may suggest that some species have a larger range of tolerance to temperature than previously thought.

6.8 Secondary Impacts of Sponge Responses to Large-Scale Climatic Variation

Global data on the impacts of thermal anomalies on sponges show contrasting responses in different geographical locations. In some cases, sponges are unaffected by the anomalies and have subsequently increased in abundance as other groups (particularly corals) have declined, while in other locations, sponges have experienced mass mortalities. Given the important functional roles that sponges play in marine systems (Bell 2008), any changes in abundance are likely to have other secondary impacts in marine systems. Furthermore, given what is already known about sponge functional roles, these secondary impacts should be relatively easy to predict but will depend on the species affected and the geographical location. For example, sponges have major impacts on the overlying water column (e.g. Perea-Blázquez et al. 2012), and changes in their abundance may have significant impacts on food availability and nutrient fluxes and therefore have important implications for other suspension-feeding organisms. However, this is likely to be most important on coral reefs, as food for sponges is not generally considered to be limiting in temperate or polar regions, although there are exceptions to this. Also of concern are changes in the abundance of bioeroding sponges on coral reefs, which seem to be far more tolerant than corals to high temperature events and then proliferate once corals die (Schönberg and Ortiz 2008), presumably as a result of increased substrate availability and reduced competition with corals. Such shifts to predominately bioeroding species are likely to alter the erosion-accretion balance and threaten longer-term reef sustainability and function. These secondary impacts need to be considered to fully understand the importance of thermal anomalies on sponges and the wider benthic community.

Substantial changes in the abundance of sponge species caused by climatic variation also have the potential to influence ecosystems at a community level. Sponges have the capacity to pump water through their aquiferous systems at high rates, with estimates that an average-sized barrel sponge can pump approximately 15,000 litres of seawater per hour (Schrope 2009). Sponges also generally have high filtering retention efficiencies of microorganisms from this pumping, for example, 89–96% retention of bacteria and picoplankton cells for *Tethya* spp. (Perea-Blázquez et al. 2012). Therefore, an increase in the abundance of sponges within an ecosystem could lead to a decrease in the concentration of picoplankton in the water column, which would potentially be detrimental for local populations of zooplankton and other benthic filter feeders. Sponges obtaining carbon from the water column also provide an important benthopelagic link in marine carbon cycle (de Goeij et al. 2013), and the photosymbionts of some sponge species represent a source of primary productivity (Wilkinson 1987), with this source of carbon utilised by spongivorous species (Wulff 2006). Furthermore, many infaunal and epifaunal taxa utilise sponges as a habitat, with this highlighted by 2235 invertebrates (>1 mm) of 75 species being found within 19 specimens of the sponge *Mycale microsigmatosa* (Ribeiro et al. 2003). Therefore, increases or decreases in sponge populations are likely to have direct effects on spongivorous taxa, such as certain nudibranch (Thompson et al. 1982), fish (Wulff 1994b) and turtle (Meylan 1988) species, and also on any sponge-associated infaunal or epifaunal invertebrates. Increased sponge population sizes will result in increased sponge benthic coverage, which could result in reduced larval settlement of other sessile benthic taxa, especially as some sponge species have been shown to have allelopathic chemicals (Chaves-Fonnegra et al. 2008) and coral disease causing microbes within their tissues (Negandhi et al. 2010). Substantial changes in the abundance of bioeroding sponge species will also likely have an impact on the benthic topography (Holmes 2000), with this having implications for marine species which rely on substrate heterogeneity for predator avoidance.

For locations where sponges constitute the dominant benthic component, temperature-related removal of these organisms could alter ecosystem functioning and stability across a very broad scale. In both the Arctic and Antarctic, polar coastal areas which are covered in sea ice for the majority of the year are dominated by a diverse community of sessile invertebrates of which sponges are often key components. However, increases in seawater temperature and the resultant decrease in the extent of sea ice and shading of the seabed have resulted in some shifts from invertebrate to algal dominated states. Such ecosystem shifts have been observed in Svalbard (Kortsch et al. 2012) and the Eastern Antarctic (Clark et al. 2013), the consequences of which are hypothesised to include (but are not limited to) a reduction in water column modification, shifts in the source of primary production and changes in upper trophic level composition.

6.9 Conclusions

Although there is an increasing amount of data becoming available on the temporal variability in sponge assemblages allowing us to gain better insights into the impacts of major climatic events, we still have a very poor understanding of responses compared to corals. Few studies have assessed long-term ecological data that are critical for assessing the effects of climate change. The information available suggests that temperature has major effects on the physiology and ecology of sponges but that some sponges do have some tolerance and resilience to these events. Given that the occurrence and severity of ENSO events are expected to increase in the future, sponges may become a more dominant feature of some benthic communities. However, it is also true that sponges have experienced some mass mortality events so the resilience may be location or species specific.

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Chapter 7
Bioeroding Sponges and the Future of Coral Reefs

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Abstract Bioeroding sponges play a central role in carbonate cycling on corals reefs. They may respond differently to habitat deterioration than many other benthic invertebrates, because at some locations, their abundances increased after disturbance. We reviewed literature on these sponges in context of environmental change and provide meta-analyses at global level. A difficult taxonomy and scarce scientific expertise leave them inadequately studied, even though they are the best-known internal bioeroders. They are sheltered within the substrate they erode, appear to be comparatively resilient against environmental change and can have heat-resistant photosymbionts and 'weedy' traits, including multiple pathways to reproduce or disperse and fast growth and healing abilities. Especially temperature stress appears to disable calcifiers stronger than bioeroding sponges. Moreover, increases in bioeroding sponge abundances have been related to eutrophication and disturbances that led to coral mortality. Chemical sponge bioerosion is forecast to double with doubled partial pressure of carbon dioxide, but reduced substrate density may counteract this effect, as dominant sponges erode more in denser substrates. Case examples portray shifting impacts of bioeroding sponges with environmental change, with some reefs already being erosional. Most available data and the largest known species record are from the Caribbean. Data from the Coral Triangle and India are largely restricted to faunistic records. Red Sea, Japanese and cold-water reef

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bioeroding sponges are the least studied. We need more quality research on functions and interaction effects, about which we are still insufficiently informed. With many calcifiers increasingly failing and bioeroding sponges still doing well, at least at intermediate levels of local and global change, these sponges may continue to significantly affect coral reef carbonate budgets. This may transform them from valuable and necessary recyclers of calcium carbonate to problem organisms.

Keywords Bioerosion • Porifera • Coral reefs • State of research • Global change • Ocean acidification

7.1 Introduction

Worldwide coral cover is declining as a consequence of various forms of disturbance (e.g. Hoegh-Guldberg 2011). In recent publications, sponges have been predicted to be more resilient to environmental change than corals, to gradually replace coral reefs and to form functional sponge habitats that may continue to provide vital ecosystem services where coral reefs succumb (Pawlik 2011; Bell et al. 2013; Kelmo et al. 2013; McMurray et al. 2015 and other contributions in this volume). However, many reef sponges have also increasingly experienced disease and mortality (e.g. Gammill and Fenner 2005; Wulff 2006; Angermeier et al. 2011, 2012; Olson et al. 2014 and references therein), and such predictions may not uniformly apply. Also, reef community shifts favouring sponges are not always beneficial. Some reports concerned epidemy-like occurrences of detrimental sponges that can themselves kill corals (e.g. Coles and Bolick 2007; Benzoni et al. 2008; Reimer et al. 2011). Bioeroding sponges may belong to these 'aggressive' sponges, but they have a special role in addition to that of other sponges. Where their abundances increase or their activities are amplified beyond normal levels, they can significantly unbalance local bioerosion rates and carbonate budgets (Rose and Risk 1985; Rützler 2002a; Ward-Paige et al. 2005; Schönberg and Ortiz 2009; Marulanda-Gómez et al. 2017). However, it remains to be seen how uniform, sustained and widespread such shifts may be, and which species and morphologies react positively to which environmental clues (Ramsby et al. 2017). Therefore, it is important to understand the biology and ecological roles of bioeroding sponges, and of bioerosion in general, and how they may change in presently changing environments (Schönberg et al. 2017).

Neumann (1966) defined bioerosion as the breakdown of hard materials by living organisms. For calcareous materials, it is the natural counterpart to biogenic calcification, and over time, it has been recognised as a vital factor for habitat health and carbonate budgets (e.g. Holmes et al. 2000; Schönberg 2015). Notwithstanding, outputs in context of bioerosion make up only a small fraction of research on calcification, but interests in bioerosion have significantly grown over time (Schönberg and Tapanila 2006a; Fang and Schönberg 2015; Schönberg 2015). The proportional contribution of bioerosion to research has particularly increased with rising concerns about coral reef demise, ocean warming and acidification (Schönberg 2017).

Within the field of bioerosion and in comparison to other taxa, our information on sponges is relatively good, and respective research extends over more than

200 years (Schönberg and Tapanila 2006a; Fang and Schönberg 2015). The first documented bioeroding sponge was '*Spongia peziza*' from South Carolina (Bosc 1802), but it was not accepted under that particular name and later synonymised with *Cliona celata*. De Lamarck (1815) produced the first formal descriptions of clionaid sponges (as *Alcyonium*), the sand-dwelling reef sponge *Cervicornia cuspidifera*, and the massive species *Spheciospongia purpurea* and *Spheciospongia vesparium*. The first clionaid recognised as a bioeroder was the Scottish *Cliona celata* described by Grant (1826), which became the type species of all clionaid sponges. Ever since, an increasing number of species of bioeroding sponges have been described at a rate of approximately 13 species per decade (Fig. 7.1), with many additional species still awaiting discovery, formal description, or clear distinction of species grouped as taxonomically difficult species complexes. With a growing understanding that this guild is diverse and has an important role in carbon-

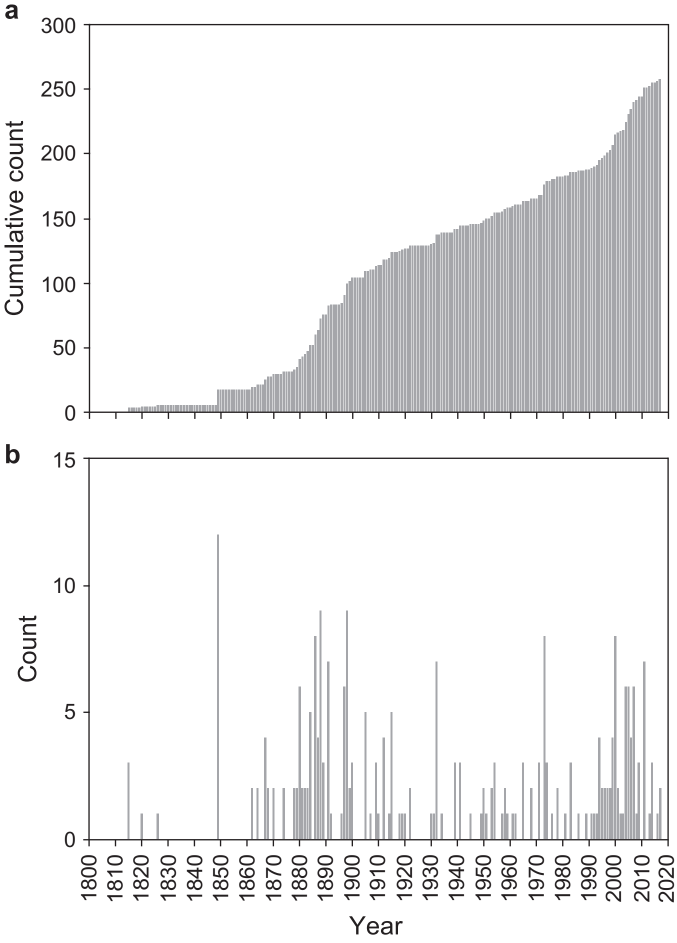


Fig. 7.1 Descriptions of new species of bioeroding sponges since 1826, based on the species listed in Table 7.1. (**a**) Cumulative count. (**b**) Counts per year. Please note that the record for 2017 is incomplete and reported two species at the time of this publication

ate cycling, related research has become increasingly intense and diverse but mostly focused on coral reefs in warm-water environments (Schönberg and Tapanila 2006a; Fang and Schönberg 2015). A full account of the historical development in bioeroding sponge research can be found in Schönberg (2008, and references therein). In short, early investigations looked into whether and how these sponges were able to bore into calcareous substrates. During the 1970s and 1980s, bioerosion research commonly assessed how much sponges proportionally contributed to macrobioerosion (e.g. MacGeachy and Stearn 1976; MacGeachy 1977; Scoffin et al. 1980). From the late 1990s onwards, the main foci in bioeroding sponge research moved further into the functional context, quantifying bioerosion rates and studying the sponges' physiology and ecology in more detail (e.g. reproduction, metabolite production, interaction of biological processes and between different organisms; see Schönberg 2008). As a result, sponges are one of the best-studied taxon groups in bioerosion research (Schönberg and Tapanila 2006a; Fang and Schönberg 2015), yet in comparison to common calcifiers such as corals, they are still not receiving enough attention (Fang and Schönberg 2015).

A recent literature review provided a summary of present knowledge on bioerosion in context with ocean acidification (OA) and overviews of definitions, research challenges and knowledge gaps (Schönberg et al. 2017). The present paper focuses specifically on bioeroding sponges in context with various local and global change parameters and in reference to coral reef environments.

7.2 Materials and Methods

The present review on bioeroding or 'endolithic' sponges is based on the authors' literature collections amended by keyword searches in Google Scholar (2016) and includes peer-reviewed publications, theses and technical reports.

All species names in this publication were checked for their present taxonomic status (van Soest et al. 2017; WoRMS Editorial Board), and taxon authorities are displayed in Appendices A (for bioeroding sponges) and B (all other taxa). As some genus names of the sponges we discuss start with the same character, we did not abbreviate species names in the text.

We screened literature on bioeroding sponges with different habits and ecological roles and aimed to establish how many bioeroding sponges are known and where they occur. For clionaid sponges, four morphologies or relationships to bioerosion were defined: *alpha* (endolithic-papillate), *beta* (mainly endolithic- or mainly epilithic-encrusting), *gamma* (free-living, different morphologies), and recently *delta* (endopsammic or buried in sediments, can be massive, encrusting or endolithic; Fig. 7.2; see also Schönberg 2015; Schönberg et al. 2017). The different morphologies represent different species or developmental stages, depending on the taxon (Ferrario et al. 2010; Xavier et al. 2010; de Paula et al. 2012). Traditionally, sponges were only regarded as active bioeroders if they were endolithic (inhabiting hard substrate; see definitions in Schönberg et al. 2017), and species with other

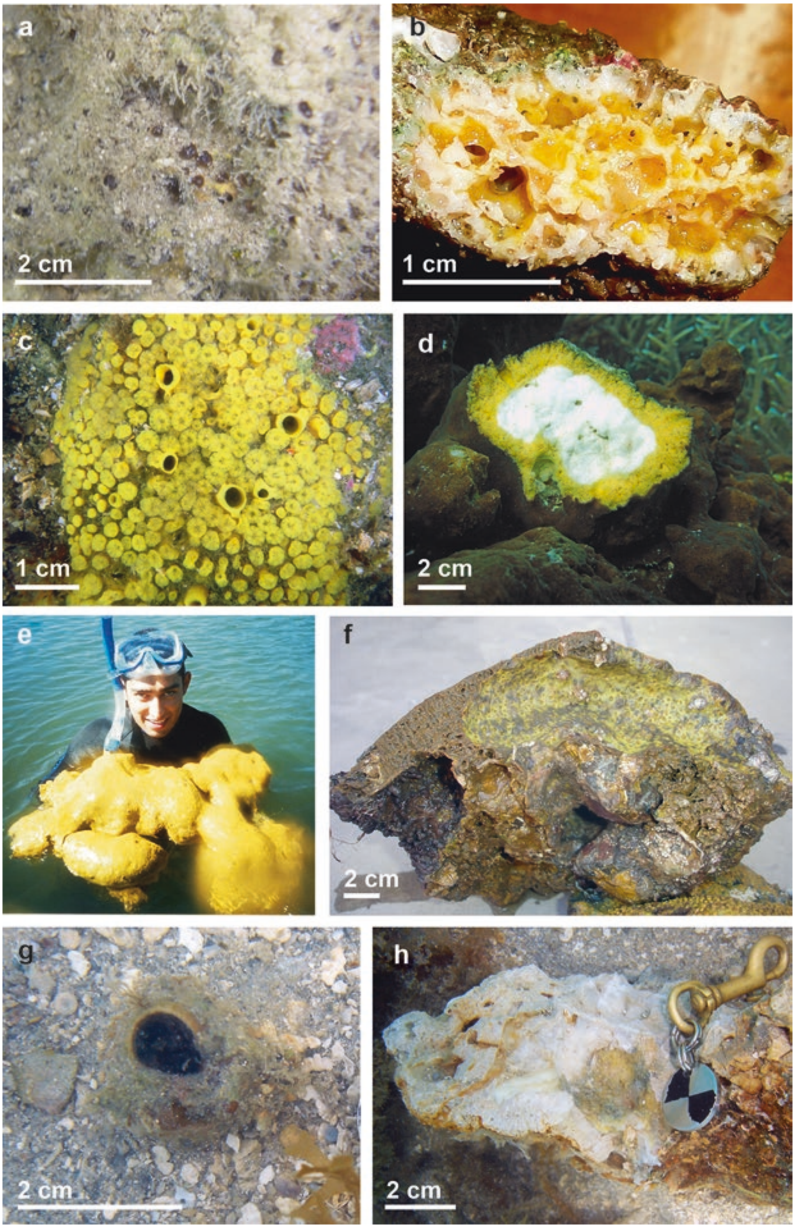


Fig. 7.2 Morphological characters of bioeroding sponges, surface (*left*) and internal views (*right*). *Alpha* morphology: (**a**) *Cliona caesia*, central Great Barrier Reef, 2 m. (**b**) *Cliona tropicalis*, Mexican Pacific, sampled from 4–5 m. *Beta* morphology: (**c**) *Cliona californiana*, Mexican Pacific, 3 m. (**d**) *Cliona orientalis*, southern Great Barrier Reef, 10 m. *Gamma* morphology: (**e**) *Cliona californiana*, Mexican Pacific, sampled from 2–3 m. (**f**) *Cliona californiana*, Mexican Pacific, sampled from 3 m. *Delta* morphology: (**g**-**h**) *Spheciospongia* sp., central Great Barrier Reef, intertidal

morphologies were largely regarded as inactive (e.g. Hatch 1980). As epilithic-encrusting *beta*, *gamma* and *delta* forms can live endolithically in early life stages or erode with basal parts (e.g. Rützler 1975; Westinga and Hoetjes 1981; Kelly 1986; Rützler 2002b, c; Pica et al. 2012) or retain their bioerosion capability and commonly degrade coarse particles they embed in their tissues (e.g. Hartman 1958; Nicol and Reisman 1976; Hatch 1980; Calcinai et al. 1999; Ise et al. 2004; Schönberg 2015), the present paper includes all four morphologies in the term 'bioeroding sponges'. The most pertaining literature was available on the *alpha*- and *beta*-growth forms, which are the forms most active in bioerosion.

We disregarded species names that were not based on a recent biotaxa, the sponges, but on fossils, or that only described the bioerosion traces they made (e.g. the *Vioa* spp. sensu Duchassaing de Fonbressin and Michelotti 1864, *Cliona bullini* sensu Annandale 1920; more detailed comments in Appendix A). We relied more strongly on recent descriptions and were more likely to ignore older ones that did not contain information on the spicules and were lacking other basic information. The lack of descriptive detail meant that we could not even tentatively match some historic descriptions against more recent ones which may have represented the same species (e.g. for the *Vioa* spp. sensu Nardo 1840 and *Thalysias saxicava* and the *Euryphylle* spp. sensu Duchassaing de Fonbressin and Michelotti 1864). While we also became aware of some doubtful genus allocations within the Clionaida, we deferred most taxonomic decisions to future publications, as this was beyond the scope of the present publication. Apart from accepted species, some partially identified species or OTUs (operational taxonomy units) were also considered if they appeared to be different from others within the same bioregion. Molecular evidence for some supposedly 'cosmopolitan' species and spicular characters of some species suggested that a number of species names likely represented unresolved species complexes (e.g. Xavier et al. 2010; de Paula et al. 2012; Appendix A). Thus, depending on sample area or spicule characters, names were displayed with 'cf.' (Latin: *conferre* or Latin: *conformis*) to indicate that these species are very similar to and possibly conspecific with the formally described species of the same name or with 'aff.' (Latin: *affinis*) to signify that the sponges shared similarities with the respective species but were likely different (see Lucas 1986). These specifiers were placed in front of the genus if the genus was in question and between genus and species names to show that the genus identity had been established but the species still needs to be confirmed (following Bengtson 1988).

We made an effort to distinguish between true bioeroding sponges and endolithic 'nestlers' that may invade, but not enlarge pre-existing cavities (e.g. Annandale 1915a). Based on available literature and pending new results, this distinction could not always be conclusive. Recent findings indicated that the ability to bioerode may be more widely distributed than previously thought (Rützler et al. 2014), but at the same time, others questioned the bioeroder status of previously accepted species (Bertolino et al. 2013). We presently included the taxa listed in Table 7.1 as actively bioeroding, which resulted in 260 valid species of distinct, putative bioeroding sponges. Another 28 OTUs were entered as well, assumed to differ from the accepted species. We caution that the bioeroder status of genera with only a small proportion of bioeroding species should be validated in the future.

Table 7.1 Demosponge taxa that are presently accepted as having bioerosion capabilities and species that are very likely bioeroders

(Subclass) and order	Family	Species considered as bioeroders	Number of species per genus	Known morphologies per genus; reasons for inclusion as bioeroders	References for bioerosion capabilities
(Heteroscleromorpha)					
Clionaida	Clionaidae	All genera and species	154	*Alpha*, *beta* (mainly endolithic-encrusting), *gamma*, *delta*	Rützler (2002b)
	Spirastrellidae	All genera and species	23	*Beta* (mainly epilithic-encrusting, with basal parts able to erode), *gamma*[a]	Rützler (2002c)
Haplosclerida	Chalinidae	*Haliclona* (*Halichoclona*) *vansoesti*	1	Thick cushions, basally eroding	Rützler et al. (2014)
	Phloeodictyidae	All *Siphonodictyon* spp.	23	*Alpha and delta*, some with cavernous, some with porous bioerosion	Desqueyroux-Faúndez and Valentine (2002)
Poecilosclerida	Acarnidae	All *Cornulella* spp.	7[b]	*Beta* or *delta*, encrusting-insinuating, with fistules rising from the basal tissue	Kirkpatrick (1900a). van Soest et al. (1994). Hooper 2002 (and original descriptions)
		Cornulum johnsoni and *Cornulum virguliferum*	2	*Alpha or delta*, with small fistules	Rützler et al. (2014)
		All *Zyzzya* spp.	5	*Alpha*, *beta* (endolithic-encrusting), *gamma*, *delta*	Hooper and Krasochin (1989), Hooper (2002)
Suberitida	Halichondriidae	*Amorphinopsis excavans*[c]	1	Thinly encrusting (*beta*, basally eroding)	Carter (1887), Thomas (1979a)
Tethyida	Timeidae	*Timea oxyasterina*	1	Thickly encrusting (*beta*, basally eroding)	Rützler et al. (2014)

(continued)

Table 7.1 (continued)

(Subclass) and order	Family	Species considered as bioeroders	Number of species per genus	Known morphologies per genus; reasons for inclusion as bioeroders	References for bioerosion capabilities
Tetractinellida (Astrophorina)	Ancorinidae	*Dercitus* (*Stoeba*) *occultus* *Dercitus* (*Stoeba*) *plicatus* *Dercitus* (*Stoeba*) *simplex*	3	Insinuating, i.e. invading cracks; mostly encrusting	Sollas (1888a), Calcinai et al. (2000, 2004, 2008), van Soest et al. (2010); but see Bertolino et al. (2013), who maintained that *Dercitus* (*Stoeba*) *plicatus* inhabited pre-existing sponge borings
		Holoxea excavans *Holoxea furtiva*	2	Encrusting-insinuating	Boury-Esnault (1971), Calcinai et al. (2004a, 2008a)
	Pachastrellidae[d]	*Triptolemma endolithica* *Triptolemma simplex* *Triptolemma strongylata*	3	Encrusting-insinuating or endolithic (*alpha*?); *Triptolemma* spp. appear to initially penetrate live sponges, but the three listed apparently established as secondary bioeroders after displacing other endolithic sponges	Van Soest (2009), Bertolino et al. (2011)
	Thoosidae	All genera and species	32	*Alpha*	Rützler (2002d)
Tetractinellida (Spirophorina)	Samidae	*Samus anonymus*	1	*Alpha*	Rützler et al. (2014); but see Bertolino et al. (2013), who maintained that *Dercitus* (*Stoeba*) *plicatus* only inhabited pre-existing sponge borings

(Verongimorpha)					
Chondrosiida	Chondrosiidae	*Chondrosia reniformis*	(1)	Free-living (*gamma*)	Bavestrello et al. (1995)[e]
Verongiida	Aplysinellidae	*Aplysinella rhax*	1	Free-living (*gamma*)	De Laubenfels (1954)
		Suberea flavolivescens	1	Free-living (mostly *gamma*, but can be encrusting)	Rützler et al. (2014)

A small number of decisions affected the species counts, as outlined in Appendix A. A few Clionaida were excluded as taxa inquirenda, but *Pione cervina* was retained, despite unusual spicule characters. We also retained *Thoosa circumflexa* and *Thoosa letellieri* as good species. Due to its spicule characters, *Dotona davidi* was here counted as a poecilosclerid, not a clionaid. Based on Schönberg and Beuck (2007), we included *Siphonodictyon rodens*, which van Soest et al. (2017) regard as a synonym of *Siphonodictyon insidiosum*. Some smaller decisions did not affect the counts at family level but are detailed in Appendix A. A total of 260 species was regarded as distinct sponge species able to bioerode calcium carbonate.

[a] According to the diagnosis provided by Rützler (2002c), Spirastrellidae are encrusting. As the World Porifera Database (van Soest et al. 2017) lists encrusting, as well as massive specimens within the Spirastrellidae, a taxonomic revision is needed.

[b] We tentatively included ‘*Spiroxya*’ *davidi* in the count for *Cornulella* as we think it is an acarnid. We do not officially change the genus, however, because we did not access the type material.

[c] *Amorphinopsis excavans* may be a facultative bioeroder. Erpenbeck and van Soest (2002) rejected the bioeroder status, and the sponge has since been found coating non-calcareous surfaces (Lim et al. 2009). However, based on the strong opinion in the original description (Carter 1887), it is tentatively retained as a bioeroder.

[d] The other known species of *Triptolemma* were reported to insinuate in skeletons of ‘lithistid’ sponges, which originally suggested that this genus contains nestlers (Bertolino et al. 2011).

[e] *Chondrosia reniformis* was observed to etch quartz, not calcium carbonate (Bavestrello et al. 1995). It was thus not presently considered in context of coral reef bioerosion, even though it is a bioeroder.

Based on these conditions, we added some analyses to this literature review. The discovery of new species of bioeroding sponges over time was appraised using the World Porifera Database (van Soest et al. 2017) and our decision what species to include. Proportional contributions by sponges to macroboring and a global biogeography were established for the following reefal bioregions, including neighbouring areas as listed in Appendix A: Caribbean, Brazil, Gulf of Guinea, Red Sea and Persian Gulf, East Africa, India, northwestern Australia, northeastern Australia to Papua New Guinea, Coral Triangle, Japan, Central Pacific, Eastern Tropical Pacific and deep- or cold-water communities with important corals. We assessed bioeroding sponge distributions with special attention to their occurrences in coral skeletons but included a few accounts of sponges eroding mollusc shells or other materials if they occurred on reefs. The outcome represents a thorough literature search but is unlikely to be exhaustive. Parts of the pre-submission manuscript were given to other colleagues for early reviews and comments. Among other things, their feedback confirmed or augmented the faunistic records for some of the bioregions.

Previously unpublished data on the massive bioeroding sponge *Cliona californiana* in the Mexican Pacific served to demonstrate wound-healing capabilities in clionaids. During this study, two cores of 1 cm depth and 1 cm diameter were extracted in the field from each of 25 marked specimens at 3–4 m water depth. At intervals, the resulting wounds were monitored over 40 days, and the healing speed was compared between summer and winter by assessing the reduction of the scar diameter.

7.3 Bioeroding Sponges on Coral Reefs

7.3.1 Why Bioeroding Sponges Are Difficult to Study

Due to a number or reasons, bioeroding sponges are regarded as a difficult taxon to study (Table 7.2). Most bioeroding sponges are cryptic and often overlooked or purposefully ignored during field studies (e.g. Cantera et al. 2003; Scaps and Denis 2008). Compared to free-living organisms, a significantly larger effort would be needed to locate and recognise them and to quantify their abundances, distributions, endolithic parts and in situ bioerosion rates (Rützler 1975; Rosell 1994; Schönberg 2001a; Daume et al. 2010; Fang et al. 2013a), especially in habitats as complex as coral reefs (Rose and Risk 1985; Schönberg 2015; Murphy et al. 2016). Moreover, sponge taxonomy in general is regarded as difficult, a situation that is aggravated by morphological plasticity and poor spicular characters of some species (e.g. Hill 1999; Schönberg and Beuck 2007; Schönberg et al. 2006), and the sponge system is constantly reassessed (see Borchiellini et al. 2004; Morrow and Cárdenas 2015). In fact more than half, 135 of the 260 valid sponge species we accepted as bioeroders (Table 7.1), have changed their genus name at least once during the past 200 years (Appendix A). Sponge science is underpinned by strong and continuous taxonomic expertise (e.g. Schönberg 2017), but related in-depth knowledge about

Table 7.2 Factors that hamper research on bioeroding sponges

Factor making research more difficult	Circumstances	References	Consequences
The sponges most active in bioerosion have a cryptic, endolithic lifestyle	Sponges are easily overlooked during field studies or simply not considered	Cantera et al. (2003), Scaps and Denis (2008)	Bioeroding sponges are less well represented in science than other reef organisms
	Endolithic portions of the sponges are difficult to quantify	Rützler (1975), Rose and Risk (1985), Rosell (1994), Schönberg (2001a), Daume et al. (2010), Fang et al. (2013a), Schönberg (2015), Murphy et al. (2016)	Values referring to bioeroding sponge abundances, biomass and in situ bioerosion rates can be very biased, especially in habitats as complex as coral reefs
The taxonomy of bioeroding sponges is difficult	Many old descriptions are very bad. Some species are morphologically variable or have poor spicular characters	Hill (1999), Schönberg and Beuck (2007), Schönberg et al. (2006), Schönberg (2013); Appendix A	During field studies, bioeroding sponges are rarely identified to species level
	Difficult species complexes exist that contain a number of species that are morphologically very similar	Barbieri et al. (1995), Bavestrello et al. (1996), Boury-Esnault et al. (1999), Rützler (2002a), Barucca et al. (2007), Ferrario et al. (2010), Xavier et al. (2010), de Paula et al. (2012), Escobar et al. (2012), León-Pech et al. (2015)	Molecular analyses are required, limiting the sample size and inflating the costs per study
	In situ identification is very difficult and only possible where the observer is familiar with the dominant species	See picture guides: Collin et al. (2005), Carballo et al. (2008a), Lim et al. (2008), Zea et al. (2016), Hall and Hooper (2016)	If species identification is necessary, destructive sampling and laboratory analyses are required, significantly inflating effort and expenses
	Bioerosion traces can provide significant taxonomic information about a given species, but traces are rarely matched with the responsible tracemakers	Hancock (1849), Bromley (1978), Bromley and D'Alessandro (1984), Bromley (2004), Calcinai et al. (2004b), Tapanila (2006), Schönberg and Shields (2008), Färber et al. (2016), Wisshak (in press)	Assessment requires destructive sampling. Some analyses are expensive and not widely available
	Taxonomic expertise is extremely restricted	Schönberg et al. (2017)	During field studies, bioeroding sponges are rarely identified to species level

(continued)

Table 7.2 (continued)

Factor making research more difficult	Circumstances	References	Consequences
Methods in research on bioeroding sponges can vary widely. Respective experimental conditions were not always ideal	Key factors are not always assessed in a consistent way	Schönberg et al. (2017)	Comparability between studies is limited. Scope for meta-analyses and generalisation is limited
	Settlement blocks and grafted substrates were made and deployed in different ways; durations of experiments varied	Schönberg et al. (2017)	Variability between different studies was at times misinterpreted, or different circumstances were used in the same context
Our present knowledge on bioeroding sponge biologies remains inadequate	Biological responses of one sponge species or genus cannot readily be assumed to match another	Schönberg et al. (2017)	Results are often used in a context that is too generalised

bioeroding sponges is very scarce. In 2016, 20 of 388 sponge scientists (5.2%) stated that they have a large research interest in bioeroding sponges, but over the last 5 years, only 1% published four or more papers on them (Google Scholar 2016; Schönberg 2016a). With increasingly restrictive museum loan policies (e.g. Paris and the Hancock Museum no longer send out holotypes) and citation and funding pressures favouring applied sciences, it will remain difficult to study bioeroding sponges (Schönberg et al. 2017). The separation of species, genus allocations and systematic placements especially of *gamma* clionaids, spirastrellids or *Cliothosa* and *Pione* persists to be problematic (Rosell and Uriz 1997; Nichols 2005; Barucca et al. 2007; Erpenbeck et al. 2016; Y. Ise pers. comm. 2017). Repeatedly, single species received several names, and single names have been represented by several species (e.g. discussed in Schönberg and Beuck 2007). Complexes for difficult species were formed, such as those similar to *Cliona celata*, *Pione vastifica* and especially *Cliona viridis* (e.g. Topsent 1932; Little 1968; Rosell and Uriz 1991; Barbieri et al. 1995; Bavestrello et al. 1996; Schönberg 2002a; Schönberg et al. 2005; Barucca et al. 2007; Leal et al. 2016). Some species complexes have been examined using molecular techniques to investigate species boundaries and phylogenetic relationships in more detail, but circumstances remain complicated (Barbieri et al. 1995; Bavestrello et al. 1996; Boury-Esnault et al. 1999; Rützler 2002b; Barucca et al. 2007; Ferrario et al. 2010; Xavier et al. 2010; de Paula et al. 2012; Escobar et al. 2012; León-Pech et al. 2015; Leal et al. 2016; Zea and López-Victoria 2016). Many species cannot easily be identified by their external morphology, but some picture guides exist that include bioeroding sponges (Collin et al. 2005; Carballo et al. 2008a; Lim et al. 2008; Zea et al. 2016; Hall and Hooper 2016). Many older descriptions are very bad (as discussed in, e.g. Schönberg and Beuck 2007; Schönberg 2013) and as a rule displayed only preserved specimens, if at all. Some excellent drawings and imagery of characteristic sponge bioerosion exist in the taxonomic context, partly reported as bioerosion traces or ichnotaxa (e.g. *Entobia* and other ichnospp.; e.g. Hancock 1849; Bromley 1978; Bromley and D'Alessandro 1984; Bromley 2004; Tapanila 2006; Schönberg and Shields 2008; Färber et al. 2016; Wisshak in press). However, one sponge species can make different traces, e.g. with growth phase or in different substrates, and different sponges were matched to the same kind of trace (e.g. Färber et al. 2016). Moreover, traces cannot be assessed unless the sponge is opened and damaged or removed from the water, e.g. for the duration of an X-ray or tomography scan.

7.3.2 *Best Practice in Research on Bioeroding Sponges and Gaps in Knowledge*

While fieldwork still poses significant challenges, recent concerns about reef health and ocean acidification seem to have triggered more research activity on bioeroding sponges (Fang and Schönberg 2015), and they are increasingly assessed for

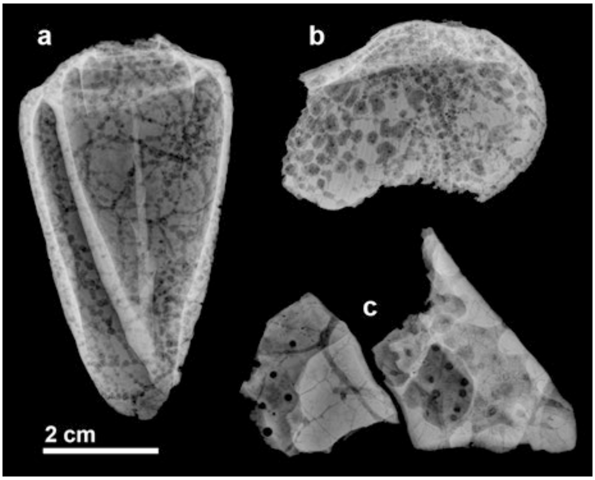


Fig. 7.3 Selected examples of sponge erosion traces illustrating how different shapes, sizes, densities and distributions of bioerosion traces might affect substrate stability. Images were obtained with X-ray that better visualises traces in dense substrates such as mollusc shells, rather than more porous substrates such as coral skeletons. However, all samples originated from reef environments. (**a**) *Pione* sp. in a corroded cone shell from One Tree Island, southern Great Barrier Reef. In two-dimensional substrates, the chain-of-bead-like arrangement of the bioerosion chambers cause an effect like a perforation seam along the edge of a stamp, creating a 'Sollbruchstelle', i.e. a predetermined breaking point. (**b**) *Pione* sp. in a bivalve shell from Ashburton Island, NW Australia. The more uniform arrangement of the comparatively small bioerosion chambers means that the breaking risk in this the shell cannot easily be predicted. In fact, the shell still felt quite solid. (**c**) Clam shell fragments inhabited by *Cliothosa hancocki* from Orpheus Island, central Great Barrier Reef, a species which produces comparatively large bioerosion chambers and tissue extensions branching from the main body that weaken the substrate more in some parts than in others

monitoring purposes (Callahan 2005; Lang et al. 2010; Makowski and Keyes 2011; Gilliam 2012). However, very few species can be recognised in situ by non-experts. It would thus be important to provide more quality in situ images of specimens that were simultaneously sampled for morphological and molecular identification. Sponges would need to be photographed in overview and close-up, with open, expanded papillae. Taxonomic samples need to include surface tissue with a few papillae and a proportionally adequate portion of the endolithic body for preparations of the spicules, the skeletal architecture and erosion structure (the latter can be assessed using broken or ground substrate, polished sections, medical X-radiography or microcomputed tomography, natural or resin casts after removal of tissue or on fixed tissue after dissolution of the substrate, e.g. Bromley and D'Alessandro 1984; Rosell 1994; Schönberg 2000; Fromont et al. 2005; Färber et al. 2016; Fig. 7.3). Long-term preservation should be in ethanol, not in formalin, to allow molecular analysis. For genetic studies, small, internal tissue fragments should be kept frozen at −20 °C or transferred into 100% laboratory-grade ethanol or another suitable fixative as soon as possible. Where the taxonomy is not fully established, it is strongly advisable to keep representative reference samples and to lodge them with a local museum.

An important factor hampering progress in research on bioeroding sponges is the lack of standardisation, with different studies not as a rule using comparable methods and analogous reference units (Table 7.2). This reduces opportunities for pattern recognition across larger spatial and time scales and for metadata analyses (see also Schönberg et al. 2017). When assessing spatial and temporal variability of bioeroding sponge abundances at community level, either quadrat, belt or line intercept studies will generate valuable and inter-comparable results if they are expressed in % of bioerodable substrate (e.g. these sponges do not recruit on sediments), which can significantly vary per habitat and thus bias the outcome (see Schönberg 2015). Alternatively, sponge bioerosion can be quantified from rubble (Holmes et al. 2000). This method will usually only capture part of the local sponge community, however, and will commonly miss the bioeroding sponges with higher bioerosion rates (Schönberg 2015). In order to compare sponge bioerosion with local calcification, sponge abundances need to be estimated more accurately, and for this purpose, the line intercept transect method may be the most appropriate (Schönberg 2015). As bioerosion rates vary widely among sponge species and with different kinds of substrate (Appendix C), the main substrate materials and their properties need to be known, as well as confirmed bioerosion rates of the dominant sponge species in the area. Community bioerosion rates obtained after settlement of macroborers on experimental blocks are unlikely to conform with bioerosion rates of single sponge species (e.g. Murphy et al. 2016).

Another way to understand the contribution of sponge bioerosion at community level is to use clean $CaCO_3$ blocks for larval settlement. The blocks will attract a succession of recruiting bioeroders and calcifiers, with sponges being late to occur and only accurately accessed after several years of exposure (e.g. Kiene and Hutchings 1994). Other people have slabbed natural substrates containing established, mature borer communities and portions of live coral. These studies measured area of sponge-generated holes in comparison to bioerosion by others and coral calcification (usually as %; Hein and Risk 1975; Hudson 1977; Scoffin et al. 1980; Appendix C). This can convey a good comparison of bioersion and accretion for budget purposes.

When conducting experiments, total sponge bioerosion rates have mostly been quantified as reduced substrate weight over time after combining sponge tissue and substrates that were originally bioeroder-free (attaching pieces of substrate to sponges, e.g. Neumann 1966; Rützler 1975; Calcinai et al. 2007a; attaching pieces of sponge to replicate substrate units, e.g. Schönberg 2002b; Duckworth and Peterson 2013). Some approaches also separately assessed chemical and mechanical parts of sponge bioerosion via the alkalinity anomaly method and by quantifying sponge-generated sediment (e.g. Zundelevich et al. 2007; Nava and Carballo 2008; but this method can be inaccurate: Fang et al. 2013b). Traditionally, the reference unit for sponge bioerosion rates is sponge tissue area on the substrate surface. Depending on whether this reference is initial or current sponge area, bioerosion rates will behave differently (Rützler 1975; Holmes et al. 2009). When using the initial area, sponge bioerosion will always increase over time, whereas they stabilise after few months when in reference to current tissue area, i.e. they stabilise when the sponge area/volume ratio stabilises (see Fig. 2 in Rützler 1975). The initial increase in sponge bioerosion over time was often erroneously interpreted as an initial burst of erosion and a later slowing (e.g. Rützler 1975; Acker and Risk 1985). However, this is an artefact, and if sponge bioerosion rates were referenced to current cell count, even the initial increase of the bioerosion rates would disappear. Resulting rates are most commonly expressed as mass of substrate lost per unit time, usually as kg m^{-2} sponge tissue $yr.^{-1}$ or as convertible units (e.g. mg cm^{-2} d^{-1} in Hill 1996 or Fang et al. 2013b). This format allows the widest range of comparisons across studies (Appendix C), and where the reference to sponge area or duration of assessment are missing, data cannot be used in a larger context (e.g. Hein and Risk 1975; Hudson 1977; Rose and Risk 1985). Upon reaching full substrate penetration, bioerosion may be limited by no longer allowing expansion into fresh $CaCO_3$. It may be advisable to sample both fully sponge-infested material and clean substrate material of the same kind and to compare the difference of weights, bulk densities or pore volumes, expressing the material loss as percentage of the original material properties (e.g. Bergman 1983; Acker and Risk 1985). More recently microcomputed tomography is widely used to generate volumetric data on bioerosion (e.g. Becker and Reaka-Kudla 1997; Beuck et al. 2010). However, sponge bioerosion was largely ignored when assessing spatial or temporal differences (e.g. Silbiger et al. 2014). This may relate to difficulties when using technologies based on X-radiography that arise from problems to distinguish empty, existing pores of the coral skeleton from those created by fine sponge bioerosion (Schönberg 2001a). Regardless of the approach, bioerosion rates vary and depend on many different circumstances (Table 7.3; Appendix C), and the minimum information needed is the taxonomic identity of the sponge and the type of substrate material. Where possible, it is valuable to assess material bulk densities of fresh and sponge-eroded substrates.

Controlled experiments need to exclude or subtract effects of other organisms and factors that may contribute residual erosion. This is best done with implementing controls—substrate that does not contain sponge tissue but is subjected to the same treatment. To date, field or aquarium experimental work was restricted to only a few species (Table 7.2), often favouring the most common or very aggressive sponges such as *Cliona celata*, *Cliona viridis* and *Pione lampa* complex species, which all can kill corals. Most of these form coherent tissue on the substrate surface (*beta* form), and some occur in free-living *gamma* morphology, which can be quickly located at many field sites. In *beta* morphology *Pione* and *Cliona* aff. *viridis* spp., fine bioerosion patterns and the dense distribution of the endolithic tissue within the substrate allow low-effort production of replicate samples for different research purposes (e.g. Schönberg and Wilkinson 2001; Fang et al. 2013a, 2016a). The dense bioerosion pattern also means that the sponge samples are comparatively pure, not commonly including other macrobioeroders that would confound results. Using explants of *gamma* morphology sponges should be the best choice, as they do not contain $CaCO_3$ that could be inhabited by microborers, but some *gamma* sponges may not bioerode as actively as fully endolithic specimens (e.g. Hatch 1980).

Table 7.3 Summary of research on reef-dwelling bioeroding sponges in context with environmental change

Factor	Species	Observed response	Reference
Nutrients, *DOM*, *POM*	Bioeroding sponges in general	Without identifying separate species except for categories based on two erosion patterns, several different studies observed that bioeroding sponge abundances and diversities as well as their bioerosion can significantly increase with eutrophication	Sammarco and Risk (1990), Risk et al. (1995), Edinger and Risk (1997, as *Cliothosa hancocki*); Holmes (1997), Holmes (2000), Holmes et al. (2000), Carreiro-Silva and McClanahan (2012), Chen et al. (2013)
	Beta-growth clionaids	Encrusting clionaids often compete with and invade live corals, which they can overwhelm more easily if the corals are stressed, e.g. by organic pollution	Rützler (2002a)
		In another Caribbean study, however, zooxanthellate *beta*-growth sponges did not clearly respond to chronic exposure of raw sewage, and only *Cliona caribbaea* abundances increased	López-Victoria and Zea (2005)
	Cliona aff. *celata*	Abundances increased with decreasing distance to a sewage outfall	Muricy (1991)
	Cliona delitrix	Abundances and individual sizes increased with nutrient levels. Positive effects of increased food concentrations appeared to be counterbalanced by sedimentation	Rose and Risk (1985), Ward-Paige et al. (2005), Chavez-Fonnegra et al. (2007)
	Cliona orientalis	Growth and bioerosion appear to be stimulated by nutrients, a factor that may interact with light and flow	Holmes et al. (2009), Achlatis et al. in press, C. Schönberg unpubl. data 1997
	Pione lampa	Abundances and individual sizes increased at eutrophicated sites	Ward-Paige et al. (2005), as *Cliona*

(continued)

Table 7.3 (continued)

Factor	Species	Observed response	Reference
Temperature (T)	*Beta*-growth clionaids	Encrusting clionaids often compete and invade live corals, which they can overwhelm easier if these are stressed, e.g. by extreme Ts	Rützler (2002a)
	Cliona aprica	While corals bleached during a heat event, the sponge did not	Vicente (1990)
	Cliona aff. *celata*	North American and Canadian *Cliona aff. celata* cease boring and become inactive over winter, reducing the size of choanocyte chambers and papillae until incurrent papillae are withdrawn at about 5 °C but without developing a 'dormant internal morphology', and they only grow significantly in $T > 15$ °C	Fell et al. (1984), Carver et al. (2010)
		The sponge was subjected to 18, 25, 31 and 33 °C, but no differences were detected with regard to the sponge's pigments. Heat causes damage to photosystem II and oxidative stress in photosynthetic symbionts of marine organisms, which can result in bleaching. As *C. celata* complex species do not contain photosymbionts or -pigments, this experiment did not target a logic goal	Miller et al. (2010)
	Cliona orientalis	Weak, apparently curvilinear response, highest bioerosion at ambient T, reduced activity at colder and warmer T, partial mortality at 31 °C. In experiments that combined T and $p\mathrm{CO}_2$, negative effect of heat appeared to be slightly reduced by positive effect of OA	Wisshak et al. (2013)
		Field studies on sponge abundances after thermal bleaching episodes attested to the hardiness of this species. However, the sponge was bleached or killed under extreme experimental temperatures. Losing its photosymbionts significantly reduced the sponge's fitness and is unsustainable for survival	Schönberg and Ortiz (2009), Fang et al. (2014, unpubl. data 2017), Ramsby et al. (2017), Achlatis et al. (in press)
	Cliona vermifera	A thermal bleaching event did not alter the rhythm of sexual reproduction	Bautista-Guerrero et al. (2014)
	Cliona varians	While corals bleached during a heat event, the sponge did not or only locally	Vicente (1990)
		C. varians partially bleached in at 10 days >31 °C in shallow water but later recovered. Specimens nearby 17 days in >33 °C and max. 41 °C did not bleach	Hill et al. (2016) and M. Hill pers. comm.
	Pione mussae	Chemical bioerosion was seasonal, with highest rates occurring during mild shoulder seasons (November, April), but April values being similar to August values (hot)	Zundelevich et al. (2007)
	Pione truitti	In cold-temperate habitats, gemmulation (formation of encapsulated resting stages) occurs towards winter, when water T falls <20 °C. Then tissue regresses for the duration of winter and physiological activity rests, including bioerosion. In spring, when T rises above 15 °C, gemmules hatch, and boring is resumed in May–June with >20 °C	Pomponi and Meritt (1990)

Overfishing	Bioeroding sponges in general	Control by grazers: comparing fished and unfished reefs, sponge bioerosion was more intense on unfished reefs that had more fish and fewer urchins (sponge bioerosion 58 versus 48% of the macroboring; see Fig. 7.5)	Carreiro-Silva and McClanahan (2012)
		Enhancement by grazers: it was assumed that most bioeroding sponges cannot settle on live coral tissue and that recruitment is more difficult on turf algae. Bite scars from parrotfish or surfaces rasped clean by other grazers such as urchins provide ideal settlement substrate, enabling the establishment of bioeroding sponges	Rützler (1971, 2002a), Cebrian (2010)
		Enhancement by grazers: lateral advance of Caribbean *beta*-form sponges was faster into freshly dead, bitten or grazed substrate (by parrotfish or urchins)	López-Victoria et al. (2004, 2006), Chaves-Fonnegra and Zea (2011), Márquez and Zea (2012)
		Control by grazers: Conversely, parrotfishes and other reef fishes as well as urchins feed on *beta*-growth bioeroding sponges (Appendix E) and can 'accidentally' remove small *alpha*-growth sponges when grazing on turfs. Grazing pressure is usually low and usually leaves the sponges unaffected, but where bottom-oriented grazing becomes intense, it may reduce sponge abundances	Hill (1998), González-Rivero et al. (2011, 2012)
	Zooxanthellate bioeroding sponges	Photosymbiotic sponges may grow faster with herbivory by fishes or urchins, which remove allelopathic macroalgae or algae that shade the photosymbiotic sponges. Overfishing can either remove the dominant herbivores (leading to fewer sponges) or the predation pressure on urchins, which then proliferate and graze more (more sponges). The data somewhat contradict Carreiro-Silva and McClanahan (2012), a situation which may relate to different sample areas or sponge species with different biologic traits	Cebrian and Uriz (2006), Cebrian (2010), González-Rivero et al. (2012)

(continued)

Table 7.3 (continued)

Factor	Species	Observed response	Reference
Ocean acidification (OA)	*Beta*-growth bioeroding sponges	A meta-analysis across various published data showed that different species of bioeroding sponges positively reacted to $p\mathrm{CO}_2$ and chemically eroded more. This was regardless of the duration of the experiment, the climate and whether or not the sponges contained zooxanthellae. The correlation suggested a doubling of the chemical bioerosion rates with doubling of $p\mathrm{CO}_2$	Schönberg et al. (2017)
	Cliona aprica (together with other naturally occurring borers in rubble)	Passive dissolution (cleaned rubble, only ambient differed from moderately and high levels of $p\mathrm{CO}_2$) and bioerosion (natural rubble, only the highest treatment differed from the others) increased with $p\mathrm{CO}_2$. As proportional contributions of bioeroders were not assessed, results may or may not apply to *Cliona aprica*	Stubler and Peterson (2016)
	Cliona celata complex spp.	Bioerosion increased with lower pH and weakened the substrate more (acid application or CO_2 perturbation). Absolute erosion rates remained lower than in zooxanthellate sponges, but the relative increase had the same slope	Duckworth and Peterson (2013), Wisshak et al. (2014)
	Cliona orientalis	Chemical bioerosion was strongly enhanced with OA (linear response, 9–31% increase for total bioerosion, depending on scenario), but mechanical bioerosion appeared to be almost unchanged. At least intermediate levels of $p\mathrm{CO}_2$ seemed to stimulate the photosynthesis of the associated zooxanthellae and the assumed transfer of photosynthates. In experiments that combined T and $p\mathrm{CO}_2$, positive effects of OA apparently yielded to negative effects of T at a threshold of >31 °C	Wisshak et al. (2012, 2013), Fang et al. (2013b, 2014)
	Cliona varians	Level of $p\mathrm{CO}_2$ did not affect survival or attachment rates of sponge grafts to live *Porites furcata* (but it is a branching coral, where attachment surface cannot be defined), but increased passive dissolution. The highest exposure reduced the coral's calcification (2014 study), or not (2015 study), and increased the sponge's bioerosion	Stubler et al. (2014, 2015)
	Pione lampa	Chemical bioerosion of the sponge increased with $p\mathrm{CO}_2$. In the sample area, 89% of the reefs are presently already erosional. Sponge erosion will aggravate this	Enochs et al. (2015)

Sedimentation	*Beta*-growth clionaids	Encrusting clionaids often compete and invade live corals, which they can easily overwhelm if these are stressed, e.g. by sedimentation	Rützler (2002a)
	Cliona aprica	The zooxanthellate sponge can tolerate turbidity and sedimentation but will occur in shallower depth than in clearer waters	Macdonald and Perry (2003)
	Cliona celata complex spp.	Can tolerate high levels of turbidity (<4 m visibility) and sedimentation	Carballo et al. (1994, 1996), Reis and Leão (2002)
	Cliona delitrix	The first and second publications found that *Cliona delitrix* tolerated and survived high levels of sedimentation and turbidity e.g. resulting from construction work and apparently benefitted from increased availability of dead substrate. The third publication noted that abundances increased along a gradient of increased food concentrations, but this appeared to be counterbalanced by sedimentation, which may have suppressed *Cliona delitrix*	McKenna and Ritter (1999), Macdonald and Perry (2003, as *Cliona laticavicola*), Chavez-Fonnegra et al. (2007)
	Cliona rhodensis	Appears to be sensitive against turbidity and sedimentation	Carballo et al. (1994, 1996)
	Cliona orientalis	Can tolerate turbidity and sedimentation, has good self-cleaning abilities, but bleaches or develops necrotic patches when smothered by excessive sedimentation; more vulnerable against fine sediments, is less abundant at sites with fine sediments	Schönberg (2001b, 2015a), Büttner and Siebler (2013), Pineda et al. (2016a, 2016b, 2017a, 2017b, 2017c), Ramsby et al. (2017)
	Cliona viridis	Can tolerate high levels of turbidity (<4 m visibility) and sedimentation	Carballo et al. (1994, 1996)
	Pione lampa	Can tolerate turbidity and sedimentation	Macdonald and Perry (2003)
	Fistulate *Spheciospongia* spp. (e.g.	Can live endopsammic, i.e. in sediments, but can withstand sedimentation by having a conical body or elongated fistules sticking up and preventing burial of the parts needed for ventilation	Cerrano et al. (2002, as *Spirastrella*); Schönberg (2016b)
	Spheciospongia florida) *Spheciospongia vagabunda*	Belongs to the dominant sponges at highly silted sites at Motupore Island, PNG, and commonly occurs in muddy or turbid habitats. The sponge's base can be buried in sandy habitats (psammobiosis). However, larval settlement can be restricted by sediment scouring	Kelly (1986, as *Spirastrella vagabunda* and *Spirastrella fungoides*)
	Large, fistulate *Siphonodictyon* spp. (e.g. *Siphonodictyon mucosum*, *Siphonodictyon siphonum*)	Often live endopsammic, i.e. in sediments, but can withstand sedimentation by having elongated fistules sticking up and preventing burial of the parts needed for ventilation	De Laubenfels (1949, as *Siphonochalina*); Cerrano et al. (2002, as *Aka*); Schönberg (2016b)

(continued)

Table 7.3 (continued)

Factor	Species	Observed response	Reference
Increased availability of substrate/severe disturbance	Bioeroding sponges in general	Abundances of bioeroding sponges increased after coral mortalities or were more abundant on reefs that had experienced bleaching. The second study found that especially species that can exist in live corals increased	Rützler (2002a), Schönberg and Ortiz (2009), Carballo et al. (2013)
	Beta-growth bioeroding sponges	During field experiments in the Caribbean sponges advanced faster into dead substrates than into live corals. *Cliona orientalis* advanced faster into live massive *Porites* in the field than into dead substrate, but behaved the opposite when spreading into cores with or without live *Porites* tissue	Chaves-Fonnegra and Zea (2011), Fang et al. (2017), C. Schönberg unpubl. data 2010–2016
	Cliona caribbaea	Corals around Puerto Rico succumbed to disease, storms, reduced water quality and anthropogenic activities. After that, the sponge became increasingly a problem	Weil et al. (2003, as *Cliona langae*)
	Cliona delitrix	Where hard coral cover decreased, *Cliona delitrix* abundances increased. In two cases, the increased environmental changes also included increased eutrophication	Rose and Risk (1985), McKenna and Ritter (1999), Ward-Paige et al. (2005)
	Pione lampa	Where hard coral cover decreased, *Pione lampa* abundances increased	Ward-Paige et al. (2005), as *Cliona*
	Pione mussae	More commonly in dead substrate	Bertram (1936)
	Cliona vermifera	More abundant in dead rubble	Carballo et al. (2008b)

Taxon authorities of sponges are listed in Appendix A. *Aff.* has affinities with this species but is not likely to be conspecific, *DOM* dissolved organic matter, *p*CO_2 partial pressure of carbon dioxide, *POM* particulate organic matter.

However, the vast amount of bioeroding sponges occurs in *alpha* morphology (e.g. Schönberg 2001b; Murphy et al. 2016). These have not been studied to the same extent and need to be increasingly targeted to allow a better integration of data and generalisation. Again, taxonomic difficulties reduce the range of opportunities.

All of the above means that although sponges are probably the best-studied endolithic bioeroders (Schönberg and Tapanila 2006a; Fang and Schönberg 2015), many questions remain unanswered, and we cannot yet adequately quantify community bioerosion rates. The lack of standard approaches to estimate sponge bioerosion in the field is a problem, because sponges are one of the most dominant taxa in bioerosion, often contributing the lion share to internal macrobioerosion on coral reefs (Appendix D).

7.4 Biogeography of Bioeroding Sponges on Coral Reefs

Of the 260 valid species of bioeroding sponges and 28 OTUs that we assessed, 240 or 92.3% commonly erode or are highly likely to erode corals. Globally 208 species or 80.0% of the assessed species are known from shallow warm-water reefs and 49 or 18.8% from corals of deep- or cold-water habitats, with just 16 species or 6.2% of these occurring in both habitats (Fig. 7.4; Appendix A). The discrepancy between species counts of bioeroding sponges on warm- and cold-water reefs may in part reflect true proportions of diversities, but they may also relate to a preference for research in warmer climates and easier access in shallow depth suitable for diving, a situation that was observed for sponges in general (Schönberg 2017). Regardless of the reason, the findings highlight the need to intensify studies on the bioerosion of cold-water reefs.

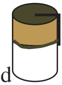
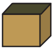
Within all shallow warm-water reefs, different bioregions again have very different diversity records (Fig. 7.4; Appendix A). The Caribbean and also the Mediterranean traditionally attracted the most intensive attention for research on bioeroding sponges, and from these areas, we have diverse data beyond species descriptions and faunistic reports (62 and 28 species, respectively, C. Schönberg unpubl. data for the Mediterranean 2010). Species numbers of bioeroding sponges from warm-water reefs of the Caribbean were followed by India (47 species) and the Coral Triangle (43 species), but here, studies mostly represented mere records. In India, mollusc aquaculture generated much research interest in the pest organisms that led to a multitude of descriptions and faunistic inventories (e.g. Annandale 1915b; Thomas 1979a). East Africa (38 species), northwestern Australia (35 species) and the Great Barrier Reef together with the Arafura Sea (33 species) had similar, mid-range diversities in warm waters. The number of bioeroding sponge species of the Central Pacific (29 species), the Eastern Tropical Pacific (27 species) and Brazil (25 species) remained lower, pending more work. In Australia, especially in the northwest, full species identification usually lagged behind ongoing surveys, and higher diversities can be expected when more taxonomic work will be completed (e.g. van Keulen and Langdon 2011; Schönberg and Fromont 2012; Hooper

Table 7.4 Healing in bioeroding sponges

Species	Fragment type	Dimensions [cm]	Undamaged surface area [cm^2]: volume [cm^3]	Surface area damaged: undamaged [cm^2]	Surface area damaged: undamaged [%]	Period allowed for healing	Reference
Cliona caribbaea	Slices of pre-infested *Acropora*	$r = 1.75$ $h = 1.3$	14.3 : 12.5	19.2 : 14.3	57.3 : 42.7	3 days	Rützler (2002a)
Cliona cf. *celata*	Tissue shreds, no ectosome included	NA	All surface was damaged, 0.05 mL	Only internal tissue used	100 : 0	Attachment: 3–4 days Fully recovered and with canal system: 2–3 weeks	Warburton (1958b)
Cliona cf. *celata*	Tissue shreds, no ectosome included	NA	All surface was damaged, 0.5 mL	Only internal tissue used	100 : 0	Attachment: 3 days Bioerosion in underlying substrate: 3–4 weeks	Cobb (1969, 1975)
Cliona cf. *celata*	Cubes	Assumed $l, w, h = 2$	Ca. 4 : 8	Ca. 20 : 4	Ca. 83.3 : 16.7	2 weeks	Duckworth and Peterson (2013)
Cliona orientalis	Cores, not bottom-trimmed	$r = 1.5$ $h = 1.32$	13.4 : 9.3	13.1 : 13.4	49.5 : 50.5	4 days	Schönberg and Suwa (2007), Wisshak et al. (2012, 2013)
Cliona orientalis	Cores, not bottom trimmed	$r = 1.5$ $h = 1.32$	13.4 : 9.3	13.1 : 13.4	49.5 : 50.5	1 week	Fang et al. (2013b, 2014)
Cliona orientalis	Cores, not bottom trimmed	$r = 1.1$ $h = 1.32$	7.2 : 5.0	9.5 : 7.2	56.9 : 43.1	1 week	Fang et al. (2016)
Cliona orientalis	Cores, bottom trimmed	$r = 1.5$ $h = 1$	13.4 : 7.1	10.1 : 13.4	42.9 : 56.9	4 days to 2 weeks ([1]with 2–5% mortality)	Schönberg and Wilkinson (2001)[1], Schönberg (2002b, 2003, 2006)
Cliona varians	Cubes	$l, w, h = 2$	Ca. 4 : 8	Ca. 20 : 4	Ca. 83.3 : 16.7	3 or 7 days	Stubler et al. (2014, 2015)

Cliona varians	Cubes?	Assumed $l, w, h = 2$	Ca. 4 : 8	Ca. 20 : 4	Ca. 83.3 : 16.7	7 days (with 8% mortality)	Hill (1996)
Spheciospongia vagabunda	Cylinder? Cube Cube	$r, h = 7.5, 16$ $l, w, h = 4, 5, 3$ $l, w, h = 3, 2, 1$	176.7 : 2827.4 20 : 60 6 : 6	930.7 : 176.7 74 : 20 16 : 6	84.0 : 16.0 78.7 : 21.3 72.7 : 27.3	100% survival 20% survival 0% survival, after 59 days; healing well underway after 22 h, fragment fusion after 10, attachment and oscules formed after 20 days	Kelly (1986)

Summary of experimental conditions of studies that used replicate sponge fragments trimmed to specific sizes. *Gamma* sponges were hand-cut, damaging all sides, except the upper surface, the ectosome. Core samples of *beta* sponges either trimmed the cores to 1 cm height to only include fully sponge-penetrated material, in which case only the ectosome remained undamaged, or they included some clean substrate material underneath—in which case the surfaces of the ectosome and that at the interface to the substrate remained unharmed. However, coring sometimes induced surface damage when the drill bit slipped or when coring too deeply so that the hole saw grated on the sponge surface. This damage is here assumed with 10% for the upper surface, as average across all used cores. Moreover, using a 3.5 cm hole saw generated cores of ca. 3 cm diameter (Wisshak et al. 2012). Irregular fragments used in experiments are not listed, as their volumes and surface areas cannot be quantified. Abbreviations: *h* height (also representing penetration depth in *beta* form sponges in cores not trimmed to contain only sponge tissue), *l* length, *r* radius, *w* width. The black angle on the symbols for the sponge cores below illustrates *h* and *r*.

Damaged surface 🟫; Core, not bottom-trimmed ; Bottom-trimmed ; Slice from branching coral ; Undamaged surface ⬛; Cube of sponge tissue. 

et al. 2013; Fromont and Sampey 2014). It should also be noted that species records listed for the Central Pacific often only relied on one site or account, and any given species may not occur across the entire bioregion. The comparatively low species counts for the Red Sea and Persian Gulf (19 species), Japanese and Korean reefs (18 species) and the Gulf of Guinea (8 species) may reflect that the existing research effort might not have been adequate to capture expected diversities (see also Fisher et al. 2011; Berumen et al. 2013). Moreover, identifications of some of the Japanese sponges appear to be unreliable and need to be revisited (Y. Ise pers. comm. 2017). Coral demise reported for some of these areas should be a strong incentive to improve the faunistic records (e.g. Nakano 2004; Yokochi 2004; Omori 2011; Riegl et al. 2012). After summation across the main oceans, the above data resulted in a more adequate picture for warm-water bioeroding sponges, with 99 species occurring on coral reefs of the Pacific, 91 in the Indian Ocean and 73 in the Atlantic. This appears to be a more realistic representation when considering that the Pacific contains the highest diversity and the largest area of warm-water coral reefs (e.g. Veron et al. 2009).

Most species of sponges eroding cold-water corals were recorded from the Mediterranean (28) and the Atlantic (20), of which 33 occur in the Mediterranean and Atlantic (Fig. 7.4). In the Pacific, 17 species of sponges have been found to erode cold-water corals, but only two in the Indian Ocean, one of which is shared with the Pacific, resulting in 18 Indo-Pacific species. These figures clearly illustrate the research need on deep-water bioeroding sponges of the Indian Ocean.

Globally, clionaids were by far the most prevalent group of bioeroding sponges and represented two thirds of the biodiversity (Fig. 7.4; Glynn 1997). Slight differences existed between bioregions, but at most warm-water sites, clionaids contributed at least two thirds to bioeroding sponge diversities on shallow warm-water reefs. In the Atlantic and on Australian reefs, the haplosclerid genus *Siphonodictyon* provided another 12–28%, whereas in other bioregions, this genus was either not as prevalent or less well studied. In the central and western Indian Ocean, the community composition was quite different to any of the other bioregions, with the Tetractinellida reaching 17% on Indian reefs. This is largely due to the unusually high diversity of *Thoosa* spp. but also to some other tetractinellids such *Triptolemma* spp., which were only recently recognised as bioeroders (Appendix A; Bertolino et al. 2011). As Rützler et al. (2014) pointed out, the capability to bioerode is far more widely distributed across sponge taxa than originally thought, and in order to better understand what other taxa may contribute to reef bioerosion, we need to more carefully assess endopsammic and chasmolithic species that were traditionally assumed to be only nestling.

Cold-water corals were mostly eroded by tetractinellids (mainly *Alectona* spp.), which contributed two thirds of the diversity in the Indo-Pacific, but only 20% of the Atlantic. Globally, the tetractinellids supplied 42.8% of the species eroding cold-water corals.

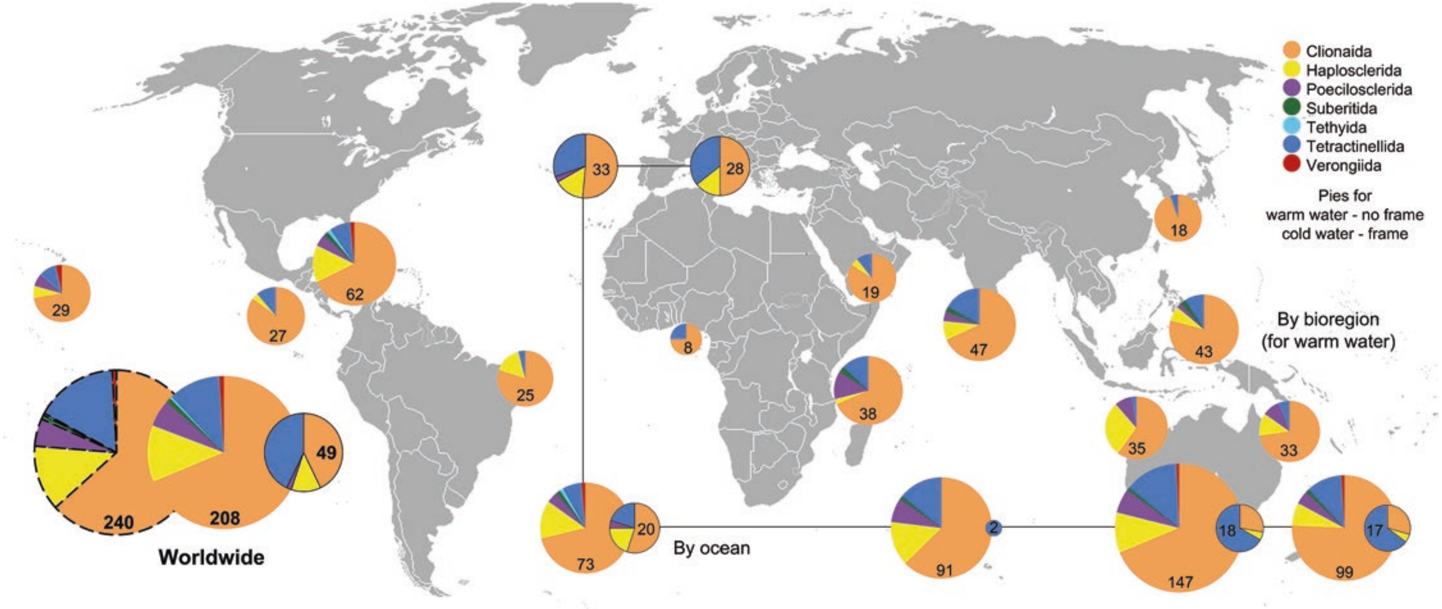


Fig. 7.4 Distribution, composition and diversity (by orders) of bioeroding sponges across bioregions with warm-water (pies without frame) and cold-water corals (pies with *black frame*). Numbers are total species counts per bioregion. Pies per ocean are connected with a *black line* and are for (from *right*) Pacific, Indo-Pacific, Indian Ocean and Atlantic (along *bottom*), Atlanto-Mediterranean and Mediterranean (from *left*, along *top*). Pies for global diversities on the *bottom left* are for all (*dashed frame*), warm-water (no frame) and cold-water habitats (*black frame*). Data for the figure were extracted from Appendix A, where respective references are listed. The background map was sourced from Educypedia (2015)

7.5 The Role of Bioeroding Sponges in Reef Ecosystems

Proportional contributions by microborers, macroborers and grazers to bioerosion can vary significantly with environmental conditions and in interaction with other biota (Schönberg et al. 2017). Regardless of such variations, sponges have been recognised as one of the leading agents of coral bioerosion in warm- and cold-water habitats and are globally the dominant macroborers on many warm-water reefs (Fig. 7.5, Appendix D; Wisshak et al. 2005). Especially in the Caribbean, sponge bioerosion is significant and uniformly strong. In the Indo-Pacific, the contribution of sponges to overall macroboring appears to be more variable but commonly reaches or surpasses one third. Bioeroding sponges play an important role in carbonate cycling, which includes structural weakening (e.g. Tunnicliffe 1979; Schönberg 2002b) and reworking of the reef matrix (e.g. Rützler 1975; Schönberg 2001b), providing structural complexity and cavities that can be inhabited by other biota (Glynn 1997; Enochs and Manzello 2012), contributing as much as 98% of the sediments in the silt size fraction (Neumann 1966; Fütterer 1974; Hein and Risk 1975; Rützler 1975; Scoffin et al. 1980; Acker and Risk 1985; Young and Nelson 1985; Carballo et al. 2016, and references therein) and dissolution of $CaCO_3$ by their etching activity (e.g. Zundelevich et al. 2007). Sponge bioerosion furthermore increases surface area exposed to passive dissolution, and in consequence, it raises ambient alkalinity and contributes to a buffering effect against ocean acidification (Andersson and Mackenzie 2011; Wisshak et al. 2014). Ironically, bioeroding sponges also consolidate reef sediments, because many *Siphonodictyon* and massive *Cliona* or *Spheciospongia* spp. can be endopsammic, which means that they live within sediments. They can bind the sediments by incorporating or agglutinating particles and through anchoring strategies (Calcinai et al. 1999; Cerrano et al. 2007; Schönberg 2016b; Figs. 7.2 and 7.6).

Other important functional roles of bioeroding sponges include, but are not restricted to, water purification and nutrient cycling. Pumping and clearance rates of bioeroding sponges that were studied to date were efficient and suggest that, like other sponges, bioeroding sponges act as natural filters and remove a large amount of particles from the water column (De Laubenfels 1950b; Kelly 1986; Lynch and Phlips 2000; Strehlow et al. 2016a; C. Schönberg and A. Pile unpubl. data 1997). This led to the hypothesis that they can prevent or reduce blooms of detrimental bacteria (Rose and Risk 1985; Lynch and Phlips 2000; Wall et al. 2012). *Cliona viridis* and *Spheciospongia vagabunda* can accumulate harmful elements—especially metals—to highly elevated levels compared to ambient conditions, but not necessarily in relation to the source of origin (Pérez et al. 2004; Padovan et al. 2012). The diet of *Cliona delitrix* and *Siphonodictyon* cf. *coralliphagum* consists to over 80% of dissolved organic carbon (Mueller et al. 2014), which is then translated into biomass (e.g. de Goeij et al. 2008, 2013). Another source of energy for larger coral reef clionaids is translocated photosynthetically fixed carbon from their symbiotic zooxanthellae of the genus *Symbiodinium*, which supports a rapid increase of sponge biomass (e.g. Weisz et al. 2010; Fang et al. 2013b, 2014, 2016, 2017b). The

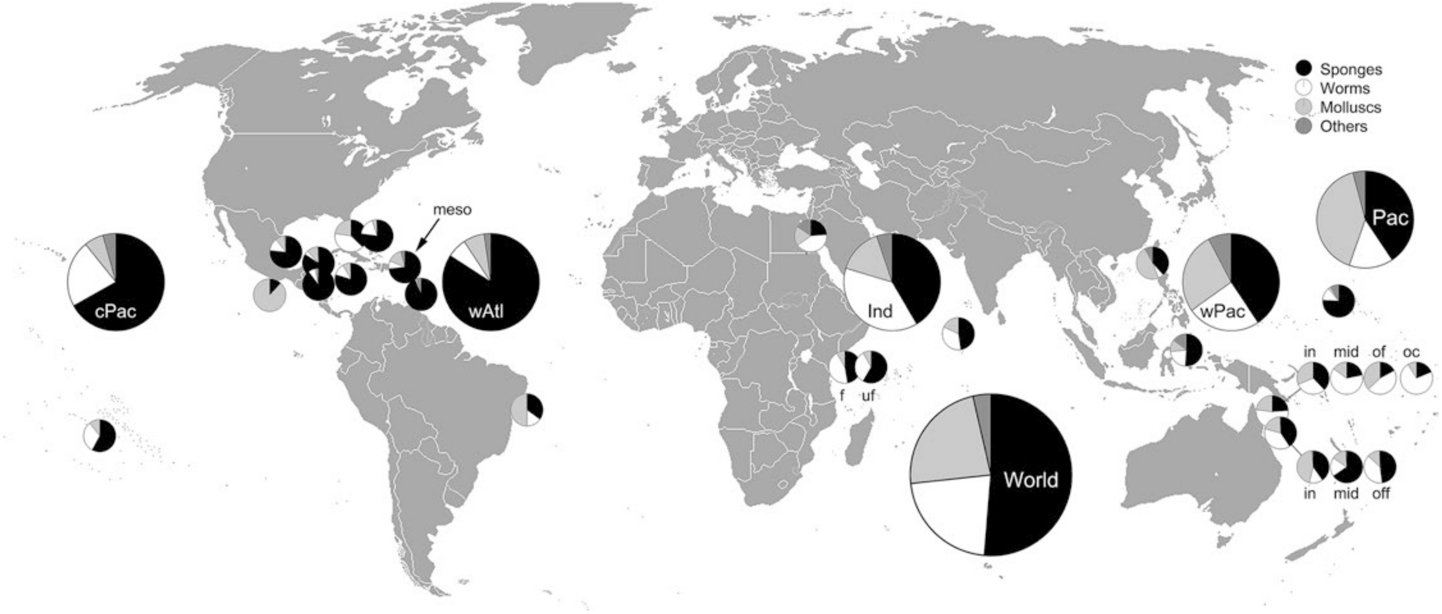


Fig. 7.5 Proportional contributions of the bioeroder guilds sponges, ‘worms’, molluscs and ‘others’ to total macroboring in warm-water corals by bioregion (*smaller pies*) and ocean (*larger pies*). One Caribbean dataset was from a mesophotic reef at St. Thomas (*meso*). For Kenya two datasets were available, for unfished (*uf*) and fished reefs (*f*). Cross-shelf studies on the Great Barrier Reef allowed the data to be divided as inshore (*in*), midshelf (*mid*), offshore or reef edge (*off*) and oceanic (*oc*). The larger pies are for the Central Pacific (*cPac*), the western Atlantic (*wAtl*), the Indian Ocean (*Ind*), the western Pacific (*wPac*) and the Pacific (*Pac*; from left to right), with global proportions displayed on the *bottom* of the figure. Data for the figure were extracted from Appendix D, where respective references are listed. The background map was sourced from Educypedia (2015)

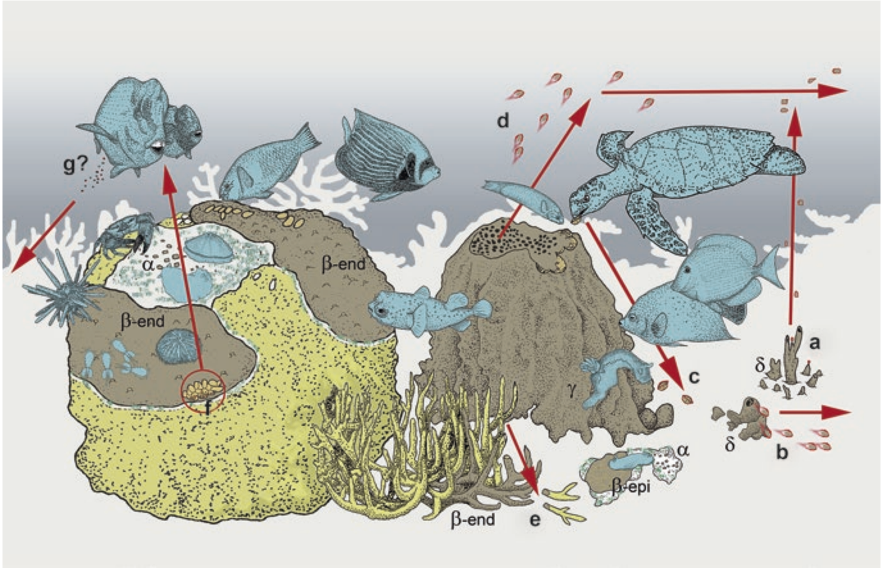


Fig. 7.6 Illustration of functions and biological traits of bioeroding sponges and interactions with other reef organisms. Bioeroding sponges (*brown*) invade dead calcium carbonate substrate (*white*) and compete with or are parasites of live corals (*yellow*): α sponges, mostly endolithic, papillate; β sponges, encrusting, either mostly endolithic (β-end) or mostly epilithic (β-epi); γ, massive, free-living; and δ, fistulate or massive, but endopsammic, living buried in sediments and agglutinating and incorporating calcium carbonate grains. Spongivorous animals feeding on bioeroding sponges in *blue*, not to scale. Pathways of reproduction and dispersal (*red*), from right to left: (**a**) Some species are able to form buds, which may be positively buoyant after detaching and may drift with currents (Ise 2010). (**b**) Clionaids have been reported to expel sticky egg parcels that adhere to the mother sponge or creeping larvae that do not move far from the origin (Warburton 1958a, 1966; Mariani et al. 2000). (**c**) Spongivorous animals may drop the fragments they bite out of the sponge, which may survive and form a new sponge (Kelly 1986). (**d**) Some clionaid species produce larvae with better swimming (drifting?) abilities than previously assumed and have a wide dispersal potential (Chaves-Fonnegra et al. 2015). (**e**) Substrate weakened by sponge bioerosion has a much larger potential to break, and branching substrates can easily fragment (Tunnicliffe 1979; Schönberg 2002b). (**f**) Clionaid sponges have been reported to produce gemmules, which are resting stages in form of encapsulated sponge cells (e.g. Schönberg 2002c). If they remain in place, they can re-establish a sponge when hatching after mortality. (**g**) It is unconfirmed but perhaps not impossible that when grazers ingest gemmules, they can carry them to other locations and defaecate possibly viable, hatchable material (see Vermeij et al. 2013 for dispersal of undigested parts of microborers)

sponges themselves become food for a multitude of other organisms, e.g. grazers such as urchins, fishes and gastropods, nudibranchs, crustaceans, and turtles (Fig. 7.6, Appendix E). Photosymbiotic bioeroding sponges can also release dissolved nutrients such as nitrate and thereby return otherwise limited compounds to the water column (Corredor et al. 1988).

Larger specimens, especially of the genus *Spheciospongia*, can house a vast diversity of epi- or endobiotically associated invertebrates and even fishes that live on the sponges' surfaces or in their canal systems (Tyler and Böhlke 1972; Nicol and Reisman 1976; Westinga and Hoetjes 1981; Martin 1996; Swain and Wulff, 2007). These relationships are often beneficial to the sponges but may occasionally incur some damage (Schönberg and Wisshak 2012). Bioeroding sponges themselves can be detrimental to live corals and molluscs they inhabit, and some sponge species are known to have coral-killing capability (e.g. Sullivan et al. 1983; McKenna 1997; Schönberg and Wilkinson 2001; López-Victoria et al. 2006; Chaves-Fonnegra and Zea 2007). Notwithstanding, on coral reefs the most significant role of this sponge guild is that of bioerosion and sediment production.

Bioerosion rates vary significantly with species and growth forms (Appendix C), likely being less pronounced in sponges in *alpha* morphology that usually form much smaller patches than in *beta*-growth sponges that are able to cover areas of several metres in diameter. *Gamma* and *delta* form sponges only erode particles they agglutinate or incorporate or the substrate at their bases (e.g. Hartman 1958; Nicol and Reisman 1976; Hatch 1980; Kelly 1986; Calcinai et al. 1999; Ise et al. 2004; Lim et al. 2012; Schönberg 2016b). Zooxanthellate species in *beta* morphology significantly contribute to coral reef bioerosion (e.g. Schönberg 2001b; Murphy et al. 2016). Our metadata show that their bioerosion rates increase with substrate density (Fig. 7.7), which may apply to all bioeroding sponges (Hernández-Ballesteros et al. 2013). The photosymbiotic species in *beta* form can laterally expand by several centimetres per year and sometimes advance faster into live or freshly dead corals than

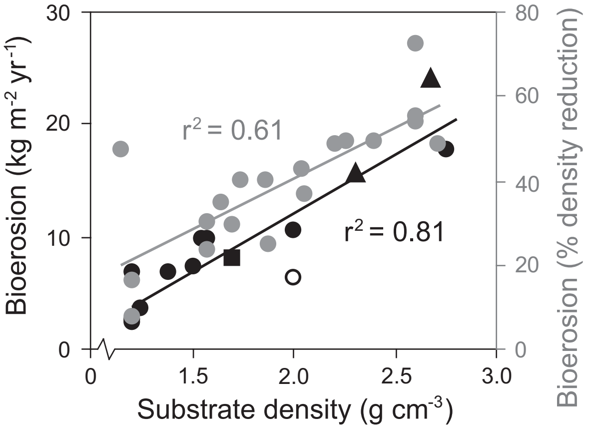


Fig. 7.7 Bioerosion rates of zooxanthellate bioeroding sponges in *beta* morphology in substrates of different bulk density, only including biological skeletons and pure mineral materials that have not been diagenetically changed and omitting all limestones, which created more variable responses. The *black trendline* uses the left *y*-axis (mass changes of substrate): (*triangles*) *Cliona albimarginata* (from Calcinai et al. 2007a), (*quadrat*) *Cliona caribbaea* (from Acker and Risk 1985), (*circles*) *Cliona orientalis* (from Schönberg 2002b; Wisshak et al. 2012; Fang et al. 2013b). The *grey trendline* uses the right *y*-axis (proportional density changes of substrate): *circles Cliona orientalis* (from Bergman 1983; Schönberg and Shields 2008). All data are from tropic or subtropic environments, with one value from a marginal reef of the subtropics, where the bioerosion rate of *C. orientalis* reached 59% of the rate determined in the same kind of substrate in the tropics (the *open circle* from the *black trendline*; from Holmes et al. 2009). Respective data are displayed in Appendix C and were extracted from various publications cited there

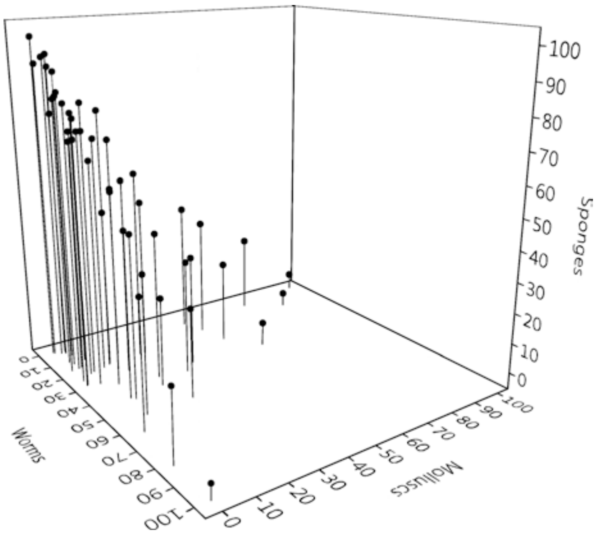


Fig. 7.8 Proportional contributions of sponges, worms and molluscs to total macroboring [%] and in relation to each other, displayed in a three-dimensional scatterplot. Bioerosion by other macroboring taxa typically remained below 5% and was here not included. Please note that where sponge bioerosion is high, both worm and mollusc bioerosion are low. No such relationship could be detected between worm and mollusc bioerosion, even though they behaved the same with respect to sponge bioerosion. Numerical data are displayed in Appendix D and were extracted from various publications cited there

into dead substrates with algal turf (Bergman 1983; Acker and Risk 1985; Hill 1996; Rützler 2002a; Schönberg 2003; López-Victoria et al. 2006; Schönberg 2006; González-Rivero et al. 2012; C. Schönberg unpubl. data 2010–2016). Species in *beta* morphology often also have penetration depths over 1 cm (Table 7.4). In contrast, *alpha*-growth sponges do not usually erode that deep into the substrate, unless they belong to groups that produce cavernous erosion, such as many species in the genera *Siphonodictyon* and *Cliothosa*. This also draws attention to the diversity of erosion traces produced by sponges (Figs. 7.2 and 7.3; see also, e.g. Bromley 1978; Bromley and D'Alessandro 1984), which will have a significant influence on how the structural stability of the infested material will be compromised.

On occasion, it has been discussed whether bioeroding sponges or worms are the more destructive internal macroborers, and why (e.g. Hutchings 1986; Hutchings et al. 2005; Osorno et al. 2005). The answer is that both can provide the largest contribution to macroboring (Fig. 7.5), but their respective roles differ temporally and spatially. Dominant sponge and worm bioeroders seem to respond divergently to environmental conditions, and overall, their contributions to total macroboring behave reciprocally (Fig. 7.8). This is also the case when comparing sponge with mollusc bioerosion, i.e. where one increases, the other one decreases. However, proportional contribution of mollusc bioerosion to total macroboring is independent of worm bioerosion and vice versa (Fig. 7.8). It thus appears that the level of sponge bioerosion is a critical factor in determining the proportional bioerosion by the other macroborers. Carreiro-Silva and McClanahan (2012) explained similar observations with organism interaction through grazer composition, in that a natural dominance of urchins is accompanied by more worm bioerosion and a dominance of fishes by more sponge bioerosion (their data were based on fished versus unfished reefs; Fig. 7.5). However, it is not clear whether this is a directly causative relationship, as our meta-analyses implied that other bioregions that are severely overfished (Caribbean and the Coral Triangle; e.g. Edinger et al. 2000; Mumby et al. 2006a) showed not only the highest proportional contributions of sponge bioerosion to total macroboring (Fig. 7.5) but also the highest recorded bioeroding sponge biodiversities (Fig. 7.4). Due to the *Diadema* mass mortality event in the Caribbean (e.g. Carpenter 1988; Mumby et al. 2006b), local fishes may still have the larger influence as grazers, but this does not seem to be the case in the Coral Triangle. We assume that the dominance of worms versus sponges may also be strongly influenced by nutrient conditions or that several covarying factors need to come into play together to determine which group proportionally erodes more (see also Hutchings et al. 2005; Osorno et al. 2005). Anthropogenically disturbed reefs often tended to have stronger sponge bioerosion (e.g. Rützler 2002a), while worm bioerosion had more influence on some less affected reefs: inshore and midshelf sites on the GBR exhibited more sponge and less worm bioerosion than offshore sites (Sammarco and Risk 1990; Risk et al. 1995; Schönberg et al. 1997; Hutchings et al. 2005; Osorno et al. 2005; Tribollet and Golubic 2005; Fig. 7.5).

7.6 Bioeroding Sponges in Changing Environments

Bioeroding sponges appear to be very resilient or resistant to drivers of environmental change that commonly negatively impact other benthic invertebrates such as corals (e.g. Vicente 1990). While species-specific differences exist, some beneficial biological traits may be widely distributed in this guild. A common trait is the cryptic habit. In contrast to free-living sponges, endolithic or endopsammic (*alpha*, *beta*, *delta*) sponges are significantly more sheltered against different kinds of adverse conditions such as strong fluctuations and extreme levels of illumination, temperature and salinity (Schönberg and Wisshak 2012; Schönberg 2016b). *Alpha*, *beta* and *delta* sponges inhabit a semi-closed and shaded environment, and the more stable pore water chemistry provides some buffering, so that the environmental conditions they are exposed to can be more easily maintained (Schönberg 2016b; Schönberg et al. 2017). Ambient water still needs to be pumped through the sponges. However, this can also be controlled during periods of altered water chemistry and heat, when bioeroding sponges can reduce or arrest pumping, presumably to minimise the associated stress (Annandale 1907; Emson 1966; Massaro et al. 2012). While still pumping, the flow appears to afford some cooling, and tissue areas around larger pores are usually the last parts of photosymbiotic sponges to bleach (C. Schönberg pers. obs. 2013 during the bleaching event described in Lafratta et al. 2016; see also Fig. 1 in Hill et al. 2016).

Clionaid sponges can be associated with zooxanthellae, dinoflagellate *Symbiodinium* spp. (Vacelet 1981; Rützler 1990; Vicente 1990; Schönberg and Loh 2005; Strehlow et al. 2016b). These photosynthetic symbionts in bioeroding sponges have been reported to increase their hosts' growth, bioerosion rates and survival in light (Rosell and Uriz 1992; Hill 1996; Schönberg 2006), circumstances which have been explained with enhanced fitness by carbon translocation from the symbionts to the sponges (Weisz et al. 2010; Fang et al. 2014, 2017b). Sponges with photosymbionts thus appear to have an advantage compared to species without, and they are often those that develop into *beta* morphology, display fast growth and high bioerosion rates and are commonly described as being especially aggressive and competitive against live corals (e.g. López-Victoria et al. 2006; Rützler 2002a; González-Rivero et al. 2013). Zooxanthellate clionaid sponges appear to be able to control the distribution of their intracellular symbionts depending on diurnal rhythms or stress parameters, and the sponges can withdraw the valuable symbionts into deeper tissue regions at night or as a measure to reduce stress, reducing the risk to lose them (Schönberg and Suwa 2007; Fang et al. 2016). While different sponge species can harbour different clades of *Symbiodinium*, the G clade seems to be most intimately associated with bioeroding sponges (Schönberg and Loh 2005; Granados et al. 2008; Hill et al. 2011). This may further explain responses to environmental stress. G clade symbionts appear to be more bleaching resistant than other clades of *Symbiodinium* and have been described as heat tolerant but potentially light vulnerable (Schönberg et al. 2008). It is thus not surprising that zooxanthellate clionaids rarely fully bleach in natural environments (Vicente 1990; Schönberg and Wilkinson 2001; Márquez et al. 2006; partial bleaching observed during severe heat events in Florida: Hill et al. 2016; C. Schönberg et al. unpubl. data 2013, e.g. for the bleaching event described in Lafratta et al. 2016). To date, experimental bleaching of zooxanthellate *Cliona* spp. has only been achieved seven times, once through an abrupt increase of light, once through exclusion of light (*Cliona varians*: Hill and Wilcox 1998), twice by removing symbiont-rich outer tissue and culturing healing sponges for 9 months in permanent darkness (*Cliona varians*: Riesgo et al. 2014; Strehlow et al. 2016b) and three times through the 2–6-month application of +3–3.5 °C above ambient, reaching >30 °C when full bleaching was attained (*Cliona orientalis*: Fang et al. 2013b; Achlatis et al. in press; J. Fang et al. unpubl. data 2017). After light stress, *Cliona varians* was observed post-bleaching. It lived for about a month azooxanthellate and then slowly regained symbionts, until it recovered normal concentrations of symbionts 90 days after bleaching (Hill and Wilcox 1998). Repopulation proceeds faster and can recover normal symbiont levels within few weeks if the sponges are exposed to concentrated symbiont suspensions (Riesgo et al. 2014; Strehlow et al. 2016b). *Cliona orientalis* and *Cliona varians* both survived partial thermal bleaching or heat-induced partial necrosis and recovered within days (Wisshak et al. 2013; Hill et al. 2016; M. Hill pers. comm. 2016). Widespread thermally induced mortality events that are increasingly common in corals still remain unknown for clionaids.

Like many other sponges, bioeroding sponges have a high capacity for regeneration. Wound healing was fast in the Mexican *gamma* form of *Cliona californiana,* and faster during the warm season. Wounds of 1 cm in diameter and 1 cm depth

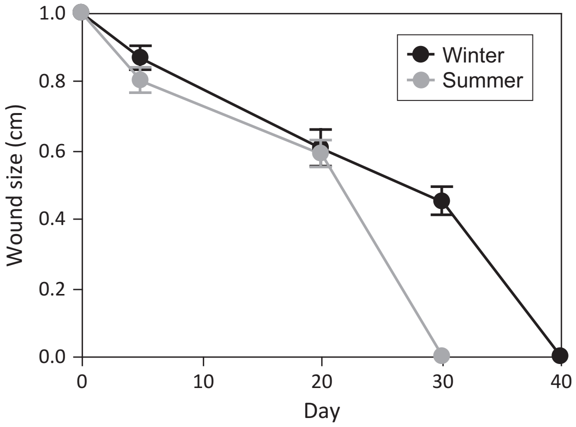


Fig. 7.9 Tissue regeneration and wound healing in *gamma* morphology *Cliona californiana* from the Mexican Pacific, assessed during the warm and the cold season. From each specimen, two cores of 1 cm diameter and 1 cm depth were removed at the beginning of the experiment, and healing was quantified by measuring the scar diameter at intervals (*N* = 25 specimens per season; error bars denote standard deviation)

healed and filled in all 25 specimens over 30 days in summer, while the same process required 40 days in winter (Fig. 7.9). Wider experimental scars in other *beta* and *gamma* sponges from which samples were taken had evened out within about half a year or longer, depending on how much tissue was removed and whether the surrounding substrate material had to be eroded down to the level of the resulting scar (Bell 2002 for *Cliona* cf. *celata*; C. Schönberg pers. obs. for *Cliona orientalis*). During a trial for remediation of clionaid infestation of live corals, all visible sponge tissue of *Cliona delitrix* was manually removed, and resulting holes were filled with cement or epoxy (Halperin et al. 2016). Yet 1 year later, *Cliona delitrix* tissue reappeared in the cleaned corals, attesting to the superior recovery potential of this sponge, even if relying on very small tissue remnants not including ectosome. Likewise, Schönberg and Burgess (2013) found a diverse community of bioeroding sponges on a reef that 6 months earlier had been destroyed and abraded by a tropical cyclone. Clionaid and *Siphonodictyon* spp. had apparently regenerated from remnant tissue in remaining coral rock. Handmade fragments of *Cliona caribbaea*, *Cliona* cf. *celata*, *Cliona varians*, *Spheciospongia vagabunda* and cores of *Cliona orientalis* sampled with a pneumatic drill for experimental work formed ectosome over the damaged surfaces within only a few days (Table 7.4). This suggests that fragments have a high potential to survive, but persistence and survival can depend on fragment size and whether oscules are present on them (Kelly 1986). Regeneration is faster in stronger flow regimes (Bell 2002) and during the warmer season (Fig. 7.9). In photosymbiotic sponges, the zooxanthellae accumulate at the edge of the damage and appear to support the healing process (Schönberg and Suwa 2007).

Recent studies showed that in contrast to congenerics from warm-temperate environments (e.g. Rosell 1993; Mariani et al. 2005; Piscitelli et al. 2011), some dominant species of bioeroding sponges on coral reefs reproduce more than once per year or generate a nearly continuous supply of reproductive elements by alternating sexual and asexual strategies (Bautista-Guerrero et al. 2010; González-Rivero et al. 2013; Bautista-Guerrero et al. 2014; Chavez-Fonnegra et al. 2016). This means that while many space competitors on the reef have short, seasonal spawning phases, several bioeroding sponges can recruit over much of the year and are ready as soon as an opportunity arises, e.g. when fresh substrate becomes exposed by mortality or grazing (Chavez-Fonnegra et al. 2016). Asexual reproduction such as budding or gemmulation can bridge gaps in sexual reproduction and facilitates near-continuous reproductive output (Fig. 7.6; Rosell 1993; Rosell and Uriz 2002a; Schönberg 2002c; Bautista-Guerrero et al. 2010). Buds can be positively buoyant, which enables dispersal by drifting (Fig. 7.6; Ise 2010). Gemmules are encapsulated omnipotent sponge cells that can ensure repopulation usually at the exact same site after dormancy during unfavourable seasons and after tissue loss due to disturbance and catastrophic events (Fig. 7.6; Schönberg 2002c and references therein). We here propose that excavating fishes such as *Bolbometopon muricatum* can bite the substrate deeply enough to remove gemmules with the grazed material (bites can be as deep as 2 cm in coral substrate, D. Bellwood, pers. comm. 2016) and that the gemmules may survive the gut passage, raining down after transport within the mobile fish, thus possibly seeding new reef areas upon defaecation (Fig. 7.6; parrotfish guts are pH neutral, D. Bellwood, pers. comm. 2016). Another pathway of dispersal not directly controlled by the sponge is fragmentation, which occurs in nature via storm damage or predation (Fig. 7.6; Kelly 1986; Schönberg and Wilkinson 2001; López-Victoria and Zea 2004), but this appears to be only a small addition to other reproductive strategies (Kelly 1986; Zilberberg et al. 2006). Some species were found to have a limited range of dispersal, and their sexual reproduction may largely depend on the production of sticky egg clusters to ensure a large recruiting mass, or creeping larvae that have only a short swimming phase and remain in the parental habitat (Fig. 7.6; Warburton 1958a, b; 1966; Kelly 1986; Mariani et al. 2000, 2001, 2005, 2006, León-Pech et al. 2015). However, the tropical coral reef species *Cliona delitrix* apparently has larvae with far better swimming abilities and a surprisingly wide dispersal range (Zilberberg et al. 2006; Chaves-Fonnegra et al. 2015). An unusual larval dispersal strategy is expressed in the hoplitomella of the Thoosidae (Trégouboff 1939, 1942; Garrone 1974; Vacelet 1999; Bautista-Guerrero et al. 2010, 2016). This larva has morphological traits of a gemmule, increasing the likelihood of survival. It also has long processes supported by spicules that enhance the viscous resistance in the water column to keep the larva afloat and ensure that it can drift across large distances even though it lacks flagellae for active propulsion.

The success of bioeroding sponges is supported by all the above traits: the sheltered life within the substrate and the ability to encapsulate dormant cells as resting stages; the bleaching resistance of photosymbiotic species by relocation of their often heat-tolerant zooxanthellae; the sponges' capacity to quickly regenerate, even from comparatively small pieces of tissue, to grow fast when the conditions are favourable; and their versatile reproduction strategies employing different pathways.

This may be the reason why bioeroding sponge species persisted, reproduced and increased their abundances when coral cover decreased under adverse conditions (Rose and Risk 1985; Vicente 1990; Rützler 2002a; Schönberg and Ortiz 2009; Marulanda-Gómez et al. 2017). Resulting community shifts appear to favour especially large, aggressive *beta*-growth species (Rützler 2002a; Ward-Paige et al. 2005; Schönberg and Ortiz 2009). Previously, shifts towards bioeroding sponges have largely been identified as a consequence of eutrophication and organic pollution (Table 7.3). Since then, increased substrate availability after coral mortality is seen more and more as another important driver advancing bioeroding sponges (Table 7.3). Recently a third strong factor was identified, ocean acidification (OA; Table 7.3), and other factors can contribute or interact (see Schönberg et al. 2017). Earlier work has shown that cells of bioeroding sponges appear to have a larger resistance against the effects of acid than non-eroding sponges (Galtsoff and Pertzoff 1926; Schönberg 1999). By experimental application of CO_2, it quickly became obvious that a lower pH greatly affects the chemical process in sponge bioerosion, the etching of fissures that will free lentil-shaped, silt-sized particles, but not so much the mechanical process, the removal of these particles (e.g. Pomponi 1980; Wisshak et al. 2012; Fang et al. 2013b; Wisshak et al. 2013, 2014; Schönberg et al. 2017). The chemical bioerosion process is strongly and consistently enhanced with lowered pH, doubling with a twofold $p\mathrm{CO}_2$, across different species and climate zones and regardless of whether the sponges are photosymbiotic or not (Table 7.3; Wisshak et al. 2014; Schönberg et al. 2017). However, for some species, the observed experimental response was not linear and resulted in a parabolic function, suggesting that physiological limits may have been reached (Table 7.3). If the parabolic responses reflected the organisms' biology, they suggest that moderate increases of $p\mathrm{CO}_2$ had beneficial effects, but higher doses beyond a presently unknown threshold became a stress factor. Other research projects used combined temperature-$p\mathrm{CO}_2$ scenarios, and the damaging effect at the final level may rather have been a consequence of the temperature application (Fang et al. 2013b), as Wisshak et al. (2013) found that temperatures above 30 °C quickly resulted in partial necrosis in the same species, *Cliona orientalis*. It is thus obvious that interaction among environmental factors can play a large role, and this is still inadequately studied (Schönberg et al. 2017). Factors such as nutrients may further enhance OA effects on macroborers with chemical bioerosion (as proposed by DeCarlo et al. 2015), but presently available data on interactions are scarce and may remain largely unconfirmed (Schönberg et al. 2017). When considering how resilient bioeroding sponges are with respect to negative developments, it is reasonable to assume that at least midterm future reefs could experience significantly more sponge bioerosion. Including sponge bioerosion in modelling approaches assessing reef health implied that the sponges had a significant impact and could determine resilience levels and recovery potentials of reef environments (Kennedy et al. 2013; Enochs et al. 2015). Under normal conditions, bioeroding sponges are a natural part of a coral reef community and should not be perceived as pest organisms. However, when coral reef health declines due to environmental change, sponge bioerosion may increase to a level that in combination with other processes may outweigh calcification. As a consequence, various management strategies may need to be considered.

Extermination of a problem group that quickly and opportunistically responds to environmental change does not seem to be advisable when it is part of the natural community, and trying to reduce the severity of the factor that produces shifts in reef health may be a better approach. As there is no known infallible remedy that could be employed to control extreme population growth in bioeroding sponges on coral reefs, mediating their advance is thus most likely best achieved by improved water quality. Integrated research on interaction effects involving different environmental and biological processes will help to gain a better understanding what triggers or controls bioeroding sponge population growth or can intensify their bioerosion rates. Further studies on bioeroding sponge reproductive strategies and population dynamics will also be of benefit in this context, as well as the knowledge about potentially preferred substrates of the more aggressive, faster-growing species. For field surveys, we require long-term, monitoring-like approaches that reveal developments over time (Schönberg 2015); standardised, large-scale investigations that identify sites that become increasingly vulnerable to bioerosion; and carbonate budget studies that assess the proportional contribution of sponge bioerosion compared to total bioerosion (Murphy et al. 2016).

7.6.1 Case Example: Caribbean

Bioerosion research in the Caribbean has traditionally been strong and still is. Similar to the situation in the Coral Triangle, over time, Caribbean reefs became heavily impacted by human activities, and coral cover declined (Fig. 7.10a). The damage includes effects of land use, reduced water quality, bleaching, coral mortality, algal bloom events and overfishing (e.g. Hughes 1994; Cramer et al. 2012). In addition, the demise of *Diadema* sea urchins caused a shift towards macroalgae on many reefs (e.g. Carpenter 1988; Mumby et al. 2006b). This led to changes in the balance between accretion and erosion and altered the roles of some bioeroders and their interactions with other biota (Perry et al. 2008; Kennedy et al. 2013; Perry and Harborne 2016; Schönberg et al. 2017).

Bioerosion studies in the Caribbean significantly contributed to our understanding of such biological interactions (Schönberg et al. 2017). Particularly *beta*-form clionaids proved to be strong space competitors against other sponges, some algae and the live corals they invade (Vicente 1978; Chavez-Fonnegra et al. 2005; López-Victoria et al. 2006; Chaves-Fonnegra and Zea 2007; Chaves-Fonnegra et al. 2008; Chaves-Fonnegra and Zea 2011). These clionaids can furthermore benefit from corallivory. Some parrotfishes occasionally target the coral lip that forms around the surface lowered by sponge bioerosion. The fish bites create fresh and undefended substrate the sponges can freely advance into (Rützler 2002a; Márquez and Zea 2012). A similar effect was observed for urchin grazing that removed turfs and crustose coralline algae and thus accelerated lateral growth of adjacent *Cliona delitrix* (Chaves-Fonnegra and Zea 2011). Single bite scars forming islands of bare substrate in live corals and algal turfs are also thought to facilitate the establishment of

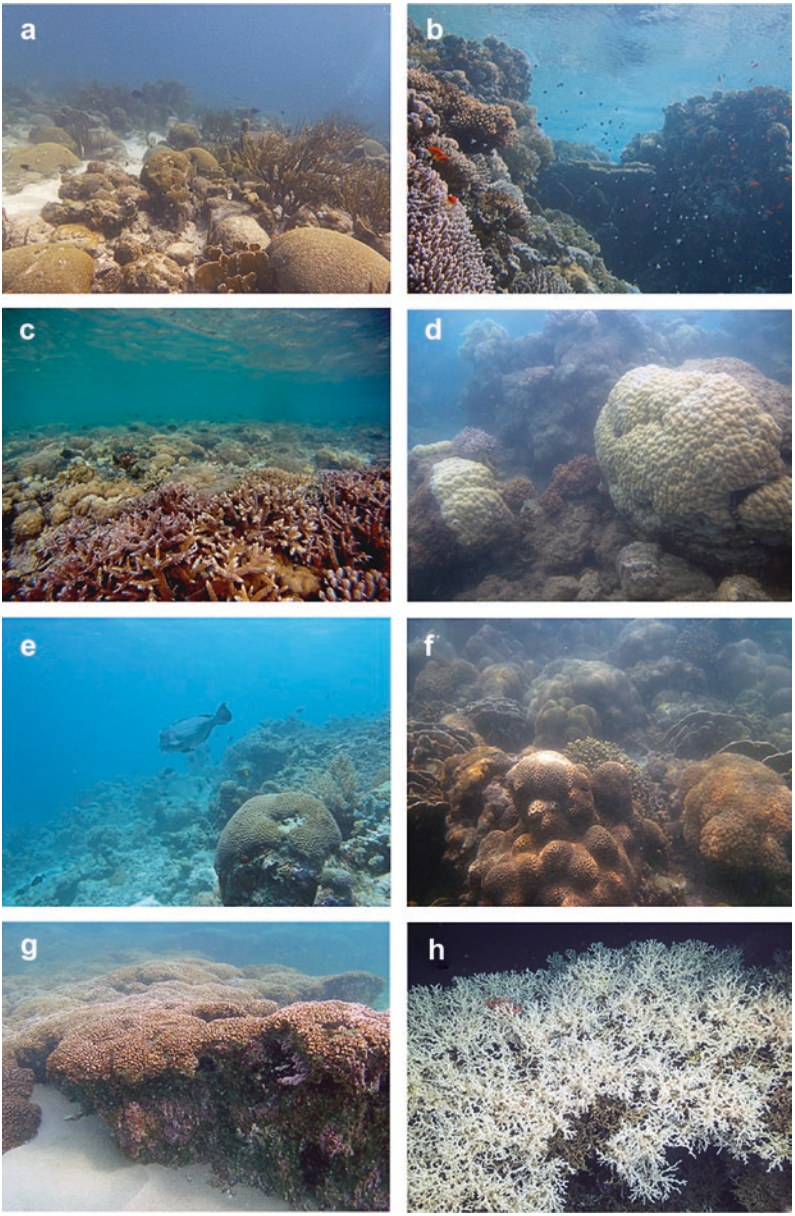


Fig. 7.10 Reef environments subject to sponge bioerosion, all except last in shallow depth of 2–5 m. (**a**) Caribbean Sea, Curaçao (courtesy M. Achlatis, Queensland University, Brisbane). (**b**) Red Sea (courtesy G. Heiss, Freie Universität, Berlin). (**c**) Lakshadweep (courtesy M. Jaini via N. Namboothri, Dakshin Foundation, Bangalore). (**d**) Central Great Barrier Reef, leeward side of Orpheus Island. (**e**) Coral Triangle, south Sulawesi (courtesy J. Marlow, Victoria University of Wellington). (**f**) Tung Ping Chau, Hong Kong. (**g**) Eastern Tropical Pacific, Mexico. (**h**) Cold-water reef at 288 m water depth (courtesy M. Wisshak, Senckenberg Institute, Wilhelmshaven)

bioeroding sponges, representing ideal settling ground for larvae that cannot recruit on live coral surfaces and not easily on turfs (Rützler 1971; López-Victoria and Zea 2005). Herbivory may further help photosymbiotic sponges by reducing the sponge-macroalgal competition that is thought to subdue the sponges by shading or by allelopathy (González-Rivero et al. 2012). On the other hand, urchins and parrotfishes also feed on different bioeroding sponges (Fig. 7.6, Appendix E), or they can entirely remove small sponges while grazing on algal turfs. Grazers therefore have an important role in bioeroding sponge recruitment, early survival and maintenance, while the sponges weaken the substrate and enhance the bioerosion effect by grazers (Schönberg et al. 2017).

Earlier research on Caribbean bioeroding sponges was largely concerned with their role in carbonate budgets and their erosion rates (e.g. Bak 1976; Stearn and Scoffin 1977; Scoffin et al. 1980; Appendix C). It quickly became evident that sponges played a predominant role in Caribbean carbonate cycling and that they produced large amounts of fine sediments (Fig. 7.5; Appendices C–D). The recognition of the key role of bioeroding sponges in Caribbean carbonate budgets has led to their inclusion in routine surveys and monitoring throughout the wider Caribbean (e.g. Callahan 2005; Lang et al. 2010; Makowski and Keyes 2011; Gilliam 2012) and in modelling efforts aiming to predict future trajectories of reef health (Kennedy et al. 2013; Enochs et al. 2015). Along with photosymbiotic clionaids, *Cliona delitrix* was recognised as a key bioeroder and good bioindicator of eutrophication in the Caribbean (Rose and Risk 1985; Callahan 2005; Ward-Paige et al. 2005; Chiappone et al. 2007). Resulting data represent one of the few examples of assessing bioeroding sponges over time and provide a guideline on how to proceed (see Schönberg 2015). As these monitoring efforts are based on imagery along standardised transects, the resulting database allowed repeated evaluation for different purposes (see Althaus et al. 2015), leading to a number of outcomes. Monitoring observed increases in bioeroding sponge abundances (Ward-Paige et al. 2005). Modelling predicticted that among other important factors, sponge bioerosion needs to be addressed in reef management to arrest and reverse coral demise in the Caribbean (e.g. Kennedy et al. 2013).

7.6.2 Case Example: Red Sea

The Indian Ocean and its neighbouring seas have globally important reef areas of significant socioeconomic value, but along with other coral reefs, they experienced serious disturbances (Fig. 7.10b, c; e.g. Souter et al. 2000). Within the region, the Red Sea stands out as a diversity hotspot with a high level of endemism (DiBattista et al. 2016). It is characterised by extreme temperatures, high salinity and water clarity that rely on low rainfall, low runoff and low nutrient influx (e.g. Berman et al. 2003; Fahmy 2003; Manasrah et al. 2006; Davis et al. 2011). Despite intensifying tourism, destructive fishing and farming practices, related nutrient enrichment, crown-of-thorn starfish outbreaks and disturbances relating to global change

(Riegl and Luke 1998; Jameson et al. 1999; Riegl and Piller 1999; Goreau et al. 2000; Kotb et al. 2004; Loya et al. 2004), until recently the Red Sea retained a comparatively high coral cover and a low occurrence of bleaching, especially in the northern half (Fig. 7.10b; Hodgson 1999; Furby et al. 2003). Combining locally unique (temperature, salinity) with widely occurring conditions (effects of human use and global change), the Red Sea thus appears to be a good location to study reef health and ecological relationships. Studies along local gradients from near pristine to highly disturbed environments may provide new insights into how various environmental parameters may affect bioeroding sponges.

While general bioerosion research in the Red Sea has generated important results (largely by H. Schuhmacher or Y. Loya and co-workers), we have only very restricted knowledge on Red Sea bioeroding sponges. Respective field surveys are virtually non-existent or did not identify the species (e.g. Sarà et al. 1979; Maier 1997). In consequence, our understanding of the diversity of Red Sea bioeroding sponges is poor (Appendix A), and more detailed knowledge is limited to a single *Pione* species of unconfirmed taxonomy.

This *Pione* species is a common bioeroder in the Red Sea and has been used for molecular and physiological studies (Beer and Ilan 1998; Steindler et al. 2001; Zundelevich et al. 2007; Ferrario et al. 2010; Erpenbeck et al. 2016). It was previously called *Pione vastifica*, *Pione lampa* or *Pione* sp., but there are good reasons to assume that it is the long-ignored species Keller described in 1891 as *Sapline mussae*. Keller overlooked the microrhabds that must have been present, but his description of the megascleres is characteristic and in agreement with data presented by Zundelevich et al. (2007) and Ferrario et al. (2010). The latter study confirmed that the sponge can occur in *alpha* and *beta* habit, and the authors did not find additional *Pione* spp. at their study sites. Morphological differences seem to exist (Ferrario et al. 2010) in comparison with *Pione lampa* (redescribed by Schönberg 2002c) and *Pione velans* (redescribed by Fromont et al. 2005), and *Pione vastifica* is an Atlantic sponge not known to occur in *beta*-growth (e.g. Hartman 1958). Until more recent material can be comprehensively compared to Keller's, we should assume that the common Red Sea clionaid is *Pione mussae*.

Pione mussae is the only species of this genus reported to have phototrophic symbionts described as zooxanthellae (*Symbiodinium*), which were studied in pioneering experiments. Beer and Ilan (1998) were the first to use pulse amplitude modulated (PAM) chlorophyll fluorometry to investigate sponge photosymbioses by targeting this sponge. They and Steindler et al. (2001) showed that it adapted its photophysiology to the predominant light environment, also displaying daily variations of photochemical performance. Since then PAM fluorometry has rapidly gained importance in this context and was employed to assess efficiency of photosystem II or photosynthetic electron transport rate (ETR) in photosymbiotic species of *Cliona* under experimental conditions, using this as an indicator of stress and health (e.g. Wisshak et al. 2012, 2013). Coral photosymbionts in the Red Sea, and especially in the Persian Gulf, are largely those adapted to high temperatures (Baker et al. 2004; Karako-Lampert et al. 2004; Sawall et al. 2014; Hume et al. 2016). Unlike for corals, we have no comparable data on the temperature tolerance of Red

Sea bioeroding sponges, even though various photosymbiotic bioeroding sponges occur there (Appendix A). Future research should thus look into their symbiotic relationships in this extreme environment.

Zundelevich et al. (2007) quantified bioerosion of *Pione mussae* not only assessing different circumstances but also for the first time comparing chemical (etching to cut out $CaCO_3$ chips) with mechanical bioerosion (chip removal; see Pomponi 1980). They estimated that two thirds of the substrate were dissolved by the sponge and only one third removed in particular form. This contrasted first estimates for the chemical part in sponge bioerosion, which ranged from 2 to <10% (Warburton 1958b; Rützler and Rieger 1973), and later measurements that commonly moved around 10% (Nava and Carballo 2008; Fang et al. 2013b; Wisshak et al. 2013). We suggest that discrepancies between studies may have been caused by the method. Assessing mechanical sponge potentially incurs losses of some of the silt-sized material during handling, presumably falsely inflating the proportion of chemical sponge bioerosion (Fang et al. 2013b; Schönberg et al. 2017). However, possible alternative explanations may include yet insufficiently understood species-specific differences and effects caused by environmental conditions.

7.6.3 Case Example: Australian World Heritage Reefs (Great Barrier and Ningaloo Reef)

Covering an area over 348,000 km^2, the Australian Great Barrier Reef (GBR; e.g. Fig. 7.10d) is the largest continuous coral reef system on earth, is of profound significance for the diversity of corals and coral-associated organisms and was inscribed as a World Heritage in 1981 (UNESCO 2016a). The GBR Marine Park Authority provided a tight focus on regulation, which led to an evolving management and protection strategy and resulted in the 2003 Zoning Plan with an area of 33% designated as no take, which received global attention (GRBMPA 2003; Miller and Sweatman 2004; Fernandes et al. 2005). The most extensive database on reef parameters is available through the 1985–2012 GBR monitoring program, further elevating the importance of this reef system (e.g. Miller and Sweatman 2004; Sweatman et al. 2011; De'ath et al. 2012). Despite global change, tropical storms, crown-of-thorn starfish outbreaks, decreasing water quality, rapidly growing coastal populations and industries and shipping traffic, the GBR initially fared better than many other reef systems, especially in the northern and southern sectors (Miller and Sweatman 2004; Sweatman et al. 2011; De'ath et al. 2012). Coral cover and calcification rates nevertheless declined due to repeated disturbances and chronic stress (e.g. De'ath et al. 2009, 2012; Brodie and Waterhouse 2016). The most recent bleaching in early 2016 has reached or surpassed the severity of the 1998 and 2002 events, with 93% of the GBR affected and with largest impact in the northern sector, resulting in high, but patchily distributed, coral mortality (Berkelmans et al. 2004; Australian National Coral Reef Task Force 2016; Ainsworth et al. 2016;

Hoegh-Gouldberg and Ridgway 2016; Stella et al. 2016). Decreasing habitat quality of the GBR and expected impacts due to harbour construction and shipping traffic led to a debate on whether a continuation of the UNESCO status for the GBR is justified (Grech et al. 2016; UNESCO 2016b, c).

The remotely located Ningaloo Reef in Northwest Australia is 260 km long and one of the longest fringing reefs of the world (UNESCO 2016d). The area is recognised for its high biodiversity and perceived endemism, not just for corals (e.g. van Keulen and Langdon 2011; Schönberg and Fromont 2012). The proximity to the coast and its importance as feeding and breeding ground for, e.g. whale sharks and turtles, give Ningaloo a special standing (UNESCO 2016d). Like the GBR, one third of the area is zoned as no-take sanctuary (Beckley and Lombard 2012). In 2011 Ningaloo Marine Park received World Heritage status (Radford and Ridgway 2011; UNESCO 2016d). For a long time, coral habitats in Northwest Australia evaded bleaching and coral mortality and were regarded as pristine, but over the last decade, they repeatedly experienced thermal stress as well, with growing impact (e.g. Feng et al. 2015; Lafratta et al. 2015). Intensifying tourism, recreational fishing, coastal, urban and industrial development and the close vicinity of Ningaloo to important carbohydrate extraction sites add to the risk for further degradation (Jones et al. 2011; UNESCO 2016d).

Research related to bioerosion was slow to start on Australian Reefs. One of the earliest reports on bioerosion for the GBR was provided by Otter (1937). Other early accounts included some isolated studies into mollusc boring (Hamner and Jones 1976) but were otherwise largely dominated by grazer studies (e.g. investigations by D. Bellwood and co-workers on parrotfish, since Bellwood 1985) and settlement experiments (e.g. block experiments by P. Hutchings and co-workers since ca. 1980, e.g. Kiene and Hutchings 1994). As sponges are slow recruiters on settlement blocks, this meant that little was known about Australian bioeroding sponges until around 1980, when GBR corals were slabbed to assess the relative impact of different bioeroders and to look into ecological relationships and interactions (e.g. Risk and Sammarco 1982; Sammarco et al. 1986, 1987; Sammarco and Risk 1990; Risk et al. 1995). The taxonomy of Australian bioeroding sponges remained virtually unexplored until the mid-1990s, when the poor species record was gradually improved by work on the GBR (Fromont 1993; Schönberg 2000, Schönberg 2001a, b; Schönberg et al. 2006; Schönberg and Tapanila 2006b; Schönberg and Beuck 2007). Respective data from Ningaloo were largely restricted to faunistic reports lacking full identification of species (van Keulen and Langdon 2011; Schönberg and Fromont 2012; Fromont and Sampey 2014). Detailed, repetitive field surveys ensued on the central GBR that showed that sponge bioerosion fluctuates with reduction or increase in live coral cover (Schönberg 2001b; Schönberg and Ortiz 2009; C. Schönberg unpubl. data 2010–2011).

Existing manipulative experiments on a single species of a bioeroding sponge have mostly been conducted with *Cliona orientalis* from the Australian east coast (Schönberg 2001a; Schönberg and Wilkinson 2001; Schönberg 2002b, 2003, 2006; Schönberg and Suwa 2007; Holmes et al. 2009; Schönberg and Shields 2008; Schönberg and Wisshak 2012; Wisshak et al. 2012; Fang et al. 2013b;

Wisshak et al. 2013; Fang et al. 2014; Wisshak et al. 2014; Fang et al. 2016; Pineda et al. 2016a, b; Fang et al. 2017a, b; Pineda et al. 2017a, b, c; Achlatis et al. in press; J. Fang et al. unpubl. data 2017). These studies showed that bioerosion rates of this species acutely react to environmental conditions, including substrate and water quality. The recent establishment of the Australian National Sea Simulator (SeaSim) research facility in Townsville opens a multitude of opportunities to work with a larger range of species, which have not yet been explored. Most importantly, the SeaSim would allow to elaborate factor and organism interaction-oriented experiments. Respective outcomes would inform on suitable management strategies that may help control the rising bioerosion rates that are expected as response to the recent large-scale bleaching and intensifying ocean acidification (Schönberg et al. 2017). This would specifically answer the question whether impacts at global scale can be reduced or slowed by controlling local factors such as water quality (Achlatis et al. in press).

7.6.4 Case Example: Coral Triangle

The Coral Triangle is the most diverse coral reef bioregion on earth and harbours 76% of the species of hermatypic corals, a situation that creates an immense demand for conservation (Roberts et al. 2002; Hoeksema 2007; Veron et al. 2009; Rudi et al. 2012; Fig. 7.10e). The area contains existing and planned coral reef World Heritage sites (UNESCO 2016e, f). However, just as for most of the other bioregions mentioned in the present paper, reefs of the Coral Triangle and the neighbouring South China Sea (Fig. 7.10f) have strongly deteriorated due to human use. Damage was most notably caused by pollution, eutrophication and increased sedimentation, destructive fishing, oil and gas extraction, coral mining and land reclamation (Gomez et al. 1994; Morton 1996; Edinger et al. 1998, 2000; Edinger et al. 2000; Fabricius 2005; Madin 2015; Schofield 2015; Southerland 2016). Especially eutrophication and the widely used practice of dynamite fishing have led to a decrease in live coral cover, reduced reef structural complexity and increased internal bioerosion, which together resulted in net reef erosion of some Indonesian reefs (e.g. Erdman 2000; Edinger et al. 2000; Holmes et al. 2000; Perry et al. 2008). In this context, sponge bioerosion was confirmed as a reliable bioindicator of reef degradation and elevated nutrients (Holmes et al. 2000; Edinger and Risk 1997). In consequence, it was proposed that coral reef monitoring programmes should collect and screen rubble for sponge bioerosion (Holmes et al. 2000; Risk et al. 2001). Schönberg (2015) discussed this method in a wider context and cautioned that unattached substrate may convey a biased picture by largely representing non-dominant bioeroding sponges. Moreover, storms can redistribute rubble pieces and decouple rubble infauna from local environmental gradients. Nevertheless, bioeroding sponge abundance is a good measure of coral reef disturbance, and depending on purpose and level of taxonomic resolution, the rubble approach can still generate vital data about reef health, which is a much-needed information.

Other research with a clear focus on the bioeroding sponges of the Coral Triangle was largely restricted to faunistic accounts and species descriptions, with Indonesia favoured over the remaining regions (e.g. Calcinai et al. 2005; Becking et al. 2013). The bioregion lacks expertise and regional coordination (Tun et al. 2004), and by far, most research efforts were contributed by foreign scientists visiting the area. A recent approach related differences in the species composition of communities of bioeroding sponges in attached substrates to environmental conditions (J. Marlow et al. unpubl. data 2017). Two other studies looked into substrate effects on bioerosion. Lescinsky et al. (2002) evaluated the relative contribution of different bioeroders per substrate quality and over time, with sponges only contributing significantly after the clean substrates were exposed to larval settlement for at least 1 year. Calcinai et al. (2007a) attached different experimental substrates to *Cliona albimarginata* and stated that denser materials became more intensely eroded. We were able to reconfirm this relationship for zooxanthellate *beta*-morphology sponges from different areas (Fig. 7.7).

The Coral Triangle is one of the areas at high risk for tsunamis. In 1976 (Philippines), 1998 (PNG) and 2004 (Indonesia, Sri Lanka, India, Thailand), the area was hit by particularly devastating seismic sea waves (Wikipedia 2016a). Reefs have been identified as natural barriers that can lessen the impact of tsunamis (Baba et al. 2008). However, bioeroding sponges reduce the structural strength of corals by increasing the porosity of coral skeleton (Tunnicliffe 1979, 1981; Schönberg 2002b). This effect is worsened by the borers preferably settling on dead parts of corals (e.g. Goreau and Hartman 1963), thus weakening their attachment and increasing the risk of their dislodgement during such catastrophic events. In the Mediterranean, sponge-bored carbonate blocks that weighed up to 75 t were assumed to have been dislocated by tsunamis (Scheffers and Scheffers 2007). Strong tropical storms can have similar effects, their frequency and strength are expected to increase (e.g. Hoegh-Guldberg et al. 2007; De'ath et al. 2012), and the same reefs that have been impacted by tsunamis may experience increased physical disturbance through storms. As prognoses are that bioerosion by sponges and other organism will intensify in the near future (Schönberg et al. 2017), physical damage by storms and tsunamis may be amplified by biological activity (Glynn 1997; Clark and Morton 1999).

7.6.5 Case Example: Eastern Tropical Pacific (ETP)

Coral reefs in the ETP are poorly developed and have a relatively low and shallow framework (thickness 1–6 m) that is mainly formed by *Pocillopora* species rather than by massive corals (Fig. 7.10g; Glynn and Colgan 1992; Cortés 1997). The reefs establish directly at the shoreline and are typically located in protected bays, being characterised by their small size of a few hectares each, a discontinuous distribution and low species diversity (Cortés 1993, 1997; Cortés et al. 2017). They do not show the zonation pattern described from other reefs: lagoon, back reef, reef flat and fore reef (Glynn 1982). Apart from human use resembling that in other bioregions (Cortés and Reyes-Bonilla 2017), bioerosion in the ETP is promoted by a suite of special environmental conditions that are responsible for the relatively ephemeral existence of local reefs over geological time (Colgan 1990; Glynn and Colgan 1992; Toth et al. 2012): productive waters and seasonal upwelling; a shallow and fluctuating thermocline; surface waters characterised by elevated $p\mathrm{CO}_2$, resulting in a relatively low pH and a low aragonite saturation state (Ω); poor reef cementation; and the considerable influence of thermal ENSO events and storms that have repeatedly led to coral bleaching and mortality over the last three decades (e.g. Glynn and Colgan 1992; Cortés 1997; Lirman et al. 2001; Millero 2007; Manzello et al. 2008; Manzello 2010; Glynn et al. 2017). The above means that the ETP combines the three conditions that have most uniformly been found to accelerate reef bioerosion: nutrient enrichment, high availability of dead substrate and a water chemistry that enhances chemical bioerosion (Glynn 1990; Eakin 1992; Manzello et al. 2017; Schönberg et al. 2017). Therefore, the currently observed degradation of eastern Pacific reefs is likely to continue under the present trends of temperature rise and ocean acidification (Glynn et al. 2001; Manzello et al. 2008; Perry et al. 2008; Carballo et al. 2013; Manzello et al. 2017). Severe bioerosion has been reported from sites within this bioregion, to an extent that eventually even the grazer-bioeroder community collapsed (Reaka-Kudla et al. 1996; Eakin 2001).

Traditionally, bioerosion research in the ETP had a large focus on grazing by sea urchins (e.g. Reaka-Kudla et al. 1996; Cortés 1997; Glynn 1997; Alvarado et al. 2016, 2017). Notwithstanding, bioeroding sponges of the Mexican Pacific are diverse and abundant, and a very good background on their taxonomy and distributions in relation to sites and environmental variables was established (Carballo et al. 2004; Carballo and Cruz-Barraza 2005; Bautista-Guerrero et al. 2006; Carballo et al. 2007, 2008b; Cruz-Barraza et al. 2011; Carballo et al. 2013; Nava and Carballo 2013). Research in the ETP furthermore contributed significantly to our knowledge on the reproduction and dispersal potential of bioeroding sponges (Bautista-Guerrero et al. 2010, 2014; León-Pech et al. 2015; Bautista-Guerrero et al. 2016; Nava and Carballo 2016). This combination of community data on boring sponges is unavailable from the rest of the Indo-Pacific Ocean, and it has considerable relevance for the assessment of how ecological factors influence coral reef health in this region.

Bioeroding sponges of the ETP live cryptically within coral bases and the reef framework, which means that they are most abundant at the reef margins, where access to dead surfaces is easiest (Carballo et al. 2008b; Fig. 7.10g). Clionaids are the most destructive and diverse group of bioeroding sponges (Fig. 7.4). *Alpha*, *beta* and *gamma* morphologies occur (Alvarado et al. 2017). *Beta*-form clionaids and large *Siphonodictyon* spp. are dominant in the Caribbean and in the western Pacific (e.g. Rützler 1971; Schönberg 2001b; Zea and Weil 2003), but they play a secondary role in the ETP (Alvarado et al. 2017). Unlike for most reefs of other bioregions, the small *alpha*-form *Cliona vermifera* is the most abundant bioeroding sponge in the ETP (Guzmán 1988; Carballo et al. 2008b; Bautista-Guerrero et al. 2014). *Cliona vermifera* is closely followed by other species that apparently favour branching corals as substrate, which is the most common material in the ETP, vis. *Siphonodictyon crypticum*, *Pione carpenteri*, *Thoosa calpulli* and *Thoosa mismalolli* (Carballo et al. 2004, 2008b; Pacheco Solano 2012). Especially *Cliona vermifera* and *Thoosa mismalolli* are locally highly destructive sponges capable of producing extensive galleries in coral skeletons (Nava and Carballo 2008; Carballo et al. 2013; Bautista-Guerrero et al. 2014). ETP boring sponges do not usually have the capacity to penetrate corals through soft tissue (Carballo et al. 2013), which is another region-specific characteristic, but *Cliona vermifera* was able to invade live corals during an experiment (Nava and Carballo 2016). The ETP coral community as well as that of the bioeroding sponges is this quite unique, which may suggest different pathways of co-evolution between the borers and the corals than elsewhere.

Bioeroding sponges appear to be most common on ETP reefs that previously experienced disturbance including thermal events (Carballo et al. 2013). It can thus be assumed that with progressing global change, sponge bioerosion in the ETP will increase further. However, Carballo et al. (2013) also reported bioeroding sponges to be less common at sites with higher rates of sedimentation. While sediment tolerance varies with species (Carballo et al. 1994; Perry 1998; Reis and Leão 2000; Schönberg 2016b; J. Marlow et al. unpubl. data 2017), evidence for an intolerance has been observed in different bioeroding sponges, especially for fine sediments (Schönberg 2001b; Chavez-Fonnegra et al. 2007; Pineda et al. 2016a, b). Sedimentation and turbidity may thus be factors that could potentially counteract predicted increases in sponge bioerosion.

7.6.6 Case Example: Cold-Water Reefs

From Atlantic, Mediterranean and Pacific *Lophelia pertusa* and Chilean *Desmophyllum dianthus*, Wisshak et al. (2005) and Wisshak (2008) described different erosion traces that likely belong to clionaid (smooth erosion scars) and non-clionaid bioeroding sponges (ring-grooved scars; see Calcinai et al. 2004a), as well as reporting mulberry-like traces that were assigned to 'micro-sponges'. Such sponge traces represented three of the most important bioeroders of a Swedish reef (Wisshak et al. 2005), which implies an important role of sponges in cold-water reef bioerosion.

In deep- or cold-water habitats, bioeroding sponges inhabit not just reef-forming, but commonly also precious corals (e.g. Schönberg and Wisshak 2014), all of which are ahermatypic and predominantly in branching habit (Fig. 7.10h; Hain and Corcoran 2004; Freiwald and Roberts 2005; Roberts et al. 2009). Cold-water coral communities contribute only 4–12% of the $CaCO_3$ flux of warm-water reefs (Lindberg and Mienert 2005) and may thus be more vulnerable to bioerosion. In many ways, warm-water calcifiers respond to sponge bioerosion in very similar ways as do those in cold and deep water, but here the corals, their habitats and the sponges eroding them are not well studied (Table 7.2; Rogers 1999; Lindberg and Mienert 2005).

Bathymetry forms the taxonomic and morphologic affiliation of bioeroding sponges, and a distinct shift in community composition occurs with water depth

(C. Schönberg et al. unpubl. data 2017). Tropical coral reefs are mostly eroded by *Cliona*, *Cliothosa*, *Diplastrella*, *Pione*, *Spirastrella* and *Zyzzya* spp. (Appendix A), while *Cervicornia*, *Spheciospongia* and large *Siphonodictyon* spp. commonly inhabit the sediments of shallow-water habitats (Ise et al. 2004; Schönberg 2016b). *Alectona*, *Delectona*, *Dercitus*, *Dotona*, *Holoxea*, *Spiroxya*, *Thoosa* and *Triptolemma* spp. play a larger role at greater depth or in colder climates (Appendix A; Cerrano et al. 2001; Calcinai et al. 2010; Fig. 7.4). *Siphonodictyon* spp. live in any of these habitats (e.g. Rützler 1971; Freiwald and Wilson 1998; Cerrano et al. 2001), but the larger, fistulate forms appear to be restricted to the shallow environments, and deep sea carbonates are invaded by smaller, papillate species (C. Schönberg et al. unpubl. data 2017; Appendix A). Shallow warm-water environments are thus characterised by larger, faster-growing sponges, some of which can receive supplementary carbon from photosymbionts (Weisz et al. 2010; Fang et al. 2014), while deeper waters exclude phototrophic species and rely on sponges in *alpha* morphology (C. Schönberg et al. unpubl. data 2017). As the dominant bioeroding sponges in ETP corals are also in *alpha* form (Alvarado et al. 2017), there may be a correlation between predominance of smaller sponges where the environment lacks massive corals.

Bioerosion rates in general decrease along a bathymetric gradient, and this is also true for sponge bioerosion (Cerrano et al. 2001). However, calcification rates also decrease, and calcifiers such as solitary or (pseudo)colonial corals usually display comparatively small growth rates compared to similar corals at shallower sites (e.g. Rogers 1999; Hain and Corcoran 2004; Gallmetzer et al. 2010; Orejas et al. 2011; Priori et al. 2013; Bramanti et al. 2014). This may result in proportionally higher bioerosion rates with depth. The cold-water coral *Lophelia pertusa* cannot easily outgrow sponge bioerosion, and while alive, it suffers from the sponges. They lead to deformation in the coral, which changes the growth direction and bends away from the main bulk of the sponges but is still severely hollowed out over time, leaving only 20–30% of the coral skeleton as a frame (Freiwald and Wilson 1998; Beuck et al. 2007). Similar changes in skeletal morphology brought about by sponge bioerosion were also observed in stylasterid hydroids (Pica et al. 2012). As bioeroding sponge larvae predominantly recruit on dead, basal parts of calcifiers (Corriero et al. 1997; Beuck and Freiwald 2005; Pica et al. 2012), they also often cause basal weakening and will aggravate the risk of fragmentation, dislodgement and toppling (Tunnicliffe 1979; Schönberg 2002b). Where fragments persist (Rogers 1999), they can even improve the dispersal potential of bioeroding sponges (Tunnicliffe 1979, 1981; López-Victoria and Zea 2004; Nava and Carballo 2016; Fig. 7.6). In small specimens of the sunset cup coral *Leptopsammia pruvoti*, a single sponge bioerosion chamber can destabilise and break the attachment of a coral specimen, and an 80% mortality through bioerosion has been observed in juveniles (Cerrano et al. 2001). This suggests that by far, most coral specimens grow too slowly to reach an escape size before their holdfast is too eroded to provide secure attachment. Corriero et al. (1997) reported that on average, 55% of the specimens of the precious red coral *Corallium rubrum* were infested with sponges. In this case, infestation rate increased with age in form of a saturation curve that behaved reciprocally to the number of live individuals, culminating in less than 10% of the corals surviving to

4 years of age, at which time 70–80% were infested. However, they only become sexually mature at year 2 or even after year 6–10 (Santangelo et al. 2003; Gallmetzer et al. 2010). Therefore, sponge erosion will significantly affect reproductive success at the community level. This again attests to the strong control bioeroding sponges can have over slow-growing calcifiers and that they can have a significant effect on the entire biocoenosis (Schönberg and Wisshak 2014).

Other unfavourable conditions may aggravate the situation for cold-water corals. Experimental studies have failed to show strong negative effects of temperature on bioeroding sponges unless they are photosymbiotic (Table 7.3). However, cold-water corals can be vulnerable to increased temperature (Torrents et al. 2008; Brooke et al. 2013; Lunden et al. 2014; Gori et al. 2016). Thermal events have led to mortality events of cold-water corals (Cerrano et al. 2000; Pérez et al. 2000; Garrabou et al. 2001; Santangelo et al. 2012), possibly facilitating more sponge bioerosion. Similar developments have previously been observed for warm-water communities (e.g. Schönberg and Ortiz 2009).

Chemical sponge bioerosion is accelerated by elevated $p\mathrm{CO}_2$ (e.g. Wisshak et al. 2014), but cold-water corals react to OA with reduced calcification rates and impaired physiological functions (e.g. Bramanti et al. 2013; Cerrano et al. 2013). Gradually increasing, long-term exposure may however allow adaptation in some corals and a return to baseline responses (Form and Riebesell 2012).

Human activities furthermore directly aggravate the situation. Precious corals have been harvested to an extent that resulted in significantly altered population structures (e.g. Bruckner 2009; Roberts and Cairns 2014). Some cold-water reefs were and are damaged by fishing practices, mining or entanglement with human litter (e.g. Rogers 1999; Hain and Corcoran 2004; Orejas et al. 2009; Bo et al. 2014; Roberts and Cairns 2014), and some are located in areas of oil and gas procurement, where they are exposed to sedimentation and contaminants that develop during construction and drilling, and to the potential risk for spills (e.g. Rogers 1999; Gass and Roberts 2006; Roberts and Cairns 2014).

Therefore, the situation for cold-water corals is similar as for those in shallow, tropical realms—multiple factors exist and interact, with local stress and damage increasingly superimposed by global change (e.g. Järnegren and Kutti 2014). Again, the circumstances are inadequately studied, but we know that sponge bioerosion interacts with some of these factors, sometimes with reinforcing loop feedback, so that net damage can be aggravated.

Overall, cold-water reefs may be more endangered than warm-water reefs, because the former do not receive as much public attention as the latter, and due to their occurrence in deeper waters, they are difficult to be monitored and are not usually covered by national jurisdiction (Hain and Corcoran 2004; Roberts and Cairns 2014). Therefore, scientists are warning of likely trajectories for these corals into extinction (Cerrano et al. 2013), which may be accelerated by sponge erosion. Even though the distribution of, e.g. *Lophelia pertusa*, depends on suitable aragonite saturation levels (Davies et al. 2008), its ability to adapt to lowered pH may be a response that merits a small amount of hope (Form and Riebesell 2012), even though interactions with further environmental factor remain unstudied, and we do not know whether other cold-water calcifiers share this trait.

7.7 Conclusions

Like many other sponges, bioeroding sponges have important ecological functions such as nutrient cycling, but they also increase habitat rugosity, and sponge bioerosion is a natural and necessary process in carbonate recycling. However, bioeroding sponge abundances have increased on many coral reefs. Being the most important internal bioeroders on most reefs, this shift has had a significant impact on carbonate cycles and may have contributed to, e.g. some Caribbean and Indonesian reefs having become erosional. Case examples demonstrate that developments in coral reef health and sponge bioerosion often rely on the same basic principles. Factors that are understood to directly promote sponge bioerosion are deteriorating water quality and eutrophication providing surplus food to the filter feeders, widespread coral mortalities that create suitable substrate for settlement and ocean acidification that reduces the energy expense required for chemical bioerosion. As a guild, bioeroding sponges are considered to be comparatively resilient in changing environments, as they are sheltered within the substrate and thought to be comparatively bleaching resistant when harbouring zooxanthellae, as well as having weedy traits such as fast growth and regeneration, and multiple pathways for reproduction and dispersal. Environmental change-related reduced substrate density may lower bioerosion rates of the most dominant species as they erode more in denser substrates, but the proportional effect will still be worsened with the substrate becoming overall weaker. At least on a midterm time scale, sponge bioerosion is expected to continue to significantly increase globally, and large-scale and repetitive monitoring of dominant species is advisable to support management and possible remediation. Locations that are insufficiently studied are eastern Atlantic, northwestern Indian Ocean, Japanese and cold-water reefs. Moreover, we only have an inadequate understanding of some biological functions of bioeroding sponges such as physiological thresholds, interactions with environmental factors and among species, and sponge bioerosion rates in comparison to calcification rates. As expert knowledge is scarce, and this taxon group is regarded as difficult to study, we are facing a challenge with high hurdles that need to be overcome by improved networking and collaboration, generating and pooling additional resources and funding and, above all, aiming for quality and widely applicable results.

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Appendix A

Annotated faunistic list of sponge species confirmed or assumed to contribute to bioerosion in corals of selected bioregions. Based on Table 7.1, van Soest et al. (2017) and explanations given below, we accepted 260 valid sponges globally as separate species of confirmed or likely coral bioeroders, including all known morphologies. From this we generated a global analysis of bioeroding sponge biogeographies (Fig. 7.4). If available, additional OTUs (operational taxonomy units) were entered in the analysis if we could be reasonably sure not to duplicate existing records. For some decisions, we used NOAA Oceanservice (2014) and Wheeler et al. (2007) to judge which areas should be considered as supporting dense coral communities and chose bioregions as indicated and grouped below. As long as sponges occurred in known coral habitats, we assumed that they at least occasionally eroded coral materials, regardless of their morphology. While we examined details of many records, we took most publications at face value and caution the readers that difficult genera and groups such as *Pione*, *Spheciospongia* and the *Cliona viridis* complex will likely contain the largest rates of inaccuracies and that we are unable to provide an error value within the scope of this study. A few taxonomic decisions were nevertheless made if we considered the reasons as obvious, and these are explained below. Pending new results, we treated unresolved species complexes as one species, unless we could distinguish species within them based on the literature. An effort was made to include mostly original accounts on primary observations and to avoid secondary records compiled from the literature, as well as to divide records by habitats that were often defined by depth (shallow warm-water reefs versus corals being eroded in cold waters, deep or shallow—anything between 0 and 50 m was immediately scored as 'shallow'). Publications on sponge biochemistry were avoided due to their often unreliable species identifications. For reasons given below, species names presented in brackets were not used for the biogeographic analysis. Abbreviations: *Unconf.* possible, but unconfirmed species record; *? author* respective record by this author here needing confirmation, possibly erroneous identification or a tentative interpretation by us that this author may have meant this species; **CS** comments by Christine Schönberg; **JLC** comments by José Luis Carballo; **AM** Atlanto-Mediterranean sponges eroding cold-water corals; **IP** Indo-Pacific sponges eroding cold-water corals. Taxon validities and authorities were confirmed in van Soest et al. (2017), where full citations of original descriptions can also be found.

Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Caribbean, Gulf of Mexico, Florida and Bermuda (62 spp. of coral-eroding sponges in warm water)			
Alectona jamaicensis	Pang, 1973	Jamaica, from 14 m	MacGeachy (1977), Scoffin et al. (1980), Pulitzer-Finali (1986), Lehnert and van Soest (1998); **CS:** The type sample was eroding *Porites furcata* in 14 m and was thus used for the warm-water analysis
Amorphinopsis sp.	Not formally described	Reported from Belize	Rützler et al. (2014); **CS:** As the authors describe evidence that this sponge was actively excavating, we counted it for the biogeography data

Cervicornia cuspidifera	(De Lamarck, 1815)	Caribbean Sea	Topsent (1933, as *Spirastrella*), Pulitzer-Finali (1986, as *Spheciospongia*), Vicente (1990, as *Spheciospongia*), Rützler (1997), Rützler and Hooper (2000), Díaz (2005), Rützler et al. (2009), Hill et al. (2011), Herrera-Moreno et al. (2012), Rützler et al. (2014)
Cliona acephala	Zea and López-Victoria, 2016	Caribbean Colombia	Very recent description, no other reports known
Cliona amplicavata	Rützler, 1974	Bermuda	Rützler (1974), MacGeachy (1977), Bromley (1978), Scoffin et al. (1980), ? van Soest (1981, as *Cliona* cf. *amplicavata*), Pulitzer-Finali (1986), Kobluk and van Soest (1989), Hofman and Kielman (1992), Holmes (2000), Rützler et al. (2014), Ugalde et al. (2015); **CS:** *Cliona amplicavata* may be a species complex and should be studied with molecular means
Cliona aprica	Pang, 1973	Jamaica	Rützler (1975), MacGeachy (1977), Pulitzer-Finali (1986), Vicente (1990), ? Gammill (1997), Lehnert and van Soest (1998), Perry (1998), Macdonald and Perry (2003), Valderrama and Zea (2003, as *Cliona aprica-langae-caribbaea*), Zea and Weil (2003), Díaz (2005), Granados et al. (2008), Rützler et al. (2009), Herrera-Moreno et al. (2012), Romero et al. (2013), Valderrama and Zea (2013), Rützler et al. (2014)
(*Cliona arenosa*) taxon inquirendum	(Schmidt, 1870)	Florida Keys	Rützler et al. (2009); **CS:** According to van Soest et al. (2017), this species is a taxon inquirendum. Based on the original description, *Cliona arenosa* appears to be different from other local *Cliona* spp. but is very similar to *Cliona tumula* from Florida. As the two species could not adequately be compared during the present approach, only the species with the more comprehensive description was included into our biogeographic analysis
Cliona barbadensis	Holmes, 2000	Barbados	No other primary records found

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona caribbaea	Carter, 1882	St. Vincent	Topsent (1889), ? Topsent (1900, as *Cliona viridis*), de Laubenfels (1936a, 1953), Pang (1973, partly as *Cliona langae*), Rützler (1974), MacGeachy (1977), Bromley (1978), Pomponi (1979, partly as *Cliona langae*), Scoffin et al. (1980), van Soest (1981, as *Cliona caribboea*), Highsmith et al. (1983), Pulitzer-Finali (1986, partly as *Cliona langae*), Scott (1987, as *Cliona langae*), Rützler (1990), Vicente (1990), Hofman and Kielman (1992), Thomas (1996), Gammill (1997), Lehnert and van Soest (1998, partly as *C. langae*), Perry (1998, partly as *Cliona langae*), Holmes (2000), Rützler (2002a, includes *Cliona aprica*), Weil et al. (2002, as *Cliona langae*), Macdonald and Perry (2003, partly as *Cliona langae*), Valderrama and Zea (2003, as *Cliona aprica-langae-caribbaea*), Zea and Weil (2003), Callahan (2005), Collin et al. (2005), Díaz (2005), Díaz and Rützler (2007), Granados et al. (2008), González-Gándara et al. (2009), Rützler et al. (2009), Baquero (2010), Hill et al. (2011), Herrera-Moreno et al. (2012), Schellinger (2013), Villamizar et al. (2014); **CS:** Most reports for this species need to be confirmed and may not have relied on an accurate identification. Accounts for *Cliona caribbaea* from 2003 and before may relate to different species, likely including *Cliona aprica* and *Cliona tenuis*
Cliona cf. *celata*	Unresolved species complex	Sensu stricto: Scotland	Topsent (1888, 1889), Arndt (1927), Hartman (1958), Little (1963), Pulitzer-Finali (1986), Rützler et al. (2009), Schellinger (2013); **CS:** *Cliona celata* was described from Scotland and represents a taxonomically difficult species complex (Xavier et al. 2010, de Paula et al. 2012). All faunistic accounts are unreliable, unless including molecular data. This report may or may not represent *Cliona celata* sensu stricto

Cliona delitrix	Pang, 1973	Jamaica	MacGeachy (1977), Pomponi (1979), Scoffin et al. (1980), van Soest (1981), Highsmith et al. (1983, as *Cliona laticavicola*), Pulitzer-Finali (1986, partly as *Cliona laticavicola*), Scott (1987, partly as *Cliona laticavicola*), Kobluk and van Soest (1989), Díaz et al. (1990), Hofman and Kielman (1992, as *Cliona laticavicola*), Lehnert (1993), Gammill (1997), Lehnert and van Soest (1998, partly as *Cliona laticavicola*), Perry (1998, partly as *Cliona laticavicola*), Holmes (2000), Rützler (2002b), Macdonald and Perry (2003, partly as *Cliona laticavicola*), Sardiñas and Alcolado (2004), Caballero et al. (2005), Callahan (2005), Collin et al. (2005), Díaz (2005), Ward-Paige et al. (2005), Zilberberg et al. (2006), Erwin and Thacker (2007), Mallela and Perry (2007, as *Cliona laticavicola*), Granados et al. (2008, as *Cliona laticavicola*), Baquero (2010, partly as *Cliona laticavicola*), González-Gándara et al. (2009), Rützler et al. (2009), Herrera-Moreno et al. (2012), Schellinger (2013), Valderrama and Zea (2013, as *Cliona laticavicola*), Mueller et al. (2014), Villamizar et al. (2014), Chaves-Fonnegra et al. (2015), Halperin et al. (2016); **CS:** Chaves-Fonnegra et al. (2017) recently showed that *Cliona laticavicola* is an ecophenotype of and conspecific with *Cliona delitrix*, with the latter being the senior synonym by a few pages in Pang (1973)
Cliona dioryssa	(De Laubenfels, 1950a)	Bermuda	Pulitzer-Finali (1986), Hofman and Kielman (1992), Lehnert (1993), Thomas (1996)
(*Cliona*? *dubbia*) taxon inquirendum	(Duchassaing de Fonbressin and Michelotti, 1864)	Caribbean	No other primary records found. **CS:** The World Porifera Database lists this species as taxon inquirendum (van Soest et al. 2017). The original description is insufficient, and apparently there is no type material for this species (van Soest et al. 1983). We disregarded this species entirely
(*Cliona*? *Pione*? *duvernoysii*): genus transfer to *Entobia duvernoysii* new comb.	(Duchassaing de Fonbressin, 1850)	Caribbean	No other primary records found. **CS:** Taxon inquirendum (van Soest et al. 2017). According to the description by Duchassaing de Fonbressin and Michelotti (1864) this is not a biotaxon and a sponge, but a description of the ichnotaxon (*Entobia duvernoysii* new comb.). It is here not accepted as a record that can conclusively be matched with a bioeroding sponge and was ignored

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona ensifera	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	MacGeachy (1977), Scoffin et al. (1980), Highsmith et al. (1983), Holmes (2000); **CS:** *Cliona ensifera* is frequently found in the Indo-Pacific (see below) and has not formally been redescribed for the Caribbean. This record should be checked. Being different from the other local species, it was still counted
Cliona euryphylle	Topsent, 1888	Campeche, Gulf of Mexico	Topsent (1889, 1900), Pulitzer-Finali (1986, as *Cliona euryphilla*), Rützler et al. (2009)
Cliona flavifodina	Rützler, 1974	Bermuda	Hechtel (1965, as *Cliona viridis*; see explanation given by Rützler 1974), MacGeachy (1977), Bromley (1978), Scoffin et al. (1980), Pulitzer-Finali (1986), Hofman and Kielman (1992, also as *Cliona* aff. *flavifodina*), Thomas et al. (1992), Thomas (1996), Holmes (2000), Rützler et al. (2014), Ugalde et al. (2015)
Cliona janitrix	Topsent, 1932	Strait of Bonifacio, Mediterranean	Pang (1973), Pulitzer-Finali (1986), Scott (1987, as *Cliona janatrix*), Kobluk and van Soest (1989), Lehnert and van Soest (1998), Perry (1998)
(*Cliona latens*) taxon inquirendum	(Duchassaing de Fonbressin and Michelotti, 1864)	Caribbean	No other primary records found. **CS:** The World Porifera Database lists this species as taxon inquirendum (van Soest et al. 2017). While the original description suggests that this species may belong to the *Cliona celata* species complex, it is insufficient. Moreover, apparently there is no type material for this species (van Soest et al. 1983). We disregarded this species entirely
Cliona laticavicola	Pang, 1973	Jamaica	Highsmith et al. (1983), Pulitzer-Finali (1986), Scott (1987), Hofman and Kielman (1992), Lehnert and van Soest (1998), Perry (1998), Macdonald and Perry (2003), Mallela and Perry (2007), Granados et al. (2008), Baquero (2010), Valderrama and Zea (2013)
Cliona lobata	Hancock, 1849	English Channel	Hartman (1958)
Cliona macgeachii	Holmes, 2000	Barbados	Scoffin et al. (1980, as *Cliona* sp. 2), Holmes (2000)

Unconf.: *Cliona millepunctata*	Hancock, 1849	Unknown. Was found in the king helmet, *Cassis tuberosa*, which occurs in the W Atlantic (N Carolina to Brazil), Caribbean and at the Cape Verde Islands	Pulitzer-Finali (1986), Rützler and Stone (1986); **CS:** These records are based on the original description by Hancock, who provided no information about the sample site. However, as the king helmet is rare in Florida and northwards but common in the West Indies (EOL Rapid Response Team 2017), we tentatively counted *Cliona millepunctata* for the Atlantic, but only for the Caribbean. Topsent (1900) reported another specimen from the Indian Ocean, but this is presently regarded as an erroneous account
(*Cliona mucronata*)	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	MacGeachy (1977), Scoffin et al. (1980), Scott (1987), Holmes (2000); **CS:** *Cliona mucronata* sensu stricto is frequently found in the Indo-Pacific (see below) and has not formally been redescribed for the Caribbean. This record should be checked and may represent *Cliona* cf. *mucronata* sensu Rützler et al. (2014; see below). Not being able to compare these two records and to avoid duplication, this one was excluded from the biogeography
Cliona aff. *mucronata*	Unresolved species complex	Sensu stricto: unknown, likely Indo-Pacific	Rützler et al. (2014, as *Cliona* cf. *mucronata*); **CS:** *Cliona mucronata* is frequently found in the Indo-Pacific (see below) and has not formally been redescribed for the Caribbean. The spicules depicted in this publication are not typical for *Cliona mucronata* sensu Sollas. But as this species is different from the other Caribbean species, it was used for the biogeography
Cliona paucispina	Rützler, 1974	Bermuda	MacGeachy (1977), Bromley (1978), Scoffin et al. (1980), Pulitzer-Finali (1986), Thomas et al. (1992)
Cliona peponaca	Pang, 1973	Jamaica	Bak (1976), MacGeachy (1977), Highsmith et al. (1983), Pulitzer-Finali (1986), Lehnert and van Soest (1998), Macdonald and Perry (2003)
(*Cliona phallica*) taxon inquirendum	Leidy, 1889	Florida, Gulf of Mexico	No other primary records found. **CS:** *Cliona phallica* was described as one of the most common sponges in the area, to be yellowish and to have a single osculum per column. As we did not access type material, the description makes it likely that this is a synonym of *Cliona varians*. Therefore, we did not consider *Cliona phallica* in our biogeography

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
(Unconf.: *Cliona radiata*)	Hancock, 1849	Unknown. Was found in the Atlantic triton, *Charonia variegata*, which occurs in the Mediterranean, Atlantic and Caribbean	See also Rützler and Stone (1986). **CS:** We do not know the exact origin of this sample. However, as confirmed sample locations for the Atlantic triton are in the western Atlantic (WoRMS Editorial Board 2017b), we ignored *Cliona radiata* for the Caribbean and Brazil but tentatively counted it for the Gulf of Guinea. It also may be a senior synonym of *Cliona amplicavata*
Cliona raphida	Boury-Esnault, 1973	Brazil	Díaz and Rützler (2007)
(*Cliona saxicava*) taxon inquirendum	(Duchassaing de Fonbressin and Michelotti, 1864)	Caribbean	No other primary records found. **CS:** The World Porifera Database lists this species as a valid species, but as incertae sedis (van Soest et al. 2017). However, while the original description suggests that this species may belong to the *Cliona viridis* species complex, it is insufficient. Apparently there is also no type material (van Soest et al. 1983), i.e. this should also be a taxon inquirendum. We disregarded this species entirely
Cliona cf. *schmidtii*	(Ridley, 1881); based on an erroneous record of a 'variety' of *Vioa johnstonii* in Schmidt, 1870 p. 5	Adriatic Sea, Mediterranean	Topsent (1889, as *Cliona johnstonii*), Pang (1973), MacGeachy (1977), Pomponi (1979), Scoffin et al. (1980), Pulitzer-Finali (1986), Kobluk and van Soest (1989, Lehnert and van Soest (1998), Perry (1998), Macdonald and Perry (2003), Mallela and Perry (2007), Rützler et al. (2009, 2014); **JLC:** Mediterranean and Caribbean *Cliona schmidtii* may be different species. **CS:** See van Soest et al. (2017) for a comment on this record. Spicules from sponges that were identified as *Cliona schmidtii* can be quite different, here leading to the assumption that the Caribbean material may not be conspecific with the type material (e.g. compare spicules pictured in Pang (1973) with those in Rosell and Uriz (2002a). However, there is at least one purple clionaid in the Caribbean; thus, it was used for the biogeographic analysis
(*Cliona*? *Pione*? *strombi*): genus transfer to *Entobia strombi* new comb.	(Duchassaing de Fonbressin and Michelotti, 1864)	Caribbean	No other primary records found. **CS:** Taxon inquirendum (van Soest et al. 2017). According to Duchassaing de Fonbressin and Michelotti (1864) this is not a biotaxon and a sponge, but a description of the ichnotaxon and the bioerosion trace (*Entobia strombi* new comb.). It is here not accepted as a record that can conclusively be matched with a bioeroding sponge and was ignored

(*Cliona subulata*)	Sollas, 1878	Unknown but sympatric with *Cliona ensifera* and *Cliona mucronata*, thus assumed as Indo-Pacific	Topsent (1889), Rützler et al. (2009); **CS:** *Cliona subulata* is assumed to be an Indo-Pacific species. It has tylostyles and spirasters with long, discrete spines. Sollas' drawings of the spicules strongly resemble those of Pang (1973) for *Cliona caribbaea*, and pending new results, we did not use this species in the biogeography for this bioregion to avoid duplication by using possibly synonymous species. Sollas' type material needs to be re-examined
Cliona tenuis	Zea and Weil, 2003	Caribbean Colombia	? Vicente (1990, as *Anthosigmella* sp.),? Gammill (1997, as *Cliona langae*), ? Valderrama and Zea (2003, as *Cliona aprica-langae-caribbaea*), Collin et al. (2005), Díaz (2005), Granados et al. (2008), Baquero (2010), González-Rivero et al. (2012, 2013), Valderrama and Zea (2013), Murphy et al. (2016)
(Unconf.: *Cliona topsenti*)	(Von Lendenfeld, 1898)	Adriatic Sea, Mediterranean	Highsmith et al. (1983); **CS:** This might be a doubtful report as *Cliona topsenti* has not otherwise been rerecorded from outside of the Mediterranean and is a *Cliona viridis* complex species similar to other Caribbean species with a difficult taxonomy. We conservatively disregarded this report for the biogeographic analysis
Cliona tumula	Friday et al., 2013	Florida Keys	Hill et al. (2011, as 'unidentified *Cliona*'), Schönberg pers. obs. (2008, as 'unidentified *Cliona*', Florida Keys); **CS**: Shares a significant number of characters with Schmidt's *Cliona arenosa* (see above), which is also from Florida. Not having type material at our disposal, we only used *Cliona tumula* for our biogeography in order to avoid duplication of possibly synonymous species
Cliona undulata	(George and Wilson, 1919)	South Carolina	? Little (1963, as *Cliona viridis*), Bass (1993), Rützler et al. (2009)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona varians	(Duchassaing de Fonbressin and Michelotti, 1864)	Caribbean	? Carter (1882, as *Suberites coronarius*), Topsent (1889, as *Papillina arcuata*), de Laubenfels (1949, 1953, as *Anthosigmella*), Little (1963, as *Anthosigmella*), Hechtel (1965, as *Anthosigmella*), Pang (1973, as *Anthosigmella*), Wiedenmayer (1977, as *Anthosigmella*), Vicente (1978, as *Anthosigmella*), ? van Soest (1981, as *Cliona* (*Anthosigmella*) sp.), van Soest et al. (1983, as *Anthosigmella*), Williams et al. (1983, as *Anthosigmella*), Pulitzer-Finali (1986, as *Anthosigmella*), Corredor et al. (1988, as *Anthosigmella*), Kobluk and van Soest (1989, as *Anthosigmella*), Díaz et al. (1990, as *Anthosigmella*), Vicente (1990, as *Anthosigmella*), Hofman and Kielman (1992, as *Anthosigmella*), Zea (1993, as *Anthosigmella*), Hill (1996, as *Anthosigmella*), Aerts and van Soest (1997, as *Anthosigmella*), Gammill (1997, as *Anthosigmella*), Lehnert and van Soest (1998, as *Anthosigmella*), Hill (1999, as *Anthosigmella*), Hill and Hill (2002, as *Anthosigmella*), Rützler (2002b), Valderrama and Zea (2003, as *Anthosigmella*), Sardiñas and Alcolado (2004), Caballero et al. (2005), Collin et al. (2005), Díaz (2005), Díaz and Rützler (2007), Erwin and Thacker (2007), Díaz and Zea (2008), Rützler et al. (2009), Baquero (2010), Amaro and Ramírez (2011), Hill et al. (2011), Stevely et al. (2011), Herrera-Moreno et al. (2012), Schellinger (2013), Valderrama and Zea (2013), Rützler et al. (2014), Stubler et al. (2014), Villamizar et al. (2014)
Cliona vermifera	Hancock, 1867	Unknown. In *Chama* sp., information which does not provide further clues	Topsent (1888, 1889), Hechtel (1965), Pang (1973), MacGeachy (1977), Bromley (1978), Scoffin et al. (1980), van Soest (1981), Highsmith et al. (1983), Pulitzer-Finali (1986), Rützler and Stone (1986), Scott (1987), Kobluk and van Soest (1989), Hofman and Kielman (1992), Lehnert and van Soest (1998), Perry (1998), Holmes (2000), Macdonald and Perry (2003), Mallela and Perry (2007), Rützler et al. (2009); **CS:** *Cliona vermifera* is thought to be a species complex (see, e.g. León-Pech et al. 2015), but pending new results is here treated as a single species
Cliona viridis	(Schmidt, 1862)	Adriatic Sea, Mediterranean	Schmidt (1870, as *Papillina suberea*), Pulitzer-Finali (1986), Rützler et al. (2009)

(*Cliothosa hancocki*)	(Topsent, 1888)	French Polynesia	Pulitzer-Finali (1986); **CS:** Pulitzer-Finali based this report on Topsent (1888, as *Thoosa hancocci*, for the Indo-Pacific) and Rützler (1973, for Tunisia). Neither of these two authors lists the species for the W Atlantic. We ignored this record for the wider Caribbean. CS regards this name as a species complex that needs to be resolved per respective bioregion
Cornulella santamartae	(Van Soest et al., 1994)	Caribbean Colombia	Díaz and Zea (2008)
Cornulum johnsoni	(De Laubenfels, 1934)	Greater Antilles	Pulitzer-Finali (1986), van Soest et al. (1994), Rützler et al. (2014)
Dercitus (*Stoeba*) *plicatus*	(Schmidt, 1868)	Algeria, Mediterranean	? Van Soest (1981, as *Dercitus* cf. *plicatus*), ? Kobluk and van Soest (1989, as *Dercitus* sp.; the authors state that this may be a new species)
Diplastrella bistellata	(Schmidt, 1862)	Adriatic Sea, Mediterranean	Zea (1993), Rützler et al. (2009, as *Spirastrella*)
Diplastrella megastellata	Hechtel, 1965	Jamaica	Kobluk and van Soest (1989), Lehnert and van Soest (1998), Díaz (2005), Díaz and Rützler (2007), van Soest (2009), Herrera-Moreno et al. (2012)
(*Diplastrella ministrella*) taxon inquirendum	Gammill, 1997	Florida	No other primary records found. **CS**: Van Soest (2017) discussed the status of this species. It was here ignored
Haliclona (*Halichoclona*) *vansoesti*	De Weerdt et al., 1999	Curaçao	Erwin and Thacker (2007), Valderrama and Zea (2013), Rützler et al. (2014)
Pione carpenteri	(Hancock, 1867)	Mazatlán	Topsent (1888, 1889, as *Cliona*), Rützler et al. (2009); **CS**: Species of the genus *Pione* are taxonomically difficult, and this record is based on very old publications on a Pacific species. Nevertheless, *Pione carpenteri* has rather robust tylostyles, and this record may thus be distinct from the other *Pione* species in the bioregion. This species was tentatively counted
(*Pione*? *dissociata*): genus transfer to *Entobia dissociata* new comb.	(Duchassaing de Fonbressin, 1850)	Caribbean	No other primary records found. **CS**: According to Duchassaing de Fonbressin and Michelotti (1864) this is not a biotaxon and a sponge, but a description of a ichnotaxon and bioerosion trace (*Entobia dissociata* new comb.). It is here not accepted as a record that can conclusively be matched with a bioeroding sponge and was ignored

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
(Unlikely record: *Pione fryeri*)	(Hancock, 1849)	Unknown. Was found in window pane oyster, *Placuna placenta*, which occurs between the Gulf of Aden and the Philippines	No other reports known for the wider Caribbean. **CS**: Van Soest et al. (2017) list the Caribbean *Vioa*/*Pione dissociata* as a synonym for *Pione fryeri*. However, as the description for *Vioa dissociata* appears to be for a bioerosion trace, it cannot conclusively be matched to a single sponge species (see comments for *Pione dissociata*). Moreover, as the type of *Pione fryeri* inhabited a windowpane oyster, its occurrence in the Caribbean is rather unlikely. *Placuna placenta* is commercially very important in the Philippines, and we tentatively assumed that the sample was from there and counted *Pione fryeri* only for the Coral Triangle
Pione lampa	(De Laubenfels, 1950b)	Bermuda	De Laubenfels (1953, as *Cliona*), Little (1963, as *Cliona*), Neumann (1966, as *Cliona*), Pang (1973, as *Cliona*), Rützler and Rieger (1973, as *Cliona*), Rützler (1975, as *Cliona*), MacGeachy (1977, as *Cliona*), Bromley (1978, as *Cliona*), Scoffin et al. (1980, as *Cliona*), van Soest (1981, as *Cliona*), Pulitzer-Finali (1986, as *Cliona*), Hofman and Kielman (1992, as *Cliona*), Thomas et al. (1992, as *Cliona*), Lehnert and van Soest (1998, as *Cliona*), Perry (1998, as *Cliona*), Holmes (2000, as *Cliona* cf. *vastifica*), Schönberg (2002b), Rützler 2002c, as *Cliona*), Macdonald and Perry (2003, as *Cliona*), Callahan (2005, as *Cliona*), Ward-Paige et al. (2005, as *Cliona*), Mallela and Perry (2007, as *Cliona*), Rützler et al. (2009), Herrera-Moreno et al. (2012), Enochs et al. (2015)
Pione truitti	(Old, 1941)	Chesapeake Bay	Hartman (1958, as *Cliona*), Little (1963, as *Cliona*), Turner (1985, as *Cliona*), Pulitzer-Finali (1986, as *Cliona*), Rützler et al. (2009); **CS**: The genus *Pione* is taxonomically difficult and confused, and the *alpha*-morphology *Pione* spp. of the Caribbean have not convincingly been redescribed or distinguished. At present, we follow Old (1941) and assume that the records for *Pione truitti* and *Pione vastifica* refer to different species

Pione cf. *vastifica*	(Hancock, 1849)	Scotland	Topsent (1888, 1889, as *Cliona*), de Laubenfels (1949, as *Cliona*), Hartman (1958, as *Cliona*), Little (1963, as *Cliona*), Bromley (1978, as *Cliona*), Pulitzer-Finali (1986, as *Cliona*), Holmes (2000, as *Cliona*), Rützler et al. (2009); **CS**: The genus *Pione* is taxonomically difficult and confused, and the *alpha*-morphology *Pione* spp. of the Caribbean have not convincingly been redescribed or distinguished. At present, we follow Old (1941) and assume that the records for *Pione truitti* and *Pione vastifica* refer to different species
Clionaid undetermined aff. *Pione enigmatica* sensu Moraes (2011)	Not formally described but reported in Rützler et al. (2014, as *Cliona* sp.)	Reported from Belize	No other reports known. **CS**: This sponge has unusual, complicated spirasters or spined rhabds not unlike those in, e.g. some Thoosidae. These microrhabds strongly resemble those in *Pione enigmatica* from Brazil, which is different from this species. It is presently not possible to conclusively allocate this material to a known genus, but it differs from all other known species and was counted
Samus anonymus	Gray, 1867	Brazil	Carter (1879), de Laubenfels (1950a), Rützler et al. (2009, 2014)
Scolopes megastra	De Laubenfels, 1953	Florida, Gulf of Mexico	Pulitzer-Finali (1986), Rützler et al. (2009)
Siphonodictyon brevitubulatum	Pang, 1973	Jamaica	? Topsent (1889, as *Cliona labyrinthica*), Rützler (1971), MacGeachy (1977), Pulitzer-Finali (1986), Zea (1987), Hofman and Kielman (1992, as *Aka* aff. *brevitubulata*), Lehnert and van Soest (1998, as *Aka*), Perry (1998, as *Aka*), Macdonald and Perry (2003, as *Aka*), Valderrama and Zea (2003, as *Aka*), Caballero et al. (2005, as *Aka*), Díaz (2005, as *Aka* cf. *brevitubulatum*), Carballo et al. (2007, as *Aka*), Mallela and Perry (2007, as *Aka*), Schönberg and Beuck (2007, as *Aka*), Murphy et al. (2016)
Siphonodictyon cachacrouense	Rützler, 1971	Dominica	MacGeachy (1977), Scoffin et al. (1980), Pulitzer-Finali (1986), Zea (1993, as *Aka*), Aerts and van Soest (1997, as *Aka*), Gammill (1997), Schönberg and Beuck (2007, as *Aka*)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Siphonodictyon coralliphagum	Rützler, 1971	Jamaica	Rützler (1971), MacGeachy (1977), Scoffin et al. (1980), van Soest (1981), Pulitzer-Finali (1986), Scott (1987), Zea (1987), Kobluk and van Soest (1989, as *Aka*), Hofman and Kielman (1992, as *Aka*), Lehnert (1993), Gammill (1997), Lehnert and van Soest (1998, 1999, as *Aka*), Luke (1998, as *Aka*), Caballero et al. (2005, as *Aka*), Collin et al. (2005, as *Aka*), Díaz (2005, as *Aka coralliphagon*), Díaz and Rützler (2007, as *Aka*), Schönberg and Beuck (2007, as *Aka*), Rützler et al. (2009, as *Aka*), Baquero (2010), Herrera-Moreno et al. (2012, as *Aka*), ? Mueller et al. (2014, as *Siphonodictyon* sp.), Rützler et al. (2014), Villamizar et al. (2014)
(*Siphonodictyon densum*)	(Schmidt, 1868)	Gulf of Mexico	Van Soest et al. (2014, as *Siphonodictyon viridescens*); **CS**: The recent redescription for *Siphonodictyon viridescens* provides spicule dimensions that very well match those of *Siphonodictyon densum*, which has characteristic, unusually large oxeas for the genus. However, the sponge was reported from depths significantly deeper than 100 m, and it was not included in the biogeographic analysis for warm-water habitats in the Caribbean
Siphonodictyon occultum	Rützler et al., 2014	Belize	To date, no other primary records available
Siphonodictyon ruetzleri	Calcinai et al., 2007a	Belize	Calcinai et al. (2007b, as *Aka*), Rützler et al. (2014)
Siphonodictyon siphonum	(De Laubenfels, 1949)	Bahamas	Rützler (1971), Wiedenmayer (1977), Williams et al. (1983), Pulitzer-Finali (1986), Hofman and Kielman (1992, as *Aka*), Lehnert and van Soest (1998, as *Aka*), Díaz and Rützler (2007, as *Aka*), Rützler et al. (2009, as *Aka*), Herrera-Moreno et al. (2012, as *Aka*)
Siphonodictyon terebrans	(Schmidt, 1870)	St. Thomas	? Carballo et al. (2007, as *Aka coralliphagum*); **CS**: After assessing a slide of the type material (2006), CS tentatively recognises this species as different from the other *Siphonodictyon* spp., and we counted it separately. Carballo et al.'s (2007) material resembles it but was not formally compared
(*Siphonodictyon viridescens*)	(Schmidt, 1880)	Barbados	No other primary records found. **CS**: The record by van Soest (2017, as *Siphonodictyon viridescens*) is here regarded as *Siphonodictyon densum*. Both species occur well below 100 m water depth and have not yet been observed to erode coral materials. Both were excluded from the biogeographic analysis for warm-water habitats in the wider Caribbean

Siphonodictyon xamaycaense	Pulitzer-Finali, 1986	Jamaica	Hofman and Kielman (1992, as *Aka* aff. *xamaycaensis*), Lehnert and van Soest (1998, 1999, as *Aka*), Rützler et al. (2014)
(Unlikely record: *Spheciospongia papillosa*)	(Ridley and Dendy, 1886)	Sydney Harbour, Australia	Rützler et al. (2009); **CS**: Unlikely report for a taxonomically comparatively difficult species that was originally found in the Pacific. As this record cannot conclusively be compared with *Spheciospongia vesparium*, it was ignored for the biogeography to avoid possible duplication
Spheciospongia vesparium	(De Lamarck, 1815)	Caribbean	Arndt (1927, as *Spirastrella pulvinata*), Topsent (1933), Schmidt (1870, as *Papillina cribrosa*), de Laubenfels (1934, as *Pseudosuberites melanos*, 1936b, 1949, 1950a, as *Spheciospongia othella*, 1953, partly as *Prianos tierney*), Little (1963), Hechtel (1965), Wiedenmayer (1977), Bromley (1978, as *Spheciospongia othella*), van Soest (1981), Westinga and Hoetjes (1981), Pulitzer-Finali (1986), Díaz et al. (1990), Vicente (1990), Hofman and Kielman (1992), Thomas et al. (1992, as *Spheciospongia othella*), Lehnert (1993), Lehnert and van Soest (1998), Macdonald and Perry (2003, as *Spheciospongia othella*), Sardiñas and Alcolado (2004, as *Cliona*), Caballero et al. (2005), Collin et al. (2005), Díaz (2005), Rützler et al. (2009, partly as *Spheciospongia cribosa*), Stevely et al. (2011), Herrera-Moreno et al. (2012), Schellinger (2013), Rützler et al. (2014)
Spirastrella coccinea	(Duchassaing de Fonbressin and Michelotti, 1864)	Caribbean	De Laubenfels (1936b), Dickinson (1945), de Laubenfels (1949, 1950a), Little (1963), Hechtel (1965), Wiedenmayer (1977), van Soest (1981), Pulitzer-Finali (1986), Kobluk and van Soest (1989), Aerts and van Soest (1997), Lehnert and van Soest (1998, 1999), Valderrama and Zea (2003), Caballero et al. (2005, as *Spitastrella*), Collin et al. (2005), Díaz (2005), Díaz and Rützler (2007), Erwin and Thacker (2007), Díaz and Zea (2008), Rützler et al. (2009), Herrera-Moreno et al. (2012), Schellinger (2013), Valderrama and Zea (2013)
Spirastrella coccinopsis	(De Laubenfels, 1953)	Gulf of Mexico	Little (1963), Pulitzer-Finali (1986), Zea (1993), Rützler et al. (2009, 2014)
Spirastrella hartmani	Boury-Esnault et al., 1999	Caribbean Panama	Arndt (1927, as *Spirastrella cunctatrix*), de Laubenfels (1936a, as *Spirastrella cunctatrix*), Wiedenmayer (1977, as *Spirastrella cunctatrix*), Pulitzer-Finali (1986, as *Spirastrella cunctatrix*), Boury-Esnault et al. (1999), Collin et al. (2005), Díaz (2005), Díaz and Rützler (2007), Amaro and Ramírez (2011), Valderrama and Zea (2013)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Spirastrella mollis	Verrill, 1907	Bermuda	Thomas et al. (1992), Thomas (1996), Collin et al. (2005), Díaz (2005, as *Spirastrella* cf. *mollis*), Díaz and Rützler (2007), Rützler et al. (2014), ? Ugalde et al. (2015, as *Spirastrella* aff. *mollis*)
(*Spirastrella phyllodes*) taxon inquirendum	(Schmidt, 1870)	Antilles	Rützler et al. (2009); **CS**: Taxon inquirendum (van Soest et al. 2017). Pending new results and confirmation of this species, it was not included into the biogeography to avoid possible duplication with other species
Spiroxya spiralis	(Johnson, 1899)	Azores	Rützler et al. (2014)
Cf. *Suberea flavolivescens*	(Hofman and Kielman, 1992)	Caribbean Colombia	? Kobluk and van Soest (1989, as 'keratose?excavating sponge'), Valderrama and Zea (2013), Rützler et al. (2014)
Thoosa armata	Topsent, 1888	Gulf of Guinea	Arndt (1927), van Soest (1981), Pulitzer-Finali (1986)
Timea oxyasterina	Rützler et al., 2014	Belize	Recent description. To date, no other reports known for the wider Caribbean
Triptolemma endolithicum	Van Soest, 2009	Caribbean Colombia	No other reports known for the wider Caribbean
(*Volzia* cf. *albicans*)	(Volz, 1939)	Adriatic Sea, Mediterranean	Highsmith et al. (1983, as *Cliona* cf. *albicans*); **CS**: Possibly same species as below? Conservatively, only one was included in the biogeography
Volzia cf. *rovignensis*	(Volz, 1939)	Adriatic Sea, Mediterranean	MacGeachy (1977, as *Cliona ?rovignensis*), Scoffin et al. (1980, as *Cliona ?rovignensis*), Holmes (2000, as *Cliona rovignensis*); **CS:** Possibly same species as above? Conservatively, only one was included in the biogeography, and we took the one more commonly mentioned
Zyzzya invemar	(Van Soest et al., 1994)	Caribbean Colombia	No other primary records found
Brazil and NE coast of South America, including Guyana (25 spp. of coral-eroding sponges in warm water)			
Cervicornia cuspidifera	(De Lamarck, 1815)	Caribbean Sea	Muricy et al. (2011), Cavalcanti (2013), van Soest (2017), F. Moraes et al. unpubl. data (2017)

Cliona carteri	(Ridley, 1881)	Victoria Bank, 20°42′S, 37°27′W	Muricy et al. (2011, as mere record), Moraes et al. unpubl. data (2017); **CS**: This species may have largely been misunderstood, which depends on its colour. Ridley described it as ‘vivid crimson’ (red) in alcohol, but red colours in clionaids normally dull over time. He also stated that the colour was identical with that of *Cliona schmidtii* (*Vioa johnstonii* sensu Schmidt 1870) and very similar to that of *Spheciospongia purpurea*, which would make the colour a bright purple, not red. Purple pigments in some clionaids are remarkably stable after sampling, and we presently consider *Cliona carteri* to be a purple sponge. The question of the colour had already been raised by Topsent (1900). Regardless of the colour, *Cliona carteri* has significantly longer tylostyles than *Cliona schmidtii* sensu Boury-Esnault (1973) reported from Brazil. For Brazil, we considered *Cliona carteri* as a separate species for our biogeographic analysis
Cliona cf. *celata* – clade C sensu de Paula et al. (2012)	Grant, 1826	Sensu stricto: Scotland	? Boury-Esnault (1973), ? Muricy and Moraes (1998), ? Reis and Leão (2002), ? Muricy and Hajdu (2006), ? Muricy et al. (2011), ? Cavalcanti (2013, as *Cliona celata* complex sp.); **CS**: *Cliona celata* is a morphologically difficult and unresolved species complex (Xavier et al. 2010). At least one of the two reported Brazilian records differs from *Cliona celata* sensu stricto; they were distinguished from each other with molecular means (de Paula et al. 2012) and are used in our analysis as two different species
Cliona aff. *celata* – clade D sensu de Paula et al. (2012)	Not formally described	Reported from Brazil	? Boury-Esnault (1973), ? Muricy and Moraes (1998), ? Reis and Leão (2002), ? Muricy and Hajdu (2006), ? Muricy et al. (2011), ? Cavalcanti (2013, as *Cliona celata* complex sp.); **CS**: *Cliona celata* is a morphologically difficult and partially unresolved species complex (Xavier et al. 2010). At least one of the two reported Brazilian records differs from *Cliona celata* sensu stricto; they were distinguished from each other with molecular means (de Paula et al. 2012) and are used in our analysis as two different species
Cliona delitrix	Pang, 1973	Jamaica	Muricy et al. (2011), F. Moraes et al. unpubl. data

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona dioryssa	(De Laubenfels, 1950)	Bermuda	Muricy and Hajdu (2006), F. Muricy et al. (2011), Zalmon et al. (2011), Moraes et al. unpubl. data (2017)
(Unconf.: *Cliona millepunctata*)	Hancock, 1849	Unknown. Was found in the king helmet, *Cassis tuberosa*, which occurs in the W Atlantic (N Carolina to Brazil), Caribbean and at the Cape Verde Islands	No other reports known. **CS**: We do not know the exact origin of this sample. However, as the king helmet 'is rare in Florida and northwards but common in the West Indies' (EOL Rapid Response Team 2017), we tentatively counted *Cliona millepunctata* within the Atlantic, but only for the Caribbean. Topsent (1900) reported another specimen from the Indian Ocean, but this is presently regarded as an erroneous account
(Unconf.: *Cliona radiata*)	Hancock, 1849	Unknown. Was found in the Atlantic triton, *Charonia variegata*, which occurs in the Mediterranean, Atlantic and Caribbean	No other reports known. **CS**: We do not know the exact origin of this sample. However, as confirmed sample locations for the Atlantic triton are in the western Atlantic (WoRMS Editorial Board 2017c), we ignored *Cliona radiata* for the Caribbean and Brazil but tentatively counted it for the Gulf of Guinea. It also may be a senior synonym of *Cliona ampliclavata*
Cliona raphida	Boury-Esnault, 1973	Brazil	Boury-Esnault (1973)
Cliona cf. *schmidtii*	(Ridley, 1881); based on an erroneous record of a 'variety' of *Vioa johnstonii* in Schmidt, 1870 p. 5	Adriatic Sea, Mediterranean	Boury-Esnault (1973), ? Cavalcanti (2013); **CS**: Spicules from sponges that were identified as *Cliona schmidtii* can be quite different, and reports require confirmation (see spicules pictured in Pang 1973, Rosell and Uriz 2002)
Cliona varians	(Duchassaing de Fonbressin and Michelotti, 1864)	Caribbean Sea	Muricy and Moraes (1998, as *Anthosigmella*), Moraes (2011), Muricy et al. (2011), Cavalcanti (2013), F. Moraes et al. unpubl. data (2017)
Cliona viridis	(Schmidt, 1862)	Adriatic Sea, Mediterranean	Leal et al. (2016; with molecular support)
Cliona sp. undetermined, red (aff. *flavifodina*?)	Awaiting assessment	From Bahía, Brazil	? Topsent (1900, as *Cliona viridis* var. *carteri*, described as 'scarlet red'), F. Moraes et al. unpubl. data (2017)
Diplastrella megastellata	Hechtel, 1965	Jamaica	Moraes (2011)

(*Diplastrella spirastrelloides*)	Van Soest, 2017	French Guiana	Very recent description, no other records known. **CS**: *Diplastrella spirastrelloides* encrusted coarse sediments in 94 m depth and was presently not counted as a coral bioeroder
Haliclona (*Halichoclona*) *vansoesti*	De Weerdt et al., 1999	Curaçao	Muricy et al. (2015)
Pione aff. *carpenteri*	Unresolved species complex	Sensu stricto: Mazatlán	Boury-Esnault (1973, as *Cliona*), Cavalcanti (2013); **CS**: The genus *Pione* is taxonomically difficult, and this record is based on very old publications on a Pacific species. While the species may not be *Pione carpenteri*, no other typical *Pione* sp. has been recorded from Brazil, and it was here counted
Pione enigmatica: recommendation to reassess genus allocation	Moraes, 2011	Brazil	No other reports known. **CS**: This species has tylostyles, smooth oxeas and microrhabds with unusual, complicated spines not unlike, e.g. in some Thoosidae. The microrhabds strongly resemble those in *Cliona* sp. sensu Rützler et al. (2014) from Belize. We cannot conclusively allocate this material to a known genus, but it differs from all the other known species
Samus anonymus	Gray, 1867	Brazil	Sollas (1888b)
Scolopes moseleyi	Sollas, 1888	Brazil	Cavalcanti (2013)
Siphonodictyon brevitubulatum	Pang, 1973	Jamaica	Moraes (2011, as *Siphonodictyon coralliphagum*)
Siphonodictyon coralliphagum	Rützler, 1971	Jamaica	F. Moraes et al. unpubl. data (2017)
Siphonodictyon sp.	Not yet formally described	From Bahía, Brazil	F. Moraes et al. unpubl. data 2017; **CS:** This *Siphonodictyon* sp. is different from the other species known from Brazil
(*Siphonodictyon* aff. *densum*)	(Schmidt, 1870)	Gulf of Mexico	Van Soest (2017); **CS**: Schmidt’s species was described with small fistules (‘barely the width of a quill’), while Van Soest (2017) reported fistules of 1 cm thickness. This may not be a strong, distinctive character, but the holotype has sharply pointed oxeas on average 240 μm long (C. Schönberg unpubl. data 2005), i.e. significantly longer oxeas than recorded by van Soest (2017). The latter material may not be *Siphonodictyon densum*. It was also sampled from 130 m depth and may thus not be a typical coral reef sponge. It was presently not counted in our biogeographic analysis

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Spheciospongia symbioticum	Hechtel, 1983	Brazil	Cavalcanti (2013)
Spheciospongia vesparium	(De Lamarck, 1815)	Caribbean Sea	Muricy et al. (2008), Cavalcanti (2013), F. Moraes et al. unpubl. data (2017)
Spirastrella coccinea	(Duchassaing de Fonbressin and Michelotti, 1864)	Caribbean Sea	Muricy and Moraes (1998), Muricy et al. (2011)
Spirastrella erylicola	Van Soest, 2017	French Guiana	Very recent description, no other records known
Spirastrella hartmani	Boury-Esnault et al., 1999	Caribbean Panama	? De Laubenfels (1956, as *Spirastrella cunctatrix*), Moraes (2011), Muricy et al. (2011), Cavalcanti (2013)
Gulf of Guinea (8 spp. of coral-eroding sponges in warm water)			
Cliona aethiopica	Burton, 1932	Gulf of Guinea	No other primary records found
Cliona lobata	Hancock, 1849	English Channel	Topsent (1918)
Unconf.: *Cliona radiata*	Hancock, 1849	Unknown. Was found in the Atlantic triton, *Charonia variegata*, which occurs in the Mediterranean, Atlantic and Caribbean	No other reports known. **CS**: We do not know the exact origin of this sample. However, as confirmed sample locations for the Atlantic triton are in the western Atlantic (WoRMS Editorial Board 2017b), we ignored *Cliona radiata* for the Caribbean and Brazil but tentatively counted it for the Gulf of Guinea. It also may be a senior synonym of *Cliona ampliclavata*
Pione carpenteri	(Hancock, 1867)	Mazatlán	Topsent (1918, as *Cliona*); **CS**: The genus *Pione* is taxonomically difficult, and this record is based on very old publications on a Pacific species. As '*carpenteri*' and '*vastifica*' were reported by the same author, we assume that they represent two different *Pione* spp. Therefore, two *Pione* spp. were counted for the biogeography analysis of this bioregion
Pione vastifica	(Hancock, 1849)	Scotland	Topsent (1918, as *Cliona*)
Samus anonymus	Gray, 1867	Brazil	Lévi (1959a)
Spirastrella cunctatrix	Schmidt, 1868	Algeria, Mediterranean	Topsent (1918), Lévi (1959a)
Thoosa armata	Topsent, 1888	Gulf of Guinea	Topsent (1918), Lévi (1959a)

Red Sea, Persian Gulf and W Arabian Sea (19 spp. of coral-eroding sponges in warm water)			
Cliona aff. *celata*	Unresolved species complex	Sensu stricto: Scotland	? Row (1911), ? Nazemi et al. (2015); **CS**: The authors' species identifications should be reassessed. For the time being, this record is counted as a separate species for the bioregion
Cliona aff. *dioryssa*	Sensu stricto: (De Laubenfels, 1950)	Sensu stricto: Bermuda	Eisapor et al. (2012), Eisapor and Safaeian (2013); **CS**: The papillae figured by the authors strongly resemble those of *Cliothosa aurivillii*. Regardless of the exact species identification, this is a different species than other species known from the area and was counted in our analysis
Cliona jullieni	Topsent, 1891	La Réunion	Ferrario et al. (2010)
(Clionaid sp. undetermined 1, aff. *Cliona jullieni* or *Cliona rhodensis*)	Not morphologically identified	Reported from the Red Sea	Erpenbeck et al. (2016, as *Cliona* sp. OTU#04); **CS**: See their 28S and COI reconstruction. Here not counted for biogeographic analysis to avoid possible duplication with either *Cliona jullieni* above or other *Cliona viridis* complex species as below
(Clionaid sp. undetermined 2, aff. *Cliona jullieni* or *Cliona rhodensis*)	Not morphologically identified	Reported from the Red Sea	Erpenbeck et al. (2016, as *Cliona* sp. GW3452); **CS**: See their 28S and COI reconstruction. Here not counted to avoid possible duplication with either *Cliona jullieni* above or other *Cliona viridis* complex species as below
(*Cliona subulata*)	Sollas, 1878	Unknown, but sympatric with *Cliona ensifera* and *Cliona mucronata*, thus assumed as Indo-Pacific	No other primary records found for this bioregion. **CS**: *Cliona subulata* has tylostyles and spirasters with long, discrete spines. Sollas' drawings of the spicules suggest that the species belongs to the *Cliona viridis* complex, of which there are other species in the area that cannot adequately be compared with *Cliona subulata*. Pending new results, we did not use *Cliona subulata* in the biogeography to avoid possible duplication. Sollas' type material needs to be re-examined
Cliona viridis complex sp. or spp.	Unresolved species complex	*Cliona orientalis* sensu stricto: Molucca Sea, Indonesia	Lévi (1958, as *Cliona orientalis*), Fishelson (1971, as *Cliona orientalis*), ? Erpenbeck et al. (2016, as *Cliona* sp. OTU#03); **CS**: This record needs to be confirmed. New, similar species were described that may occur in the area, and there may be more than one *Cliona viridis* complex species.
Cliothosa aff. *hancocki*	Unresolved species complex	Sensu stricto: French Polynesia	Lévi (1965a); **CS** regards this name as a species complex that needs to be resolved per respective bioregion, and Lévi's spicules look odd. It is here still counted as a species distinct from the others occurring in this region

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
(Unconf.: *Cornulella purpurea*)	(Hancock, 1849)	Unknown, sample found in *Tridacna gigas*, which has an Indo-Pacific distribution	Referring to Hancock's sample and thus not reporting a confirmed sample site: Kirkpatrick (1900a, as *Dyscliona*), Topsent (1907, as undetermined genus), Hallmann (1920, as *Paracornulum*), Rützler and Stone (1986, as *Cliona*), van Soest et al. (1994); **CS**: It is possible that *Cornulella purpurea* occurs in this bioregion, but as the sample site is unknown and cannot be conclusively matched to our bioregions, this species did not become part of our analysis
Diplastrella gardineri	Topsent, 1918	Maldives	Lévi (1958)
Pione carpenteri	(Hancock, 1867)	Mazatlán	Doroudi (1996, as *Cliona*), Ferrario et al. (2010); **CS**: The genus *Pione* is taxonomically difficult, and this record is based on a very old publication of an E Pacific species. However, while the exact species identification may need to be reconfirmed, the latter authors distinguished three species of *Pione* by molecular means, so it can here be counted for the biogeography
Cf. *Pione cervina*	(Hancock, 1849)	Unknown. Found in a pearl shell, *Pinctada* cf. *albina*, which occurs in the Red Sea	No other primary records found. **CS**: Taxon inquirendum (van Soest et al. 2017). Has tuberculate diactines unusual for *Pione* (Rützler and Stone 1986). But as it differs from the other species, it is here tentatively counted (based on the vague identification of the host shell)
Pione margaritiferae	(Dendy, 1905)	Gulf of Mannar	Doroudi (1996, as *Cliona*), Ferrario et al. (2010); **CS**: The genus *Pione* is taxonomically difficult, and this record is based on a comparatively old publication of an Indian species. However, while the exact species identification may need to be reconfirmed, the authors distinguished three species of *Pione* by molecular means, so it can here be counted for the biogeographic analysis

Pione mussae	(Keller, 1891)	Central Red Sea, Sudan	Bertram (1936, as *Cliona*), Lévi (1958, as *Cliona vastifica*), ? Doroudi (1996, as *Cliona vastifica*), Beer and Ilan (1998, as *Cliona vastifica*), Steindler et al. (2001, as *Cliona vastifica*), Ferrario et al. (2010, as *Pione* cf. *vastifica* and *Pione* cf. *lampa*), Bruckner and Dempsey (2015, as 'bioeroding sponge'), Nazemi et al. (2015, as *Cliona vastifica*), Erpenbeck et al. (2016, as *Pione* cf. *vastifica* OTU#07); **CS**: This refers to the bright orange-red, papillate or encrusting-endolithic species that is most commonly reported in beta morphology, and the authors separated this species from the other two *Pione* spp. in the Red Sea by molecular analysis. Three species were counted
Siphonodictyon sp.	Not formally described, noticed by C. Schönberg pers. obs. (2006)	Gulf of Aden	No other primary records found. **CS** thinks this is an undescribed *Siphonodictyon* sp. (working name 'zipallapiz')
Spheciospongia inconstans	(Dendy, 1887)	Madras	Lévi (1965a, as *Spirastrella*), Fishelson (1971, as *Spirastrella*), ? Van Soest and Beglinger (2008, as *Spheciospongia tentorioides*)
Spheciospongia mastoidea	(Keller, 1891)	Southern Red Sea, Eritrea	No other primary records found
Spheciospongia cf. *vagabunda*	(Ridley, 1884)	Torres Straits	Erpenbeck et al. (2016, as *Spirastrella* OTU#05); **CS**: Gamma morphology. See their 28S reconstruction
Spirastrella decumbens	Ridley, 1884	Torres Straits	Keller (1891), Lévi (1958), Lévi (1965a, as *Spirastrella cunctatrix*), Fishelson (1971, as *Spirastrella cunctatrix*), ? Erpenbeck et al. (2016, as OTU #06), **CS**: See their 28S and COI reconstructions. Van Soest et al. (2017) consider records of *Spirastrella cunctatrix* as incorrect for the Red Sea. As this species is very similar to *Spirastrella decumbens*, we tentatively listed respective reports as *Spirastrella decumbens*
Spirastrella cf. *hartmani*	Boury-Esnault et al., 1999	Caribbean Panama	Erpenbeck et al. (2016, as GW5949), **CS**: See their 28S and COI reconstructions
Spirastrella pachyspira	Lévi, 1958	E Red Sea, Saudi Arabia	No other records known from the Red Sea

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
(Unconf.: *Thoosa cactoides*)	Hancock, 1849	Unknown. In the pearl oyster, *Pinctada margaritifera*, which has an Indo-Pacific distribution	No other primary records found. **CS**: As we do not know the exact type location of this species, we did not count it for any specific bioregion
Unconf.: *Thoosa circumflexa*	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	? Lévi (1965a, as *Thoosa armata*), ? Fishelson (1971, as *Thoosa armata*); **CS**: According to van Soest et al. (2017), *Thoosa circumflexa* is a taxon inquirendum, but after viewing Topsent's samples in Paris (2006–2007), CS finds this to be a good species. The Red Sea records are for *Thoosa armata*, which is an Atlantic species, and according to van Soest et al. (2017) it does not occur in the Red Sea. Lévi's drawings appeared to be most similar to drawings CS made of spicules of *Thoosa circumflexa*, which is an Indo-Pacific sponge and may possibly occur in the Red Sea. The present decision is very tentative, but the species counted for our biogeographic analysis
Unconf.: *Thoosa letellieri*	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Red Sea. According to van Soest et al. (2017), this is a taxon inquirendum, but after viewing Topsent's samples in Paris (2006–2007), CS finds this to be a good species. As we decided that *Thoosa circumflexa* might occur in the Red Sea (see above) and the type of *Thoosa letellieri* was found in the same shell, we tentatively counted the latter as well
E Africa, Madagascar, Seychelles, Reunion and Mauritius (38 spp. of coral-eroding sponges in warm water)			
Alectona primitiva	Topsent, 1932	Kangaroo Island, S Australia, in the whirling abalone *Haliotis cyclobates* (as *Haliotis excavata*)	Vacelet and Vasseur (1971, from shallow water)

Alectona wallichii	(Carter, 1874)	Agulhas Bank, S of Africa (Carter: also from the ‘South Sea’ and Seychelles), first reported as spicules in sediment	Vacelet (1999, from shallow water)
Amorphinopsis excavans	Carter, 1887	W Andaman Sea	Thomas (1973); **CS**: *Amorphinopsis excavans* is seen as an Indo-Pacific species, but characters described in older accounts vary. The species (complex?) needs to be re-examined and revised (Carvalho et al. 2004)
Aff. *Cervicornia cuspidifera*	Unresolved species complex	Sensu stricto: Caribbean Sea	Thomas (1973, 1981, as *Spirastrella cuspidifera*); **CS**: *Cervicornia cuspidifera* is a Caribbean species. Other endopsammic clionaids exist in the Indo-Pacific, and this account needs to be re-examined. It was still counted as a species different from the others in the area
Cliona albimarginata	Calcinai et al., 2005	N Sulawesi	? Thomas (1981, as *Cliona viridis*), ? Pulitzer-Finali (1993, as *Cliona viridis*), ? Calcinai et al. (2000, as *Spheciospongia varians*), ? Schleyer et al. (2006, as *Anthosigmella orientalis*), Azzini in Calcinai et al. (2008a)
Cliona aff. *celata*	Unresolved species complex	Sensu stricto: Scotland	Dendy (1922), Vacelet and Vasseur (1971), Thomas (1973, 1979a), Calcinai et al. (2000); **CS**: *Cliona celata* was described from Scotland and represents a taxonomically difficult species complex (Xavier et al. 2010, de Paula et al. 2012). All faunistic accounts are unreliable unless including molecular data. This report is unlikely to be *Cliona celata* sensu stricto but was still counted as a clionaid different from others in the bioregion
Cliona ensifera	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide useful information. Assumed from Indo-Pacific	Vacelet et al. (1976)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona johnstonii	(Carter, 1886)	Bass Strait	Ridley (1884, as *Vioa schmidti*), Topsent (1900, as *Cliona schmidti*), Vacelet et al. (1976, as *Cliona schmidtii*); **CS**: We tentatively listed all '*Cliona schmidtii*' reported from the Indo-Pacific as *Cliona johnstonii* to imply that the two species are different. See van Soest et al. (2017) for comments on the distribution of *Cliona schmidtii*
Cliona jullieni	Topsent, 1891	La Réunion	Vacelet et al. (1976)
Cliona aff. *lobata*	Unresolved species complex	Sensu stricto: English Channel	Vacelet et al. (1976); **CS**: The Atlantic species *Cliona lobata* has been widely reported, but maybe not always accurately. These accounts have to be re-examined. The present record is possibly misidentified but is here counted as a morphologically different clionaid for the bioregion
(Unconf.: *Cliona michelini*)	Topsent, 1888	Indian Ocean, in shell of rock snail	No other primary records found for this bioregion. **CS**: This species may occur in the bioregion, but as the exact sample origin is unknown, it was not included here. Based on notes on a slide preparation, *Cliona michelini* was listed for India, however
Cliona mucronata	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	Vacelet et al. (1976), Thomas (1979a), Calcinai et al. (2000)
Cliona aff. *mucronata* sensu Vacelet and Vasseur (1971)	Unresolved species complex	Sensu stricto: Unknown, likely Indo-Pacific	Vacelet and Vasseur (1971); **CS**: Their figure of the short tylostyle is not typical for *Cliona mucronata* sensu stricto. As *Cliona* aff. *mucronata* and sensu stricto can both be found on the Great Barrier Reef (C. Schönberg unpubl. data 2010–2011), the species were here considered separately

(*Cliona subulata*)	Sollas, 1878	Unknown, but sympatric with *Cliona ensifera* and *Cliona mucronata*, thus assumed as Indo-Pacific	No other primary records found for this bioregion. **CS**: *Cliona subulata* has tylostyles and spirasters with long, discrete spines. Sollas' drawings of the spicules suggest that the species belongs to the *Cliona viridis* complex, of which there are others in the area that cannot adequately be compared with *Cliona subulata*. Pending new results, we did not use this species in the biogeography to avoid possible duplication. Sollas' type material needs to be re-examined
(Unconf.: *Cliona thoosina*)	Topsent, 1888	Unknown, in *Tucetona* shell (as *Pedunculus*), which does not provide helpful information. However, a tissue preparation of the type DT2538 at the Paris Museum was marked 'Indian Ocean' (C. Schönberg pers. obs. 2006–2007)	No other primary records found for this bioregion. **CS**: The species could possibly occur in this bioregion, but we were unable to confirm the exact type location and could not consider this species in our biogeographic analysis. Other records were from the Mediterranean (e.g. Pulitzer-Finali 1983, as *Cliona cretensis*, in calcareous rock; Rosell and Uriz 2002b, Ponti et al. 2011)
Cliothosa hancocki	(Topsent, 1888)	French Polynesia	Topsent (1888, also as *Cliona quadrata*, does not state exact sample site, in *Tridacna* sp.), Vacelet et al. (1976), Thomas (1979a), Pulitzer-Finali (1993); **CS** regards this name as a species complex that needs to be resolved per respective bioregion. It is here still counted as a species distinct from others occurring in this region
(Unconf.: *Cliothosa quadrata*)	(Hancock, 1849)	In the giant clam, *Tridacna gigas*, which occurs in the Indo-Pacific	**CS**: After accessing Topsent's samples at the Paris Museum (2006–2007), CS regards *Cliothosa hancocki* as a species complex. *Cliothosa hancocki* and *Cliothosa quadrata* are very similar (e.g. Calcinai et al. 2005) but have not yet been formally compared. To avoid possible duplication only *Cliothosa hancocki* was counted for our biogeographic analysis (more commonly used name), despite records from the area under the name *Cliothosa quadrata* (see entries above)
Cornulella amirantensis	Van Soest et al., 1994	Seychelles	No other primary records found

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cornulella lundbecki	Dendy, 1922	Seychelles	Van Soest et al. (1994)
Cornulella minima	(Vacelet et al., 1976)	Madagascar	Van Soest et al. (1994)
(Unconf.: *Cornulella purpurea*)	(Hancock, 1849)	Unknown, sample found in *Tridacna gigas*, which has an Indo-Pacific distribution	Referring to Hancock's sample and thus not reporting a confirmed sample site: Kirkpatrick (1900a, as *Dyscliona*), Topsent (1907, as undetermined genus), Hallmann (1920, as *Paracornulum*), Rützler and Stone (1986, as *Cliona*), van Soest et al. (1994); **CS**: It is possible that *Cornulella purpurea* occurs in this bioregion, but as the sample site is unknown and cannot be conclusively matched to our bioregions, this species did not become part of our analysis
Cornulella tyro	Van Soest et al., 1994	Seychelles	No other primary records found
Diplastrella gardineri	Topsent, 1918	Maldives	Vacelet et al. (1976), Pulitzer-Finali (1993)
Pione carpenteri	(Hancock, 1867)	Mazatlán	Thomas (1979a, 1981), Calcinai et al. (2000); **CS**: *Pione* species are difficult to identify, but as the three species reported for this bioregion have different spicule dimensions, they were all counted
Pione margaritiferae	(Dendy, 1905)	Gulf of Mannar	? Vacelet and Vasseur (1971); **CS**: But no tylostyles were recovered, and the displayed microscleres represent a mix of *Pione* microrhabds and non-*Pione* spirasters); Thomas (1979a, 1981)
Pione aff. *vastifica*	Unresolved species complex	Sensu stricto: Scotland	Thomas (1973, 1979a, 1981, as *Pione vastifica*), Calcinai et al. (2000, as *Pione vastifica*); **CS**: *Pione vastifica* was originally reported from the Atlantic, and this may be a different species, but it is here counted as a third *Pione* species different from the other two in this bioregion
Samus anonymus	Gray, 1867	Brazil	Thomas (1973)
Siphonodictyon minutum	(Thomas, 1972)	Sri Lanka	Thomas (1973, 1979a, 1981)
(*Spheciospongia capensis*)	(Carter, 1882)	Agulhas Bank	No other primary records found. **CS**: May not occur far enough north to be a coral reef sponge, was not counted for the biogeography
Spheciospongia excentrica	(Burton, 1931)	Natal	Vacelet et al. (1976, as *Spirastrella*), Schleyer et al. (2006)
Spheciospongia florida	(Von Lendenfeld, 1897)	Tanzania	Lévi (1965b), Barnes and Bell (2002), Díaz et al. (2007)
Spheciospongia globularis	(Dendy, 1922)	Chagos	Lévi (1961, as *Spirastrella*), Schleyer et al. (2006)

Spheciospongia inconstans	(Dendy, 1887)	Madras	Lévi (1961, as *Spirastrella*), Vacelet and Vasseur (1971, as *Spirastrella*), Thomas (1973, as *Spirastrella*), Vacelet et al. (1976, as *Spirastrella*), Thomas (1979a, 1981, as *Spirastrella*), Pulitzer-Finali (1993, as *Spirastrella*)
Spheciospongia poterionides	(Vacelet and Vasseur, 1971)	Madagascar	No other primary records found
Spheciospongia solida	(Ridley and Dendy, 1886)	Philippines	Barnes and Bell (2002, as *Spirastrella*)
Spheciospongia transitoria: reversed comb. to *Spirastrella transitoria*	Ridley, 1884	Seychelles	No other primary records found. **CS**: The original description places this species into the genus *Spirastrella* and clearly mentions the encrusting habit. The sponge has tylostyles and large, robust, conically spined spirasters and derivates. Based on these characters, the species is here returned to *Spirastrella*
Spheciospongia vagabunda	(Ridley, 1884)	Torres Straits	Dendy (1922 as *Spirastrella*, including the varieties *tubulodigitata* and *gelatinosa*, the former being accepted as *Spheciospongia vagabunda*—van Soest et al. 2017), Lévi (1965a, as *Spirastrella*), Thomas (1973), Pulitzer-Finali (1993), Barnes and Bell (2002, as *Spirastrella*), Schleyer et al. (2006)
Spirastrella cunctatrix	Schmidt, 1868	Algeria, Mediterranean	? Carter (1882, described either with purple colour or as 'variety' on a crab's back), Vacelet and Vasseur (1971), Vacelet et al. (1976), Calcinai et al. (2000)
Spirastrella decumbens	Ridley, 1884	Torres Straits	Dendy (1922), Lévi (1956)
Spirastrella pachyspira	Lévi, 1958	E Red Sea, Saudi Arabia	Lévi (1961), Vacelet and Vasseur (1971), Vacelet et al. (1976), Thomas (1973), Barnes and Bell (2002)
Spirastrella punctulata	Ridley, 1884	Mozambique	No other primary records found
(Unconf.: *Thoosa cactoides*)	Hancock, 1849	In the pearl oyster, *Pinctada margaritifera*, which has an Indo-Pacific distribution	No other primary records found. **CS**: As we do not know the exact type location of this species, we did not count it for any specific bioregion

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
(Unconf.: *Thoosa circumflexa*)	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Indian Ocean. According to van Soest et al. (2017), this is a taxon inquirendum, but after viewing Topsent's samples in Paris (2006–2007), CS finds this to be a good species. As we cannot confirm the exact origin of Topsent's sample, we did not include this species in our biogeographic analysis for the W Indian Ocean
Thoosa cf. *fischeri*	Topsent, 1891	Sri Lanka	? Thomas (1973, as *Thoosa armata*); **CS**: *Thoosa armata* is an Atlantic species, and unlike the material of Thomas (1973), it does not have tylostyles. Given the spicule complement and the sampling area, Thomas' material is likely *Thoosa fischeri*. It differs from *Thoosa radiata* (below) and was counted
(Unconf.: *Thoosa letellieri*)	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Indian Ocean. According to van Soest et al. (2017), this is a taxon inquirendum, but after viewing Topsent's samples in Paris (2006–2007), CS finds this to be a good species. As we cannot confirm the exact origin of Topsent's sample, we did not include this species in our biogeographic analysis for the W Indian Ocean
Thoosa radiata	Topsent, 1888	Unknown, in *Tridacna* sp., a genus which has an Indo-Pacific distribution	Thomas (1981)
Zyzzya fuliginosa	(Carter, 1879)	Torres Straits	Dendy (1922), Vacelet et al. (1976, as *Paracornulum atoxa*), Hooper and Krasochin (1989, as *Zyzzya massalis*), van Soest et al. (1994)
India, Maldives, Laccadives, British Ocean Territory and Andaman Islands (47 spp. of coral-eroding sponges in warm water)			
Alectona wallichii	(Carter, 1874)	Agulhas Bank, S of Africa (Carter: also from the 'South Sea' and Seychelles), first reported as spicules in sediment	? Namboothri and Fernando (2012, as *Alectona* sp.), Sunil Kumar and Thomas (2012, 2015)

Amorphinopsis excavans	Carter, 1887	W Andaman Sea	Carter (1887), Annandale (1915a), Kumar (1925), Thomas (1972, 1979b, 1989), Venkataraman et al. (2007), Pattanayak (2009); **CS**: *Amorphinopsis excavans* is seen as an Indo-Pacific species, but characters described in different accounts vary, and the species (complex?) needs to be revised (Carvalho et al. 2004). Pattanayak lists three forms or varieties. This material needs to be re-examined to see whether they all belong to the same species. It was still counted as a separate species for the bioregion
Aff. *Cervicornia cuspidifera*	Unresolved species complex	Sensu stricto: Caribbean Sea	Thomas (1972, 1979b, 1989, as *Spirastrella*), Venkataraman et al. (2007 as *Spirastrella*); **CS**: *Cervicornia cuspidifera* is a Caribbean species. Other endopsammic clionaids exist in the Indo-Pacific, and this account needs to be re-examined. It was still counted as a different species in the bioregion
Cliona annulifera	Annandale, 1915a	Sri Lanka	Thomas (1979b, from shallow water), Pattanayak (2009)
Cliona aff. *celata*	Unresolved species complex	Sensu stricto: Scotland	Carter (1881, as *Cliona warreni*), Annandale (1915b, partly as *Cliona warreni*), Thomas (1972, 1979b, 1989), Venkataraman et al. (2007), Sunil Kumar and Thomas (2011), Namboothri and Fernando (2012), Sunil Kumar and Thomas (2015); **CS:** *Cliona celata* was described from Scotland and represents a taxonomically difficult species complex (Xavier et al. 2010, de Paula et al. 2012). All faunistic accounts are unreliable unless including molecular data. This report is unlikely to be *Cliona celata* sensu stricto but was still counted as a clionaid different from other species in the bioregion
Cliona ensifera	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	Sollas (1878), Annandale (1915b), Thomas (1972, 1979b, 1989), Calcinai et al. (2000), Pattanayak (2006), Immanuel et al. (2015), Raghunathan (2015), Kiruba-Sankar et al. (2016)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
(Unconf.: *Cliona insidiosa*)	Hancock, 1849	In the giant clam, *Tridacna gigas*, occurs in the Indo-Pacific	No other primary records found. **CS**: The sponge could possibly occur in this bioregion but was not observed since its description. As the exact type location is unknown, it was not included in the biogeographic analysis
Cliona johnstonii	(Carter, 1886)	Bass Strait	Calcinai et al. (2000, as *Cliona schmidti*); **CS**: We tentatively listed all '*Cliona schmidtii*' reported from the Indo-Pacific as *Cliona johnstonii* to imply that the two species are different. See van Soest et al. (2017) for comments on the distribution of *Cliona schmidtii*
Cliona kempi	Annandale, 1915a	Andaman Islands	Thomas (1979b), Pattanayak (2006, 2009), Namboothri and Fernando (2012), Immanuel et al. (2015)
Cliona aff. *lobata*	Unresolved species complex	Sensu stricto: English Channel	Thomas (1979b), Pattanayak (2006), Sunil Kumar and Thomas (2011), Namboothri and Fernando (2012), ? Sivaleela (2014), ? Kumar and Jogani (2014), ? Kumar and Shah (2014), Immanuel et al. (2015); **CS**: The Atlantic species *Cliona lobata* has been widely reported, but maybe not always accurately. These accounts have to be re-examined. The present record is possibly misidentified but is here counted as a morphologically different clionaid for the bioregion
Cliona michelini	Topsent, 1888	Indian Ocean, in shell of rock snail	Annandale (1915b); **CS**: The listing by Annandale is based on Topsent's description. However, slide DX425 of *Cliona michelini* at the Paris Museum was marked 'Bombay' (C. Schönberg pers. obs. 2006–2007), suggesting that the species was found at least once in Indian waters
Cliona mucronata	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	Annandale (1915a, b), Thomas (1972, 1979b, 1989), Calcinai et al. (2000), Pattanayak (2006), Bhagirathan et al. (2008), Namboothri and Fernando (2012), Immanuel et al. (2015)

Cliona nodulosa	Calcinai et al., 2000	Maldives	No other primary records found
Cliona patera	(Hardwicke, 1820)	Singapore	Annandale (1915b)
(*Cliona subulata*)	Sollas, 1878	Unknown, but sympatric with *Cliona ensifera* and *Cliona mucronata*, thus assumed as Indo-Pacific	No other primary records found for this bioregion. **CS**: *Cliona subulata* has tylostyles and spirasters with long, discrete spines. Sollas' drawings of the spicules suggest that the species belongs to the *Cliona viridis* complex, of which there are others in the area that cannot adequately be compared with *Cliona subulata*. Pending new results, we did not use this species in the biogeography to avoid possible duplication. Sollas' type material needs to be re-examined
(Unconf.: *Cliona thoosina*)	Topsent, 1888	Unknown, in *Tucetona* shell (as *Pedunculus*), which does not provide helpful information. However, a tissue preparation of the type DT2538 at the Paris Museum was marked 'Indian Ocean' (C. Schönberg pers. obs. 2006–2007)	No other primary records found for this bioregion. **CS**: The species could possibly occur in this bioregion, but we were unable to confirm the exact type location and could not consider this species in our biogeographic analysis. Other records were from the Mediterranean (e.g. Pulitzer-Finali 1983, as *Cliona cretensis*, in calcareous rock; Rosell and Uriz 2002a; Ponti et al. 2011)
Cliona aff. *viridis* sp. 1 (aff. *cuspidifera*?) *Cliona* aff. *viridis* sp. 2 (aff. *orientalis*?)	Unresolved species complex	Sensu stricto: Adriatic Sea, Mediterranean	Carter (1887, as *Suberites coronarius*), Dendy (1916, as *Cliona coronaria*), Annandale (1915b, as *Cliona viridis* and *Cliona orientalis*), Kumar (1925, as *Cliona viridis*), Thomas (1972, 1979b, 1989, as *Cliona viridis* and *Cliona orientalis*), Calcinai et al. (2000, as *Cliona orientalis* and *Spheciospongia varians*?), Namboothri and Fernando (2012), Immanuel et al. (2015, as *Cliona varians*), Raghunathan (2015, as *Cliona varians*), Kiruba-Sankar et al. (2016, as *Cliona varians*); **CS**: The group is taxonomically difficult, and there are several species that may possibly occur (e.g. *Cliona albimarginata*, *Cliona orientalis* as common ones). As some of the authors listed two separate species in their publications, two species were counted, but local material will need to be investigated with molecular means

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliothosa aurivillii	(Lindgren, 1897)	Java Sea	Thomas (1972, 1989, as *Spirastrella*), Venkataraman et al. (2007, as *Spirastrella*), Namboothri and Fernando (2012)
Cliothosa dichotoma	(Calcinai et al., 2000)	Maldives	Calcinai et al. (2000)
Cliothosa hancocki	(Topsent, 1888)	French Polynesia	Topsent (1888, as *Cliona quadrata*), Annandale (1915a, as *Thoosa hancocci* and *Cliona quadrata*, 1915b, as *Thoosa*), Thomas (1972, as *Cliona quadrata*, 1979b, as *Thoosa*), Pattanayak (2006, partly as *Cliona quadrata*), Sivaleela (2014, as *Cliothosa quadrata*), Sunil Kumar and Thomas (2015), Immanuel et al. (2015, partly as *Cliothosa quadrata*); **CS** regards this name as a species complex that needs to be resolved per respective bioregion. It is here counted as one species distinct from the others occurring in this region
(*Cliothosa quadrata*)	(Hancock, 1849)	In the giant clam, *Tridacna gigas*, occurs in the Indo-Pacific	**CS**: After accessing Topsent's samples at the Paris Museum (2006–2007), CS regards *Cliothosa hancocki* as a species complex. *Cliothosa hancocki* and *Cliothosa quadrata* are very similar (e.g. Calcinai et al. 2005) but have not yet been formally compared. To avoid possible duplication, only *Cliothosa hancocki* was counted for our biogeographic analysis, despite records from India under the name *Cliothosa quadrata* (see entries above)
(Unconf.: *Cornulella purpurea*)	(Hancock, 1849)	Unknown, sample found in *Tridacna gigas*, which has an Indo-Pacific distribution	Referring to Hancock's sample and thus not reporting a confirmed sample site: Kirkpatrick (1900a, as *Dyscliona*), Topsent (1907, as undetermined genus), Hallmann (1920, as *Paracornulum*), Rützler and Stone (1986, as *Cliona*), van Soest et al. (1994); **CS**: It is possible that *Cornulella purpurea* occurs in this bioregion, but as the sample site is unknown and cannot be conclusively matched to our bioregions, this species did not become part of our analysis.
(*Delectona higgini*)	(Carter, 1880)	Sri Lanka	Thomas (1972, 1979b); **CS**: But Thomas apparently referred to Carter's account or sample, did not state a sampling depth either and reported coralline algae as substrate. The three other *Delectona* spp. occur in deep water. As this sponge may not occur in shallow water, it was not included in the biogeographic analysis related to warm-water corals

Dercitus (*Stoeba*) *simplex*	(Carter, 1880)	Sri Lanka	Sollas (1888a), ? Annandale (1915a, as *Stoeba plicata*), ? Calcinai et al. (2000 as *Dercitus plicatus*), van Soest et al. (2010), Immanuel et al. (2015); **CS**: Reports outside the Mediterranean are unlikely to be *Dercitus* (*Stoeba*) *plicatus* (see e.g. van Soest et al. 2010). The species was tentatively included here as one species of *Dercitus*
(*Dotona pulchella*)	Carter, 1880	Sri Lanka	Thomas (1972, 1979b); **CS**: But Thomas' account seems to rely on other people's samples, which were largely from deep water (see below). The present record was not included into the warm-water analysis
Pione carpenteri	(Hancock, 1867)	Mazatlán	Carter (1887, as *Cliona bacillifera*), Topsent (1888, as *Cliona*), Annandale (1915a, b, as *Cliona*), Thomas (1979b, 1989, as *Cliona*), Calcinai et al. (2000), Immanuel et al. (2015), Sunil Kumar and Thomas (2015); **CS**: This may not be *Pione carpenteri*, but it represents the local *Pione* species with straight, spindle-shaped microrhabds
(Unconf.: *Pione fryeri*)	(Hancock, 1849)	Unknown. Was found in window pane oyster, *Placuna placenta*, which occurs between the Gulf of Aden and the Philippines	No other primary records found. **CS**: This species could potentially occur in the bioregion, but as we do not know the exact sample site, we could not conclusively assign it to any one of our bioregions. *Placuna placenta* is commercially very important in the Philippines, and we tentatively assumed that the sample was from there and counted *Pione fryeri* only for the Coral Triangle
Pione indica: recommendation to reassess genus allocation	(Topsent, 1891)	Sri Lanka	Annandale (1915b, as *Cliona*), (Thomas 1979b, as *Cliona*); **CS** saw a slide of the type material in Paris (2006–2007). The species shares *Pione* and *Cliona* characters: Pro-*Pione* characters are that the tylostyles are always very straight and that the sponge contains acanthose microrhabds (spirasters?). Pro-*Cliona* characters are that the tylostyles are always robust, the tyles contain occasional vesicles, and there are no oxeas. This species may be close to the *Cliona lobata* group? The species was found in a pearl oyster shell and was thus assumed to be from shallow water
Pione margaritiferae	(Dendy, 1905)	Sri Lanka	Annandale (1915b, as *Cliona*), Thomas (1972, 1979b, as *Cliona*), Venkataraman et al. (2007 as *Cliona*), Sunil Kumar and Thomas (2011, 2015); **CS**: This has been described from the bioregion and represents the local *Pione* with helical microrhabds

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Pione aff. *vastifica*	Unresolved species complex	Sensu stricto: Scotland	Annandale (1915b, c, as *Cliona*), Thomas (1972, 1979b, 1989, as *Cliona*), Pattanayak (2006 as *Cliona*), Venkataraman et al. (2007 as *Cliona*), Sunil Kumar and Thomas (2011), Namboothri and Fernando (2012), Immanuel et al. (2015), Sunil Kumar and Thomas (2015)
Samus anonymus	Gray, 1867	Brazil	Carter (1880), Bhagirathan et al. (2008)
Siphonodictyon diagonoxeum	(Thomas, 1968a)	Sri Lanka	Thomas (1972, 1979b, as *Aka*), Pattanayak (2009, as *Aka*)
Siphonodictyon maldiviense	Calcinai et al., 2000	Maldives	Calcinai et al. (2007b)
Siphonodictyon minutum	(Thomas, 1972)	Sri Lanka	Thomas (1972, 1979b, 1989, as *Aka*), Pattanayak (2009, as *Aka*), Sunil Kumar and Thomas (2015)
Siphonodictyon mucosum	Bergquist, 1965	Palau	Namboothri and Fernando (2012, as *Aka*)
(*Siphonodictyon laccadiviense*) taxon inquirendum	(Thomas, 1989)	Laccadives	No other primary records found. **CS**: This name has been synonymised with *Zyzzya fuliginosa* (van Soest et al. 2017), but it is here assumed that Thomas really meant a *Siphonodictyon* species. However, we were unable to find a formal description or to locate any type material (which is supposed to exist at the Calcutta Museum, P. Thomas pers. comm. 2012). At this stage we cannot adequately avoid possible species duplication and ignored this name
Spheciospongia florida	(Von Lendenfeld, 1897)	Zanzibar	Kumar (1925, as *Spirastrella*)
Spheciospongia globularis	(Dendy, 1922)	Chagos	Dendy (1922, as *Spirastrella*)
Spheciospongia inconstans	(Dendy, 1887)	Madras	Dendy (1887, as *Suberites*, 1922), Thomas (1972, 1979b, 1989, as *Spirastrella*), Calcinai et al. (2000), Pattanayak (2006), Venkataraman et al. (2007, as *Spirastrella*), Sivaleela (2014), Immanuel et al. (2015)
Spheciospongia tentorioides	(Dendy, 1905)	Sri Lanka	No other primary records found

Spheciospongia vagabunda	(Ridley, 1884)	Torres Straits	Carter (1887, as *Spirastrella trincomaliensis*), Dendy (1905, as *Spirastrella*), Dendy (1916, as *Spirastrella vagabunda* var. *tubulodigitata*), Dendy (1922, as *Spirastrella* and the varieties *tubulodigitata* and *gelatinosa*), Immanuel et al. (2015), Raghunathan (2015), Kiruba-Sankar et al. (2016, as *Spirastrella*)
Spirastrella andamanensis	Pattanayak, 2006	Andaman Islands	Pattanayak (2009), Immanuel et al. (2015)
(*Spirastrella* aff. *coccinea*)	Unresolved species complex	Sensu stricto: Caribbean	Thomas (1989), Venkataraman et al. (2007); **CS**: See comments for *Spirastrella* aff. *cunctatrix*
Spirastrella aff. *cunctatrix* (*sabogae*?)	Unresolved species complex	Sensu stricto: Algeria, Mediterranean	Carter (1887), Immanuel et al. (2015), Raghunathan (2015), Kiruba-Sankar et al. (2016); **CS**: Related records require confirmation. See Boury-Esnault et al. (1999) for the distribution of similar *Spirastrella* spp. *Spirastrella coccinea* and *Spirastrella cunctatrix* are morphologically very similar. To avoid possible duplication, we excluded one of the locally unexpected species from our analyses. We assumed that the more likely species to occur might be *Spirastrella cunctatrix*, possibly introduced to the Indo-Pacific via the Suez Canal. Alternatively, this could be *Spirastrella sabogae*
Timea curvistellifera: genus transfer to *Spirastrella curvistellifera* new comb.	(Dendy, 1905)	Sri Lanka	No other primary records found. **CS:** *Timea curvistellifera* is transferred into *Spirastrella*, because according to the original description, it is a thinly encrusting sponge that has no asters as typical for *Timea* but an ectosomal crust of spirasters with robust, conical spines either terminally arranged or following the convex sides of the axis, which is congruent with *Spirastrella*
Spirastrella pachyspira	Lévi, 1958	E Red Sea, Saudi Arabia	Thomas (1968), ? Kumar and Jogani (2014), ? Kumar and Shah (2014)
Spirastrella punctulata	Ridley, 1884	Mozambique	Kumar (1925)
Spiroxya acustella	(Annandale, 1915b)	Bay of Bengal	Thomas (1979b, as *Donotella*), Pattanayak (2009, as *Cliona*); **CS:** Reported from shallow water
Spiroxya levispira	(Topsent, 1898)	Acores	Calcinai et al. (2000); **CS:** Reported from shallow water
Thoosa armata	Topsent, 1888	Gulf of Guinea	Annandale (1915b), Thomas (1979b, 1989), Sunil Kumar and Thomas (2015)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Thoosa bulbosa	Hancock, 1849	In the giant clam, *Tridacna gigas*, occurs in the Indo-Pacific	Topsent (1888), Namboothri and Fernando (2012)
(Unconf.: *Thoosa cactoides*)	Hancock, 1849	In the pearl oyster, *Pinctada margaritifera*, which has an Indo-Pacific distribution	No other primary records found. **CS:** As we do not know the exact type location of this species, we did not count it for any specific bioregion
(Unconf.: *Thoosa circumflexa*)	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS:** It is an Indo-Pacific sponge and may possibly occur in the Indian Ocean. According to van Soest et al. (2017), this is a taxon inquirendum, but after viewing Topsent's samples in Paris (2006–2007), CS finds this to be a good species. As we cannot confirm the exact origin of Topsent's sample, we did not include this species in our biogeographic analysis for Indian sites
Thoosa fischeri	Topsent, 1891	Sri Lanka	Thomas (1979b)
Thoosa laeviaster	Annandale, 1915b	Myanmar	Thomas (1979b, as *Annandalea*)
(Unconf.: *Thoosa letellieri*)	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Indian Ocean. According to van Soest et al. (2017), this is a taxon inquirendum, but after viewing Topsent's samples in Paris (2006–2007), CS finds this to be a good species. As we cannot confirm the exact origin of Topsent's sample, we did not include this species in our biogeographic analysis for Indian sites
(Unconf.: *Thoosa radiata*)	Topsent, 1888	Unknown, in *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: This Indo-Pacific sponge might occur in the Indian Ocean. However, as we cannot confirm the exact type location, we did not include this species in our biogeographic analysis for Indian sites
Thoosa socialis	Carter, 1880	Gulf of Mannar	Cater (1881), Thomas (1972, 1979b, as *Thooce*)
Zyzzya fuliginosa	(Carter, 1879)	Torres Straits	Dendy (1922, as *Lissodendoryx massalis*), Thomas (1981, 1989, partly as *Damirina laccadiviensis*), van Soest et al. (1994), Calcinai et al. (2000)
Zyzzya papillata	(Thomas, 1968a)	Sri Lanka	Van Soest et al. (1994)

NW Australia, Cocos and Christmas Islands (35 spp. of coral-eroding sponges in warm water)			
Cliona caesia	(Schönberg, 2000)	Central Great Barrier Reef	C. Schönberg pers. obs. (2012, Ningaloo)
Cliona aff. *celata*	Unresolved species complex	Sensu stricto: Scotland	Hentschel (1909), Schönberg and Fromont (2012), Fromont and Sampey (2014); **CS**: *Cliona celata* was described from Scotland and represents a taxonomically difficult species complex (Xavier et al. 2010, de Paula et al. 2012). All faunistic accounts are unreliable unless including molecular data. This report is unlikely to be *Cliona celata* sensu stricto but was still counted as a clionaid different from others in the bioregion
Cliona dissimilis	Ridley and Dendy, 1886	Arafura Sea	Hooper and Wiedenmayer (1994), Fromont and Sampey (2014)
Cliona ensifera	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	C. Schönberg pers. obs. (2012, Ningaloo)
(Unconf.: *Cliona insidiosa*)	Hancock, 1849	In the giant clam, *Tridacna gigas*, occurs in the Indo-Pacific	No other primary records found. **CS**: The sponge could possibly occur in this bioregion but was not noted since its description. As the exact type location is unknown, it was not included in the biogeographic analysis
Unconf.: *Cliona johannae*	Topsent, 1932	W Australia. But reported from the red abalone, *Haliotis rufescens*, which occurs in the E Pacific, Oregon to Baja California	No other primary records found. **CS**: This species has been published as being from Western Australia (sometimes: Shark Bay). However, in that case, the host material must have been misidentified, as it has an E Pacific distribution. We presently rely on the published statement for the type location. W Australian abalone spp. do not extend into Shark Bay, and it may even be a sample from further south than always assumed
(Unconf.: *Cliona michelini*)	Topsent, 1888	Indian Ocean, in shell of rock snail	No other primary records found for this bioregion. **CS**: This species may occur in the bioregion, but as the exact sample origin is unknown, it was not included here. Based on notes on a slide preparation, *Cliona michelini* was listed for India, however

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona minuscula	Schönberg et al., 2006	Central Great Barrier Reef	C. Schönberg pers. obs. (2012, Ningaloo)
Cliona mucronata	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	C. Schönberg pers. obs. (2012, Ningaloo)
Cliona orientalis	Thiele, 1900	Molucca Sea, Indonesia	C. Schönberg pers. obs. (2012, Kimberley, Ningaloo); ? Schönberg and Fromont (2012), Fromont and Sampey (2014)
(*Cliona subulata*)	Sollas, 1878	Unknown, but sympatric with *Cliona ensifera* and *Cliona mucronata*, thus assumed as Indo-Pacific	No other primary records found for this bioregion. **CS**: *Cliona subulata* has tylostyles and spirasters with long, discrete spines. Sollas' drawings of the spicules suggest that the species belongs to the *Cliona viridis* complex, of which there are others in the area that cannot adequately be compared with *Cliona subulata*. Pending new results, we did not use this species in the biogeography to avoid possible duplication. Sollas' type material needs to be re-examined
(Unconf.: *Cliona thoosina*)	Topsent, 1888	Unknown, in *Tucetona* shell (as *Pedunculus*), which is not helpful information. A tissue preparation of the type DT2538 at the Paris Museum was marked 'Indian Ocean' (C. Schönberg pers. obs. 2006)	No other primary records found for this bioregion. **CS**: The species could possibly occur in this bioregion, but we were unable to confirm the exact type location and could not consider this species in our biogeographic analysis. Other records were from the Mediterranean (e.g. Pulitzer-Finali 1993, as *Cliona cretensis*, in calcareous rock; Rosell and Uriz 2002b; Ponti et al. 2011)
Cliona cf. *tinctoria*	Schönberg, 2000	Central Great Barrier Reef	Schönberg and Fromont (2012), Fromont and Sampey (2014)

Cliona vermifera	Hancock, 1867	Unknown. In *Chama* sp., information which does not provide further clues	C. Schönberg pers. obs. (2012, Ningaloo); **CS:** *Cliona vermifera* is thought to be a species complex (see e.g. León-Pech et al. 2015), but pending new results is here treated as a single species
(*Cliona* spp. undetermined)	Not formally described	Reported from NW Australia	Fromont and Sampey (2014, as *Cliona* sp. 8, sp. 17, sp. K1, sp. NW1); **CS**: Apart from *Cliona celata*, *Cliona dissimilis*, *Cliona orientalis* and *Cliona tinctoria*, the authors reported four other *Cliona* spp. as OTUs. As we cannot presently match these against the other listed *Cliona* spp., we did not count them for the biogeographic analysis
(Unconf.: *Cornulella purpurea*)	(Hancock, 1849)	Unknown, sample found in *Tridacna gigas*, which has an Indo-Pacific distribution	Referring to Hancock's sample and thus not reporting a confirmed sample site: Kirkpatrick (1900a, as *Dysclíona*), Topsent (1907, as undetermined genus), Hallmann (1920, as *Paracornulum*), Rützler and Stone (1986, as *Cliona*), van Soest et al. (1994); **CS**: It is possible that *Cornulella purpurea* occurs in this bioregion, but as the sample site is unknown and cannot be conclusively matched to our bioregions, this species did not become part of our analysis
Dercitus (*Stoeba*) *occultus*	Hentschel, 1909	Shark Bay	Van Soest et al. (2010)
Pione carpenteri	(Hancock, 1867)	Mazatlán	Hentschel (1909, as *Cliona carpenteri* var. *gracilis*), Hooper and Wiedenmayer (1994, as *Cliona*); **CS:** The genus *Pione* is taxonomically difficult. However, as Hentschel distinguished four *Pione* spp. in the same publication, we accept that they were different from each other
(Unconf.: *Pione fryeri*)	(Hancock, 1849)	Unknown. Was found in window pane oyster, *Placuna placenta*, which occurs between the Gulf of Aden and the Philippines	No other primary records found. **CS**: This species could potentially occur in the bioregion, but as we do not know the exact sample site, we could not conclusively assign it to any one of our bioregions. *Placuna placenta* is commercially very important in the Philippines, and we tentatively assumed that the sample was from there and counted *Pione fryeri* only for the Coral Triangle

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Pione aff. *lampa*	Unresolved species complex	Sensu stricto: Bermuda	Fromont and Sampey (2014, as *Pione lampa*); **CS**: This record needs to be revisited; *Pione lampa* has not yet been recorded from anywhere apart from the Caribbean. As another species known to grow in encrusting morphology—*Pione velans*—was listed in the same publication, this one was accepted as different and different from the papillate *Pione* spp. listed by Hentschel (1909)
Pione margaritiferae	(Dendy, 1905)	Gulf of Mannar	Hentschel (1909, as *Cliona*), Hooper and Wiedenmayer (1994, as *Cliona*)
Pione aff. *vastifica*	Unresolved species complex	Sensu stricto: Scotland	Hentschel (1909, as *Cliona vastifica*)
Pione velans	(Hentschel, 1909)	Shark Bay	Hooper and Wiedenmayer (1994, as *Cliona*), Fromont et al. (2005), Fromont and Sampey (2014)
(*Pione* spp. undetermined)	Not formally described	Reported from NW Australia	Fromont and Sampey (2014, as *Pione* sp. 2781, sp. 2782); **CS**: Apart from *Pione lampa* and *Pione velans*, the authors reported two other *Pione* spp. as OTUs. As we cannot presently match these against the other listed *Pione* spp., we did not count them for the biogeographic analysis
Siphonodictyon minutum	(Thomas, 1972)	Sri Lanka	C. Schönberg pers. obs. (2012, Ningaloo)
Siphonodictyon mucosum	Bergquist, 1965	Palau	Fromont and Sampey (2014)
Siphonodictyon paratypicum	(Fromont, 1993)	Central Great Barrier Reef	Fromont and Sampey (2014); **CS:** This species is similar to *Siphonodictyon maldiviense*, and this record needs reassessment. However, it represents a different species from the other ones in the bioregion and was counted
7 *Siphonodictyon* spp. undetermined	Not formally described	Reported from NW Australia	Schönberg and Fromont (2012, as 10 *Siphonodictyon* spp.), Fromont and Sampey (2014, as 6 *Siphonodictyon* spp.); **CS:** We counted seven of these species in addition to the identified species, because without reassessing the material, we could not rule out species duplication

Spheciospongia digitata	(Hentschel, 1909)	Shark Bay	Hooper and Wiedenmayer (1994, as *Spirastrella*)
Spheciospongia papillosa	(Ridley and Dendy, 1886)	Sydney Harbour, Australia	Schönberg and Fromont (2012, as 'cf.'), Fromont and Sampey (2014); **CS:** This species is better known from colder water (e.g. Dendy 1897), but according to the authors, it occurred on northwestern Australian reefs and was counted for the NW Australian biogeography
Spheciospongia purpurea	(De Lamarck, 1815)	Bass Strait	Carter (1882, as *Alcyonium purpureum*), Topsent (1933, as *Spirastrella*), Hooper and Wiedenmayer (1994, as *Spirastrella*); **CS:** The sponge is best known from southwestern Australia, but it has been sampled as far north as the Abrolhos Islands and was counted (C. Schönberg pers. obs. 2015, accessing samples of the Western Australian Museum)
Spheciospongia tentorioides	(Dendy, 1905)	Sri Lanka	Hentschel (1909, as *Spirastrella tentorioides* var. *australis*), Hooper and Wiedenmayer (1994, as *Spirastrella*)
Spheciospongia vagabunda	(Ridley, 1884)	Torres Straits	Dendy and Frederick (1924, as *Spirastrella*), Hooper and Wiedenmayer (1994, as *Spirastrella*), Schönberg and Fromont (2012, as 'cf.'), Fromont and Sampey (2014)
(*Spheciospongia* spp. undetermined)	Not formally described	Reported from NW Australia	Schönberg and Fromont (2012), Fromont and Sampey (2014); **CS:** Not fully identified *Spheciospongia* spp. could not be adequately be compared to other *Spheciospongia* spp. in our data table. We did not count them for the biogeographic analysis
(*Spirastrella* sp. undetermined)	Not formally described	Reported from the Kimberley	Fromont and Sampey (2014, as *Spirastrella* WA1); **CS:** As this species could not adequately be compared with the record of *Spirastrella decumbens*, it was here ignored to avoid duplication
Spirastrella decumbens	Ridley, 1884	Torres Straits	Kirkpatrick (1900b), ? Hentschel (1909, as *Spirastrella cunctatrix*), Hooper and Wiedenmayer (1994)
(Unconf.: *Thoosa cactoides*)	Hancock, 1849	In the pearl oyster, *Pinctada margaritifera*, which has an Indo-Pacific distribution	No other primary records found. **CS:** As we do not know the exact type location of this species, we did not count it for any specific bioregion

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
(Unconf.: *Thoosa circumflexa*)	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS:** This Indo-Pacific sponge might occur in the Indian Ocean. According to van Soest et al. (2017), this is a taxon inquirendum, but after viewing Topsent's samples in Paris (2006–2007), CS finds this to be a good species. Without the exact type location, we did not include this species in our biogeographic analysis for the NW Australia
(Unconf.: *Thoosa letellieri*)	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: This Indo-Pacific sponge might occur in the Indian Ocean. Taxon inquirendum (van Soest et al. 2017), but after viewing Topsent's samples in Paris (2006–2007), CS finds this to be a good species. Without the exact type location, we did not use this species here
(Unconf.: *Thoosa radiata*)	Topsent, 1888	Unknown, in *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Indian Ocean. However, as we cannot confirm the exact origin of Topsent's sample, we did not include this species here
Zyzzya cf. *criceta*	Schönberg, 2000	Central GBR	Fromont and Sampey (2014)
Zyzzya fuliginosa	(Carter, 1879)	Torres Straits	Hooper and Krasochin (1989, as *Zyzzya massalis*), Schönberg and Fromont (2012 as 'aff.'), Fromont and Sampey (2014, as 'cf.'), van Soest et al. (1994)
Zyzzya sp. undetermined	Not formally described	From Carnarvon Shelf	Schönberg and Fromont (2012, as Zyzzya sp. 1)
Coral Sea, including Great Barrier Reef (GBR), Arafura Sea, Papua New Guinea and New Caledonia (33 spp. of coral-eroding sponges in warm water)			
Aff. *Cervicornia* sp.	Not formally described	Observed on the central and southern GBR	C. Schönberg pers. obs. (2010–2014, endopsammic, zooxanthellate, with tylostyles and spirasters, agglutinating and incorporating particles); **CS**: This is at least one species, different from the other ones here listed
Cliona caesia	(Schönberg, 2000)	Central GBR	Schönberg (2000, 2001a, as *Pione*), Schönberg et al. (2006), Hill et al. (2011), C. Schönberg pers. obs. (2014, southern GBR)

Cliona aff. *celata*	Unresolved species complex	Sensu stricto: Scotland	? Kelly-Borges and Vacelet (1998, as *Cliona* sp.), Schönberg (2000, 2001a), Schönberg et al. (2006), C. Schönberg pers. obs. (2014, southern GBR); **CS:** *Cliona celata* was described from Scotland and represents a taxonomically difficult species complex (Xavier et al. 2010, de Paula et al. 2012). All faunistic accounts are unreliable unless including molecular data. This report is unlikely *Cliona celata* sensu stricto but was still counted as a clionaid different from others. It may represent more than one species; some samples had raphides as well as tylostyles. Bioerosion traces differed with sample
Cliona dissimilis	Ridley and Dendy, 1886	Arafura Sea	Hooper and Wiedenmayer (1994)
Cliona ensifera	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	Schönberg et al. (2006), Pica et al. (2012, depth unknown), C. Schönberg pers. obs. (2010–2014, central and southern GBR)
(Unconf.: *Cliona insidiosa*)	Hancock, 1849	In the giant clam, *Tridacna gigas*, occurs in the Indo-Pacific	No other primary records found. **CS:** The sponge could possibly occur in this bioregion but was not noted since its description. As the exact type location is unknown, it was not included in the biogeographic analysis
Cliona johnstonii	(Carter, 1886)	Bass Strait	Schönberg et al. (2006, as *Cliona* cf. *schmidti*); **CS:** We tentatively listed all '*Cliona schmidtii*' reported from the Indo-Pacific as *Cliona johnstonii* to imply that the two species are different. See van Soest et al. (2017) for comments on the distribution of *Cliona schmidtii*
Cliona cf. *jullieni*	Topsent, 1891	La Réunion	Kelly-Borges and Vacelet (1998), Hill et al. (2011), C. Schönberg pers. obs. (2010–2011, central GBR)
Cliona minuscula	Schönberg et al., 2006	Central GBR	Schönberg et al. (2006), C. Schönberg pers. obs. (2014, southern GBR)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona mucronata	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	Schönberg et al. (2006), C. Schönberg pers. obs. (2010–2014, central and southern GBR)
Cliona aff. *mucronata* sensu Vacelet and Vasseur (1971)	Unresolved species complex	Sensu stricto: Unknown, likely Indo-Pacific	C. Schönberg pers. obs. (2011, central GBR)
Cliona orientalis	Thiele, 1900	Molucca Sea, Indonesia	Vacelet (1981), Kelly-Borges and Vacelet (1998), Schönberg (2000, 2001), Schönberg et al. (2006), Hill et al. (2011), Ramsby et al. (2017)
Cliona tinctoria	Schönberg, 2000	Central GBR	? Carter (1882, as purple-coloured *Spirastrella cunctatrix*, for 'Australia'), ? Pulitzer-Finali (1982, as *Cliona carteri* from Heron Island; CS observed *Cliona tinctoria* at Heron Island 2002–2004, a similar, but more likely species), Schönberg (2000), Schönberg et al. (2006)
Cliona vermifera	Hancock, 1867	Unknown. In *Chama* sp., information which does not provide further clues	Schönberg (2001a, as *Bernatia*), Schönberg et al. (2006), C. Schönberg pers. obs. (2010–2014, central and southern GBR); **CS**: *Cliona vermifera* is thought to be a species complex (see e.g. León-Pech et al. 2015), but pending new results is here treated as a single species
Cliothosa aurivillii	(Lindgren, 1897)	Java Sea	Burton (1934, as *Spirastrella*), Hooper and Wiedenmayer (1994, as *Spirastrella*), Schönberg and Wisshak (2012)
Cliothosa hancocki	(Topsent, 1888)	French Polynesia	Risk et al. (1995), Schönberg (2000, 2001a), C. Schönberg pers. obs. (2014, southern GBR); **CS** regards this name as a species complex that needs to be resolved per respective bioregion. It is here still counted as a species distinct from the others occurring in this region

(Unconf.: *Cliothosa quadrata*)	Hancock, 1849	In the giant clam, *Tridacna gigas* occurs in the Indo-Pacific	No record found for this bioregion. **CS**: After accessing Topsent's samples at the Paris Museum (2006–2007), CS regards *Cliothosa hancocki* as a species complex. *Cliothosa hancocki* and *Cliothosa quadrata* are very similar (e.g. Calcinai et al. 2005). To avoid possible duplication, only *Cliothosa hancocki* was counted for our biogeographic analysis (more commonly used name)
(Unconf.: *Cornulella purpurea*)	(Hancock, 1849)	Unknown, sample found in *Tridacna gigas*, which has an Indo-Pacific distribution	Referring to Hancock's sample and thus not reporting a confirmed sample site: Kirkpatrick (1900a, as *Dyscliona*), Topsent (1907, as undetermined genus), Hallmann (1920, as *Paracornulum*), Rützler and Stone (1986, as *Cliona*), van Soest et al. (1994); **CS**: *Cornulella purpurea* might occur in the bioregion, but as the sample site is unknown and cannot be conclusively matched to our bioregions, this species did not become part of our analysis
Cornulum virguliferum	(Lévi and Lévi, 1983)	New Caledonia	Van Soest et al. (1994)
Pione aff. *vastifica*	Unresolved species complex	Sensu stricto: Scotland	Schönberg (2001); **CS**: Unlikely to be *Pione vastifica* sensu stricto, but counted as the only *Pione* species recorded in the bioregion
Neamphius huxleyi	(Sollas, 1888)	Vanuatu	Díaz et al. (2007)
(Unconf.: *Siphonodictyon labyrinthicum*)	(Hancock, 1849)	Unknown type location, but found in the giant clam, *Tridacna gigas*, which occurs in the Indo-Pacific	Pica et al. (2012, as *Aka*, likely New Caledonia, in *Distichopora* sp., but depth unknown); **CS**: Presently not counted
Siphonodictyon minutum	(Thomas, 1972)	Sri Lanka	Schönberg et al. (2006)
Siphonodictyon mucosum	Bergquist, 1965	Micronesia	Kelly (1986), Kelly-Borges and Bergquist (1988), Fromont (1993, as *Aka*), Hooper and Wiedenmayer (1994, as *Aka*), Schönberg (2000, 2001, as *Aka*), Schönberg and Wisshak (2012, as *Aka*)
Siphonodictyon paratypicum	(Fromont, 1993)	Central GBR	Hooper and Wiedenmayer (1994, as *Aka*), Schönberg and Tapanila (2006, as *Aka*)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Siphonodictyon sp. yellow	Not formally described	Central GBR	C. Schönberg pers. obs. (2011, endopsammic, may or may not be conspecific with the species observed at the Marianas; see Kelly et al. 2003); **CS**: This record is different from the species known from the bioregion and was counted for the biogeography analysis
Spheciospongia congenera	(Ridley, 1884)	Torres Straits	Hooper and Wiedenmayer (1994, as *Spirastrella*)
Spheciospongia inconstans	(Dendy, 1887)	Madras	Burton (1934, as *Spirastrella*), Vacelet (1981, as *Spirastrella*), Hooper and Wiedenmayer (1994, as *Spirastrella*), Kelly-Borges and Vacelet (1998)
Spheciospongia lacunosa	(Kieschnick, 1898)	Torres Straits	Hooper and Wiedenmayer (1994, as *Spirastrella*)
(*Spheciospongia purpurea*)	(De Lamarck, 1815)	Bass Strait	? Hentschel (1912); **CS**: Hentschel approached this species using a wide scope. It may not be *Spheciospongia purpurea* and likely represents more than one species. As we could not rule out duplication, we did not count it
Spheciospongia ramulosa	(Von Lendenfeld, 1888)	Sydney Harbour	No other primary records found
Spheciospongia semilunaris	(Lindgren, 1897)	Java Sea	Burton (1934, as *Spirastrella*), Hooper and Wiedenmayer (1994, as *Spirastrella*)
Spheciospongia spiculifera	(Kieschnick, 1898)	Torres Straits	Hooper and Wiedenmayer (1994, as *Spirastrella*)
Spheciospongia vagabunda	(Ridley, 1884)	Torres Straits	Bergquist and Tizard (1967, as *Spirastrella*), Kelly (1986, partly as *Spheciospongia fungoides* or *Spheciospongia gallensis* or *Spheciospongia trincomaliensis*), Kelly-Borges and Bergquist (1988), Kelly-Borges and Vacelet (1998), Sutcliffe et al. (2010)
Spirastrella decumbens	Ridley, 1884	Torres Straits	Hooper and Wiedenmayer (1994)
(Unconf.: *Thoosa cactoides*)	Hancock, 1849	In the pearl oyster, *Pinctada margaritifera*, which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Coral Sea. As we cannot confirm the exact origin of Hancock's sample, however, we did not use it for this bioregion

(Unconf.: *Thoosa circumflexa*)	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Coral Sea. As we cannot confirm the exact origin of Topsent's sample, however, we did not use it for this bioregion
(Unconf.: *Thoosa letellieri*)	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Coral Sea. As we cannot confirm the exact origin of Topsent's sample, however, we did not use it for this bioregion
(Unconf.: *Thoosa radiata*)	Topsent, 1888	Unknown, in *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Coral Sea. As we cannot confirm the exact origin of Topsent's sample, however, we did not use it for this bioregion
Thoosa sp.	Not yet formally described	Reported from the central GBR (C. Schönberg pers. obs. 2012)	No other primary records found. **CS**: At this stage, the material has only been identified to genus
Zyzzya criceta	Schönberg, 2000	Central Great Barrier Reef	Schönberg (2000, 2001a), ? Harper (2014, as *Zyzzya fuliginosa*), C. Schönberg pers. obs. (2014, on the southern GBR)
Zyzzya fuliginosa	(Carter, 1879)	Torres Straits	Van Soest et al. (1994)
Coral Triangle, including Indonesia, South China Sea, Taiwan, Gulf of Thailand, Singapore, Malaysia, Vietnam, the Philippines and Palau (43 spp. of coral-eroding sponges in warm water)			
Amorphinopsis excavans	Carter, 1887	W Andaman Sea	Hooper et al. (2000), Azzini et al. (2007b), Lim et al. (2009, 2016); **CS**: *Amorphinopsis excavans* is seen as an Indo-Pacific species, but characters described in older accounts vary, and the species (complex?) needs to be re-examined and revised (Carvalho et al. 2004)
Aff. *Cervicornia cuspidifera*	Unresolved species complex	Sensu stricto: Caribbean Sea	Hooper et al. (2000), Putchakarn (2007); **CS**: *Cervicornia cuspidifera* is a Caribbean species. Other endopsammic clionaids exist in the Indo-Pacific, and this account needs to be re-examined. It was still counted as different

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona albimarginata	Calcinai et al., 2005	N Sulawesi	? Hooper et al. (2000, as *Cliona* cf. *caroboea*), Calcinai et al. (2005), Putchakarn (2007), Lim et al. (2016); **CS**: *Cliona albimarginata* and *Cliona orientalis* have both been recorded from this bioregion and are very similar
Cliona aff. *celata*	Unresolved species complex	Sensu stricto: Scotland	Dawydoff (1952), ? van Soest (1990, as *Cliona* sp. orange), Hooper et al. (2000, as *Cliona* cf. *celata*), Calcinai et al. (2006), Azzini et al. (2007b), Chervyakova (2007), Lim et al. (2009, 2012, 2016); **CS**: *Cliona celata* was described from Scotland and represents a taxonomically difficult species complex (Xavier et al. 2010, de Paula et al. 2012a). All faunistic accounts are unreliable unless including molecular data. This report is unlikely to be *Cliona celata* sensu stricto but was still counted as a clionaid different from others in the bioregion
(*Cliona dissimilis*)	Ridley and Dendy, 1886	Arafura Sea	? Lim et al. (2012a, as *Cliona* sp. 'orange encrusting'); **CS**: This is not a confirmed record. To avoid possible duplication, we did not count it
Cliona ensifera	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	Hooper et al. (2000)
Cliona favus	Calcinai et al., 2005	N Sulawesi	No other primary records found
(Unconf.: *Cliona insidiosa*)	Hancock, 1849	In the giant clam, *Tridacna gigas*, occurs in the Indo-Pacific	No other primary records found. **CS**: The sponge could possibly occur in this bioregion but was not noted since its description. As the exact type location is unknown, it was not included in the biogeographic analysis
Cliona johnstonii	(Carter, 1886)	Bass Strait	De Laubenfels (1954), Hooper et al. (2000, as *Cliona* cf. *schmidtii*); **CS**: We tentatively listed all '*Cliona schmidtii*' reported from the Indo-Pacific as *Cliona johnstonii* to imply that the two species are different. See van Soest et al. (2017) for comments on the distribution of *Cliona schmidtii*

Cliona kempi	Annandale, 1915a	Andaman Islands	Hooper et al. (2000)
Cliona liangae	Calcinai et al., 2005	N Sulawesi	No other primary records found
Cliona aff. *lobata*	Hancock, 1849	English Channel	Hooper et al. (2000); **CS**: The Atlantic species *Cliona lobata* has been widely reported but maybe not always accurately. These accounts have to be re-examined. The present record is possibly misidentified but is here counted as a morphologically different clionaid for the bioregion
Cliona mucronata	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	Dawydoff (1952), Desqueyroux-Faúndez (1981), Hooper et al. (2000), Calcinai et al. (2005), Lim et al. (2016)
Cliona orientalis	Thiele, 1900	Molucca Sea, Indonesia	Hooper et al. (2000), Calcinai et al. (2006), Azzini et al. (2007b), Lim et al. (2012a), Lim et al. (2016); **CS**: *Cliona albimarginata* and *Cliona orientalis* have both been recorded from this bioregion and are very similar
Cliona patera	(Hardwicke, 1820)	Singapore	Schlegel (1857, as *Spongia* (*Poterion*) *neptuni*), Dawydoff (1952, as *Poterion*), Hooper et al. (2000, as *Poterion neptuni*), Lim et al. (2009, 2012a, 2012b), Low (2012), Lim et al. (2016)
Cliona utricularis	(Calcinai et al., 2005)	N Sulawesi	Lim et al. (2012a, 2016)
(*Cliona* aff. *viridis*)	Unresolved species complex	Sensu stricto: Adriatic Sea, Mediterranean	Hooper et al. (2000, as *Cliona* cf. *viridis*); **CS:** *Cliona viridis* complex species are taxonomically difficult. This account is a tentative identification and would have incurred the risk of duplication. We did not count it
Cliothosa aurivillii	(Lindgren, 1897)	Java Sea	Dawydoff (1952, as *Spirastrella*), Bergquist (1965), Hooper et al. (2000, as *Spirastrella*), ? Calcinai et al. (2006, as *Cliona*), ? Azzini et al. (2007b, as *Cliona*), Putchakarn (2011), Lim et al. (2016, listed as *Cliona* and *Cliothosa*), J. Marlow pers. comm. (2015, Celebes Sea); **CS:** The tylostyles in Calcinai et al. (2006) very much resemble those of *Spheciospongia peleia*. Azzini et al. (2007b) followed Calcinai et al.'s decision

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliothosa dichotoma	(Calcinai et al., 2000)	Maldives	Calcinai et al. (2005)
Cliothosa hancocki	(Topsent, 1888)	French Polynesia	Lindgren (1898, as *Thoosa*), Dawydoff (1952, as *Thoosa*), Hooper et al. (2000, as *Thoosa* (*Cliothosa*) *hancocki* and *Cliona quadrata*), Calcinai et al. (2006), Azzini et al. (2007b), Chervyakova (2007, as *Thoosa*), Lim et al. (2016), J. Marlow pers. comm. (2016, Celebes Sea); **CS** regards this name as a species complex that needs to be resolved per respective bioregion. It is here still counted as a species distinct from the others occurring in this region
(*Cliothosa quadrata*)	(Hancock, 1849)	In the giant clam, *Tridacna gigas*, occurs in the Indo-Pacific	**CS**: After accessing Topsent's samples at the Paris Museum (2006–2007), CS regards *Cliothosa hancocki* as a species complex. *Cliothosa hancocki* and *Cliothosa quadrata* are very similar (e.g. Calcinai et al. 2005). To avoid possible duplication, only *Cliothosa hancocki* was counted (more commonly used name), even though *Cliothosa quadrata* was also recorded (see above)
(Unconf.: *Cornulella purpurea*)	(Hancock, 1849)	Unknown, sample found in *Tridacna gigas*, which has an Indo-Pacific distribution	Referring to Hancock's sample and thus not reporting a confirmed sample site: Kirkpatrick (1900a, as *Dyscliona*), Topsent (1907, as undetermined genus), Hallmann (1920, as *Paracornulum*), Rützler and Stone (1986, as *Cliona*), van Soest et al. (1994); **CS:** It is possible that *Cornulella purpurea* occurs in this bioregion, but as the sample site is unknown and cannot be conclusively matched to our bioregions, this species did not become part of our analysis
(*Dercitus* (*Stoeba*) *plicatus*)	(Schmidt, 1868)	Algeria, Mediterranean	Sollas (1902, as *Dercitus plicata*), Hooper et al. (2000, as *Dercitus plicatus*); **CS**: Doubtful record. Was not counted for the biogeographic analysis
Dercitus (*Stoeba*) *simplex*	(Carter, 1880)	Gulf of Mannar	Thiele (1900), Hooper et al. (2000)
(*Diplastrella spiniglobata*): recommendation to reassess genus allocation	(Carter, 1879)	'South Sea'	Hooper et al. (2000); **CS**: The spicules depicted by Carter suggest that it is not a bioeroding sponge but it may be closer to a *Placospongia*. The species needs to be reassessed and was not counted
Holoxea excavans	Calcinai et al., 2001	Taiwan	Lim et al. (2016)

Neamphius huxleyi	(Sollas, 1888)	Vanuatu	Díaz et al. (2007), Lim et al. (2016)
Pione carpenteri	(Hancock, 1867)	Mazatlán	Hooper et al. (2000, as *Cliona* and partly as *Cliona bacillifera*), Calcinai et al. (2006), Azzini et al. (2007b)
Unconf.: *Pione fryeri*	(Hancock, 1849)	Unknown. Was found in window pane oyster, *Placuna placenta*, which occurs between the Gulf of Aden and the Philippines	No other primary records found. **CS**: This species might occur in the bioregion, but as we do not know the exact sample site, we could not assign it to any one of our bioregions. *Placuna placenta* is commercially very important in the Philippines, and we tentatively assumed that the sample was from there and counted *Pione fryeri* only for the Coral Triangle
(*Pione* aff. *vastifica*)	Unresolved species complex	Sensu stricto: Scotland	Hooper et al. (2000, as *Cliona*); **CS**: This record could not adequately be verified and was not used for the biogeographic analysis
Samus anonymus	Gray, 1867	Brazil	Sollas (1902), de Laubenfels (1954), Hooper et al. (2000)
Siphonodictyon maldiviense	Calcinai et al., 2000	Maldives	Calcinai et al. (2007b), ? Putchakarn (2007, as *Aka* sp.), Lim et al. (2012a, 2016, as *Aka*)
Siphonodictyon microterebrans	Calcinai et al., 2007b	N Sulawesi	No other primary records found
Siphonodictyon mucosum	Bergquist, 1965	Palau	Rützler (1971), Cerrano et al. (2002, as *Aka*), Hooper et al. (2000, as *Aka*), Calcinai et al. (2005, 2006, as *Aka*), Azzini et al. (2007b, as *Aka*), Putchakarn (2007, as *Aka*), de Voogd and Cleary (2009, as *Aka*), Lim et al. (2012a, as *Aka*), Becking et al. (2013), Lim et al. (2016)
(*Siphonodictyon* sp. undetermined)	Not formally described	Reported from Singapore	Lim et al. (2012a, as *Siphonodictyon* sp. 'white fistules soft'); **CS**: Conservatively, we treat this as a doubtful record and did not count it
(*Siphonodictyon* sp. undetermined)	Not formally described	Reported from Vietnam	Chervyakova (2007, as *Aka* sp. – 'yellow soft sponge'); **CS**: Possibly doubtful genus allocation? Conservatively not counted
Spheciospongia areolata	(Dendy, 1897)	Port Phillip Bay, South Australia	Dawydoff (1952, as *Spirastrella*), Hooper et al. (2000, as *Spirastrella*), Lim et al. (2016)
Spheciospongia carnosa	(Topsent, 1897)	Ambon, Banda Sea	Desqueyroux-Faúndez (1981, as *Spirastrella*), Hooper et al. (2000, as *Spirastrella*)
Spheciospongia congenera	(Ridley, 1884)	Torres Straits	Putchakarn (2011)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Spheciospongia inconstans	(Dendy, 1887)	Madras	Thiele (1899, as *Spirastrella*); Sollas (1902, as *Spirastrella*); Hooper et al. (2000, as *Spirastrella*); Lévi (1959b, as *Spirastrella*); Chervyakova (2007), Lim et al. (2016)
Spheciospongia lacunosa	(Kieschnick, 1898)	Ternate	Kieschnick (1900, as *Spirastrella*), Dragnewitsch (1906, as *Spirastrella*), Hooper et al. (2000, as *Spirastrella*), Lim et al. (2016)
Spheciospongia peleia	(De Laubenfels, 1954)	Palau	? Calcinai et al. (2006, as *Cliona aurivillii*), ? Azzini et al. (2007b, as *Cliona aurivillii*), Becking et al. (2013)
Spheciospongia purpurea	(De Lamarck, 1815)	Bass Strait	Hooper et al. (2000, as *Spirastrella*, including the taxon inquirendum *Spirastrella purpurea glaebosa*), Lim et al. (2016); CS: The sponge is best known from southwestern Australia, but it has been sampled as far north as the Abrolhos Islands and was tentatively counted (C. Schönberg pers. obs. 2015, accessing samples of the Western Australian Museum)
Spheciospongia semilunaris	(Lindgren, 1897)	Java Sea	Hooper et al. (2000, as *Spirastrella*)
Spheciospongia solida	(Ridley and Dendy, 1886)	Philippines	Topsent (1897, as *Spirastrella*), Lindgren (1898, as *Spirastrella*), Desqueyroux-Faúndez (1981, as *Spirastrella*), van Soest (1989, 1990, as *Spirastrella*), Hooper et al. (2000, as *Spirastrella*), Cerrano et al. (2002, as *Spirastrella*), Calcinai et al. (2006, as *Spirastrella*), Azzini et al. (2007b), Putchakarn (2007, 2011, as *Spirastrella*), Pica et al. (2012, as *Spheciospongia* cf. *solida*, enveloping and eroding basal parts of *Stylaster* sp.), Becking et al. (2013), Lim et al. (2016)
Spheciospongia spiculifera	(Kieschnick, 1898)	Ambon	Kieschnick (1900, as *Spirastrella*), Hooper et al. (2000, as *Spirastrella spiculifer*)
Spheciospongia tentorioides	(Dendy, 1905)	Sri Lanka	Calcinai et al. (2006, as *Spirastrella*), Azzini et al. (2007b), ? Li (2013, as *Spheciospongia* sp.), Lim et al. (2016)

Spheciospongia vagabunda	(Ridley, 1884)	Torres Straits	Kieschnick (1896, as *Spirastrella cylindrica*), Thiele (1900, as *Spirastrella cylindrica*), Wilson (1925, as *Spirastrella*), de Laubenfels (1935, as *Spirastrella*), Bergquist (1965, as *Spirastrella*), van Soest (1989, 1990, as *Spirastrella*), Hooper et al. (2000, as *Spirastrella*, also as ‘cf.’ and *Suberites trincomaliensis*), Longakit et al. (2005), Chervyakova (2007), de Voogd and Cleary (2009), Lim et al. (2012a, as *Spheciospongia* cf. *vagabunda*), Becking et al. (2013), Hadi et al. (2016), Lim et al. (2016)
(*Spirastrella* aff. *coccinea*)	Unresolved species complex	Sensu stricto: Caribbean	Hooper et al. (2000); **CS**: See comments for *Spirastrella* aff. *cunctatrix*
Spirastrella aff. *cunctatrix* (*sabogae*?)	Unresolved species complex	Sensu stricto: Algeria, Mediterranean	Desqueyroux-Faúndez (1981), Hooper et al. (2000), Azzini et al. (2007b); **CS**: This record requires confirmation. See Boury-Esnault et al. (1999) about the distribution of similar *Spirastrella* spp. *Spirastrella coccinea* and *Spirastrella cunctatrix* are morphologically very similar. To avoid possible duplication, we excluded one of the locally unexpected species from our biogeographic analysis. We assumed that the more likely species to occur might be *Spirastrella cunctatrix*, which might have been introduced to the Indo-Pacific via the Suez Canal. Alternatively, this could be *Spirastrella sabogae*
Spirastrella decumbens	Ridley, 1884	Torres Straits	Topsent (1897), van Soest (1990), Hooper et al. (2000), Calcinai et al. (2006; sensu Kirkpatrick 1900a), Azzini et al. (2007b), Lim et al. (2012a, as *Spirastrella decumbens* var. *robusta*), Becking et al. (2013), Lim et al. (2016)
Spirastrella pachyspira	Lévi, 1958	E Red Sea, Saudi Arabia	Hooper et al. (2000)
Spirastrella tristellata	Topsent, 1897	Ambon	Topsent (1897), Hooper et al. (2000)
(Unconf.: *Thoosa cactoides*)	Hancock, 1849	In the pearl oyster, *Pinctada margaritifera*, which has an Indo-Pacific distribution	No other primary records found. **CS**: As we do not know the exact type location of this species, we did not count it for any specific bioregion

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
(Unconf.: *Thoosa circumflexa*)	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Coral Triangle. According to van Soest et al. (2017), this is a taxon inquirendum, but after viewing Topsent's samples in Paris (2006–2007), CS finds this to be a good species. As we cannot confirm the exact origin of Topsent's sample, we did not include this species here in our biogeographic analysis
(Unconf.: *Thoosa letellieri*)	Topsent, 1891	Unknown, sample found in Caen, on *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Coral Triangle. According to van Soest et al. (2017), this is a taxon inquirendum, but after viewing Topsent's samples in Paris (2006–2007), CS finds this to be a good species. As we cannot confirm the exact origin of Topsent's sample, we did not include this species here
(Unconf.: *Thoosa radiata*)	Topsent, 1888	Unknown, in *Tridacna* sp., a genus which has an Indo-Pacific distribution	No other primary records found. **CS**: It is an Indo-Pacific sponge and may possibly occur in the Coral Triangle. However, as we cannot confirm the exact origin of Topsent's sample, we did not include this species here
Zyzzya criceta	Schönberg, 2000	Central GBR	J. Marlow, pers. comm. (2016, Celebes Sea); **CS**: See also http://www.kudalaut.eu/en/dph/5483/Photos-Sale/Boring-sponge; http://www.kudalaut.eu/en/dph/4793/Photos-Sale/Sponge
Japan, especially the Ryukyu Islands, Korea (18 spp. of coral-eroding sponges in warm water) – Y. Ise pers. comm. (2017): Species identifications partly unconfirmed, need re-assessment			
Cliona cf. *amplicavata*	Rützler, 1974	Bermuda	C. Schönberg pers. obs. (2004, Ryukyu Islands, preliminary identification only)
(*Cliona argus*) (*Cliona argus* var. *laevicollis*)	Thiele, 1898	Hakodate, Tsugaru Strait, in mollusc and brachiopod shells	No other primary records found. **CS:** The type location is cold temperate, and in addition, the variety was sampled from 140 m. *Cliona argus* was thus not included in the biogeographic analysis
Cliona caesia	(Schönberg, 2000)	Central Great Barrier Reef	C. Schönberg pers. obs. (2004, Ryukyu Islands); Hill et al. (2011)

Cliona aff. *celata*	Unresolved species complex	Sensu stricto: Scotland	Hoshino (1981), Hoshino (1987), C. Schönberg pers. obs. (2004, Ryukyu Islands); **CS**: *Cliona celata* was described from Scotland and represents a taxonomically difficult species complex (Xavier et al. 2010, de Paula et al. 2012). All faunistic accounts are unreliable unless including molecular data. This report is unlikely to be *Cliona celata* sensu stricto but was still counted as a clionaid different from others in the bioregion
Cliona infrafoliata	(Thiele, 1898)	Hakodate, Tsugaru Strait, in mollusc and brachiopod shells	Hoshino (1981, as *Suberites infrafoliatus*), Tanita and Hoshino (1989, as *Suberites infrafoliata*); **CS**: The type location is cold temperate, but the sponge has later been recorded from Bingonada Sea, which has a mild, warm climate. Japanese waters are influenced by the Kuroshio Current, which supports corals further north than at some other places. The sponge was tentatively counted into the biogeographic analysis
Cliona cf. *minuscula*	Schönberg et al., 2006	Central Great Barrier Reef	C. Schönberg pers. obs. (2004, Ryukyu Islands)
(Unconf.: *Cliona orientalis*)	Thiele, 1900	Molucca Sea, Indonesia	C. Schönberg pers. obs. (2004, Ryukyu Islands), Schönberg et al. (2008); **CS**: Several characters of *Cliona raromicrosclera*, *Cliona reticulata* and *Cliona orientalis* are very similar. *Cliona orientalis* and *Cliona reticulata* have almost identical spicule dimensions, but in both, tylostyles are about 100 µm shorter than those of *Cliona raromicrosclera*. Pending a direct comparison, we avoided possible duplication of the same species; only *Cliona raromicrosclera* and *Cliona reticulata* were counted into the biogeography
Cliona aff. *raromicrosclera*	Unresolved species complex	Sensu stricto: Gulf of California	Hoshino (1981, as *Anthosigmella*), Hoshino (1987), Tanita and Hoshino (1989, as *Anthosigmella*); **CS & JLC**: This might be an unlikely record for Japan and belongs to the taxonomically difficult *Cliona viridis* complex. For example, several characters of *Cliona raromicrosclera* and *Cliona reticulata* are very similar. However, as *Cliona reticulata* tylostyles are about 100 µm shorter than those of *Cliona raromicrosclera*, both species were tentatively counted
Cliona reticulata	Ise and Fujita, 2005	Ryukyu Islands	No other primary records found

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliothosa hancocki	(Topsent, 1888)	French Polynesia	C. Schönberg pers. obs. (2004, Ryukyu Islands); **CS** regards this name as a species complex that needs to be resolved per respective bioregion. It is here still counted as a species distinct from the others occurring in this region
(Unconf.: *Cornulella purpurea*)	(Hancock, 1849)	Unknown, sample found in *Tridacna gigas*, which has an Indo-Pacific distribution	Referring to Hancock's sample and thus not reporting a confirmed sample site: Kirkpatrick (1900a, as *Dyscliona*), Topsent (1907, as undetermined genus), Hallmann (1920, as *Paracornulum*), Rützler and Stone (1986, as *Cliona*), van Soest et al. (1994); **CS**: It is possible that *Cornulella purpurea* occurs in this bioregion, but as the sample site is unknown and cannot be conclusively matched to our bioregions, this species did not become part of our analysis
(*Pione concharum*)	(Thiele, 1898)	Hakodate, Tsugaru Strait (maybe also Sagami Bay), in mollusc and brachiopod shells	No other primary records found. **CS**: The confirmed sampling area is cold temperate, and *Pione concharum* was thus conservatively excluded from the biogeographic analysis
Pione aff. *vastifica*	Unresolved species complex	Sensu stricto: Scotland	Hoshino (1981, 1987, as *Cliona*); Schönberg pers. obs. (2004, Ryukyu Islands)
Spheciospongia panis	(Thiele, 1898)	Sagami Bay	Hoshino (1976, 1977, 1982, 1987, as *Spirastrella*), Tanita and Hoshino (1989, as *Spirastrella*); **CS**: This is a massive species that was sampled from 51–80 m but was found as far south as subtropical Amami Oshima
Spheciospongia peleia	(De Laubenfels, 1954)	Palau	Hoshino (1981, as *Ridleya*); **CS**: Recorded from Ishigaki Island that is described as semi-tropical and counted. Ise et al. (2004) synonymised *Spheciospongia peleia* with *Spheciospongia vagabunda* (or *inconstans*), a decision that is not here followed
(*Spheciospongia rotunda*)	(Tanita and Hoshino, 1989)	Sagami Bay	Tanita and Hoshino (1989, as *Spirastrella*); **CS**: This is a massive species that was sampled from 80–90 m and was conservatively excluded from the biogeographic analysis
Unconf.: *Spheciospongia* cf. *vagabunda*	(Ridley, 1884)	Torres Straits	? Ise et al. (2004, as *Spheciospongia inconstans*)

Speciospongia sp. undetermined	Presently not adequately resolved	Reported from various sites in Japan	Hoshino (1977, 1981, 1987 as *Cliona lobata*); **CS**: Reported from Kii Channel, but apparently inconsistent with the original description for *Cliona lobata*. This is a massive sponge with exceptionally fine spirasters that does not match any of the other Japanese *Spheciospongia* species and was counted for the biogeographic analysis as an undetermined clionaid
Spirastrella abata	Tanita, 1961	Kurushima Strait	Tanita (1967, 1968, 1969), Hoshino (1981, 1987), Tanita and Hoshino (1989); **CS**: Was recorded from the Ariake Sea and tentatively counted
Spirastrella aff. *coccinea* (*cunctatrix*?, *sabogae*?)	Unresolved species complex	Sensu stricto: Caribbean	Hoshino (1981, 1987); **CS**: See Boury-Esnault et al. (1999) on the distribution of similar *Spirastrella* spp. *Spirastrella coccinea* and *Spirastrella cunctatrix* are morphologically very similar
Spirastrella insignis	Thiele, 1898	Sagami Bay	Thiele (1898), Tanita (1961, 1965, 1967, 1968, 1969), Hoshino (1977, 1987), Tanita and Hoshino (1989); **CS**: Was recorded from the Ariake Sea
Spirastrella yongmeoriensis	Kim and Sim, 2009	East China Sea	No other primary records found
Thoosa sp.	Not formally described	Reported from Okinawa	C. Schönberg pers. obs. (2004, Ryukyu Islands, only identified to genus)
Central Pacific Islands (Fiji, Hawaii, French Polynesia, Funafuti, Vanuatu, Marshall Islands, Marianas, Easter Islands) (29 spp. of coral-eroding sponges in warm water)			
Alectona wallichii	(Carter, 1874)	Agulhas Bank, S of Africa (Carter: also from the 'South Sea' and Seychelles), first reported as spicules in sediment	? Smyth (1990, as *Alectona* sp.?), Vacelet (1999, in calcareous rock, but also from Tuléar in intertidal scleractinians)
Aplysinella rhax	(De Laubenfels, 1954)	Marshall Islands	Tabudravu et al. (2002)
Cliona aff. *celata*	Grant, 1826	Scotland	Topsent (1932); **CS**: *Cliona celata* was described from Scotland and represents a taxonomically difficult species complex (Xavier et al. 2010, de Paula et al. 2012). All faunistic accounts are unreliable unless including molecular data. This report is unlikely to be *Cliona celata* sensu stricto but was still counted as a clionaid different from others in the bioregion

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona ecaudis	Topsent, 1932	Society Islands	Topsent (1932), S. Pohler pers. comm. (2009, Fiji); **CS:** Spicules of *Cliona ecaudis* could easily be interpreted as immature spicules of *Cliona mucronata*. After viewing *Cliona ecaudis* type material (C. Schönberg pers. obs. 2006–2007), it is here accepted as separate species
Cliona ensifera	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	Smyth (1990), Kelly et al. (2003)
Cliona euryphylle	Topsent, 1888	Campeche, Gulf of Mexico	De Laubenfels (1954, as *Cliona euryphylla*)
(Unconf.: *Cliona insidiosa*)	Hancock, 1849	In the giant clam, *Tridacna gigas*, occurs in the Indo-Pacific	No other primary records found. **CS**: The sponge could possibly occur in this bioregion but was not noted since its description. As the exact type location is unknown, it was not included in the biogeographic analysis
Cliona johnstonii	(Carter, 1886)	Bass Strait	Kirkpatrick (1900a, as *Cliona schmidti*); **CS**: We tentatively list all '*Cliona schmidtii*' reported from the Indo-Pacific as *Cliona johnstonii* to imply that the two species are different. See van Soest et al. (2017) for comments on the distribution of *Cliona schmidtii*
Cliona mucronata	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which is not useful information. Assumed to be from the Indo-Pacific	Kirkpatrick (1900a)

Cliona aff. *orientalis*	Unresolved species complex	Sensu stricto: Molucca Sea, Indonesia	? Topsent (1932, as *Cliona viridis* and a variety of *Cliona caribbaea*), ? de Laubenfels (1954, as *Cliona lobata*), Smyth (1990, as *Cliona viridis*), Kelly et al. (2003, as *Cliona viridis*)
Cliona raromicrosclera	(Dickinson, 1945)	Gulf of California	No other primary records found
Cliona aff. *topsenti*	Unresolved species complex	Sensu stricto: Adriatic Sea	Topsent (1932)
Cliona valentis	(De Laubenfels, 1957)	Hawaii	Bergquist (1977, as *Anthosigmella* or *Spirastrella*)
Cliona vermifera	Hancock, 1867	Unknown. In *Chama* sp., information which does not provide further clues	Topsent (1932); **CS**: *Cliona vermifera* is thought to be a species complex (see e.g. León-Pech et al. 2015), but pending new results is here treated as a single species
Cliothosa hancocki	(Topsent, 1888)	French Polynesia	Topsent (1932), Highsmith (1981a, as *Cliona* cf. *quadrata*); **CS** regards this as a species complex that needs to be resolved per bioregion. It is here still counted as a species distinct from the others occurring in this region
(*Cliothosa quadrata*)	Hancock, 1849	In the giant clam, *Tridacna gigas*, occurs in the Indo-Pacific	**CS**: After accessing Topsent's samples at the Paris Museum (2006–2007), CS regards *Cliothosa hancocki* as a species complex. *Cliothosa hancocki* and *Cliothosa quadrata* are very similar (e.g. Calcinai et al. 2005). To avoid possible duplication, only *Cliothosa hancocki* was counted for our biogeographic analysis (more commonly used name), even though *Cliothosa quadrata* has been reported in the area (see above)
(Unconf.: *Cornulella purpurea*)	(Hancock, 1849)	Unknown, sample found in *Tridacna gigas*, which has an Indo-Pacific distribution	Referring to Hancock's sample and thus not reporting a confirmed sample site: Kirkpatrick (1900a, as *Dyscliona*), Topsent (1907, as undetermined genus), Hallmann (1920, as *Paracornulum*), Rützler and Stone (1986, as *Cliona*), van Soest et al. (1994); **CS**: It is possible that *Cornulella purpurea* occurs in this bioregion, but as the sample site is unknown and cannot be conclusively matched to our bioregions, this species did not become part of our analysis

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
(*Diplastrella spiniglobata*): recommendation to reassess genus allocation	(Carter, 1879)	'South Sea'	Bergquist (1967, 1977); **CS**: The spicules depicted by Carter suggest that it is not a bioeroding sponge but it may be closer to a *Placospongia*. The spicules in the figure in Bergquist (1967) may suggest a tethyid? The species needs to be reassessed and was not counted
Dotona davidi: recommendation to reassess genus allocation	(Kirkpatrick, 1900a)	Tuvalu	No other primary records found. **CS**: The species is described to have microacanthose subtylotes and may be an acarnid. Without examining the type material, we were unable to make a clear decision on a genus allocation, but we presently counted this record into the Poecilosclerida for the biogeographic analysis
Pione carpenteri	(Hancock, 1867)	Mazatlán	Topsent (1932, as *Cliona*); **CS:** The material was reported to have two colours and may represent two different species but was counted as one
Pione aff. *vastifica*	Unresolved species complex	Sensu stricto: Scotland	Topsent (1932, as *Cliona*), de Laubenfels (1950b, 1954, as *Cliona*), Bergquist (1977, as *Cliona*), Desqueyroux-Faúndez (1990, as *Cliona*), Smyth (1990), Kelly et al. (2003); **CS**: The *Pione* species complex is taxonomically difficult and confused. However, this species was counted as different to *Pione carpenteri*
Siphonodictyon cf. *diagonoxeum*	(Thomas, 1968)	Sri Lanka	Highsmith (1981, as *Aka* cf. *diagonoxeum*); **CS:** This record needs to be checked against *Siphonodictyon maldiviense* but was counted as a separate *Siphonodictyon* sp.
Siphonodictyon sp. yellow	Not formally described	Reported from the Mariana Islands	Kelly et al. (2003); **CS**: May or may not be conspecific with the yellow *Siphonodictyon* sp. from the central Great Barrier Reef
Spheciospongia globularis	(Dendy, 1922)	Chagos	Kelly et al. (2003)
Spheciospongia potamophera: reversed comb. to *Spirastrella potamophera*	De Laubenfels, 1954	Marshall Islands	Kelly et al. (2003, as *Spheciospongia*); **CS**: The original description characterises this species as encrusting; having tylostyles and large, robust, conically spined spirasters and derivates; and inflated surface canals in branching-radiate, raylike arrangement typical for *Spirastrella*. The sponge is thus presently returned to *Spirastrella*
Spheciospongia solida	(Ridley and Dendy, 1886)	Philippines	Tendal (1969, as *Spirastrella*)

Spheciospongia vagabunda	(Ridley, 1884)	Torres Straits	? De Laubenfels (1954, as *Anthosigmella*), Bergquist (1967, as *Spirastrella*), Bergquist et al. (1971, as *Spirastrella*), Bergquist (1977, as *Spirastrella*), Tendal (1969, as *Spirastrella*), Kelly et al. (2003)
(*Spirastrella* aff. *coccinea*)	Unresolved species complex	Sensu stricto: Caribbean	Bergquist (1967), Bergquist et al. (1971), Bergquist (1977); **CS**: See comments for *Spirastrella* aff. *cunctatrix*
Spirastrella aff. *cunctatrix* (*sabogae*?)	Unresolved species complex	Sensu stricto: Algeria, Mediterranean	Desqueyroux-Faúndez (1990); **CS**: This record requires confirmation. See Boury-Esnault et al. (1999) about the distribution of similar *Spirastrella* spp. *Spirastrella coccinea* and *Spirastrella cunctatrix* are morphologically very similar. To avoid possible duplication, we excluded one of the locally unexpected species from our biogeographic analysis. We assumed that the more likely species to occur might be *Spirastrella cunctatrix*, which might have been introduced to the Indo-Pacific via the Suez Canal. Alternatively, this could be *Spirastrella sabogae*
Spirastrella decumbens	Ridley, 1884	Torres Straits	De Laubenfels (1954)
Spirastrella keaukaha	De Laubenfels, 1951	Hawaii	De Laubenfels (1951), Ball (1975, as *Spirastrella keaukaha* (*coccinea*?))
Thoosa amphiasterina	Topsent, 1920	French Polynesia, presumably in shallow water, because of *Tridacna* sp.	Topsent (1932), Azzini et al. (2007a)
Thoosa bulbosa	Hancock, 1849	In the giant clam, *Tridacna gigas*, occurs in the Indo-Pacific	Smyth (1990), Kelly et al. (2003)
Zyzzya fuliginosa	(Carter, 1879)	Torres Straits	Luke (1998, partly as *Zyzzya massalis*), Van Soest et al. (1994)
Eastern Tropical Pacific (ETP) between S California and Galápagos Islands (27 spp. of coral-eroding sponges in warm water)			
Cliona amplicavata	Rützler, 1974	Bermuda	Carballo et al. (2004, 2008a), Verdín Padilla et al. (2010), Pacheco Solano (2012, 2015), Alvarado et al. (2017)
Cliona californiana	De Laubenfels, 1932	N California	? De Laubenfels (1939, as *Cliona celata*), ? Luke (1998, partly as *Cliona celata*, partly as *Cliona celata* var. *californica*), Carballo et al. (2004), Carballo et al. (2008a), Verdín Padilla et al. (2010), Pacheco Solano (2012, 2015), Ávila et al. (2012), Alvarado et al. (2017)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona cf. *chilensis*	Thiele, 1905	Chilean Patagonia	Desqueyroux-Faúndez and van Soest (1997); **CS**: The name *Cliona chilensis* apparently comprises two species, with one of them extending at least as far north as N Chile (de Paula et al. 2012)
Cliona ensifera	Sollea, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	Cortés (1992), Guzmán and Cortés (1993)
Cliona euryphylle	Topsent, 1888	Campeche, Gulf of Mexico	Carballo et al. (2004, as *Cliona euryphylla*), Carballo et al. (2008a, as *Cliona euryphylla*), Verdín Padilla et al. (2010, as *euryphylla*), Ávila et al. (2012, as *Cliona euryphylla*), Pacheco Solano (2012, 2015, both as *Cliona euryphylla*), Alvarado et al. (2017, as *Cliona euryphylla*)
Cliona flavifodina	Rützler, 1974	Bermuda	Carballo et al. (2004), Carballo et al. (2008a), Verdín Padilla et al. (2010), Alvarado et al. (2017)
(Unconf.: *Cliona johannae*)	Topsent, 1932	Unknown. In the red abalone, *Haliotis rufescens*, which occurs in the E Pacific, Oregon to Baja California, but published for Western Australia	No other primary records found. **CS:** This species was previously published to be from Western Australia. However, the host material suggests an E Pacific distribution, but the sponge was not reported since its description. We more strongly relied on the stated type location and counted this sponge for W Australia, not here
Cliona medinae	Cruz-Barraza et al., 2011	Isla Clarion, Mexican Pacific	Carballo et al. (2008a, as *Cliona* sp. 2), Cruz-Barraza et al. (2011), Alvarado et al. (2017)
Cliona microstrongylata	Carballo and Cruz-Barraza, 2005	Gulf of California	Carballo and Cruz-Barraza (2005), Carballo et al. (2008a), Pacheco Solano (2015)

Cliona aff. *mucronata*	Unresolved species complex	Sensu stricto: Unknown, likely Indo-Pacific	Bautista-Guerrero et al. (2006), Carballo et al. (2008a, 2008b), Pacheco Solano (2012, 2015, as *Cliona* cf. *mucronata*), Alvarado et al. (2017); **JLC**: *Cliona mucronata* is a species complex (see Pacheco Solano 2015); **CS**: Local spicule shapes strongly resemble those displayed by Rützler et al. (2014), but their spicules are longer (see also Pacheco Solano 2015). Neither of the authors described spirasters, as occur in *C. mucronata* sensu stricto
Cliona papillae	Carballo et al., 2004	Mazatlán	Carballo et al. (2004), Carballo et al. (2008a), Verdín Padilla et al. (2010)
Cliona pocillopora	Bautista-Guerrero et al., 2006	Nayarit	Bautista-Guerrero et al. (2006), Carballo et al. (2008a), Pacheco Solano (2012, 2015), Alvarado et al. (2017)
Cliona raromicrosclera	(Dickinson, 1945)	Gulf of California	Carballo et al. (2004), Carballo et al. (2008a), Alvarado et al. (2017)
Cliona tropicalis	Cruz-Barraza et al., 2011	Nayarit	Carballo et al. (2008a, as *Cliona* sp. 1), Cruz-Barraza et al. (2011), Pacheco Solano (2015), Alvarado et al. (2017)
Cliona vallartense	Carballo et al., 2004	Jalisco	Carballo et al. (2004), Carballo et al. (2008a), Alvarado et al. (2017)
Cliona vermifera	Hancock, 1867	Unknown. In *Chama* sp., information which does not provide further clues	Carballo et al. (2004, 2008a, b), Pacheco Solano (2012), Bautista-Guerrero et al. (2014), León-Pech et al. (2015), Pacheco Solano (2015), Alvarado et al. (2017); **CS**: *Cliona vermifera* is thought to be a species complex (see e.g. León-Pech et al. 2015), but pending new results is here treated as a single species
Cliothosa tylostrongylata	Cruz-Barraza et al., 2011	Oaxaca	Carballo et al. (2008a, b, as *Cliothosa hancocki*), Cruz-Barraza et al. (2011), Pacheco Solano (2015), Alvarado et al. (2017)
(Unconf.: *Cornulella purpurea*)	(Hancock, 1849)	Unknown, sample found in *Tridacna gigas*, which has an Indo-Pacific distribution	Only referring to Hancock's sample: Kirkpatrick (1900a, as *Dyscliona*), Topsent (1907, as undetermined genus), Hallmann (1920, as *Paracornulum*), Rützler and Stone (1986, as *Cliona*), van Soest et al. (1994); **CS**: *Cornulella purpurea* might occur in this bioregion, but as the type location is unknown, this species did not become part of our analysis
Pione carpenteri	(Hancock, 1867)	Mazatlán	Carballo et al. (2004, 2008a, 2008b), Verdín Padilla et al. (2010), Pacheco Solano (2012, 2015, both as 'cf.'), Alvarado et al. (2017)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Pione mazatlanensis	(Hancock, 1867)	Mazatlán	Carballo et al. (2004), Carballo et al. (2008a), Verdín Padilla et al. (2010), Pacheco Solano (2015, as 'cf.'), Alvarado et al. (2017)
Siphonodictyon crypticum	(Carballo et al., 2007)	Oaxaca	Carballo et al. (2007, 2008a, 2008b, as *Aka*), Alvarado et al. (2017)
Spheciospongia confoederata	De Laubenfels, 1930	California	De Laubenfels (1932), Luke (1998)
Spheciospongia incrustans	Carballo et al., 2004	Jalisco	Carballo et al. (2004), Carballo et al. (2008a), Alvarado et al. (2017)
Spheciospongia ruetzleri	Carballo et al., 2004	Nayarit	Carballo et al. (2004), Carballo et al. (2008a)
Spirastrella decumbens	Ridley, 1884	Torres Straits	Carballo and Nava (2007), Verdín Padilla et al. (2010, as *Spiastrella decubens*)
Spirastrella sabogae	Boury-Esnault et al., 1999	Pacific Panama	? Dickinson (1945, as *Spirastrella coccinea*), Boury-Esnault et al. (1999)
Thoosa calpulli	Carballo et al., 2004	Nayarit	Carballo et al. (2004, 2008a, 2008b), Pacheco Solano (2015, as 'cf.'), Bautista-Guerrero et al. (2016), Alvarado et al. (2017)
Thoosa mismalolli	Carballo et al., 2004	Jalisco	Carballo et al. (2008a), Bautista-Guerrero et al. (2010), Verdín Padilla et al. (2010), Pacheco Solano (2012, 2015), Bautista-Guerrero et al. (2016), Alvarado et al. (2017)
Thoosa purpurea	Cruz-Barraza et al., 2011	Revillagigedo Archipelago	Alvarado et al. (2017)
Corals in cold-water habitats of the Atlanto-Mediterranean (AM) or Indo-Pacific (IP) (e.g. Lophelia/*Madrepora*/hydrozoan communities or precious corals such as *Corallium, Paracorallium*; most samples from deeper than 100 m but also partly from diving depths if in colder water) (49 spp. of coral-eroding sponges in cold water)			
(*Alectona mesatlantica*)	Vacelet, 1999	Mid-Atlantic Ridge, in 2030 m, in calcareous rock	**AM**: No other primary record known from cold-water reefs. **CS**: According to Wheeler et al. (2007), the sponge's type location is not known for coral carbonate mounds with, e.g. *Lophelia*. This species has not yet been recorded from corals and was not counted for the cold-water coral eroders
Alectona microspiculata	Bavestrello et al., 1998	Philippines, depth not stated, in *Distichopora* sp.	**IP**: No other primary record known. **CS**: No depth stated, but samples from commercial fisheries. We counted it assuming it was from some depth

Alectona millari	Carter, 1879	N Atlantic between N Scotland and Faroe Islands, 653 m, in *Madrepora oculata* (latter as *Amphihelia*)	**AM**: Jennings (1891, Denmark, from shallow depths?, in mollusc shells), Topsent (1900, at the Faroes, Norway, Azores, French Mediterranean, in corals), Topsent (1904, Azores, 880 m, in a coral, 1920, Gulf of Lion, Mediterranean, 500–600 m, substrate not described), Alander (1935, 1942, Norway and Sweden, 85–1190 m, in *Lophelia*), Barletta and Vighi (1968, Strait of Bonifacio, 100 m, in *Corallium rubrum*), Vacelet (1969, Ligurian Sea, 146–170 m, in *Dendrophyllia cornigera*), Templado et al. (1986, Alboran Sea, 100–200 m, from *Corallium rubrum* community, but maybe not in the coral), Jensen and Frederiksen (1992, Faroe Islands, 252–260 m, in dead *Lophelia pertusa*), Maldonado (1992, Alboran Sea, 70–120 m, in *Corallium rubrum*), Freiwald and Wilson (1998, as *Alectona millaris*, Norway, 200–400 m, in *Lophelia pertusa*), Hansson (1999, Scandinavia, depth and substrate not specified), Borchiellini et al. (2004, NW Atlantic off Ireland, 590–880 m, in corals), Beuck and Freiwald (2005, Porcupine Bight, 780 m, in *Lophelia pertusa*), Beuck et al. (2007, Porcupine Bight, 1039 m, in *Lophelia pertusa*), Roberts et al. (2009, Porcupine Bight, in *Lophelia pertusa*), van Soest and Beglinger (2009, Mingulay Reefs, in *Lophelia* and *Madrepora* spp.), Calcinai et al. (2010, Mediterranean, depth not stated, in precious coral); **CS**: The species can also occur in shallow depths
Alectona sarai	Calcinai et al., 2008a	Japan, 120 m, in *Paracorallium japonicum*	**IP**: Calcinai et al. (2010, Pacific, depth not stated, in precious coral)
Alectona sorrentini	Bavestrello et al., 1998	Japan Sea, depth not stated, in *Corallium elatius*	**IP**: Calcinai et al. (2010, Pacific, depth not stated, in precious coral); **CS**: Sample obtained through commercial fisheries and assumed to be from some depth. It was counted into the cold-water category of the analysis
Alectona triradiata	Lévi and Lévi, 1983	New Caledonia, 290–350 m, in calcareous substrate	**IP**: Bavestrello et al. (1998, Japan Sea, depth not stated, in *Corallium elatius*), Calcinai et al. (2010, Pacific, depth not stated, in precious coral)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Alectona verticillata	(Johnson, 1899)	Madeira, 'from deep water', in *Corallium johnsoni* (as *Pleurocorallium*) and *Dendrophyllia ramea*	**AM, IP**: Calcinai et al. (2004b, Ryukyu Islands, 195–300 m, in *Corallium elatius*), Calcinai et al. (2010, Mediterranean and Pacific, depth not stated, in precious coral)
Alectona wallichii	(Carter, 1874)	Agulhas Bank, S of Africa (Carter: also from the 'South Sea' and Seychelles), 144–180 m, first reported as spicules in sediment	**IP, AM?**: Carter (1879, as *Corticium*, in the 'South Seas' in *Stylaster sanguineus*), Bavestrello et al. (1998, Japan Sea, depth not stated, in *Corallium elatius*), Hansson (1999, Scandinavia, depth and substrate not specified), Calcinai et al. (2010, Pacific, depth not stated, in precious coral); **CS**: Hansson's record requires reassessment and is presently not accepted as correct
Alectona sp.	Not formally described, but reported by Bavestrello et al. (1998)	Japan Sea, depth not stated, in *Corallium elatius*	**IP**: No other original report known from cold-water reefs. **CS:** The species appears to be different to all other known *Alectona* spp. and was counted
(*Cliona annulifera*)	Annandale, 1915b	Sri Lanka, 1265 m, in mollusc shells	Thomas (1979b), Pattanayak (2009); **CS**: This species was not included in the cold-water analysis, because it was only found in mollusc shells and it was not clear whether it was sampled from a coral habitat
Cliona caledoniae	Van Soest and Beglinger, 2009	Scotland, Mingulay Reefs in *Lophelia* and *Madrepora* spp., 127 m (paratypes 82–131 m)	**AM**: No other original report known from cold-water reefs
Cliona cf. *celata*	Grant, 1826	Scotland, from shore, in *Ostrea edulis* shells	**AM**: Alander (1942, Sweden, to 200 m, in thick-shelled bivalves), Hansson (1999, Scandinavia, depth and substrate not specified), Cruz Simó (2002, depth not stated, in *Dendrophyllia ramea*); **CS**: These accounts of *Cliona celata* may refer to different species. It was described from Scotland and represents a taxonomically difficult species complex (Xavier et al. 2010, de Paula et al. 2012). All faunistic accounts are unreliable unless including molecular data. These reports are unlikely to represent *Cliona celata* sensu stricto but were still counted as a clionaid different from others in the bioregion

Cliona chilensis	Thiele, 1905	Chilean Patagonia, 18 m, massive or on shells	**IP, AM**: Försterra et al. (2005, Chilean Patagonia, shallow water, in *Desmophyllum dianthus*), Willenz et al. (2009, Chilean Patagonia, 1–30 m, in 'stony corals'); **CS**: It also occurs in the Atlantic (e.g. de Paula et al. 2012)
Cliona desimoni	(Bavestrello et al., 1995)	W Pacific, off Taiwan, 150–200 m, in *Corallium elatius*	**IP**: Calcinai et al. (2010, Pacific, depth not stated, in precious coral)
(Unconf.: *Cliona ensifera*)	Sollas, 1878	Unknown, found in an octocoral (*Isis* sp.), which does not provide further information about the sample site. Assumed to be from the Indo-Pacific	**IP?**: Pica et al. (2012, likely New Caledonia, in *Distichopora* sp., but depth unknown); **CS**: This record was not counted, because it might have been for a shallow, warm-water environment
Cliona janitrix	Topsent, 1932	Strait of Bonifacio, Mediterranean, depth not stated, in oyster shell	**AM**: Melone (1965, Strait of Bonifacio, 60 m, in *Corallium rubrum*), Barletta and Vighi (1968, different sites in the Mediterranean, 25–100 m, in *Corallium rubrum*), Corriero et al. (1997, Ligurian Sea, 20–45 m, in *Corallium rubrum*), Calcinai et al. (2002, Ligurian Sea, 15–35 m, in *Corallium rubrum* and *Leptopsammia pruvoti*), Rosell and Uriz (2002, Balearic Sea, Mediterranean, 30 m, in *Corallium rubrum*), Calcinai et al. (2010, Mediterranean, depth not stated, in precious coral)
Cliona lobata	Hancock, 1849	English Channel	**AM**: Alander (1942, Sweden, down to 1265 m, in thin-shelled bivalves), Topsent (1900, in England, Denmark, Belgium and France, but the substrate mentioned referred to mollusc shells), Hansson (1999, Norway, depth and substrate not specified), Calcinai et al. (2010, Mediterranean, depth not stated, in precious coral)
Cliona cf. *schmidtii*	(Ridley, 1881); based on an erroneous record of a 'variety' of *Vioa johnstonii* in Schmidt, 1870 p. 5	Adriatic Sea, Mediterranean, depth not stated, substrate not specified	**AM**: Cruz-Simó (2002, Canary Islands, depth not stated, in *Dendrophyllia ramea*)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona vermifera	Hancock, 1867	Unknown. In *Chama* sp., information which does not provide further clues	**AM, IP?**: Corriero et al. (1997, Ligurian Sea, 20–45 m, in *Corallium rubrum*); **CS**: *Cliona vermifera* is thought to be a species complex (see e.g. León-Pech et al. 2015). Pending new results, it is treated as a single species
Cliona viridis	(Schmidt, 1862)	Adriatic Sea, Mediterranean, depth not stated, as massive sponge and in *Cladocora caespitosa* (as *Caryophyllaea*)	**AM**: ? Templado et al. (1986, as *Cliona copiosa*, Alboran Sea, 100–200 m, from *Corallium rubrum* community, but maybe not in the coral), Corriero et al. (1997, Ligurian Sea, 20–45 m, in *Corallium rubrum* community but not in the coral itself), Hansson (1999, Norway, depth and substrate not specified), Sitjà and Maldonado (2014, Alboran Sea, 52–92 m, substrate not specified); **CS**: Only tentatively counted, because it has access to corals
(*Cornulum virguliferum*)	(Lévi and Lévi, 1983)	New Caledonia, 175–430 m, in foraminiferan	**IP**: No other primary record known from cold-water reefs. **CS**: As the sponge was reported at depth from a foraminiferan, it was only included in the warm-water coral-related biogeographic analysis
Delectona alboransis	Rosell, 1996	Alboran Sea, W Mediterranean, 70–120 m, in *Corallium rubrum*	**AM**: No other primary record known from cold-water reefs
Delectona ciconiae	Bavestrello et al., 1996	Alboran Sea, W Mediterranean (but also found at Elba Island, Bosa Marina, 80–120 m, in *Corallium rubrum*)	**AM:** ? Barletta and Vighi (1968, as *Thoosa* sp., different sites in the Mediterranean, 25–100 m, in *Corallium rubrum*), Calcinai et al. (2002, Ligurian Sea, 25 m, in *Corallium rubrum*, 2010, Mediterranean, depth not stated, in precious coral)
Delectona higgini	(Carter, 1880)	Sri Lanka, depth not stated, in coralline algae	**IP:** No other primary record known from cold-water reefs. **CS:** Carter did not state a sampling depth and reported coralline algae as substrate. The sample may have originated in shallow, warm water. However, as the three other *Delectona* spp. occur in deep water, *Delectona higgini* was tentatively included in the cold-water count as well

Delectona madreporica	Bavestrello et al., 1997	Ligurian Sea, 22 m, in *Leptopsammia pruvoti* and *Madracis pharensis*	**AM:** ? Barletta and Vighi (1968, as *Thoosa* sp., different sites in the Mediterranean, 25–100 m, in *Corallium rubrum*), Calcinai et al. (2002, Ligurian Sea, 15 m, in *Leptopsammia pruvoti*)
Dercitus (*Stoeba*) *plicatus*	(Schmidt, 1868)	Algeria, Mediterranean, depth not stated, in coralline algae	**AM:** Templado et al. (1986, Alboran Sea, 80–120 m, from *Corallium rubrum* community, but maybe not in the coral), ? Calcinai et al. (2002, as *Dercitus* sp., Ligurian Sea, 25 m, in *Corallium rubrum*, 2010, as *Stoeba* spp., Mediterranean and Pacific, depth not stated, in precious coral), Mastrototaro et al. (2010, as *Stoeba plicata*, Ionian Sea, 513–747 m, in *Madrepora oculata* and *Lophelia pertusa*), Sitjà and Maldonado (2014, Alboran Sea, 52–112 m, substrate not specified)
Diplastrella bistellata	(Schmidt, 1862)	Adriatic sea, Mediterranean, depth or substrate not stated	**AM:** Vacelet (1969, Gulf of Lion, substrate not described), Maldonado (1992, Alboran Sea, 70–120 m, on *Corallium rubrum*), Sitjà and Maldonado (2014, Alboran Sea, 87–92 m, substrate not specified)
Dotona pulchella	Carter, 1880	Sri Lanka, depth not stated, in coralline algae	**AM, IP:** Topsent (1904, Azores, 880 m, in corals), Calcinai et al. (2001, Taiwan, between 250 and 400 m, in *Corallium elatius*), Rosell and Uriz (2002, as *Dotona pulchella* subsp. *mediterranea*, Alboran Sea, Mediterranean, 70–120 m, in *Corallium rubrum*), Calcinai et al. (2010, Mediterranean and Pacific, depth not stated, in precious coral); **CS:** As all the reports from the Atlanto-Mediterranean region are from deeper waters, the Sri Lankan sample was also counted for deep water
Holoxea excavans	Calcinai et al., 2001	Taiwan, between 250 and 400 m, in *Corallium elatius*	**IP:** Calcinai et al. (2008b Japan, depth not stated, in *Paracorallium japonicum*, 2010, Pacific, depth not stated, in precious coral)
Holoxea furtiva	Topsent, 1892	Gulf of Lion, Mediterranean, depth not stated, in coralline algae	**AM:** Templado et al. (1986, Alboran Sea, 100–200 m, from *Corallium rubrum* community, but maybe not in the coral), Calcinai et al. (2001, Cape Verde Islands, depth not stated, in *Corallium rubrum*, 2010, as *Holoxea furtive*, Mediterranean, depth not stated, in precious coral)
(*Neamphius huxleyi*)	(Sollas, 1888)	Vanuatu, 108–126 m, massive sponge	**IP:** No other primary record known from cold-water reefs. **CS:** But numerous (here ignored) publications on the biochemistry of this species are available that suggest that the species is widely distributed in the Pacific. As we have no knowledge whether this sponge erodes corals, we did not use this record

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Pione vastifica	(Hancock, 1849)	Scotland, depth not stated, from mollusc shells	**AM:** Alander (1942, as *Cliona*, Sweden, 65–600 m, in *Lophelia*), Templado et al. (1986, as *Cliona*, Alboran Sea, 100–200 m, from *Corallium rubrum* community, but maybe not in the coral), Maldonado (1992, as *Cliona*, Alboran Sea, 70–120 m, in *Corallium rubrum*), Cruz-Simó (2002, as *Cliona*, Canary Islands, depth not stated, in *Dendrophyllia ramea*), Hansson (1999, Scandinavia, depth and substrate not specified)
Siphonodictyon corallirubri	(Calcinai et al., 2007b)	Tyrrhenian Sea, depth unknown, in *Corallium rubrum*	**AM:** Calcinai et al. (2010, Mediterranean, depth not stated, in precious coral)
Siphonodictyon infestum	(Johnson, 1899)	Madeira, depth not stated, in bivalve shells	**AM:** ? Topsent (1904, as *Cliona labyrinthica*), ? Alander (1942, as *Aka labyrinthica*, W Norway and Sweden, 85–300 m, in *Lophelia*), ? Melone (1965, as *Cliona labyrinthica*, 60–75 m, Strait of Bonifacio in *Corallium rubrum*), ? Jensen and Frederiksen (1992, as *Siphonodictyon labyrinthicum*, Faroe Islands, 252–260 m, in dead *Lophelia pertusa*), ? Corriero et al. (1997, as *Aka labyrinthica*, Ligurian Sea, 20–45 m, in *Corallium rubrum*), ? Freiwald and Wilson (1998, as *Aka labyrinthica*, Norway in *Lophelia pertusa*), ? Hansson (1999, as *Siphonodictyon labyrinthica*, Scandinavia, substrate or depth not described), ? Calcinai et al. (2002, as *Aka labitinthyca*, Ligurian Sea, 25 m, in *Corallium rubrum*), ? Rosell and Uriz (2002a, as *Aka labyrinthica*, Balearic Sea, Mediterranean, 30 m, in *Corallium rubrum*), Beuck et al. (2007, as *Aka infesta*, Porcupine Bight, 1030 m, in *Lophelia pertusa*), Schönberg and Beuck (2007, Ionian Sea, 671–679 m, in *Madrepora oculata*), Beuck et al. (2010, Ionian Sea, 671–679 m, in *Madrepora oculata*), Calcinai et al. (2010, Mediterranean, depth not stated, in precious coral)
Siphonodictyon insidiosum	(Johnson, 1899)	Madeira, depth not stated, in bivalve shells	**AM:** ? Barletta and Vighi (1968, as *Cliona labyrinthica*, different sites in the Mediterranean, 25–100 m, in *Corallium rubrum*), Calcinai et al. (2008b, Mediterranean, depth not stated, in *Corallium rubrum*, 2010, Mediterranean and Pacific, depth not stated, in precious coral)

Siphonodictyon labyrinthicum	(Hancock, 1849)	Unknown type location, but found in the giant clam, *Tridacna gigas*, which occurs in the Indo-Pacific in shallow water	**IP:** Pica et al. (2012, as *Aka*, likely New Caledonia, in *Distichopora* sp., but depth unknown), Calcinai et al. (2008b, 2010, Pacific, depth not stated, in precious coral); **CS:** This species has been widely—and erroneously—reported from the Atlanto-Mediterranean region (see Schönberg and Beuck 2007 for details). None of the presently available accounts can be considered as reliable, but the species was tentatively counted for cold-water reefs, because its spicule shape was more congruent with deep-water species
Siphonodictyon rodens	(Johnson, 1899)	Madeira, 'from deep water' in *Dendrophyllia ramea*	**AM:** ? Vacelet (1969, as *Cliona labyrinthica*, Gulf of Lion, 175–235 m, in rock debris); **CS:** The spicules of Vacelet's material may be too thin to match this species (his oxea dimensions given as 130–170 × 2.5–5 μm). Van Soest et al. (2017) synonymised it with *Siphonodictyon insidiosum*. It is here listed, tentatively recognised as a valid species and counted, because a morphometric study on the spicules revealed differences between the Johnson species (Schönberg and Beuck 2007; although this was based on hand drawings of the spicules)
(*Siphonodictyon* spp.)	Not formally described, reported by Cruz in a few publications	Canary Islands, depth not stated, in corals, calcareous algae and mollusc shells	**AM:** Cruz and Bacallado (1983) and Cruz Simó (2002, Canary Islands, depth not stated, e.g. in *Dendrophyllia ramea* and *Cladocora debilis*); **CS**: After observing some of Cruz's vouchers, it became clear that he had misidentified and combined more than one species under the same name. At least one species very much resembled *Siphonodictyon brevitubulatum* and is thus different from the other species listed here. However, as we cannot exactly allocate which record belongs to which substrate, we did not include this record in our biogeographic analysis
Spirastrella cunctatrix	Schmidt, 1868	Algeria, Mediterranean, depth and substrate not stated	**AM**: Templado et al. (1986, Alboran Sea, 100–200 m, from *Corallium rubrum* community, but maybe not in the coral); **CS**: The sponge erodes coral materials in shallow depths and was not excluded from the biogeographic analysis for cold-water habitats

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Pione abyssorum: genus transfer to *Spiroxya abyssorum* new comb.	(Carter, 1874)	English Channel, 900 m, in *Lophelia pertusa* (as *Lophohelia prolifera*)	**AM:** Hansson (1999, as *Cliona abyssorum*, Scandinavia, depth and substrate not specified); **CS**: The species was listed as a *Pione* on the World Porifera Database (van Soest et al. 2017). However, based on the spicule combination of subtylostyles, smooth oxeas and helical microstrongyles, the species is here transferred to *Spiroxya*. Carter (1974) and Topsent (1904) already stated that the present species resembles other *Spiroxya* spp.
Spiroxya acus	(Bavestrello et al., 1995)	W Pacific, 150–200 m, in *Corallium elatius*	**IP**: Calcinai et al. (2010, Pacific, depth not stated, in precious coral)
Spiroxya corallophila	(Calcinai et al., 2002b)	Ligurian Sea, Mediterranean, 30–35 m (but also other sites in the Mediterranean), in *Corallium rubrum*	**AM:** Calcinai et al. (2010, Mediterranean, depth not stated, in precious coral)
Spiroxya heteroclita	Topsent, 1896	Gulf of Lion, Mediterranean, depth not stated, in stones	**AM:** Corriero et al. (1997, Ligurian Sea, 20–45 m, in *Corallium rubrum*), Beuck and Freiwald (2005, also as *Entobia laquea*, Porcupine Bight, 780 m, in *Lophelia pertusa*), Longo et al. (2005, Ionian Sea, 640–662 m, substrate not specified), Beuck et al. (2007, Porcupine Bight, 1030 m, in *Lophelia pertusa*), Calcinai et al. (2010, Mediterranean, depth not stated, in precious coral), Mastrototaro et al. (2010, Ionian Sea, 640–662 m, in *Madrepora oculata* and *Lophelia pertusa*)

Spiroxya levispira	(Topsent, 1898)	Azores, 880 m, in coral	**AM:** Topsent (1904, Azores, as *Cliona levispira*, 1165–1360 m, in coral), Boury-Esnault et al. (1994, as *Cliona*, Maroccan Atlantic, 1378 m, in pebbles or madrepores), Hansson (1999, as *Cliona*, Scandinavia, depth and substrate not specified), Rosell and Uriz (2002a, as *Scantiletta*, Balearic and Alboran Sea, Mediterranean, 30–120 m, in *Corallium rubrum*, 100 m, in *Lophelia pertusa*), Borchiellini et al. (2004, NW Atlantic off Ireland, 590–880 m, in corals), Longo et al. (2005, Ionian Sea, 634–809 m, substrate not specified), van Soest and Beglinger (2009, Mingulay Reefs and Rockall Bank, 82–762 m, in *Lophelia* and *Madrepora* spp.), Beuck et al. (2010, Ionian Sea, 300–1100 m, in *Desmophyllum dianthus*, *Lophelia pertusa*, *Madrepora oculata*, *Pseudamussium peslutrae*), ? Calcinai et al. (2010, Pacific, depth not stated, in precious coral), Mastrototaro et al. (2010, Ionian Sea, 642–809 m, in *Madrepora oculata* and *Lophelia pertusa*), Bavestrello et al. (2014, Tyrrhenian Sea, Mediterranean, 45–280 m, in *Corallium rubrum*); **CS:** The record for the Pacific by Calcinai et al. (2010) is here regarded as a possible mistake
Spiroxya macroxeata	(Calcinai et al., 2001)	Taiwan, between 250 and 400 m, in *Corallium elatius*	**IP:** No other original report known from cold-water reefs
Spiroxya pruvoti	(Topsent, 1900)	Gulf of Lion, 5–600 m, in coral	**AM:** Hansson (1999, Scandinavia, depth and substrate not specified)
Spiroxya sarai	(Melone, 1965)	Strait of Bonifacio, 68 m, in *Corallium rubrum*	**AM:** Barletta and Vighi (1968, different sites in the Mediterranean, 25–100 m, in *Corallium rubrum*), Corriero et al. (1997, as *Cliona*, Ligurian Sea, 20–45 m, in *Corallium rubrum*), Calcinai et al. (2002, as *Cliona*, Ligurian Sea, 30–35 m, in *Corallium rubrum*, 2010, Mediterranean, depth not stated, in precious coral)
Thoosa armata	Topsent, 1888	Gulf of Guinea, depth and substrate not specified	**AM:** Topsent (1904, Azores, 599 m, in a coral), Barletta and Vighi (1968, Tyrrhenian Sea, 50–65 m, in *Corallium rubrum*), Templado et al. (1986, Alboran Sea, 100–200 m, from *Corallium rubrum* community, but maybe not in the coral), Calcinai et al. (2010, Mediterranean, depth not stated, in precious coral)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Thoosa bulbosa	Hancock, 1849	In the giant clam, *Tridacna gigas*, occurs in shallow waters of the Indo-Pacific	**IP:** Calcinai et al. (2001, Taiwan, between 250 and 400 m, in *Corallium elatius*, 2010, Pacific, depth not stated, in precious coral)
(*Cliothosa investigatoris*): recommendation to reassess genus allocation and to consider *Thoosa*, the genus used in the original description, or alternatively a sample including *Cliothosa* and *Thoosa* spicules	(Annandale, 1915b)	Sri Lanka, 1265 m, in gastropod shell	**IP:** Pattanayak (2009, as *Thoosa*); **CS:** The original description of *Cliothosa investigatoris* shares taxonomic characters that make it difficult to decide whether this species is a *Cliothosa* or a *Thoosa* (or both?). The species is presently listed as a *Cliothosa* (van Soest et al. 2017), which would however be a very unusual genus in deep water. Based on the occurrence of microacanthose, bulbous amphiasters, the species is more likely *Thoosa*. Nevertheless, lacking access to the type material, we have not made a firm decision. As this species has not yet been reported to erode coral materials, it was not counted
Thoosa midwayi	Azzini et al., 2007a	Midway Atoll, central N Pacific, between 100 and 1500 m, in *Corallium* sp.	**IP:** Calcinai et al. (2001, as *Thoosa amphiasterina*, Midway Atoll, central N Pacific, between 100 and 1500 m, in *Corallium* sp., 2010, Pacific, depth not stated, in precious coral)
Thoosa mollis	Volz, 1939	Adriatic Sea, Mediterranean, 2–8 m, in calcareous stones	**AM:** Calcinai et al. (2010, Mediterranean, depth not stated, in precious coral)
(*Thoosa* sp.)	Not fully identified	Reported for bathyal depths at New Caledonia, in *Vaceletia crypta* Borchiellini et al. (2004)	**CS:** No further information provided. As we could not decide which species this could be and wanted to avoid duplication, we did not use this account
Triptolemma simplex	(Sarà, 1959)	Tyrrhenian Sea, Mediterranean, 0–1 m in calcareous rock wall of cave	**AM:** Templado et al. (1986, Alboran Sea, 100–200 m, from *Corallium rubrum* community, but maybe not in the coral), ? Corriero et al. (1997, as *Triptolemus* sp., Ligurian Sea, 20–45 m, in *Corallium rubrum*), Bertolino et al. (2011, Ligurian and Tyrrhenian Sea, 30–40 m, in calcareous rock and *Corallium rubrum*)

Triptolemma strongylata	Bertolino et al., 2011	Japan, ca. 200 m, in *Paracorallium japonicum*	**IP:** No other original report known from cold-water reefs
Zyzzya coriacea	(Lundbeck, 1910)	N Atlantic, Mid-Atlantic Ridge, 1438 m, massive sponge	**AM:** No other original report known. **CS:** The species' distribution overlaps that of *Lophelia* reefs (van Soest et al. (2017), enabling us to count it
Valid species of bioeroding sponges that to date have neither been found in coral reef environments nor are known for eroding coral material (31 spp.)			
Cliona adriatica	Calcinai et al., 2011	Adriatic Sea, Mediterranean, in calcareous rock	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs
Cliona burtoni	Topsent, 1932	Bonifacio, W Mediterranean, in oyster shell	To date only known from the Mediterranean (e.g. Bertolino et al. 2013, Calcinai et al. 2015). Not yet reported for eroding coral materials or for occurring on coral reefs
Cliona diversityla	Sarà, 1978, in serpulid tubes and mollusc shells	Tierra del Fuego	To date, only known from the Tierra del Fuego (e.g. Gappa and Landoni 2005). Not yet reported for eroding coral materials or for occurring on coral reefs
Cliona labiata	(Keller, 1880)	Capri, Tyrrhenian Sea, Mediterranean, massive sponge	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs, not described to embed or agglutinate calcareous materials. **JLC and CS:** It may well be that this is a synonym for the massive form of *Cliona viridis*, but we did not access type material
Cliona lesueuri	Topsent, 1888	Kangaroo Island, S Australia, in the whirling abalone *Haliotis cyclobates* (as *Haliotis excavata*)	No other primary records found. Reported to erode in mollusc shells, not yet for eroding coral materials or for occurring on coral reefs
Cliona lisa	Cuartas, 1991	Patagonia, in pebble	Only known from Argentina (e.g. Gappa and Landoni 2005). Not yet reported for eroding coral materials or for occurring on coral reefs
Cliona parenzani	Corriero and Scalera-Liaci, 1997	Ionian Sea, Mediterranean, massive, eroding calcareous rock	Only known from the Mediterranean (e.g. Vacelet et al. 2008). Not yet reported for eroding coral materials or for occurring on coral reefs. **CS**: Vacelet et al. (2008) may in part include *Cliona burtoni*, which, however, presents the same situation (see above)

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Cliona rhodensis	Rützler and Bromley, 1981	Rhodes, E Mediterranean, 0.5–8 m, in Mesozoic limestone, coralline algae and pebbles	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs
Cliona spissaspira	Corriero and Nonnis Marzano, 2007	Ionian Sea, Mediterranean, in calcareous rock	No other primary records found. Reported to erode in calcareous rock, not yet for eroding coral materials or for occurring on coral reefs
Clionaopsis platei	Thiele, 1905	Patagonia, massive sponge	Only known from Patagonia (e.g. Willenz et al. 2009, referring to massive sponge, Diez et al. 2014, in oyster shell). Not yet reported for eroding coral materials or for occurring on coral reefs
Diplastrella ornata	Rützler and Sarà, 1962	Adriatic Sea, Mediterranean	Only known from the Mediterranean. The sponge was found on the lower surface of a stone. Not yet reported for eroding coral materials or for occurring on coral reefs
Pione angelae	Urteaga and Pastorino, 2007	Mar del Plata, Argentina, in gastropod shells	Only known from Patagonia and the Chilean fjords (e.g. Diez et al. 2014, in oyster shell). Not yet reported for eroding coral materials or for occurring on coral reefs. **CS**: *Pione muscoides* and *Pione angelae* need to be compared, they may be synonymous
Pione gibraltarensis	Austin et al., 2014	W Canada, Gulf of Alaska, in bivalve shells	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs
Pione hancocki taxon inquirendum	(Schmidt, 1862)	Adriatic Sea, Mediterranean	No other primary records found. **CS**: The species type has a very unusual spicule combination that seems to include *Pione*-like tylostyles and spined or nodulose rhabdostyles as they may occur in poecilosclerids. This species requires reassessment, and we have ignored it entirely
Pione hixoni	(Von Lendenfeld, 1886)	Sydney Harbour, Australia, massive sponge	No other primary records found. **CS**: The massive sponge was reported from 40 m depth and ‘attached to the sand’ of a subtropical habitat. It was thus not included in our biogeographic analysis

Pione muscoides	(Hancock, 1849)	Unknown. Reported from the gastropod *Chorus giganteus* (as *Monoceros fusoides*), which occurs along the Chilean coastline	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs. **CS**: The only other record under this name is likely erroneous, as the spicule dimensions differ (Bergquist 1961, as *Cliona muscoides*, from New Zealand). *Pione muscoides* and *Pione angelae* need to be compared; they have very similar spicule dimensions and may be synonymous
Pione rhabdophora	(Hentschel, 1914)	Cape Verde Islands, in *Strombus* shell	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs
Pione robusta	(Old, 1941)	Chesapeake Bay, in oysters	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs
Pione spirilla	(Old, 1941)	Chesapeake Bay, in oysters	Only known from the east of the USA and from oysters (e.g. Wells 1959, 1961). Not yet reported for eroding coral materials or for occurring on coral reefs
Pione stationis	(Nassonow, 1883)	Black Sea, in bivalve shells	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs. **CS**: The original description is insufficient for comparisons; the type material needs to be re-examined
Scolopes lignea	(Hallmann, 1912)	New South Wales coast, Australia, massive sponge	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs
Siphonodictyon nodosum	(Hancock, 1849)	Unknown type location, but found in the giant clam, *Tridacna gigas*, which occurs in the Indo-Pacific	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs
Spheciospongia albida	(Carter, 1886)	Port Phillip Bay, massive sponge that incorporates sediments	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs

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Species	Taxon authority	Type locality	References for reports in bioregion since original description (e.g.)
Spheciospongia alcyonoides	(Hallmann, 1912)	S Queensland, massive sponge	Hooper and Wiedenmayer (1994); **CS**: This species is known from the subtropics but has not yet been reported to occur on coral reefs of erode corals and was not counted for the biogeographic analysis
Spheciospongia australis	(Von Lendenfeld, 1888)	Sydney Harbour, Australia, massive sponge	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs
Spheciospongia massa	(Ridley and Dendy, 1886)	Bass Straits, Australia, massive sponge	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs
Spheciospongia montiformis	(Hallmann, 1912)	S Queensland, massive sponge	Hooper and Wiedenmayer (1994, as *Spirastrella*); **CS**: This species is known from the subtropics but has not yet been reported to occur on coral reefs of erode corals and was not counted for the biogeographic analysis
Spheciospongia poculoides	(Hallmann, 1912)	New South Wales coast, Australia, massive sponge	No other primary records found. Not yet reported for eroding coral materials or for occurring on coral reefs
Spheciospongia robusta	(Carter, 1886)	Port Phillip Bay, South Australia, massive sponge	Only known from South Australia (e.g. Dendy 1897). Not yet reported for eroding coral materials or for occurring on coral reefs
Thoosa tortonesei	(Sarà, 1958)	Ligurian Sea, Mediterranean	No other primary records found. Reported to erode in calcareous rock, not yet for eroding coral materials or for occurring on coral reefs. **CS**: The spicules pictured by Sarà may suggest that at least part of the sample was contributed by a *Cliona viridis*-like sponge. They may represent more than one species, and the material needs to be re-examined
Volzia azzaroliae	(Sarà, 1978)	Patagonia, in rock material made of coralline algae	Only known from Patagonia (e.g. Pansini and Sarà 1999, Gappa and Landino 2005). Not yet reported for eroding coral materials or for occurring on coral reefs

Appendix B

Taxonomic list of non-sponge species mentioned in the publication (with the exception of *Vaceletia crypta*, a hypercalcified sponge that was used by bioeroding sponges as substate). Taxon validities and authorities were verified in the World Register of Marine Species (WoRMS Editorial Board).

Context: Bioerosion rates and host organisms (background information for main text and Appendices C and D)

Phylum	Class	Family	Species	Taxon authority	Common name
Mollusca	Bivalvia (Heterodonta)	(Cardioidea) Cardiidae (Tridacninae)	*Tridacna gigas*	(Linnaeus, 1758)	Giant clam
			Tridacna squamosa	(De Lamarck, 1819)	Fluted giant clam
	Bivalvia (Pteriomorphia)	(Anomioidea) Placunidae	*Placuna placenta*	(Linnaeus, 1758)	Windowpane oyster
		(Arcoidea) (Glycimerididae)	*Tucetona* sp.	Iredale, 1931	Bittersweet clam
		(Chamoidea) Chamidae	*Chama macerophylla*	Gmelin, 1791	Leafy jewelbox
		(Ostreoidea) Ostreidae (Ostreinae)	*Ostrea edulis*	Linnaeus, 1758	Edible oyster
		(Pectinoidea) Pectinidae (Palliolinae)	*Pseudamussium peslutrae*	(Linnaeus, 1771)	Seven-rayed scallop
		(Pterioidea) Pteriidae	*Pinctada margaritifera*	(Linnaeus, 1758)	Black-lip pearl oyster
	Gastropoda (Caenogastropoda)	(Muricoidea) Muricidae (Ocenebrinae)	*Chorus giganteus*	(Lesson, 1831)	Giant unicorn snail
		(Stromboidea) Strombidae	*Lobatus gigas*	(Linnaeus, 1758)	Queen conch
		(Tonnoidea) Cassidae	*Cassis tuberosa*	(Linnaeus, 1758)	King helmet
		(Tonnoidea) Ranellidae (Cymatiinae)	*Charonia variegata*	(De Lamarck, 1816)	Atlantic triton
	Gastropoda (Vetigastropoda)	(Haliotoidea) Haliotidae	*Haliotis cyclobates*	Péron and Lesueur, 1816	Whirling abalone
			Haliotis rufescens	Swainson, 1822	Red abalone

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Phylum	Class	Family	Species	Taxon authority	Common name
Cnidaria	Anthozoa (Hexacorallia)	Acroporidae	*Acropora muricata*	(Linnaeus, 1758)	Spiny coral
			Acropora palmata	(De Lamarck, 1816)	Elkhorn coral
			Astreopora listeri	Bernard, 1896	Starflower coral
			Montipora digitata	(Dana, 1846)	Pore coral
		Agariciidae	*Agaricia agaricites*	(Linnaeus, 1758)	Lettuce coral

Cnidaria ctnd.	Anthozoa (Hexacorallia)	Astrocoeniidae	*Madracis myriaster*	(Milne Edwards and Haime, 185)	Striate finger coral
			Madracis pharensis	(Heller, 1868)	Encrusting star coral
		Caryophylliidae	*Desmophyllum dianthus*	(Esper, 1794)	Cockscomb cup coral
			Lophelia pertusa	(Linnaeus, 1758)	Spider hazard, cold-water coral, deep-sea coral
		Dendrophylliidae	*Dendrophyllia cornigera*	(De Lamarck, 1816)	Doe cup coral
			Dendrophyllia ramea	(Linnaeus, 1758)	Branching cup coral
			Leptopsammia pruvoti	Lacaze-Duthiers, 1897	Sunset cup coral
		Meandrinidae	*Dichocoenia stokesii*	Milne Edwards and Haime, 1848	Pineapple coral
			Meandrina meandrites	(Linnaeus, 1758)	Meander coral
		Merulinidae	*Cyphastrea serailia*	(Forskål, 1775)	Lesser knob coral
			Dipsastraea pallida	(Dana, 1846)	Knob coral
			Favites halicora	(Ehrenberg, 1834)	Larger star coral
			Goniastrea retiformis	(De Lamarck, 1816)	Lesser star coral
			Orbicella annularis	(Ellis and Solander, 1786)	Caribbean or boulder star coral
		Montastraeidae	*Montastraea cavernosa*	(Linnaeus, 1767)	Great star coral, false knob coral
		Mussidae	*Manicina areolata*	(Linnaeus, 1758)	Porous coral
			Pseudodiploria clivosa	(Ellis and Solander, 1786)	Knobby brain coral
			Pseudodiploria strigosa	(Dana, 1846)	Symmetrical brain coral
		Oculinidae	*Madrepora oculata*	Linnaeus, 1758	Zigzag coral
		Pocilloporidae	*Pocillopora verrucosa*	(Ellis and Solander, 1786)	Cauliflower coral

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Phylum	Class	Family	Species	Taxon authority	Common name
Cnidaria ctnd.	Anthozoa (Hexacorallia)	Poritidae	*Goniopora tenuidens*	(Quelch, 1886)	Anemone coral
			Porites astreoides	De Lamarck, 1816	Yellow *Porites*, mustard hill coral
			Porites cylindrica	Dana, 1846	Cylindrical hump coral
			Porites furcata	De Lamarck, 1816	Split hump coral
			Porites lobata	Dana, 1846	Lobate hump coral
			Porites lutea	Milne Edwards and Haime, 1851	Mound coral
			Porites porites	(Pallas, 1766)	Hump coral
			Porites rus	(Forskål, 1775)	Knobbly hump coral
		Siderastreidae	*Siderastrea radians*	(Pallas, 1766)	Lesser starlet coral
			Siderastrea siderea	(Ellis and Solander, 1768)	Massive starlet coral
			Siderastrea stellata	Verrill, 1868	Starry starlet coral
			Cladocora caespitosa	(Linnaeus, 1767)	Pillow coral
		Scleractinia *incertae sedis*	*Cladocora debilis*	Milne Edwards and Haime, 1849	Thin tube coral
	Anthozoa (Octocorallia)	Coralliidae	*Corallium elatius*	Ridley, 1882	Japanese pink coral
			Corallium johnsoni	Gray, 1860	Johnson’s precious coral
			Corallium rubrum	(Linnaeus, 1758)	Red coral, precious coral
			Paracorallium japonicum	(Kishinouyi, 1903)	Japanese red coral
		Isididae	*Isis* sp.	Linnaeus, 1758	Bamboo coral
	Hydrozoa	Stylasteridae	*Distichopora* sp.	De Lamarck, 1816	Lace stick coral
Porifera	Demospongiae (Keratosa)	Verticillitidae	*Vaceletia crypta*	(Vacelet, 1977)	Cryptic hypercalcified sponge

Context: Spongivory (background information for Appendix E)					
Chordata (Vertebrata)	(Tetrapoda) Reptilia	Cheloniidae	*Eretmochelys imbricata*	(Linnaeus, 1766)	Hawksbill turtle
	(Pisces) Actinopterygii	Acanthuridae	*Acanthurus coeruleus*	Bloch and Schneider, 1801	Blue tang surgeonfish
			Acanthurus pyroferus	Kittlitz, 1834	Chocolate surgeonfish
		Chaetodontidae	*Chaetodon kleinii*	Bloch, 1790	Sunburst butterflyfish
			Chaetodon vagabundus	Linnaeus, 1758	Vagabond butterflyfish
		Zanclidae	*Zanclus cornutus*	(Linnaeus, 1758)	Moorish idol
		Pomacentridae	*Stegastes partitus*	(Poey, 1868)	Bicolour damselfish
			Stegastes planifrons	(Cuvier, 1830)	Threespot damselfish
		Scaridae	*Chlorurus microrhinos*	(Bleeker, 1854)	Blunt-head parrotfish
			Scarus coelestinus	Valenciennes, 1840	Midnight parrotfish
			Scarus iseri	(Bloch, 1789)	Striped parrotfish
			Sparisoma viride	(Bonnaterre, 1788)	Stoplight parrotfish
	(Pisces) Coelacanthi	Pomacanthidae	*Holacanthus ciliaris*	(Linnaeus, 1758)	Queen angelfish
			Holacanthus passer	Valenciennes, 1846	King angelfish
			Holacanthus tricolor	(Bloch, 1795)	Rock beauty
			Pomacanthus arcuatus	(Linnaeus, 1758)	Gray angelfish
			Pomacanthus paru	(Bloch, 1787)	French angelfish
			Pomacanthus zonipectus	(Gill, 1862)	Cortez angelfish
Echinodermata (Asterozoa)	Asteroidea	Oreasteridae	*Oreaster reticulatus*	(Linnaeus, 1758)	Red cushion sea star, West Indian sea star
	Ophiuroidea	Ophiotrichidae	*Ophiothrix* (*Ophiothrix*) *angulata*	(Say, 1825)	Angular brittle star
Echinodermata (Echinozoa)	Echinoidea (Cidaroidea)	(Cidaroidea) Cidaridae	*Eucidaris tribuloide*	(De Lamarck, 1816)	Slate pencil urchin
	Echinoidea (Euechinoidea)	Arbaciidae	*Arbacia punctulata*	(De Lamarck, 1816)	Purple-spined sea urchin
		Toxopneustidae	*Lytechinus variegatus*	(De Lamarck, 1816)	Variegated sea urchin, green urchin
Arthropoda (Crustacea)	(Multicrustacea) (Copepoda)	Asterocheridae	*Asterocheres suberitis*	Giesbrecht, 1879	*Suberites* copepod

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Phylum	Class	Family	Species	Taxon authority	Common name
Arthropoda (Crustacea) ctnd.	(Multicrustacea) Malacostraca (Eumalacostraca)	(Alpheoidea) Alpheidae	*Alpheus heterochaelis*	Say, 1818	Bigclaw snapping shrimp
		(Eriphioidea) Menippidae	*Menippe mercenaria*	(Say, 1818)	Southern or Florida stone crab
		(Palaemonoidea) Palaemonidae (Palaemoninae)	*Palaemonetes vulgaris*	(Say, 1818)	Marsh grass shrimp
		(Pilumnoidea) Pilumnidae (Pilumninae)	*Pilumnus sayi*	Rathbun, 1897	Spineback hairy crab
		(Sphaeromatoidea) Sphaeromatidae	*Paracerceis caudata*	(Richardson, 1899)	Tailed isopod
		(Xanthoidea) Panopeidae (Panopeninae)	*Dyspanopeus sayi*	(Smith, 1869)	Say's mud crab
			Panopeus herbstii	Milne Edwards, 1834	Atlantic mud crab
Annelida	Polychaeta	Syllidae	*Branchiosyllis oculata*	Ehlers, 1887	Eyed gillworm
Mollusca	Gastropoda (Caenogastropoda)	(Triphoroidea) Cerithiopsidae	*Seila adamsi*	(Lea, 1845)	Adam's cerith snail
	Gastropoda (Heterobranchia)	(Doridoidea) Chromodorididae	*Doriprismatica sedna*	(Marcus and Marcus, 1967)	Sedna prism nudibranch
			Felimare agassizii	(Bergh, 1894)	Agassizi's coloured nudibranch
		(Doridoidea) Discodorididae	*Platydoris argo*	(Linnaeus, 1767)	Doris argo nudibranch
		(Phyllidioidea) Dendrodorididae	*Doriopsilla albopunctata*	(Cooper, 1863)	Whitespot Doris nudibranch
			Doriopsilla pharpa	Marcus, 1961	Lemon drop nudibranch
	Gastropoda (Vetigastropoda)	(Fissurelloidea) Fissurellidae (Diodorinae)	*Diodora cayenensis*	(De Lamarck, 1822)	Cayenne keyhole limpet

Appendix C

Published sponge bioerosion rates with reference to substrate types. For separate sponge species, we aimed to use data that had the same units or could be converted to match other published data (e.g. we looked for rates over time with reference to sponge tissue area or to reef area). Values for all sponges together may not be as easily related to each other, and caution is advisable when comparing these data. Data from settlement block experiments were not included, because in this context, they are not as meaningful and incur a high risk of variation or bias due to attachment mode and duration of exposure. Some means were hierarchically calculated to weigh data according to the subgrouping in the respective study (see Appendix D). Specific gravity of bulk densities refers to water at 4 °C, and references for material densities are referenced by highset numbers and citations at the bottom of the table. Part of the data displayed below were used for Fig. 7.7 (used only for zooxanthellate β-morphology sponges eroding biological skeleton or pure calcite, but excluding building materials such as limestone). *GBR* Great Barrier Reef. Bioeroding sponge morphologies are *α* papillate-endolithic, *β* encrusting-endolithic, *γ* free-living, *δ* endopsammic (for explanations, see main text or Schönberg et al. 2017). Further taxon information can be found in Appendix A (for bioeroding sponges) and in Appendix B (for non-sponge taxa).

Species, morphology	Location	Substrate material	Specific gravity	% substrate removed	Annual bioerosion [kg] per m^2 sponge tissue	Annual bioerosion per m^2 reef area	References
Photosymbiotic spp. (Percentages refer to the area of full sponge penetration only.)							
Cliona albimarginata, β	N Sulawesi	Prun limestone	2.6[1, 19]		2.9		Calcinai et al. (2007a)
		Vicenza limestone	2[1], 1.9[19]		11.0		
		Conero majolica	2.8[1]		12.6		
		Coral: *Acropora* sp.	2.3[1], 2.9[7]		15.6		
		Clam shell: *Hippopus* sp.	2.7[1], 2.9[17]		24.0		
		Finale calcarenite	2.0[1, 19]		24.2		
		Carrara marble	2.7[1, 19]		29.5		
		Mean across substrates	1.9–2.9		17.1		

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Species, morphology	Location	Substrate material	Specific gravity	% substrate removed	Annual bioerosion [kg] per m^2 sponge tissue	Annual bioerosion per m^2 reef area	References
Cliona aprica, α	Caribbean	Conch shells: *Lobatus gigas*		Ca. 50	7.0		Rützler (1975, snail as *Strombus*)
Cliona caribbaea, β	Grand Cayman	Coral (unspecified)	1.7^1	20.0	8.0*	0.4	Acker and Risk (1985)
Cliona flavifodina, α	Mexican Pacific	Coral: *Pocillopora verrucosa*	2.8^2		0.5		Nava and Carballo (2008)
Cliona orientalis, β	Central GBR	Mollusc shell: bivalve?	2.6^1	71.9			Bergman (1983)
		Coral: coral rubble	2.6^1	53.5			
		Mollusc shell: cockscomb oyster	2.6^1	55.0			
		Coral (unspecified)	1.2^1	47.0			
		Mollusc shell: cockscomb oyster	1.9^1	24.6			
		Coral (unspecified)	2.4^1	49.2			
		Coral (unspecified)	2.3^1	49.1			
		Coral (unspecified)	2.2^1	48.2			
		Coral (unspecified)	1.2^1	7.4			
		Coral (unspecified)	1.7^1	39.7			
		Coral (unspecified)	1.2^1	15.8			
		Coral (unspecified)	1.6^1	23.4			
		Coral (unspecified)	2.0^1	42.2			
		Coral (unspecified)	1.7^1	28.8			
		Coral (unspecified)	2.1^1	36.1			
		Coral (unspecified)	1.9^1	39.8			
		Coral (unspecified)	1.6^1	29.9			
		Coral (unspecified)	1.6^1	34.1			
		Mean across all substrates	1.2–2.6	38.6			

Cliona orientalis, β	Central GBR	Coral: *Astreopora listeri*	1.3[1]		3.4		Schönberg (2002c, *Dipsastrea* as *Favia*)
		Coral: *Goniopora tenuidens*	1.2[1]		6.7		
		Coral: *Favites halicora*	1.4[1]		6.8		
		Coral: *Cyphastrea serailia*	1.5[1]		7.1		
		Coral: *Dipsastraea pallida*	1.6[1], 1.4[6]		9.6		
		Coral: massive *Porites*	1.6[1], 1.2[14]		9.7		
		Coral: *Goniastrea retiformis*	2.0[1], 1.7[6]		10.3		
		Clam shell: *Tridacna squamosa*	2.8[1]		17.6		
		Mean across substrates	1.2–2.0		8.9		
Cliona orientalis, β	Central GBR	Mineral: Iceland spar	2.7[19]	51.6 (central) 57.7 (marginal)			Schönberg and Shields (2008)
Cliona orientalis, β	Central GBR	Coral: massive *Porites*	1.6[1], 1.2[14]		2.2		Wisshak et al. (2012)
Cliona orientalis, β	Southern GBR	Coral: massive *Porites*	1.6[1], 1.2[14]		2.5		Fang et al. (2013b)
Cliona orientalis, β	S Queensland	Coral: *Goniastraea* sp.	2.0[1], 1.7[6] (for *G. retiformis*)		6.1		Holmes et al. (2009)
Cliona varians, γ	Florida Keys	Calcite material	NA, ca. 2.5		22.8		Hill (1996, as *Anthosigmella*)
?*Pione mussae*, β	Aqaba	Reef rock	NA		0.3 (2.6?)***		Zundelevich et al. (2007)

? – The predominant Red Sea *Pione* species has occasionally been reported to be photosynthetic (Beer and Ilan 1998; Steindler et al. 2001, both as *Cliona vastifica*), but it is not a typical species to contain dinoflagellate zooxanthellae

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Species, morphology	Location	Substrate material	Specific gravity	% substrate removed	Annual bioerosion [kg] per m^2 sponge tissue	Annual bioerosion per m^2 reef area	References
Heterotrophic spp. (Percentages refer to the area of full sponge penetration only.)							
Cliona cf. *celata*, α	Bahía, Brazil	Coral: *Siderastrea stellata*	1.8[1], 1.3–1.5[5]			1.0	Reis and Leão (2000)
Cliona aff. *celata*, α	Central GBR	Mineral: Iceland spar	2.7[19]	90.7 (central) 79.1 (marginal)			Schönberg and Shields (2008)
Cliona delitrix, α-β	Grand Cayman	Coral: *Montastraea cavernosa*	1.7[1]	53.0			Rose and Risk (1985)
		Coral: *Porites astreoides*	1.3[1], 1.4[18]	47.0			
		Mean across substrates	1.3–1.7	50.0			
Cliona peponaca, α	Curaçao	Coral: *Orbicella annularis*	1.7–2.1[6], 1.8[9], 1.4[18]		2.5–3.3**		Bak (1976, *Orbicella* as *Montastrea*)
Cliona vermifera, α	Mexican Pacific	Coral: *Pocillopora verrucosa*	2.8[2]		1.2		Bautista-Guerrero et al. (2014)
Clionaid sp. undet. (*Pione lampa*?)	Belize	Bivalve shells: *Chama macerophylla*	NA, >2.5	Ca. 50	1.7–4.4		Rützler (1975)
Pione lampa, β	Bermuda	Porous dolomite	2.8[3] or <		2.9		Neumann (1966)
	Bermuda	Dense aragonite	2.9[3]		4.0–15.0		
Pione lampa, β	Bermuda	Iceland spar	2.7[20]		6.6–14.2		Rützler (1975)
	Bermuda	Dense calcite	2.7[3]		18.9–23.8		
Entire guild of bioeroding sponges (Please note! Values below refer to the entire coral or to reef area studied and are thus these are different values than the above percentages, even if in the same column.)							

All sponge bioerosion	Bermuda	Different materials, mostly reef framework	NA			0.26, or 3.0 where sponges dense	Rützler (1975)
All sponge bioerosion	Florida Keys	Coral: *Dichocoenia stokesii*	2.0^{9}	8.5			Hein and Risk (1975, *Pseudodiploria* as *Dodiploria*, *Orbicella* as *Montastrea*)****
		Coral: *Pseudodiploria strigosa*	1.2^{10}	7.3			
		Coral: *Orbicella annularis*	$1.7–2.1^{6}$, 1.8^{9}, 1.4^{18}	3.5, 11.6			
		Coral: *Manicina areolata*	NA	2.8			
		Coral: *Siderastrea radians*	1.8^{1}, $1.3–1.5^{5}$ (for *S. stellata*)	33.4, 31.7			
		Coral: all massive corals		12.3			
All sponge bioerosion	Veracruz	Coral: *Orbicella annularis*	1.3^{1}	1.3			Hernández-Ballesteros et al. (2013, *Orbicella* as *Montastraea*)
		Coral: *Porites astreoides*	1.4^{1}	2.7			
		Mean across all substrates	1.3–1.4	2.0			
All sponge bioerosion	Yucatán	Coral: *Orbicella annularis*	1.4^{1}	3.6			Hernández-Ballesteros et al. (2013, *Orbicella* as *Montastraea*)
		Coral: *Porites astreoides*	1.6^{1}	6.7			
		Mean across all substrates	1.4–1.6	5.2			
All sponge bioerosion	Yucatán	Coral: different species	NA	16.4 per reef area			Hepburn et al. (2006)

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Species, morphology	Location	Substrate material	Specific gravity	% substrate removed	Annual bioerosion [kg] per m^2 sponge tissue	Annual bioerosion per m^2 reef area	References
All sponge bioerosion	Belize	Coral: *Orbicella annularis*	1.8[8]	7.4			Highsmith et al. (1983)
		Coral: *Montastraea cavernosa*	1.6[1]	4.6			
		Coral: *Porites astreoides*	1.5[1]	4.1			
		Mean across substrates	1.5–1.8	5.4			
All sponge bioerosion	St. Thomas	Rubble, unspecified	NA	47.0–88.5			Weinstein et al. (2014)
All sponge bioerosion	St. Croix	Coral cores: *Acropora palmata*	1.9[16]	41.3 (41.1–41.4)		0.22 (0.21–0.23)	Moore and Shedd (1977)
		Coral cores: *Millepora* sp.	2.3[13]	31.5 (31.0–32.0)		5.23 (1.2–3.5)	
		Mean across all substrates	1.9–2.3	36.4		0.37	
All sponge bioerosion	Barbados	Coral: *Orbicella annularis*	1.7–2.1[6], 1.8[9], 1.4[18]	9.4–11.6			MacGeachy (1977, *Orbicella* as *Montastrea*)
		Coral: *Porites astreoides*	1.4[18]	3.3–6.2			
		Coral *Siderastrea siderea*	1.6[18]	1.3–7.8			
		Mean across all substrates	1.4–1.8			0.28	
All sponge bioerosion	Barbados	Rubble, unspecified	NA	24.0–41.0			Holmes (2000)

All sponge bioerosion	Barbados	Coral: *Agaricia agaricites*	1.9[18]			0.35	Stearn and Scoffin (1977, *Orbicella* as *Montastraea*)*****
		Coral: *Orbicella annularis*	1.7–2.1[6], 1.8[9], 1.4[18]			0.35	
		Coral: *Porites astreoides*	1.4[18]			0.14	
		Coral *Siderastrea siderea*	1.6[18]			0.07	
		Mean across all substrates	1.4–1.9			0.23	
All sponge bioerosion	Barbados	Coralline algae	0.5–0.7[11]			0.47	Scoffin et al. 1980, *Orbicella* as *Montastraea*)*****
		Coral: *Agaricia agaricites*	1.9[17]			0.29	
		Coral: *Orbicella annularis*	1.7–2.1[6], 1.8[9], 1.4[18]			0.44	
		Coral: *Porites astreoides*	1.4[18]			0.19	
		Coral: *Porites porites*	1.2[18]			0.18	
		Coral *Siderastrea siderea*	1.6[17]			0.09	
		Mean across all substrates	0.5–1.9			0.28	
All sponge bioerosion	Curaçao	Coral: *Orbicella annularis*	1.7–2.1[6], 1.8[9], 1.4[18]	2.4			Bak (1976, *Orbicella* as *Montastrea*)
		Coral: *Meandrina meandrites*	1.9[10]	1.7			
		Mean across substrates	1.4–2.1	2.1			

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Species, morphology	Location	Substrate material	Specific gravity	% substrate removed	Annual bioerosion [kg] per m^2 sponge tissue	Annual bioerosion per m^2 reef area	References
All sponge bioerosion	Bonaire	Different coral spp. dominating	NA			0.04	Perry et al. (2012, *Orbicella* as *Montastraea*, *Madracis myriaster* as *Madracis mirabilis*; sponge bioerosion rates were estimated by using values from other oceans and species, partly not congeneric; development of the algorithm remains unclear as some of the cited works did not provide data for sponge tissue area—Scoffin et al. 1980—or did not separate sponge bioerosion from macroboring—Chazottes et al. 1995.)
		Mean across all substrates at non-diving sites, dominated by *Orbicella annularis* and *Madracis myriaster*	*O. annularis*: 1.7–2.1[6], 1.8[8], 1.4[18] *M. myriaster*: 1.6[4]			0.02	
		Mean across all substrates				0.03	
All sponge bioerosion	Red Sea	Coral: *Porites* sp.	NA	1.0			Klein et al. (1991)

All sponge bioerosion	Kenya	Branching coral: *Porites cylindrica*, *Porites rus*, *Montipora digitata*				0.10–0.15 (fished and unfished)	Carreiro-Silva and McClanahan (2012, *Montipora digitata* as *Porites palmata*)
All sponge bioerosion	Maldives	Coral rubble	NA			0.03	Morgan (2014)
All sponge bioerosion	South China Sea	Coral: *Porites lutea*	1.6[6]	3.7			Chen et al. (2013)
All sponge bioerosion	Indonesia	Coral: *Porites lobata*	1.4[12]	2.8			Holmes et al. (2000)
All sponge bioerosion	Central GBR	Coral: *Porites lobata*	1.4[12]	1.8			Sammarco and Risk (1990)
All sponge bioerosion	Central GBR	Coral: *Acropora muricata*	2.6[6]	Ca. 0.5–3.0			Risk et al. (1995, as *Acropora formosa*)
All sponge bioerosion	Central GBR	Massive *Porites* sp.	Likely 1.4–1.6, see above	2.2			Schönberg et al. (1997)

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Species, morphology	Location	Substrate material	Specific gravity	% substrate removed	Annual bioerosion [kg] per m^2 sponge tissue	Annual bioerosion per m^2 reef area	References
All sponge bioerosion	Enewetak	Coral: *Goniastraea retiformis*	1.7[1], 2.0[15]	6.0			Highsmith (1981a, *Dipsastraea* as *Favia*, *Orbicella* as *Montastrea*)
		Coral: *Porites lutea*	1.4[1]	2.0			
		Coral: *Dipsastraea pallida*	1.4[1], 1.6[15]	0.9			
		Rubble	NA	3.8			

References for material densities: [1]Same reference as listed on the right. [2]Al-Sofyani and Floos (2013), [3]Barthelmy (1997–2014), [4]Bruggemann et al. (1994), [5]Carricart-Ganivet et al. (2013), [6]Coraltraits (2016), [7]Dunn et al. (2012), [8]Dunstan (1975), [9]Highsmith (1981b), [10]Mallela (2004), [11]McCoy (2013) for *Pseudolithophyllum*, [12]Morgan and Kench (2012). [13]Odum and Odum (1955), [14]Risk and Sammarco (1991), [15]Schönberg (2002b), [16]Schuhmacher and Plewka (1981), [17]Sowa et al. (2014), [18]Stearn et al. (1977), [19]StoneContact (2016), [20]Wikipedia (2016b). *Acker and Risk (1985) calculated their value by using average growth rates and average sponge areas, and while the value was obtained by a different method than used by the other authors, the value aligns well (Fig. 7.7). **Bak (1976) did not state whether the areal reference for his bioerosion rates was sponge surface area or block area. In the latter case, the values would be meaningless, and it is here assumed that the reference is the sponge surface area. ***Zundelevich et al.'s (2007) total bioerosion rate was calculated by adding together their measures for chemical and mechanical bioerosion. However, they estimated mechanical bioerosion by quantifying the resulting sediment, which is likely an inaccurate method (see Discussion in Fang et al. 2013a; Schönberg et al. 2017). Chemical sponge bioerosion has previously been determined as being closer to 10% (Wisshak et al. 2013; Schönberg et al. 2017), which would mean that Zundelevich's total bioerosion rates for *P. mussae* may have been around 2.6 kg m^{-2} $yr.^{-1}$ instead of 0.3, a value which would be more similar to other published bioerosion rates for this genus. ****Hein and Risk's (1975) values per coral species are all based on only one or two specimens. Their bioerosion rates were given as mm^3 $yr.^{-1}$, without reference to area. Therefore, the values could not be recalculated as standardised data. *****The sponge bioerosion rates from Stearn and Scoffin (1977) and Scoffin et al. (1980) were calculated by using their average contribution of sponges to total macroboring of 92%.

Appendix D

Proportional contributions of sponge, worm, mollusc and other bioerosion to total macroboring. Means were calculated hierarchical, e.g. first within a given study, then across studies, then across ocean, as outlined below. Where the published total did not exactly match the sum of the partial bioerosion, we set the sum of the partial bioerosion values to 100%. Taxonomic information for non-sponge taxa that form the substrate for bioeroding sponges can be found in Appendix B. Data were used for Figs. 7.5 and 7.8. A selection of data of block settlement experiments was here included, because by calculating values into %, they were all relative and thus comparable. However, block data were only used after a minimum of 1 year of exposure.

Ocean	Location	Substrate	Proportion of macrobioerosion [mean % of total]				References
			Sponges	'Worms'	Molluscs	Others	
W Atlantic 1	Florida Keys	*Dichocoenia stokesii*	70.7	19.6	9.7	NA	Hein and Risk (1975, *Orbicella* as *Montastrea*, *Pseudodiploria* as *Diploria*). Data were calculated from their Table 1
		Orbicella annularis	36.0	62.5	1.5	NA	
		Pseudodiploria strigosa	31.5	34.0	34.5	NA	
		Pseudodiploria clivosa	0.0	12.9	87.1	NA	
		Manicina areolata	18.4	81.6	0.0	NA	
		Siderastrea radians	66.7	29.7	3.6	NA	
	Means Florida Keys across substrates		**37.2**	**40.1**	**22.7**	**NA**	
W Atlantic 2	Bahamas	*Orbicella annularis*	X-ray: 79.3	X-ray: 16.0	X-ray: 3.6	X-ray: 1.1	Becker and Reaka-Kudla (1997, *Orbicella* as *Montastrea*). Calculated from their Table 1. The paper compared X-ray and CAT scan
			CAT: 75.1	CAT: 19.9	CAT: 5.0	CAT: 0.0	
	Means Bahamas across different methods		**Mean: 77.2**	**Mean: 17.9**	**Mean: 4.3**	**Mean: 0.6**	
	Jamaica 1, 1–30 m	Dead corals and rubble	81.5	15.9	2.5	0.1	Perry (1998). Calculated from his Table 3

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Ocean	Location	Substrate	Proportion of macrobioerosion [mean % of total]				References
			Sponges	'Worms'	Molluscs	Others	
W Atlantic 3	Jamaica 2, 0–8 m	Different coral spp.	84.4	11.8	2.4	1.4	Macdonald and Perry (2003). Calculated from their Table 3
	8–16 m		77.3	8.0	14.4	0.3	
	16–25 m		71.1	6.4	20.4	2.1	
	Means Jamaica 2, across depths		**77.6**	**8.7**	**12.4**	**1.3**	
	Means across Jamaica 1–2		**79.6**	**12.3**	**7.4**	**0.7**	
W Atlantic 4	St. Thomas (mesophotic)	Coral rubble	73.4	7.9	14.5	4.2	Weinstein et al. (2014). Data were read off their Fig. 4, lowest part
	Barbados	*Orbicella annularis*, 0–15 m	95.7*	1.8*	0.3	2.2	MacGeachy and Stearn (1976, *Orbicella* as *Montastrea*). Data were calculated from their Table 7.2. *The value for sponges includes bioerosion from spionids and should be smaller; the one for worms should be larger
W Atlantic 5	Barbados	*Orbicella annularis*, 0–15 m	92.0	1.4	0.0	6.6	Scoffin et al. 1980, *Orbicella* as *Montastrea*). Data were calculated from their p. 486. Data are part of the above study. These values are only for the part of the study in which worms were common. As they accounted for <3% of macroboring, they were ignored at the other sites, which were part of the studies for MacGeachy and Stearn (1976)
	Means Barbados across studies		**93.9**	**1.6**	**0.1**	**4.4**	
W Atlantic 6	Veracruz Reefs	*Orbicella annularis*	79.3	5.3	12.4	3.0	Hernández-Ballesteros et al. (2013, *Orbicella* as *Montastrea*). Data were calculated from their Table 1
		Porites astreoides	73.7	20.7	5.6	0.0	
	Means Veracruz across different substrates		**76.5**	**13.0**	**9.0**	**1.5**	

W Atlantic 7	Puerto Morelos, N Yucatán	Coral rubble	76.2	4.9	18.2	0.7	Hepburn et al. (2006). Data were read off their Fig. 3
	S Yucatán	*Orbicella annularis*	94.5	0.5	4.2	0.8	Hernández-Ballesteros et al. (2013, *Orbicella* as *Montastrea*). Data were calculated from their Table 1
		Porites astreoides	89.8	6.2	4.0	0.0	
	Means S Yucatán across different substrates		**92.1**	**3.4**	**4.1**	**0.4**	
	Means Yucatán across N and S		**84.1**	**4.2**	**11.2**	**0.5**	
W Atlantic 8	Belize, 2–7 m	*Orbicella annularis*	93.8	2.3	2.2	1.7	Highsmith et al. (1983, *Orbicella* as *Montastrea*). Data were calculated from their Table 2. Where the sum of their percentages did not reach 100%, values were recalculated so that it did
		Montastrea cavernosa	91.0	3.0	3.5	2.5	
		Porites astreoides	84.0	16.0	0.0	0.0	
	Means Belize across different substrates		**89.6**	**7.1**	**1.9**	**1.4**	
W Atlantic 9	Bahía, Brazil	*Siderastrea stellata*	35.0	15.0	50.0	0.0	Reis and Leão (2000). Data were read off their Fig. 2
Means W Atlantic 1–9			**71.8**	**13.2**	**13.5**	**1.5**	
Indian Ocean 1	Red Sea	*Porites* spp.	23.9	41.3	19.2	15.6	Klein et al. (1991). Data were calculated from their Table 1. Only their recent material was considered, not the fossil substrate

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Ocean	Location	Substrate	Proportion of macrobioerosion [mean % of total]				References
			Sponges	‘Worms’	Molluscs	Others	
(Indian Ocean)	Persian Gulf	Dead corals	(2.2)	(27.4)	(46.9)	(23.5)	Jafari et al. (2016). It seems that the authors included embedding barnacles as bioeroders (?), and perhaps sponge bioerosion is underestimated? The values are here displayed, but not used in the overall calculations
			Without barnacles:				
			(2.8)	(35.8)	(61.3)	(NA)	
Indian Ocean 2	Kenya fished	Branching coral: *Porites cylindrica*, *Porites rus*, *Montipora digitata* – 6 years after coral death	47.4	44.3	8.4	NA	Carreiro-Silva and McClanahan (2012, *Montipora digitata* as *Porites palmata*). Data were calculated from their App. 1
	Kenya unfished		58.4	33.4	8.1	NA	
	Means Kenya		**52.9**	**38.9**	**8.2**	**NA**	
	Maldives 1 at 5 m	*Porites* sp. (blocks – 14-month exposure)	62.4	28.5	9.1	NA	Zahir (2002) Data were read off his Fig. 3
	Maldives 1 at 10 m		23.6	48.7	27.7	NA	
	Means Maldives 1		**43.0**	**38.6**	**18.4**	**NA**	
Indian Ocean 3	Maldives 2 lagoon	*Acropora* rubble	74.1	22.2	3.7	NA	Morgan (2014). Data were read off his Fig. 4.5.
	Maldives 2 inner reef		51.2	29.1	19.7	NA	
	Maldives 2 outer reef		32.0	37.7	30.3	NA	
	Means Maldives 2		**52.4**	**29.7**	**17.9**	**NA**	
	Means Maldives across 1–2		**47.7**	**34.2**	**18.1**	**NA**	
Means Indian Ocean 1–3			**41.5**	**38.1**	**15.2**	**5.2**	
W Pacific 1	Daya Bay, South China Sea	*Porites lutea*	38.3	5.7	48.0	8.0	Chen et al. (2013). Data were calculated from their Fig. 3

W Pacific 2	Lizard Island, northern GBR 1, windward	*Porites lutea* (blocks – 5-year exposure, at 1–20 m)	33.3	39.4	27.3	NA	Kiene and Hutchings (1994). Data were read off their Fig. 3. The eight sites were grouped by us, so that leeward sites included the channel and leeward slope and deep sites
	Flat and lagoon		10.2	86.2	3.6	NA	
	Leeward sites		66.1	26.5	7.4	NA	
	Means northern GBR 1		**36.5**	**50.7**	**12.8**	**NA**	
	Northern GBR 2, two inshore sites	Massive *Porites* (blocks – 4-year exposure, at 7–10 m)	35.8	34.6	29.6	NA	Hutchings et al. (2005). Data were read off their Fig. 7.3. The sites for this and the following two studies were inshore sites, Snapper Island and Low Isles; midshelf site, Lizard Island; reef edge sites, Harrier Reef and Ribbon Reef 3; and an oceanic site, Osprey Reef
	One midshelf site		11.7	71.6	16.7	NA	
	Two reef edge sites		18.1	44.7	37.2	NA	
	One oceanic site		18.4	75.8	5.8	NA	
	Means northern GBR 2		**21.0**	**56.7**	**22.3**	**NA**	
	Northern GBR 3, two inshore sites	Massive *Porites* (blocks – 4-year exposure, at 7–10 m)	41.7	26.7	31.6	NA	Osorno et al. (2005). Data were calculated from their Table 1
	One midshelf site		21.9	63.3	14.9	NA	
	Two reef edge sites		17.2	45.9	36.9	NA	
	One oceanic site		18.8	72.4	8.8	NA	
	Means northern GBR 3		**24.9**	**52.1**	**23.0**	**NA**	
	Northern GBR 4, two inshore sites	Massive *Porites* (blocks – 3-year exposure)	35.6	32.0	32.4	NA	Tribollet and Golubic (2005). Data were calculated from their Table 3
	One midshelf site		20.1	74.8	5.1	NA	
	Two offshore sites		15.8	58.2	26.0	NA	
	One oceanic site		18.0	69.1	12.9	NA	
	Means northern GBR 4		**22.4**	**58.5**	**19.1**	**NA**	

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Ocean	Location	Substrate	Proportion of macrobioerosion [mean % of total]				References
			Sponges	‘Worms’	Molluscs	Others	
	Means northern GBR across studies 1–4		**23.9**	**53.2**	**22.9**	**NA**	Averaged by distance from shore first, then across studies
	Central GBR, One inshore site	*Porites lobata*, from 7–9 m	22.6	24.8	52.6	NA	Sammarco and Risk (1990). Data were calculated from their Table 3. The sites were inshore, Orpheus Island; midshelf, Britomart, Rib and Davies Reef; and offshore, Myrmidon Reef
	Three midshelf sites		58.3	26.7	15.0	NA	
	One offshore site		38.7	54.6	6.7	NA	
	Means central GBR for *Porites* 1		**39.9**	**35.4**	**24.7**	**NA**	
	Central GBR, one inshore site	Massive *Porites*	20.4	4.1	75.5	NA	Schönberg et al. (1997). Data were read off their Fig. 1. ‘Worms’ included ‘other’ bioerosion. The sites were inshore, Pandora Reef; midshelf, Rib Reef; and offshore, Myrmidon Reef
	One midshelf site		68.5	14.8	16.7	NA	
	One offshore site		57.7	19.2	23.1	NA	
	Means central GBR for *Porites* 2		**48.9**	**12.7**	**38.4**	**NA**	
	Means central GBR for *Porites* across studies 1–2		**44.4**	**24.0**	**31.6**	**NA**	
	Central GBR, Two inshore sites	*Acropora muricata*, at 6–8 m	77.8	12.0	6.2	4.0	Risk et al. (1995, as *Acropora formosa*). Data were calculated from their Table 3
	Three midshelf sites		69.7	15.5	11.5	3.3	
	One offshore site		48.0	42.5	7.5	2.0	
	Means central GBR for *Acropora*		**65.2**	**23.3**	**8.4**	**3.1**	
	Means central GBR across substrates		**54.8**	**23.7**	**20.0**	**1.5**	
	Means across GBR		**39.5**	**38.5**	**21.4**	**0.7**	

Western Pacific 3	Java Sea, low resuspension	Coral: *Porites lobata*	54.1	27.4	8.1	10.4	Holmes et al. (2000). Data were read off their Figs. 1 and 4. Data were grouped by us with respect to resuspension levels
	Ambon, low resuspension		57.0	24.9	15.1	3.0	
	Means low resuspension		**55.6**	**26.1**	**11.6**	**6.7**	
	Java Sea, high resuspension	Coral: *Porites lobata*	46.6	18.6	12.1	22.7	
	Means Indonesia across suspension levels		**51.1**	**22.3**	**11.9**	**14.7**	
Means Western Pacific 1–3			**43.0**	**22.1**	**27.1**	**7.8**	
Central Pacific 1	Enewetak, 0–30 m	*Goniastrea retiformis*	76.1	1.3	4.0	18.6	Highsmith (1981b). Data were calculated from his Table 5
		Porites lutea	82.3	10.9	1.5	5.3	
		Dipsastraea pallida	75.0	25.0	0.0	0.0	
		Rubble	69.8	15.4	3.7	11.1	
	Means Enewetak across substrates		**75.8**	**13.2**	**2.3**	**8.7**	
Central Pacific 2	Moorea and Tahiti	*Porites lutea* (blocks – 5-year exposure)	42.9	36.3	20.8	NA	Pari et al. (2002). Data were read off their Fig. 3
	Polynesia atolls		72.8	26.7	0.5	NA	
	Means French Polynesia across sites		**57.9**	**31.5**	**10.6**	**NA**	
Means Central Pacific 1–2			**66.9**	**22.4**	**6.4**	**4.3**	
Eastern Tropical Pacific (*ETP*)		*Porites lobata*	**11.9**	**0.0**	**88.1**	**0.0**	Carballo unpubl. data (2017)
Means Pacific			**40.6**	**14.8**	**40.5**	**4.1**	
Means World			**51.3**	**22.0**	**23.1**	**3.6**	

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Appendix E

Spongivorous organisms feeding on bioeroding sponges (see also Fig. 7.6). Only examples of feeding directly on the sponges are here reported; experiments using sponge-extract infused artificial pellets are not listed. Taxonomic information can be found in Appendix A (for bioeroding sponges) and in Appendix B (for non-sponge taxa).

Sponge species	Predator species	Location	Observation	Reference
Cervicornia cuspidifera	Sea star, *Oreaster reticulatus*	San Blas, Caribbean	The sea star fed on the sponge in a feeding choice experiment	Wulff (1995)
Cliona albimarginata	Parrotfish, *Bolbometopon* sp.	N Sulawesi	The fish feeding on the sponge	Calcinai et al. (2005)
Cliona ampliclavata	Nudibranch, *Doriprismatica sedna*	Mexican Pacific	The nudibranch consumed *C. ampliclavata*	Verdín Padilla et al. (2010, as *Glossodoris sedna*)
Cliona californiana	Nudibranchs, *Doriprismatica sedna* and *Felimare agassizii*	Mexican Pacific	The nudibranchs consumed *C. californiana*	Verdín Padilla et al. (2010, as *Glossodoris sedna* and *Hypselodoris agassizii*)
Cliona caribbaea	Parrotfishes, wrasses, surgeonfishes	Caribbean	Evidenced by occasional bite marks	Acker and Risk (1985)
Cliona cf. *celata*	Nudibranch, *Doriopsilla albopunctata*	California?	From the literature	Bloom (1976)

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Sponge species	Predator species	Location	Observation	Reference
Cliona cf. *celata*	Keyhole limpet, *Diodora cayenensis*, cerithid snail, *Seila adamsi*, isopod, *Paracerceis caudata*, snapping shrimp, *Alpheus heterochaelis*, grass shrimp, *Palaemonetes vulgaris*, brachyurid crabs, *Menippe mercenaria*, and *Pilumnus sayi*, xanthid crabs, *Panopeus herbstii*, and *Dyspanopeus sayi*, urchins, *Arbacia punctulata* and *Lytechinus variegatus*, and possibly the brittle star *Ophiothrix* (*Ophiothrix*) *angulata*	N Carolina	Feeding experiments with starved potential predators using undisturbed *C.* cf. *celata* specimens and specimens of which the endosome was exposed revealed that many organisms will feed on that sponge, depending on access	Guida (1976, as *Cilicaea cordata* and *Neopanope sayi*)
Cliona cf. *celata*	Nudibranch, *Doriopsilla pharpa*	S Carolina	Faeces and laboratory observations confirmed that the nudibranch fed on *C.* cf. *celata* but less during winter when C. celata cf. retracted	Eyster and Stancyk (1981)
	Snapping shrimp, *Alpheus heterochaelis*	S Carolina	The shrimp consumed the nudibranch and C. cf. celata papillae	
Cliona euryphylle	Angelfishes, *Holacanthus passer* and *Pomacanthus zonipectus*	Mexican Pacific	The fishes consumed *C. euryphylle*	Verdín Padilla et al. (2010)

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Sponge species	Predator species	Location	Observation	Reference
Cliona flavifodina	Nudibranch, *Doriprismatica sedna*	Mexican Pacific	The nudibranch consumed *C. flavifodina*	Verdín Padilla et al. (2010, as *Glossodoris sedna*)
Cliona orientalis	Parrotfish, *Chlorurus microrhinos*	Central Great Barrier Reef	*C. orientalis* was observed with occasional parrotfish bite marks	Schönberg et al. (2017)
Cliona papillae	Angelfishes, *Holacanthus passer*, *Pomacanthus zonipectus* and the nudibranchs, *Doriprismatica sedna* and *Felimare agassizii*	Mexican Pacific	The fishes and the nudibranchs consumed *C. papillae*	Verdín Padilla et al. (2010, as *Glossodoris sedna* and *Hypselodoris agassizii*)
Cliona tenuis	Parrotfishes, *Scarus iseri*, *Scarus coelestinus* and *Sparisoma viride*; damselfishes, *Stegastes planifrons* and *Stegastes partitus* and the surgeonfish *Acanthurus coeruleus*	Belize, Caribbean	The fishes were observed to feed on *C. tenuis*, and bite frequency decreased in listed sequence	González-Rivero et al. (2012)
Cliona varians	Sea star, *Oreaster reticulatus*	San Blas, Caribbean	The sea star fed on the sponge in the field and in a feeding choice experiment	Wulff (1995, as *Anthosigmella varians*)
Cliona varians	Angelfish, *Pomacanthus paru*	Caribbean	Gut content analysis confirmed that the fishes ate *C. varians*	Randall and Hartman (1968, as *Anthosigmella varians*)
Cliona varians	Angelfishes, *Pomacanthus arcuatus* and *Pomacanthus paru*	US Virgin Islands, Caribbean	The fishes consumed *C. varians*	Hourigan et al. (1989)
Cliona varians	Angelfish, *Pomacanthus arcuatus*	Florida Keys	Uncaged *C. varians* exhibited bite marks	Hill (1998)

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Sponge species	Predator species	Location	Observation	Reference
Cliona varians	Angelfishes, *Holacanthus ciliaris*, *Pomacanthus arcuatus* and *Pomacanthus paru*, hawksbill turtle *Eretmochelys imbricate* (It is not clear, however, which of these, or all, targeted the sponge.)	Florida Keys	Uncaged branching *C. varians* morphs were eaten and lost their branches	Hill and Hill (2002, as *Anthosigmella varians*)
Cliona varians	Angelfish, *Pomacanthus paru*	Brazil	*C. varians* was consumed by the angelfish, as evidenced by gut content	Batista et al. (2012)
Cliona viridis	Copepod, *Asterocheres suberitis*	W Mediterranean	Copepod behaviour was studied with videography	Mariani and Uriz (2001)
Cliothosa aurivillii	Copepod, *Tisbe* sp.	Central Great Barrier Reef	*C. aurivillii* became infested with copepods that produced faeces in the colour of the sponge	Schönberg and Wisshak (2012)
Cliona sp.	Angelfishes, *Holacanthus tricolor*, *Pomacanthus arcuatus* and *Pomacanthus paru*	US Virgin Islands, Caribbean	The fishes consumed *Cliona* sp.	Hourigan et al. (1989)
Cliona sp. or spp.	Sea star, *Oreaster reticulatus*	San Blas, Caribbean	The sea star fed on *Cliona* sp. in the field and in a feeding choice experiment	Wulff (1995)
Cliona spp.	Sea urchin, *Eucidaris tribuloides*	Bahía, Brazil	Spicules found in the urchin guts showed that it fed on clionaid sponges	Santos et al. (2002)

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Sponge species	Predator species	Location	Observation	Reference
Cliona sp.	Angelfishes, *Holacanthus passer* and *Pomacanthus zonipectus*	Mexican Pacific	The fishes consumed *Cliona* sp.	Verdín Padilla et al. (2010)
Unidentified clionaid	Angelfish, *Pomacanthus paru*	Brazil	The clionaid was consumed by the angelfish, as evidenced by gut content	Batista et al. (2012)
Pione carpenteri	Angelfish, *Holacanthus passer*, and the nudibranch, *Doriprismatica sedna*	Mexican Pacific	The fish and the nudibranch consumed *P. carpenteri*	Verdín Padilla et al. (2010, as *Cliona mazatlanensis*)
Pione mazatlanensis	Angelfish, *Holacanthus passer*, and the nudibranchs, *Doriprismatica sedna* and *Felimare agassizii*	Mexican Pacific	The fish and the nudibranch consumed *P. mazatlanensis*	Verdín Padilla et al. (2010, as *Cliona mazatlanensis, Glossodoris sedna* and *Hypselodoris agassizii*)
Pione vastifica	Nudibranch, *Platydoris argo*	Strait of Gibraltar	Gut contents were studied to find that the nudibranch fed on *P. vastifica*	Megina et al. (2002, as *Cliona vastifica*)
Spheciospongia vagabunda	Wrasse, puffer fish and the hawksbill turtle, *Eretmochelys imbricata*?	Papua New Guinea	Sponges were found with feeding damage and rejected fragments strewn near them. Predators were tentatively identified from the form of the feeding scars	Kelly (1986, as *Spirastrella vagabunda*)
Spheciospongia vesparium	Angelfishes, *Holacanthus ciliaris*, *Holacanthus tricolor* and *Pomacanthus paru*	Caribbean	Gut content analysis confirmed that the fishes ate *S. verparium*	Randall and Hartman (1968)

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Sponge species	Predator species	Location	Observation	Reference
Spheciospongia vesparium	Polychaete, *Branchiosyllis oculata*	Bermuda	Polychaetes changed colour, depending on which sponge they were, and feeding was confirmed by examining the gut content	Pawlik (1983, as *Spheciospongia othella*)
Spheciospongia vesparium	Sea star, *Oreaster reticulatus*	San Blas, Caribbean	The sea star fed on the sponge in a feeding choice experiment	Wulff (1995)
Spheciospongia sp.	Hawksbill turtle, *Eretmochelys imbricata*	Seychelles	Oesophageal lavage yielded the material that showed that the turtles were eating *Spheciospongia* sp.	Cuevas et al. (2007), von Brandis et al. (2014)
Spheciospongia sp.	Surgeonfish, *Acanthurus pyroferus*; butterfly fishes, *Chaetodon kleinii*, *Chaetodon vagabundus*; and idol, *Zanclus cornutus*	Wakatobi, Banda Sea	The fishes fed on the sponge	Powell et al. (2015)
Spirastrella coccinea	Angelfishes, *Holacanthus ciliaris*, *Holacanthus tricolor*, *Pomacanthus arcuatus* and *Pomacanthus paru*	Caribbean	Gut content analysis confirmed that the fishes ate *S. coccinea*	Randall and Hartman (1968)
Spirastrella coccinea	Angelfishes, *Pomacanthus arcuatus* and *Pomacanthus paru*	San Blas, Caribbean	During field observations the bites were counted the fishes took from *S. coccinea*	Wulff (1994)

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Sponge species	Predator species	Location	Observation	Reference
Spirastrella coccinea	Hawksbill turtle, *Eretmochelys imbricata*	Dominican Republic, Caribbean	Oesophageal lavage yielded the material that showed that the turtles were eating *S. coccinea*	León and Bjorndal (2002)
Spirastrella cf. *cunctatrix*	Sea star, *Oreaster reticulatus*	San Blas, Caribbean	The sea star was observed to feed on the sponge in the field	Wulff (1995)
Spirastrella decumbens	Angelfishes, *Holacanthus passer* and *Pomacanthus zonipectus*	Mexican Pacific	The fishes consumed *S. decumbens*	Verdín Padilla et al. (2010)
Spirastrella hartmani	Angelfish, *Pomacanthus paru*	Brazil	*S. hartmani* was consumed by the angelfish, as evidenced by gut content	Batista et al. (2012)
Spirastrella sp.	Angelfishes, *Pomacanthus paru*, *Holacanthus ciliaris* and *H. tricolor*	Bahía, Brazil	*Spirastrella* sp. was commonly consumed by the angelfishes, as evidenced by gut content	Andréa et al. (2007)
Thoosa mismalolli	Angelfishes	Mexican Pacific	The fishes consumed *T. mismalolli*	Verdín Padilla et al. (2010)
Thoosa sp.	Angelfishes, *Holacanthus passer* and *Pomacanthus zonipectus*	Mexican Pacific	The fishes consumed *Thoosa* sp.	Verdín Padilla et al. (2010)

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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)

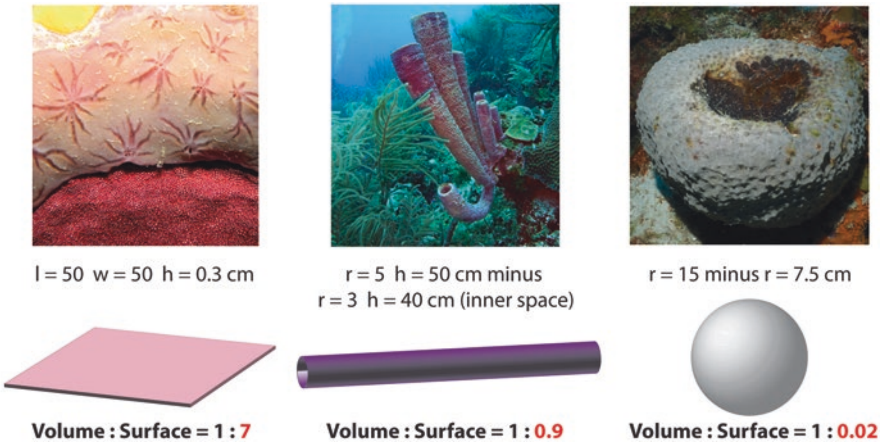

Fig. 8.1 Volume-to-surface area ratio of a thin encrusting sheet-shaped sponge *Halisarca caerulea*, a massive tubular sponge *Aplysina archeri*, and a massive ball-shaped sponge *Ircinia strobilina*. Shown are their representative geometrical forms (*thin cuboid*, *hollow cylinder*, and *dented ball*) 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 multi-oscular 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

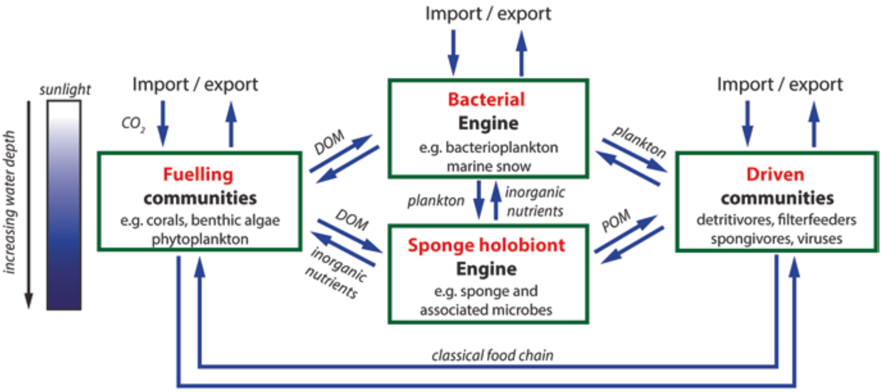

Fig. 8.2 Concept of sponge-driven food web framework along a depth gradient, indicating the direction and size of energy and nutrient fluxes (*arrows*) as well as the biomass and composition of benthic and pelagic reef communities (*boxes*). A simplified overview of predicted dominant pathways for a 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?

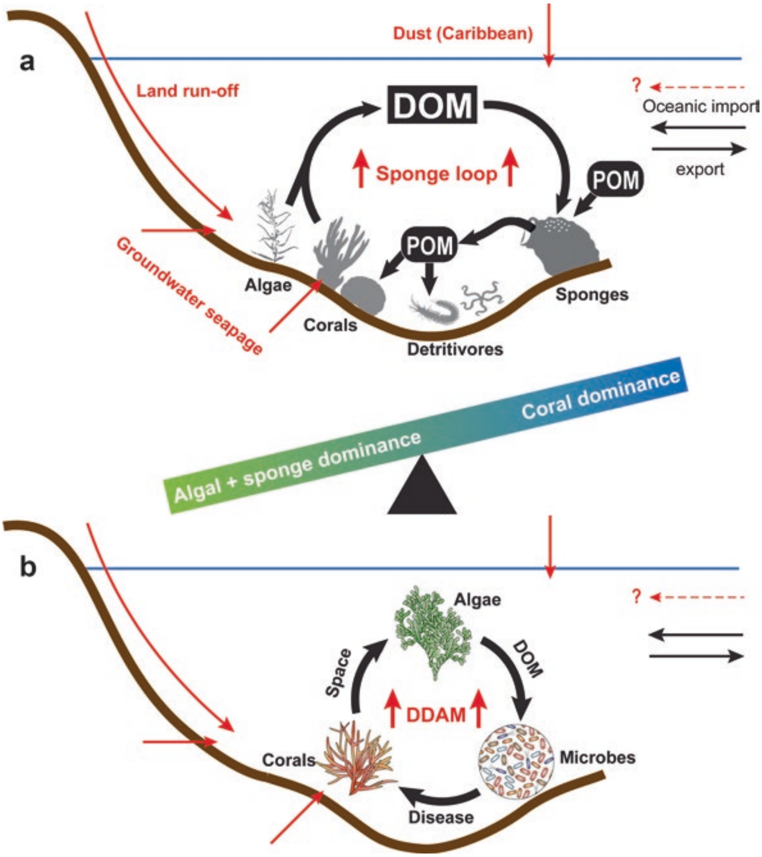

Fig. 8.3 The hypothetical role of the sponge loop (**a**) and the microbial loop (**b**) in catalyzing reef community shifts through enhanced anthropogenic input (indicated by *red arrows*). (**a**) Dissolved organic matter (DOM) is released by algae and corals and converted to particulate organic matter (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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Chapter 9
Sponge Disease and Climate Change

Heidi M. Luter and Nicole S. Webster

Abstract Reports of sponge disease have increased in recent years, impacting a wide range of species from tropical, temperate and freshwater environments. In this chapter, we provide a current overview of reported sponge diseases, focusing particularly on the symptoms of disease, the microbial shifts that occur in affected sponges and the identification of putative pathogens. In addition, we explore the potential role of climate-driven dysbiosis in disease aetiology.

Keywords Porifera • Disease • Microbial shifts • Pathogens

9.1 Introduction

Reports of diseases affecting marine organisms have increased in recent decades, impacting a wide range of species including fish, seals, dolphins, shellfish, starfish, urchins, corals, sponges, seagrass, kelp and coralline algae (Harvell et al. 1999, 2002, 2009; Lafferty et al. 2004; Haapkylä et al. 2007; Bally and Garrabou 2007). A particularly notable example was a recent study of coral loss on the Great Barrier Reef (GBR) which found that 6.8% of the total coral cover lost between 1995 and 2009 was attributed to disease (Osborne et al. 2011). It is currently difficult, however, to determine if the increasingly reported outbreaks are a result of improvements in monitoring, opportunistic pathogens, increased pathogen virulence, reduced host resistance and resilience and/or changed environmental conditions. Nevertheless, environmental parameters associated with reduced water quality and global climate change are known to compromise the fitness of coral reef organisms, likely contributing to the increased prevalence of diseases in marine species globally (Bourne et al. 2016).

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Reports of sponge disease span a broad geographic range but have predominantly affected the Mediterranean and Caribbean sponge populations, although there are also reports from isolated sponge species throughout Papua New Guinea, the GBR and Mexico (previously reviewed in Webster 2007), as well as freshwater sponge communities in Lake Baikal, Russia (Denikina et al. 2016). Affected individuals display a wide array of symptoms including brown spots, black patches, white patches, red bands, orange bands, pustules, bleaching and generalised necrosis (Table 9.1 and Fig. 9.1). These disease epidemics can have severe impacts on the survival of sponge populations and the associated ecology of the reef. For instance, one of the most severe epidemics which occurred in the Caribbean resulted in the loss of 70–95% of commercial sponge species (Galstoff 1942). Similar devastation occurred in the Mediterranean where an epidemic reduced the annual output of the commercial sponge fishery by over 90% (Vacelet 1994). In addition, 60% of the commercial sponges in the Ligurian Sea succumbed to disease (Gaino et al. 1992). From 1984 to 1998, disease affected between 6–15% of *Aplysina fulva*, 2–12% of *Amphimedon compressa* and 1–4% of *Iotrochota birotulata* populations at San Blas, Panama (Wulff 2007). The most recent large-scale sponge disease epidemic occurred in the Mediterranean during the summers of 2008 and 2009 where 80–95% of sponges surveyed were affected (Cebrian et al. 2011). Although not on a large scale, diseased sponges have also been reported in the Red Sea. For instance, two diseased *Crella cyathophora* individuals were collected 30 km apart, and both displayed the same symptoms of a green film on their surface (Gao et al. 2015). In addition, incidents of the disease have also been described in freshwater habitats, most notably, *Lubomirskia baicalensis* populations endemic to Lake Baikal, Russia, where diseased individuals display an uncharacteristic pink colour compared to the green pigmentation of their healthy counterparts (Fig. 9.2) (Denikina et al. 2016).

Until recently, most studies focused on describing the increasing incidence of sponge disease with comparatively few studies examining the associated microbiomes of healthy and affected individuals (Webster 2007; Webster and Blackhall 2008). However, with the increasing application of molecular tools, there has been an increase in the number of studies attempting to elucidate putative sponge pathogens.

9.2 Pathogens and Disease Aetiology

In 1998, isolated individuals of *Rhopaloeides odorabile* on the GBR displayed extensive necrosis and exposure of skeletal fibres (Fig. 9.1a). Microbiological examinations revealed the presence of a bacterium burrowing through the spongin fibres, which was identified as an Alphaproteobacteria (strain NW4327) (Webster et al. 2002). This strain was successful in inducing disease symptoms in healthy sponges, making it the first confirmed sponge pathogen. Strain NW4327 produces a collagenase enzyme that acts in degrading sponge skeletal fibres (Mukherjee et al. 2009) and also contains virulence genes related to collagenase activity which is the

Table 9.1 Comprehensive table of reported sponge diseases

Sponge species	Geographic location	Year(s)	Disease name	Microbial characterisation	References
Callyspongia (Euplacella) aff. *biru*	Maldives	2013	Sponge necrosis syndrome	Polymicrobial disease—combination of a bacterium and fungus from the *Rhodobacteraceae* and *Rhabdocline* genera induce disease symptoms	Sweet et al. (2015)
Crella cyathophora	Red Sea	2012	Generalised necrosis	Diseased individuals enriched with a clade within the phylum Verrucomicrobia	Gao et al. (2015)
Lubomirskia baicalensis	Lake Baikal, Russia	2011	Uncharacterised pink necrosis	Diseased individuals dominated by *Synechococcus* and higher abundances of Verrucomicrobia	Denikina et al. (2016)
Ircinia variabilis, Sarcotragus spinosulus, Spongia officinalis	Adriatic Sea	2009	Generalised necrosis	SEM used to observe cyanobacterial mat, but no other microbial characterisation attempted	Di Camillo et al. (2013)
Ircinia fasciculata	Mediterranean and Africa	2008–2010	Pustule disease	Twisted rod bacteria identified by TEM, community shift detected in healthy individuals	Maldonado et al. (2010) and Blanquer et al. (2016)
Ianthella basta	Torres Strait and GBR	2008–2010	Brown spot syndrome	No bacterial community shifts or distinct pathogens detected	Luter et al. (2010 a, b)
Ircinia fasciculata, Sarcotragus spinosulum	Mediterranean	2007–2010	Generalised necrosis	TEM revealed degraded cyanobacteria associated with necrotic zones as well as an unidentified boring bacteria	Cebrian et al. (2011)

(continued)

Table 9.1 (continued)

Sponge species	Geographic location	Year(s)	Disease name	Microbial characterisation	References
Amphimedon compressa	Florida Keys	2007–2010	Sponge white patch	Sponge-boring morphotype identified by TEM, shift in bacterial community associated with diseased individuals	Angermeier et al. (2012)
Aplysina aerophoba	Slovenia, Adriatic Sea	2007	Black patch disease	Multiple sequences unique to diseased samples identified, including a Deltaproteobacteria implicated in coral black band disease	Webster et al. (2008a, b)
Spongia officinalis	Mediterranean	2006	Generalised necrosis	None	T Perez (personal communication)
Coscinoderma mathewsii, Rhopaloeides odorobile	GBR	2006	Generalised necrosis	None	CN Battershill (personal communiation)
Xestospongia muta	Florida Keys and Bahamas	2005, 2007–2009	Sponge orange band	Shift in cyanobacterial community associated with orange band	Cowart et al. (2006) and Angermeier et al. (2011)
X. muta, Geodia spp., *Ircinia* spp. *Verongula gigantea, Callyspongia plicifera*	Mexico	2004–2005	Generalised necrosis	None	Gammill and Fenner (2005)
Aplysina cauliformis	Bahamas	2004	*Aplysina* red band syndrome	Band coloration attributed to a Cyanobacterium but aetiological agent unknown	Olson et al. (2006), Gochfeld et al. (2007), and Olson and Gao (2013)
Cinachyra antarctica, Inflatella belli, Isodictya setifera	Antarctica	2002	Generalised necrosis	None	NS Webster (unpublished data)
A. aerophoba	Greece	2001	Generalised necrosis	None	Skoufas (2003)

X. muta	Curacao	2000	Generalised necrosis	None	Nagelkerken et al. (2000)
I. basta	Papua New Guinea	1996–2000	Brown lesion necrosis	Bacterial strains within the *Bacillus* and *Pseudomonas* genera correlated with diseased tissue	Cervino et al. (2006)
R. odorobile	GBR	1998	Sponge-boring necrosis	Causative agent identified as an Alphaproteobacterium that burrows through spongin fibres	Webster et al. (2002)
X. muta	Belize	1996	Generalised necrosis	None	Paz (1997)
Ircinia spinosula and *Ircinia* spp.	Mediterranean	1994–1996	Generalised necrosis	None	Corriero et al. (1996)
Haliclona oculata and *Halichondria panicea*	North Wales	1988–1989	Generalised necrosis	White bacterial film noted in diseased *H. panicea*	D. Moss (personal communication)
Commercial sponge spp.	Libya	1987	Generalised necrosis	None	Gashout et al. (1989)
Spongia and *Hippospongia* spp., *Petrosia ficiformis, Ircinia variabilis, Anchinoe paupertas*	Sicily and Ligurian Coast	1986–1995	Generalised necrosis	Ovoid bacteria filled the canaliculi of exposed skeletal fibres	Gaino et al. (1992) and Rizzello et al. (1997)
Hippospongia spp., *Spongia* spp.	Mediterranean	1986–1990	Generalised necrosis	Unidentified bacterium burrowing through tissues and white film postulated to be an *Oscillatoria* spp.	Economou and Konteatis (1988), Vacelet (1994), and Vacelet et al. (1994)
Geodia papyracea	Belize	1985	Generalised necrosis	Tissue decay attributed to a Cyanobacterium	Rützler (1988)

(continued)

Table 9.1 (continued)

Sponge species	Geographic location	Year(s)	Disease name	Microbial characterisation	References
Iotrochota spp., *A. compressa, Aplysina fulva, Callyspongia vaginalis, Niphates* spp., *Xestospongia* spp., *Verongula rigida, Ircinia* spp.	Panama	1984–1995	Generalised necrosis	None	Wulff (2006a, b, 2007)
Hippospongia spp.	Caribbean	1938	Generalised necrosis	Fungi always present in diseased specimens	Galstoff (1942) and Storr (1964)
Commercial sponge spp.	British Honduras	1939	Generalised necrosis	Unbranched fungal filaments between live and dead tissue	Walton Smith (1939) and Smith (1941)
Commercial sponge spp.	Cuba	1939	Generalised necrosis	Unidentified fungal filaments in diseased specimens	Galstoff et al. (1939) and Smith (1941)
Commercial sponge spp.	Bahamas	1938–1939	Generalised necrosis	Unidentified fungal filaments in diseased specimens	Galstoff et al. (1939) and Smith (1941)
Commercial sponge spp.	Florida Keys	1939	Generalised necrosis	Unidentified fungal filaments in diseased specimens	Smith (1941)
Hippospongia equina	Tunisia	1906	Generalised necrosis	None	Allemand-Martin (1906, 1914)
Commercial sponge spp.	Florida	1895	Generalised necrosis	None	Brice (1896)
Ircinia spp.	Indian Ocean	1884	Generalised necrosis	Fungal filaments in diseased tissue	Carter (1878)

Disease syndromes that were not originally named when published have been assigned the disease name of generalised necrosis. Diseases prior to 2006 were previously reported in Table 1 of Webster (2007)

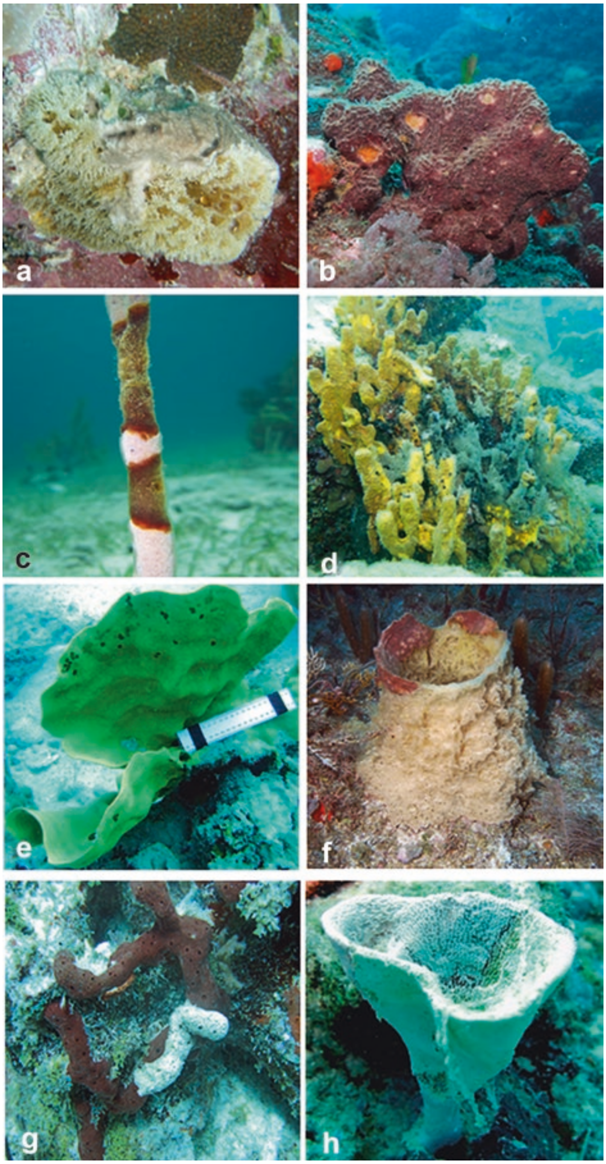

Fig. 9.1 Images showing a wide range of sponge disease symptoms: (**a**) sponge-boring necrosis in the GBR sponge, *Rhopaloeides odorabile*; (**b**) *Ircinia* pustule disease affecting populations throughout the Mediterranean and Africa (photo: Luis Sanchez, UG and Manuel Maldonado, CEAB-CSIC); (**c**) Aplysina red band syndrome (photo: Julie Olson); (**d**) black patch disease in *Aplysina aerophoba* (photo: Joana Xavier); (**e**) brown spot syndrome in the GBR sponge, *Ianthella basta*; (**f**) sponge orange band/bleaching in *Xestospongia muta* populations in the Florida Keys and Bahamas (photo: Joseph Pawlik); (**g**) sponge white patch affecting *Amphimedon compressa* in the Florida Keys (photo: Hilde Angermeier); and (**h**) suspected disease in *Carteriospongia foliascens* on the GBR (photo: Craig Humphrey)

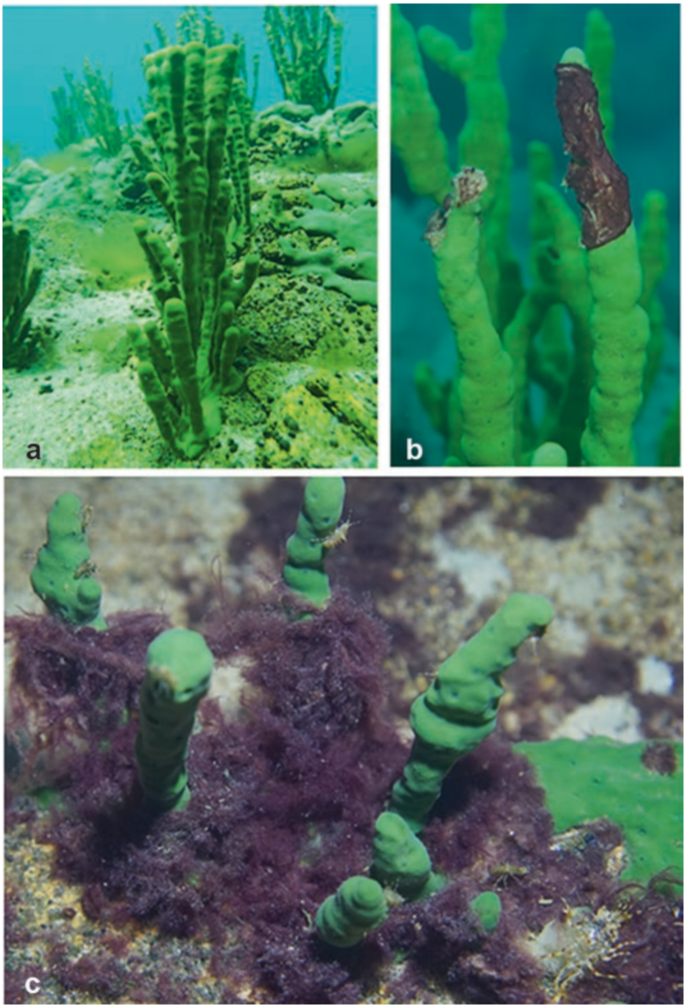

Fig. 9.2 The first reported freshwater sponge disease affecting populations of *Lubomirskia baicalensis* endemic to Lake Baikal, Russia. (**a**) Healthy individual with normal green pigmentation, (**b**) diseased individual displaying pink-red colouration and (**c**) advanced stages of disease. Photo: Igor Khanaev and Sergei Belikov

primary cause of pathogenicity (Choudhury et al. 2015). Although elevated seawater temperature has been shown to increase the virulence of some coral pathogens (Kushmaro et al. 1997; Toren et al. 1998), this was not the case for NW4327 which displayed the highest collagenase activity at ambient seawater temperatures (Mukherjee et al. 2009; Choudhury et al. 2015).

In 2013, a disease epidemic was reported in the Maldives affecting between 30 and 36% of the *Callyspongia (Euplacella)* aff. *biru* population (Sweet et al. 2015). The disease was characterised as ‘sponge necrosis syndrome’, and monitoring revealed a disease progression rate of 0.34 ± 0.08 cm d^{-1}. In addition, the authors identified a combination of one *Rhodobacteraceae*-affiliated bacterium (GenBank Accession No. KP001553) and one *Rhabdocline*-affiliated fungus (GenBank Accession No. KP001552) capable of inducing the syndrome in healthy individuals (Sweet et al. 2015). This is only the second study to successfully confirm the aetiological agent of disease.

Sponges host highly complex communities of symbiotic bacteria and archaea (Thomas et al. 2016) which can make identifying causative agents of disease particularly difficult. Defining the disease aetiology is further complicated by the fact that sponge skeletons can rapidly degrade after mortality, leaving behind no signs that a disease event has occurred. Whilst there are only two confirmed cases where sponge disease has been linked to a specific pathogen, there are numerous examples in which putative pathogens have been linked to disease symptoms but not unequivocally identified or verified as primary pathogens. For instance, disease in many dictyoceratid species was commonly associated with an unidentified bacteria burrowing through the sponge fibres (Vacelet et al. 1994; Gaino and Pronzato 1989). In addition, in the Western Mediterranean and African coasts, an epidemic of 'pustule disease' severely affected populations of *Ircinia* spp. throughout 2008–2009 (Maldonado et al. 2010). As the name suggests, symptoms include small pustules on the sponge surface, which eventually unite to form large necrotic lesions (Fig. 9.1b). The infection process advances from the outside to the inner sponge body, and infected sponges appear to employ a primitive immune response involving laying down concentric barriers of collagen to stop the spread of the disease. This was the first study to describe a host mechanism for combatting an infection. Whilst no molecular microbial characterisation was undertaken, extensive transmission electron microscopy (TEM) investigations revealed the consistent presence of a bacterium with twisted rod morphology that may have been responsible for the infection. Disease outbreaks have continued to impact *Ircinia* in the Mediterranean with recent bacterial analyses revealing an early disruption in the microbiome of healthy sponges which leads to a decline in host health, thereby increasing the susceptibility to infections through opportunistic pathogens (Blanquer et al. 2016).

Aplysina red band syndrome (ARBS) is a disease affecting *Aplysina* sponges throughout the Caribbean (Olson et al. 2006; Gochfeld et al. 2007; Olson and Gao 2013). Symptoms of this syndrome include a rust-coloured leading edge often followed by a trail of necrotic tissue (Olson et al. 2006) (Fig. 9.1c). Microscopic examination of affected sponges revealed the consistent presence of a cyanobacterium within the red band although its role in disease causation is still unknown (Olson and Gao 2013). Black patch disease also affects *Aplysina* sponges, with over 40% of the *Aplysina aerophoba* population in Slovenia affected by this disease (Webster et al. 2008b) (Fig. 9.1d). Microbial profiling of healthy and black patch-affected sponges revealed multiple sequences that were only present in diseased *A. aerophoba*, including a Deltaproteobacteria with similarity to a strain implicated in coral black band disease (Webster et al. 2008b).

A disease syndrome affecting the abundant sponge species *Ianthella basta* has been reported from reefs throughout the GBR, Torres Strait and Papua New Guinea (Cervino et al. 2006; Luter et al. 2010a, b) (Fig. 9.1e). Sponges displaying symptoms of brown spot lesions and necrosis were identified in 43 and 66% of the surveyed populations in the Palm Islands and Torres Strait, respectively (Luter et al. 2010b). Comprehensive comparisons of diseased and healthy individuals using various molecular and microbiological techniques were unsuccessful at revealing any primary pathogens. Moreover, infection trials failed to successfully transmit brown spot lesions to healthy individuals, even after physical damage (Luter et al. 2010a).

Giant barrel sponges in the Caribbean (*Xestospongia muta*) are also displaying signs of a disease commonly referred to as sponge orange band syndrome (SOB) (Fig. 9.1f), which occurs in conjunction with fatal bleaching (Cowart et al. 2006). Microbiological examinations of SOB-affected individuals show destruction of the pinacoderm, and microbial profiling concomitantly revealed a shift in the cyanobacterial community away from the clade of sponge-specific symbionts (e.g. *Synechoc occus/Prochlorococcus*) known to inhabit healthy individuals towards nonspecific cyanobacteria reflecting the community of the ambient environment, including lineages such as *Leptolyngbya* which have been associated with coral disease (Angermeier et al. 2011). Similarly, *Amphimedon compressa* in the Caribbean are displaying symptoms of a new sponge disease called sponge white patch (SWP). Diseased specimens possess distinctive white patches on their branches (Fig. 9.1g), with TEM detecting a spongin-boring bacterium similar to that reported by Webster et al. (2002) and microbial profiling revealing a distinct community shift in diseased individuals (Angermeier et al. 2012). However, no putative pathogens have yet been described for SOB or SWP, and infection assays with healthy *X. muta* and *A. compressa* have been similarly unsuccessful at transmitting the disease.

The first comprehensive microbial comparison of a disease outbreak in a freshwater habitat revealed that diseased *L. baicalensis* individuals (Fig. 9.2b,c) were dominated by *Synechococcus* and had higher relative abundances of Verrucomicrobia compared to healthy individuals (Denikina et al. 2016). In this instance, the authors suggested that the shift in the microbial community of diseased individuals might be a result of increased methane production in Lake Baikal. In addition to disease, bleaching has also been reported in this endemic species, with bleached patches characterised by dominance of cyanobacterial sequences and lower abundances of Bacteroidetes and Betaproteobacteria than their healthy counterpart (Kaluzhnaya and Itskovich 2015).

In addition to the published literature, anecdotal reports of disease-affected sponges are also increasing. For example, images of the dominant reef species *Carteriospongia foliascens* show affected individuals with a white bacterial mat and necrosis (Fig. 9.1h). Furthermore, Deignan and Pawlik recently described a new disease 'agelas wasting syndrome' in *Agelas tubulata* at the 2016 International Coral Reef Symposium (Abstract ID 28815).

However, the frequent failure to identify specific causative agents combined with the general inability to transmit infection to healthy individuals suggests that microorganisms may not always be responsible for disease-like symptoms. Alternatively, some diseases or disease-like syndromes may be a result of complex functional interactions occurring within the holobiont, and future experimental research is required to generate a better understanding of the links between host health, symbionts, pathogens and the environment.

9.3 Environmental Stress and Disease Symptoms

There is some evidence for correlations between sponge disease and environmental factors such as elevated temperatures and urban/agricultural runoff. Mass sponge mortalities have occurred during abnormally high seawater temperatures (Vicente 1990; Vacelet 1994; Vacelet et al. 1994; Cerrano et al. 2001), including a recent die-off that affected 80–100% of the *I. fasciculata* populations in the Western Mediterranean (Cebrian et al. 2011). Similarly, an outbreak affecting three dictyoceratid sponge species in the north Adriatic Sea was directly correlated with high seawater temperatures in conjunction with calm seas, with 22% of sponges displaying disease symptoms (Di Camillo et al. 2013). Whether these mortality events involve pathogenic agents, cause a breakdown in important microbial symbioses or relate solely to exceeding the sponge's physiological thresholds is a critical question for future research.

Being active filter feeders with few external barriers, sponges and their symbionts need to be able to acclimate to the local conditions of their environment. Environmental disturbance is known to destabilise host-bacterial associations and likely contributes to declining host fitness as has been described for other systems such as the human microbiome (Cho and Blaser 2012).

Over the past decade, numerous studies have examined how sponge microbiomes respond to a suite of environmental pressures including temperature (López-Legentil et al. 2008, 2010; Webster et al. 2008a, 2011; Fan et al. 2012; Simister et al. 2012a, b), nutrients (Simister et al. 2012b; Luter et al. 2014), pH (Morrow et al. 2015), sediment loads (Luter et al. 2012; Pineda et al. 2015) and contaminants (Webster et al. 2001; Selvin et al. 2007; Saby et al. 2009; Tian et al. 2014). Whilst some species maintain remarkably stable microbial communities irrespective of environment and/or host health, others undergo major shifts in the microbiome, which often correlate with declining host health.

Elevated seawater temperature associated with global climate change is expected to have the largest impact on the health and microbiome dynamics of sponges and has therefore been the focus of most field-based and experimental research to date. For instance, the giant barrel sponge *Xestospongia muta* is known to be dominated by a *Synechococcus*-type cyanobacteria and a stable *Crenarchaeota* community consistent with the archaeal community found in other sponge species (López-Legentil et al. 2008, 2010). However, López-Legentil and colleagues demonstrate that this archaeal symbiosis is maintained when the sponge undergoes cyclical bleaching from which it is able to recover but shifts to reflect the archaeal community in the surrounding sediment when the sponges become fatally bleached (López-Legentil et al. 2010). This shift leads to an increased expression of *amoA*, likely a result of elevated ammonia associated with tissue death (López-Legentil et al. 2010). Similarly, changes in the microbiome of *Halichondria bowerbanki* occur when the sponge is exposed to seawater temperatures only 1–2 °C above ambient. This shift includes the disappearance of specific microbes from thermally stressed sponges and the appearance of new microbes, perhaps due to a rare species increasing in relative frequency within the microbial community (Lemonie et al. 2007). Major changes in the symbiotic microbial community have also been detected in the GBR sponge *R. odorabile* when adult sponges were exposed to temperatures of 33 °C. The microbiome shift included the immediate loss of the primary culturable symbiont, a rapid increase in Bacteroidetes and Firmicutes and the development of a microbial community reflecting that of diseased corals (Webster et al. 2008a). Importantly, these microbial changes were not observed when the sponges were exposed to sublethal temperature regimes (Simister et al. 2012a). In contrast to the adult sponges, larvae of the same species exhibit a markedly higher thermal tolerance, with adverse health effects and accompanying microbial shifts not occurring until 36 °C (Webster et al. 2011). These studies revealed distinct thermal tolerances in each of the *R. odorabile* life history stages and confirmed that the *R. odorabile* larvae can maintain highly stable symbioses at seawater temperatures exceeding those predicted under climate change. Whilst experimental research has not revealed a direct link between environmental stressors and specific disease symptoms, the shifts in sponge-associated microbial communities that occur in conjunction with necrosis and mortality of the host provide for a strong link between host health and the stability of symbiont communities.

Coastal marine systems are increasingly being exposed to rising levels of nutrients, sediments and pollutants from terrestrial runoff, particularly with more frequent storm events associated with climate change (Fabricius et al. 2014). In fact, nutrient-rich runoff has been linked with facilitating disease outbreaks in coral populations (Haapkylä et al. 2011), as well as increasing the virulence of coral-associated pathogens (Bruno et al. 2003). Conversely, no positive links have been made between sponge disease outbreaks and/or pathogen virulence and eutrophication. In fact, the only study to examine the potential effects of elevated nutrients on disease progression found that ARBS lesions in *Aplysina cauliformis* progressed no faster when exposed to high levels of nitrogen (Gochfeld et al. 2012). In addition, experimental studies examining the impacts of elevated nutrients on various sponge species have described no adverse effects on host health (Simister et al. 2012b; Luter et al. 2014), indicating nutrients alone may not lead to increased incidences of disease in sponge populations.

In comparison to thermal stress and eutrophication, little is known about how sponges will respond to ocean acidification (OA), and there are currently no studies that directly link OA to sponge disease. Surveys of sponges at volcanic CO_2 seeps have reported both increased (Goodwin et al. 2013) and decreased (Fabricius et al. 2011) sponge diversity at low pH sites, shifts in abundance of some sponge species between high and low pH sites (Morrow et al. 2015) and changes in the host-associated microbiomes of some sponge species (Morrow et al. 2015). However, none of these studies reported any adverse health effects evident in sponges at low pH environments. Similarly, with the exception of reduced spicule biomineralisation in *Mycale grandis* (Vicente et al. 2015) and reduced growth rates in *Chondrosia reniformis* (Ribes et al. 2016) at elevated $p\mathrm{CO}_2$ conditions, experimental research has demonstrated little adverse impact of OA (Wisshak et al. 2012; Duckworth and Peterson 2013; Fang et al. 2013). Importantly, a recent study by Bennett and colleagues which explored the interactive effects of elevated seawater temperature and $p\mathrm{CO}_2$ on four different GBR sponge species found that elevated $p\mathrm{CO}_2$ alone did not cause any sponge stress, but the interactive effects of temperature and $p\mathrm{CO}_2$ varied according to nutritional mode, with elevated $p\mathrm{CO}_2$ exacerbating temperature stress in heterotrophic species but mitigating temperature stress in phototrophic species (Bennett et al. 2016). It is therefore not expected that OA alone will be a major driver of future disease outbreaks.

Whilst many studies have assessed changes in sponge microbiomes in response to environmental stressors, very few studies have established cause-effect pathways for environmental stress-related dysbiosis. A notable exception was a thermal stress study which employed expression profiling of the host in conjunction with phylogenetic, functional and expression analysis of the symbiont community (Fan et al. 2013). Persistent exposure to elevated seawater temperature altered the sponge-associated microbial community of *R. odorabile* from one with predominantly symbiotic functions to one characterised by opportunistic bacterial functions. Importantly, sensitive host gene expression and metaproteomic analyses revealed that thermal stress triggered an immediate stress response in both the host and symbiont community which involved a decrease in expression of functions that mediate the holobiont symbiosis. For example, the nutritional interdependence between host and symbionts was disrupted, and an array of other molecular interactions were affected including reduced expression of transporters involved in the uptake of sugars, peptides and other substrates. These changes occurred in immediate response to heat stress and likely lead to destabilisation of the holobiont and subsequent loss of the stable microbiome and the introduction of new microorganisms with functional and expression profiles indicative of a scavenging lifestyle (e.g. a lack of virulence functions and high growth rates) (Fan et al. 2013).

9.4 Conclusion

Since the comprehensive review of sponge disease in 2007 (Webster 2007), there have been nine additional disease syndromes described globally, as well as numerous unpublished descriptions of ‘disease-like’ symptoms. This trend highlights how sponge disease continues to pose a threat, not only to coral reefs but also to sensitive freshwater habitats. However, recent developments in DNA and RNA sequencing, advanced imaging technologies and state-of-the-art experimental aquarium facilities now provide the community with a set of customised tools for investigating the causative agents of sponge disease and exploring the interaction between climate stressors and disease events. In addition, future research should focus not only on describing the microbial community shifts associated with declining sponge health but also explore the complex molecular interactions occurring between the host and the microbial community using a holobiont research approach (Webster and Thomas 2016). Understanding the environmental forces that influence the diversity, specificity and function of microbial symbionts, including analysis of the molecular pathways mediating holobiont health and stability, will be critical for determining how sponge populations will respond to future disease epidemics in a rapidly changing ocean. Furthermore, the advent of bioinformatic tools such as HoloVir (Laffy et al. 2016) opens the door for future research to better explore the potential role of viruses in sponge disease processes, which to date have received little attention.

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Chapter 10
Sponge Reefs of the British Columbia, Canada Coast: Impacts of Climate Change and Ocean Acidification

K.W. Conway, F. Whitney, S.P. Leys, J.V. Barrie, and M. Krautter

Abstract Sponge reefs living in deeper shelf waters on the western margin of North America are somewhat insulated from surface water effects of localized ocean warming but are susceptible to increasing hypoxia associated with ocean stratification and increasing upwelling. The largest reef complexes are projected to experience increasing upwelling and low-oxygen events in the future as part of the observed and projected changes in ocean ventilation accompanying increased atmospheric carbon dioxide concentrations. Inshore and shallow reefs are subjected to surface water warming in fiords. Surface water productivity is anticipated to change slightly likely having limited negative impact on the sponge reefs which are adapted to relatively low-nutrient situations. It is unknown the extent to which glass sponges might be resilient to lower oxygen conditions. While filtration is an energetically costly method of feeding, glass sponges appear to be adapted to reduce their energetic needs by using ambient flow to assist filtration. Populations that experience extreme hypoxia in some fiords may be extirpated by extreme anoxic events. Ocean acidification will not have as large an effect on the siliceous skeleton sponges as it will on corals and other carbonate-dependent organisms though it is possible changing pH will affect tissue functioning and homeostasis by compromising membrane pumps. Hexactinellid sponges and sponge reefs have been resilient to changing climate and ocean environments in the geologic past.

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Keywords Porifera • Deep water • Hexactinellids • Hypoxia

10.1 Introduction

Framework reefs constructed by hexactinellid sponges of the order Hexactinosida are found on the continental shelf of British Columbia and in fiords along the entire mainland coast from Howe Sound to Lynn Canal, Alaska, a distance of roughly 1300 km (Fig. 10.1). They are found in water depths of 20–240 m and form mounds (bioherms), meadows (biostromes), or ridges (Conway et al. 1991, 2005). They can occur as a small reef of a hectare in size to reef complexes hundreds of km^2. The reefs form long-term and stable benthic communities and are thought to have been growing since the stabilization of modern sea levels and oceanographic conditions approximately 9000 years ago (Krautter et al. 2001). Habitat requirements include exposed glaciated surfaces that are gravel-rich, elevated silicic acid nutrient concentrations with no wave energy at the seabed. Suspended sediments rich in flocculated organic matter and moderate tidal currents are also normally associated with reef sites (Whitney et al. 2005a). The reefs have been mapped using multibeam bathymetric and other acoustic methods, and spatial resolution of their deeper water distribution is readily assessed (Conway et al. 2005). Glacial shelf crossing troughs and elevated locations in fiord settings are preferred growth sites where isolation from basin sedimentation and also access to current feeding opportunities are augmented by topographic position. The glacial erosion of the broad troughs provided the flat seabed areas for extensive reef development seen in the very large reef complexes of the continental shelf. Although coastal BC was carved and topographically steepened, while fiords were overdeepened by glaciers, the effect of the glaciers on the shelf paradoxically created a very low-slope shelf ramp that is the ideal situation for the development of extensive siliceous sponge reefs (Leinfelder et al. 1994). Reefs have not been found in the open exposed western shelves of Vancouver Island or Haida Gwaii nor in the fiords that have their termini in these shelf settings.

The reefs have apparently survived changes to the coastal ocean climate system imparted by climatic events during the Holocene, including the Holocene hypsithermal and other warm and cold intervals and the Pacific Decadal Oscillation and ENSO cycles. The deep shelf benthic situation of the reefs presumably renders them insulated from perturbations that are more immediately and directly experienced by biota in surface waters. The sponges are efficient sediment traps that baffle seafloor tidal currents and the organic-rich-flocculated marine snow arriving from surface water productivity that accumulates on the reef surface. The rate of growth of the reefs is unknown, but the largest reefs may grow as fast as 12 m vertically in 3000 years (Stone et al. 2014).

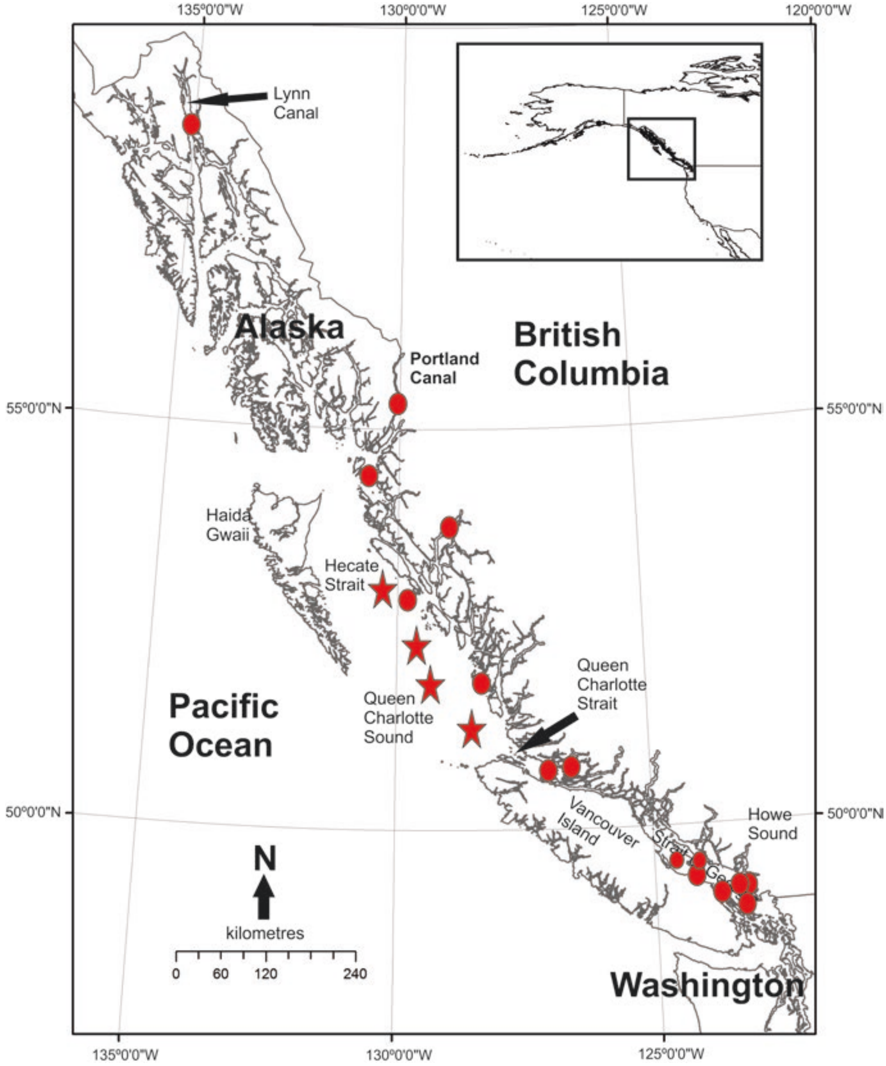

Fig. 10.1 Location of known sponge reefs on the Pacific margin of North America. *Red star symbols* indicate large reef complexes and *red dots* smaller reefs

10.2 Sponge Reefs and Changing Postglacial Climates

The existence of the modern sponge reefs is due to climatic change at the close of the last glaciation that caused ice margins to recede from continental shelves. Without the foundation of glacial deposits left in deep water after extensive glaciation during the late Wisconsinan ice advance, reefs would not be possible. The seabed hosts many glacial landforms including glacial flutes and drumlins as well as ground and terminal moraine deposits. Especially important to the development of the shelf sponge reefs are iceberg furrows which are common in the area where the reefs are found. The three reef-forming species require hard substrate to grow upon and cannot anchor in soft sediments such as sand or mud (Reiswig 2002). The coarse boulder margins of the furrows (Conway et al. 1991) are optimal initiation sites of sponge growth and subsequent reef development. In addition, the berms of iceberg furrows provide a raised surface off the generally flat seafloor. Observations from newly created scours on the Labrador shelf indicate that berm heights may reach 6 m (Josenhans and Barrie 1989). With time the berms are reworked, and in areas where a significant coarse sediment component exists, a lag of gravel, cobbles, and boulders is formed. In the southern reef areas within the Strait of Georgia, the reefs are situated on the top of ice-streamlined banks or drumlins such as the Fraser Ridge (Conway et al. 2004) or Halibut and McCall Bank (Conway et al. 2005) that originated during glaciation of the Georgia Basin. In fiords terminal moraines or elongate ice-streamlined banks are sites where reefs develop (Stone et al. 2014). Future changes to ice distribution in Alaska may open new sponge reef habitat as ice recedes from fiords. The habitat may expand as roughly 60 tidewater glaciers recede from seaward termini exposing new areas for reef development on moraines and banks. Sea level adjustments normally accompany ice recession in the fiords as isostacy accounts for loading from ice mass reduction. In addition sedimentation rates are often very high at ice front positions. As ice moved offshore from the Coast Mountains of the Canadian Cordillera, it only covered portions of the continental shelf with different timings, depending on region. With climate warming deglaciation of the Pacific North Coast was rapid with an eastward-retreating ice shelf rapidly depositing sediment and producing icebergs, while in the Strait of Georgia, ice mostly remained in place with rapid downwasting and limited sediment deposition (Barrie and Conway 2002). Consequently, resulting sea level change is both rapid and heterogeneous. On the Pacific North Coast, isostatic rebound occurred after deglaciation at the western extreme, while close to the thick ice load of the cordilleran ice sheet, the crust remained depressed (Hetherington and Barrie 2004). Changing sediment supply with sea level regression resulted in the formation of large outwash plains, channel systems, deltas, wave-cut terraces, and areas of limited to no deposition (Barrie and Conway 2013). Subsequent transgression drowns these coastal features, redistributing the sediment, and ultimately cuts off sediment supply to the shelf. This resulted in some extensive areas of exposed iceberg-furrowed glacial deposits, ideal for the generation of sponge reefs. In the Strait of Georgia, sea level fell and most deposition was in the deeper waters leaving the raised glacial features exposed. Consequently, a changing climate resulted in a rapid change from an ice-covered continental shelf to an exposed shelf on the North Coast and deeply submerged Strait of Georgia, to near present conditions in less than 2000 years. The exposure of glacial and deglacial features, such as drumlins and iceberg furrows, in a submerged shelf environment provided the seed habitat for sponge reef formation, similar to what is happening at a smaller scale in Alaskan fiords today (Barclay et al. 2009). Glass sponges, recruited from the south and from slope depth waters, would have rapidly colonized the newly available habitat as ice receded from the shelf.

Under modern conditions, the Fraser River delta has expanded during the Holocene into the deep water of the Strait of Georgia. As the suspended plume is transported north by flooding tide, the sediments are mantling glacial banks such as Halibut and McCall Bank. Fraser Ridge is a prominent glacial streamlined knoll that hosts sponge reefs in the midst of the expanding delta. As the river delta expands, sponge reef habitat will be buried by the prodelta sediments.

10.2.1 Hexactinellid Sponges and Sponge Reefs in Earth's History: Ancient Ocean Environments

Hexactinellid sponges are the first-known multicellular organisms in Earth's history. This implies a very significant resilience in the face of environmental changes and challenges. They occur in deposits of Ediacaran age (late Proterozoic, >542 million years) (Gehling and Rigby 1996). In the oldest sponge taxa, their lyssacinosidan spicules were isolated and not yet fused together to a rigid skeletal framework. In the late Devonian, another hexactinellid sponge group evolved: hexactinosidan sponges. Their characteristic skeletal architecture consists of fused hexactine spicules so forming a rigid and stable skeleton which stays intact as a whole after the death of the individual sponge. The acquisition of this feature was fundamentally important for a reef-building potential of this sponge group. Several extant genera originated in the Mesozoic including two of the three genera involved in modern BC bioherm construction (*Aphrocallistes* and *Heterochone*) which appeared in the Cretaceous (Krautter 2002), an indication of the conservative and long-term successful life histories of these sponges. The fused skeletons act as a hard, firm substrate on the seafloor. Hexactinosidan larvae require hard substrate as the larvae are not able to settle on an unconsolidated soft or muddy seafloor. In the Late Triassic of China, the first modern sponge reefs occur (Wendt et al. 1989). They are very similar to the Late Jurassic sponge reefs in regard of facies, architecture, and faunal assemblage. In the course of the Late Jurassic, the glass sponge reefs spread out on the tectonically stable northern shelf of the Tethys and reached their widest spatial distribution in the late Oxfordian (Krautter 1997, Krautter et al. 2001, and references therein), where they formed a discontinuous deepwater siliceous sponge reef belt, which was the largest bioconstruction that ever existed in Earth's history (Fig. 10.2). The ocean conditions which supported this vast sponge reef belt were inferred to have been a broad low-slope shelf with a more stratified ocean than today with sluggish ocean circulation partly driven by evaporation with some upwelling of lower oxygen waters (Leinfelder et al. 1994) onto the sponge reef shelf habitat. The temperature during this time period is thought to have been at least as warm as existing Pacific Ocean temperatures at the sponge reefs because of the proximity of well-developed carbonate platform and coral reefs that were abundant in a belt

Fig. 10.2 Distribution of sponge reefs (*red tone*) during the Upper Jurassic (Hogg et al. 2010)

inshore of the Jurassic sponge reefs. Periodic very low oxygen conditions caused these sponge reefs to be replaced by microbial reefs (thrombolites).

After Jurassic times, there was a remarkable decline in the distribution of hexactinosidan reefs. In the Cretaceous, glass sponge reefs are known mostly from Central and Western Europe. The steady decline of deepwater siliceous sponge reefs continued during the Paleogene and finally comes to an end in the Middle Paleocene. No younger fossil siliceous sponge reefs have been described, and—until the discovery of the reefs off British Columbia—it was thought that this reef type created by glass sponges had become extinct (Krautter et al. 2001). Fossil and recent sponge reef-associated benthos include sponge-encrusting fauna mainly consisting of serpulids, foraminifera, brachiopods, bryozoans, echinoderms, and bivalves to a minor degree. The ecological niche of the glass sponge reefs off British Columbia can be characterized as ultraconservative, as it has not changed over more than 220 million years (Krautter et al. 2006).

10.2.2 Overview of Environmental Controls of Sponge Reef Distribution in the Upper Jurassic

During the Late Jurassic, a stratified Tethys Ocean was present (Leinfelder et al. 1994; Danise et al. 2015). This time interval has been regarded as the time of maximum sponge reef success (Leinfelder et al. 2002). Upwelling of hypoxic waters has been inferred for portions of the northern shelf of the Tethys where sponge reefs were most common during the Upper Jurassic (Fig. 10.2). Some authors propose decoupling of the direct effects of warming on benthic communities and propose indirect effects (such as hypoxia) as being more important (Danise et al. 2015). Reduced or fluctuating oxygenation has been correlated in some studies with eventual replacement of siliceous sponge reefs with microbial reefs (Leinfelder et al. 1994 and references therein). In summary the time of maximal sponge reef distribution occurred during a period with a warmer, more stratified ocean during a time of an inferred "greenhouse climate" with at least periodic low-oxygen upwelling events. The widespread Jurassic sponge reefs thus thrived in a relatively warm and, at least periodically, low oxygen setting. An important difference with today is that the Late Jurassic Tethys Ocean was strongly buffered against ocean acidification along the Tethys margins by so-called alkalinity pumps that were generated by anaerobic basins in the opening Atlantic margin (Leinfelder et al. 1994 and references therein).

10.3 Oceanographic and Contemporary Climate Trends

10.3.1 Shelf Circulation

In the North Pacific, the eastward-flowing subarctic current splits several hundred kilometers from the coast into the Alaska and California Currents (Fig. 10.3). A major gyre in the NE Pacific, the Alaska gyre, upwells deep, nutrient-rich waters toward the ocean surface. Ocean ventilation is weak in this region, creating an oxygen minimum zone in which concentrations below 500 m are <40 μM (Whitney et al. 2007). Along the North American coast, the California Current mixes with the California Undercurrent (CUC) as it flows northward from Mexico, which further decreases oxygen levels in BC shelf and slope waters. The CUC is a major component of subsurface waters found along the outer coast of southern BC. In this region, oxygen drops below 60 μM (a concentration which is hypoxic to many marine animals, Gray et al. 2002) at between 120 and 400 m, depending on the season and location (Crawford and Pena 2013).

On the BC North Coast (Queen Charlotte Sound, Hecate Strait, and adjoining inland waters), the influence of the CUC is weaker, comprising 30–40% of continental slope waters below the mixed layer (Thomson and Krassovski 2010). The broadly open shelf behaves like an estuary in summer, with fresh surface waters flowing toward the ocean and deep waters flowing landward through canyons. In winter, downwelling winds reverse this flow pattern (Whitney et al. 2005a).

During the strong El Niño in 1998, a mesoscale eddy transported a large portion of the North Coast shelf water to open ocean (Whitney and Robert 2002). Depending on their trajectory and time of formation, these eddies could export larval communities from the BC coast toward SE Alaska or open ocean.

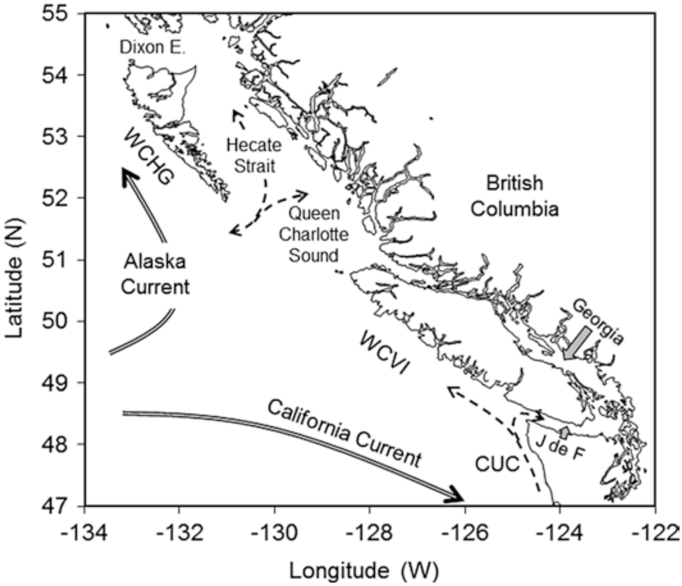

Fig. 10.3 Coastal British Columbia where both coastal (surface, *thin lines* of WCVI and WCHG; subsurface, *dashed lines* entering Juan de Fuca and Hecate Straits) and oceanic (*double lines*) currents determine the composition of coastal waters. Some place names are abbreviated: *J de F* Juan de Fuca Strait, *Georgia* Strait of Georgia, *CUC* California Undercurrent, *WCVI* west coast of Vancouver Island, *WCHG* west coast of Haida Gwaii, *Dixon E.* Dixon Entrance

Nutrient supply from winter storms, tidal mixing, and estuarine circulation maintain high levels of primary productivity along the BC coast from spring through fall (Whitney et al. 2005b). The most productive regions occur at the southern and northern ends of Vancouver Island, where tidal mixing and estuarine flow discharge nutrient-rich waters onto the outer shelf. The Strait of Georgia (SoG) is also a highly productive region as a result of the estuarine circulation forced by freshwater discharges from land. A buoyant surface layer flows toward open ocean, creating a return flow of nutrient-rich waters at depth. Waters are mixed from top to bottom in tidal passes before entering the SoG. Summer upwelling supplies cooler, more saline water to the BC shelf. These waters flow into Juan de Fuca Strait where they are lightly mixed on neap tides to produce the densest waters of the year. Basin waters in the SoG and adjacent inlets are typically replaced in late summer with waters low in oxygen (Pickard 1975). Occasionally, coastal upwelling is weak enough that basin renewal does not occur (perhaps a consequence of weaker coastal upwelling during an El Niño). Some southern BC fiords may experience severe hypoxia and sponge mortality in deep waters as a consequence (Leys et al. 2004). In the southern SoG, late spring productivity is controlled by the muddy waters of the Fraser River which both stratify the surface layer and reduce light levels. The Fraser is a large source of dissolved Si to coastal waters, an essential glass sponge nutrient (Whitney et al. 2005b).

10.3.2 Climate Changes on the BC North Coast and in Adjacent Inlets

The largest of the sponge reefs on the BC coast is found in troughs running into Hecate Strait and Queen Charlotte Sound, to depths where oxygen levels do not drop below ~60 μM (~250 m). Their upper limit is likely controlled by the depth of winter mixing (~150 m in Hecate Strait), which would isolate them from winter extremes. Thus, if their optimal habitat is one that is stable (low sedimentation), is protected from strong currents, receives a reasonable input of detrital organic matter to supply nutrition, has sufficient dissolved Si for growth (~40 μM), and does not go hypoxic (Whitney et al. 2005a; Leys et al. 2004), then changes to these conditions may stress them. Glass sponge sensitivity to ocean acidification is not understood. Silica deposition requires acidic vesicles and is not known to be impaired by acidic water; freshwater sponges, for example, produce siliceous spicules in ponds and rivers that often have a pH of 6. Still, a more acidic ocean (an ocean with higher levels of carbon dioxide) may impair sponge respiration and increase stresses caused by warming and low oxygen (Brewer and Peltzer 2009). The proton pumps used by plankton (Flynn et al. 2012), bacteria, and sponges to maintain tissue homeostasis, and to generate flagella beat, are adapted to present CO_2 levels; changes in pH are therefore expected to affect the sponge filtration activity as well as the availability of food. This is especially an issue if upwelling intensifies, bringing waters with higher CO_2 and lower oxygen levels onto the shelf in summer, or if a warming ocean releases substantial amounts of methane which will place a microbial demand on oxygen and add CO_2. The BC coast is known to store large amounts of methane (Capelle and Tortell 2016) and gas hydrates along the continental slope (Riedel et al. 2002).

Climate trends currently detected in the NE Pacific include warming, decreasing surface salinity, enhanced ocean stratification, strengthening upwelling at the northern extreme of the upwelling domain, decreasing oxygen levels at depth, and increased acidity of coastal waters (e.g., Whitney et al. 2007; Feeley et al. 2010; Whitney 2011; Rykaczewski et al. 2015). Sampling on the BC North Coast has been only sporadic over the past 60 years, making assessments of some trends suspect. Available data show surface warming (~0.7 °C/century) and loss of oxygen at depths where sponge reefs occur (Fig. 10.4). Oxygen losses cannot be quantified well from data collected in Hecate Strait, however, are calculated to be 0.5 to >1.2 μM/year in waters of sponge reef depth along the BC coast (Whitney et al. 2007; Crawford and Pena 2013; Whitney et al. 2013), and can be linked with reduced ventilation of the subarctic Pacific Ocean along the Russian coast. Warming is not apparent near Hecate Strait sponge reefs (Fig. 10.2), although it is observed at similar depths offshore (Whitney et al. 2007, 2013).

Oxygen levels are hypoxic to a wide variety of marine organisms (Gray et al. 2002) at maximum sponge reef depths (seasonally as low as 60 μM at 250 m depth, Fig. 10.4). Lowest concentrations occur during periods of summer upwelling (Whitney et al. 2005a) which means that any intensification of upwelling will likely

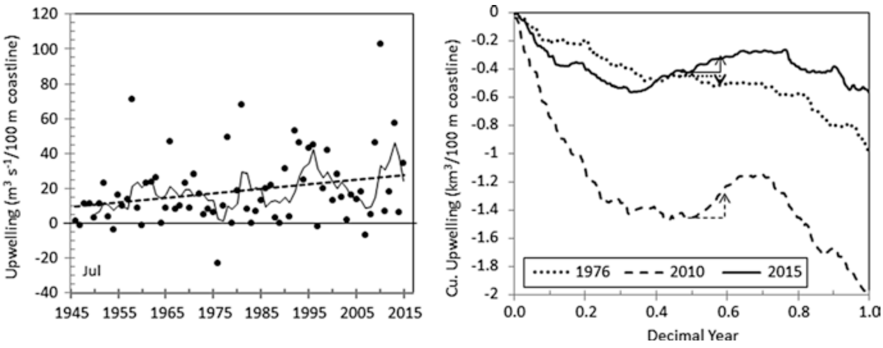

Fig. 10.4 Trends in temperature (*top*) and oxygen (*bottom*) in Hecate Strait (*left*) and Strait of Georgia (*right*) for depths shown in the legends. NCEP temperatures for February and August from 50.4 to 52 N and 129.4 to 131.2 W (*upper left panel*) show a warming trend in surface waters of 0.7 °C/century between 1946 and 2015. Deep waters in SoG are warming at 2.3 and 1.7 °C/century and losing oxygen at 0.75 and 0.69 μmol/kg/year at depths of 75 and 150 m between 1961 and 2011. The *dashed line* in the bottom, *left panel* indicates a level at which hypoxia is felt for many marine animals. Data are too sparse to assess trends in subsurface waters of Hecate Strait. Trends in temperature and oxygen in Hecate Strait and the Strait of Georgia

damage the deepest of this sponge community. Modeling suggests an intensification of the poleward extents of coastal upwelling regions (Rykaczewski et al. 2015). Using data from 51 N, 131 W (NOAA/NMFS data, www.pfeg.noaa.gov), upwelling trends are assessed over the period 1946–2015 (Fig. 10.5). On average, upwelling occurs from May through September, with significant change (intensification 1.4%/year) being observed only in July. In late September, a change in prevailing wind direction begins the winter downwelling season. The trend in fall months is toward weaker downwelling, but in winter (January–March) downwelling is strengthening by ~1%/year (data not shown). Sponge reefs will be threatened by hypoxia only during upwelling periods, with the persistence and strength of upwelling determining the impact. Along the Oregon Coast, extended periods of upwelling have decimated crab and fish communities in recent years (Grantham et al. 2004).

10.3.3 Climate Changes on the BC South Coast (Strait of Georgia and Adjacent Inlets)

Glass sponge communities are found in many BC fiords and in several sites within the Strait of Georgia Basin (Leys et al. 2004). Waters throughout this area are better oxygenated than on the North Coast due to the strong tidal mixing of deep waters flowing into the SoG basin (Johannessen et al. 2014). During mixing, waters exchange heat and oxygen with the atmosphere. Waters are also rich in dissolved Si due to riverine inputs (Whitney et al. 2005b). Trends in both temperature and oxygen are strong (Fig. 10.4) at sponge depths. Oxygen losses of ~0.7 μM/year are

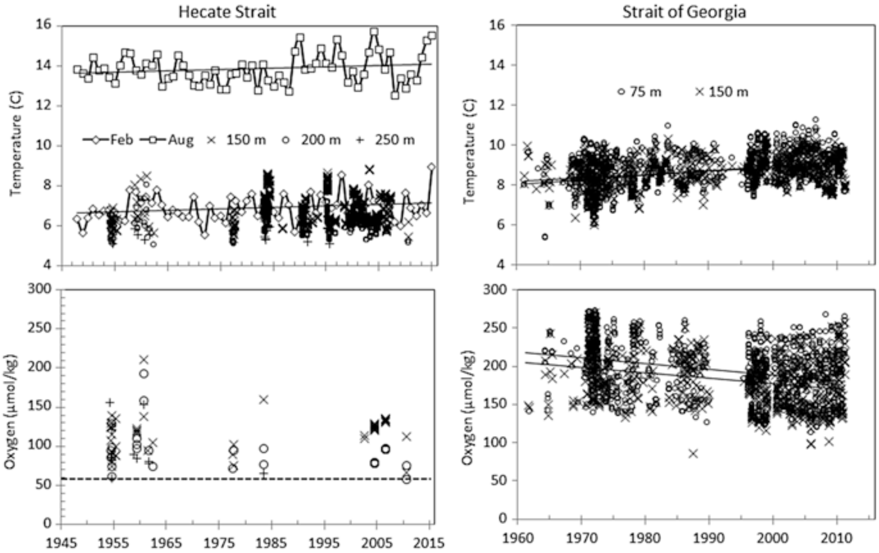

Fig. 10.5 *Left*, average upwelling rate for July from 1946 to 2015 at 51 N, 131 W. A linear regression (*dashed line*) shows upwelling increasing by 0.26 m^3/s/100 m of coastline. A 5-year smoothed line identifies periods of stronger or weaker summer upwelling. *Right*, cumulative upwelling over selected years. Winter downwelling generally abates in May and resumes in September. *Arrows* indicate July upwelling intensity, with downwelling occurring in 1976

similar to those found on the outer coast of Vancouver Island (Crawford and Pena 2013), and warming of 1.7 and 2.2 °C/century at 75 and 150 m is only slightly higher than what has been found in the NE Pacific (Whitney et al. 2007). Oxygen levels are higher in winter than summer but are declining more rapidly (0.9 and 1.5 µM/year at 75 and 150 m).

Warming rates of 1.5 °C/century in summer and 4 °C/century in winter (from Fig. 10.4) are substantially greater than what is observed in surface seawater and the atmosphere. Lighthouse observations in central SoG (1915–2015) show warming of 0.8 °C/century in February and only 0.07 °C/century in August (Departure Bay data, http://www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.html). Air temperatures are warming more in August (1.4 °C/century) than in February (0.8 °C/century) at a local weather station (Victoria International Airport, http://climate.weather.gc.ca). SoG winter warming at sponge depths must arise because either the waters are forming earlier in the fall when surface waters are warmer or the contribution of the warmer water mass is increasing.

Johannessen et al. (2014) point out that oxygen levels in SoG will not drop below ~90 µM because of the oxygenation occurring during mixing of inflow waters and thus should not stress most mid-water organisms. However, a combination of warming and oxygen loss may stress cool water organisms (see glass sponge biology below).

10.3.4 Other Climate Considerations

Measurements of ocean acidity along the BC coast are sparse. Surveys in recent years have shown that acidic waters upwell onto the shelf in summer (Feeley et al. 2010), causing considerable concern to shellfish industries. These studies and unpublished data (Ianson, personal communication) show that pH varies between 7.5 and 8.1 at depths where sponge reefs are found along the BC coast. Sponges in the Strait of Georgia experience greater acidity than those on the North Coast (by 0.1–0.2 pH units) but in waters that are better oxygenated.

Rising sea level will increase erosion in some areas. This may increase the amount of lithogenic material being transported to sponges in shelf canyons, thereby decreasing the nutritional content in suspended particles being transported to reefs. If sedimentation increases and growth slows due to poorer nutrition, or due to clogging if unable to arrest their feeding current (see above), sponge reefs may struggle to stay above deposited sediments. Sponges near the Fraser River delta, situated on a ridge in a sloping seascape, handle large fluxes of sediment. Local currents and the structure of a reef complex should control deposition among sponges.

Melting ice fields in BC and Alaska are increasing the supply of freshwater to the NE Pacific (Larsen et al. 2007), likely causing the declines being observed in surface salinity (e.g., Whitney 2011). The resulting increase in ocean stratification may lead to declines in nutrient supply to the mixed layer and consequently the productivity of the subarctic Pacific. In coastal waters, nutrition is largely dependent on tidal mixing, upwelling, and estuarine circulation. Changes in river discharge (e.g., less snowpack leading to weaker summer flow) or in upwelling (summer intensification) alter nutrient supplies. Tidal mixing will not be affected; thus, any productivity changes in coastal waters may be slight. Okey et al. (2014) reviewed possible climate impacts on the BC coast, summarizing the main impacts on sponge habitat (not specifically sponges) as warming, hypoxia, and acidification.

10.4 Biology of Glass Sponges and Climate Change: Vulnerability and Resilience

In addition to requiring elevated silica levels, hard substrates, and sediment to cement reefs together, glass sponge reefs benefit from elevated bathymetry where tidal currents provide a consistent directional flow. The need for steady ambient currents relates to the sponges' energetic balance: the energy it costs to filter the water and the energy gained by ingesting the bacteria filtered from the water. Glass sponges have very limited complement of microbial symbionts (they are "low microbial abundance" (LMA) sponges), and since dissolved organic carbon is negligible at the depths of the reef, bacteria make up all of the particulate organic carbon (POC) that the sponges feed on (Yahel et al. 2007). To extract bacteria from the water, the sponges generate a filtration current using flagellated "pump" cells that work in batteries (called chambers) to draw the water through the tissues. That activity is energetically costly and requires most of the energy attained by ingesting bacteria; a small portion remains for growth, repair, and reproduction (Leys et al. 2011).

At the depths of the reefs, the concentration of bacteria is about a tenth of that in surface waters, and so elevated bathymetry which enhances the ambient currents brings new water to replenish that grazed by the sponges, and at the same time, it generates resuspension of some bottom sediments rich with bacteria (Kahn et al. 2015). But perhaps most importantly, it allows the sponges to take advantage of viscous entrainment to process more water at the same or lower energetic cost (Leys et al. 2011).

The climate changes described above could potentially affect this very finely tuned balance in a number of ways. Any changes that resulted in lower productivity might reduce bacterial concentrations below the level that sustains sponge filtration, which would affect their scope for growth and reproduction. Although the reef-building sponges only use 0.5 μM of oxygen for each liter filtered, that amount is extracted from oxygen-rich water (120–140 μM) (Leys et al. 2011; Kahn et al. 2013); reduced ambient oxygen levels would be expected to make extraction of oxygen more difficult and drive up the cost of filtration.

Glass sponges are also particularly sensitive to temperature change ($Q_{10} = 3$) because of their electrical conduction system (Leys and Meech 2006). Glass sponge tissue is unique among multicellular animals in being largely syncytial, a tissue construction that allows them to propagate electrical signals that control and arrest the feeding current. Feeding current arrest occurs in response to irritation such as intake of sediment that presumably might damage their filter structures (Leys et al. 1999). The electrical conduction system is unusually sensitive to temperature. Below 7 °C the sponge *Rhabdocalyptus dawsoni* did not pump, and it was not until the temperature reached 10 °C that filtration started (Leys et al. 1999), but more importantly, in the same experiments, feeding arrests could not be evoked when the temperature was higher than 13 °C (Fig. 10.6; Leys and Meech 2006). In later work some sponges continued to arrest at temperatures as high as 19 °C (Tompkins-MacDonald in Leys and Meech 2006). Presumably different glass sponge species have different temperature sensitivities, but if reef sponges are less likely to be able to arrest their feeding current in warmer water, then they would be more susceptible to clogging and damage by sediment at higher temperatures. Whereas other sponges can remove particles by a series of contractions to expel the water (Ludeman et al. 2014), glass sponges do not contract, and so arresting their filtration current is their only protection against taking in damaging particles.

10.5 Summary and Conclusions

The main effects of climate change in BC coastal ocean may be an increased upwelling of oxygen-poor waters into the troughs of the northern shelf and warming of surface waters in the Georgia Basin and adjacent fiords. The large reef complexes are thus more subject to reduced oxygen concentrations than the Strait of Georgia reefs

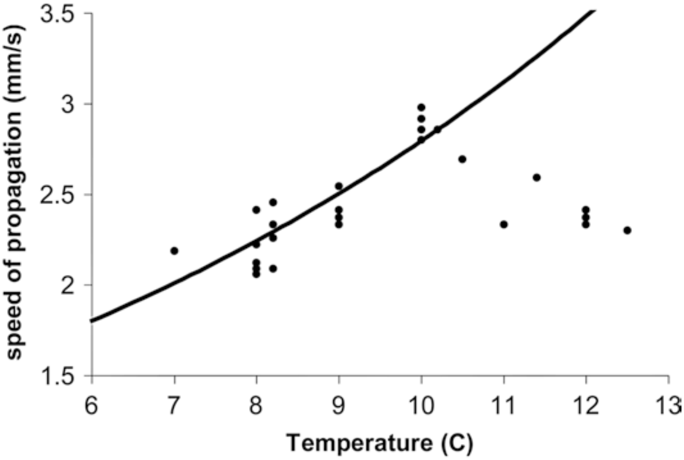

Fig. 10.6 The rate of propagation of action potentials through the glass sponge *Rhabdocalyptus dawsoni* is temperature sensitive ($Q_{10} = 3$). Sponges did not filter below 7 °C and were unable to arrest their feeding current at temperatures above 12.5 °C. Distribution of Upper Jurassic siliceous sponge reefs

(Fig. 10.7) since they are more exposed to the effects of an increasingly stratified ocean and episodic or long-term changes in summer upwelling. While fiord sponge communities in southern BC may be most at risk from warming in shallow water, reduced dissolved oxygen concentration that will occur in waters deeper than sponges is found. A very small increase in potential sponge reef habitat is anticipated in the next century as tidewater glaciers recede in Alaskan fiords. The degree to which sponge reefs are susceptible to oxygen depletion is not known, but it is possible that local populations in some fiords may face extirpation with warming and greatly reduced dissolved oxygen levels. It is probable that taxa which utilize the sponge reefs such as rockfish species and some invertebrates will be impacted by low oxygen before the reef-forming sponge species are themselves affected. Ocean acidification may not affect the siliceous sponge populations as directly as marine taxa which are heavily dependent on carbonate at various life history stages such as cnidarians, mollusks, and many crustacean species with tiny pelagic larval forms. Hexactinellids may, however, suffer detrimental effects by reducing the efficiency of the sponge membrane pumps, which in turn will affect feeding efficiency. They may also suffer other effects through changes to circulation patterns which may disrupt larval dispersion and increasing sedimentation at some sites. In addition some reduction of primary productivity may reduce bacterial concentrations in bottom waters.

Siliceous sponges are the earliest metazoan fossils known and have survived several mass extinction events during the last 560 million years. Hexactinellid sponges and sponge reefs have been resilient to changing climates over the longest geologic time scales. The acme of sponge reef occurrence in geologic time, during the Upper Jurassic, was a time of stratified oceans with very high atmospheric carbon dioxide concentrations thought to have been several times that of today.

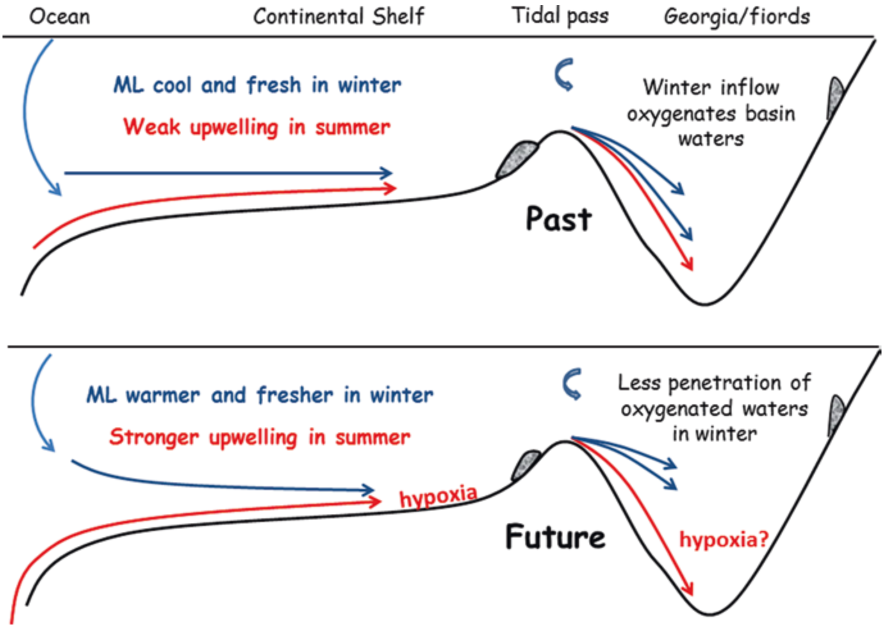

Fig. 10.7 Past circulation across BC shelf regions and into fiords (*upper panel*) has kept sponge reef habitat (stippled regions) oxygenated due to the transport of mixed layer (ML) waters into basins and fiords and also due to weak summer upwelling which has limited impact on reefs. In the future, less dense waters may be imported in winter, and stronger upwelling will supply denser, hypoxic waters onto the continental slope. The density contrast between winter and summer waters should result in weaker oxygenation of basins and fiords

Although the BC sponge reefs have existed for most of Holocene time, with survival through warming and cooling intervals during the epoch, the synergistic effects of changing climate with other human impacts, including widespread bottom trawling and coastal pollution, are unknown.

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Chapter 11
Future Research Directions and Gaps in Our Knowledge

James J. Bell and José Luis Carballo

Abstract In this final chapter, we explore the current gaps in our understanding of ocean acidification and increased sea surface temperature on sponges and highlight some future research directions to address these gaps. We particularly focus on the geographic spread of the currently available studies, the mechanisms of acclimation and the potential for long-term adaptation. We also highlight the need for more multiple stressor impact studies and a better understanding of the ecosystem consequences of changing sponge abundance. With this information, we will be able to better predict future impacts of environmental change on sponges.

Keywords Porifera • Climate change • Ocean acidification • Ocean warming • Adaptation • Acclimation • Multiple stressor

11.1 Taxonomic and Geographical Spread of Studies

There are currently over 8000 known species of sponge, although the total number is likely to be considerably higher given the levels of cryptic speciation that are increasingly being uncovered by the application of molecular tools (e.g. Xavier et al. 2010; Bell et al. 2014). As would be expected the number of sponge studies on climate change has increased over time, peaking in 2013. However, the total contribution of studies that have studied OA and OW combined represents only a small portion of all studies (Fig. 11.1), with less than fifteen species studied to date. Of

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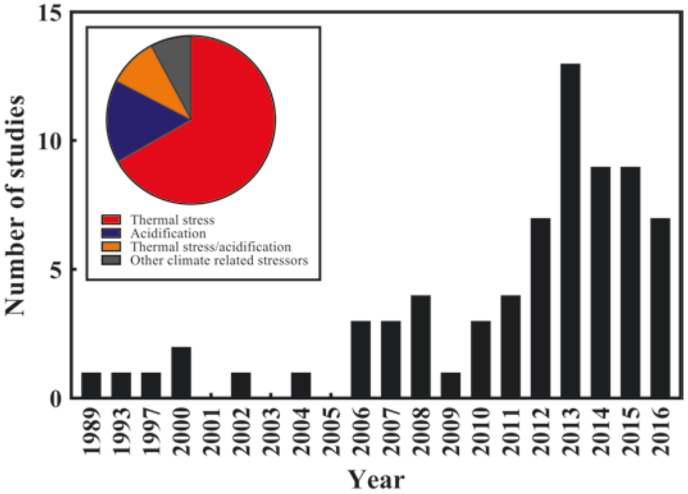

Fig. 11.1 The number of studies focused on climate change impacts over time on sponges based on a Scope and Google Scholar search (climate change, ocean acidification, sponge, porifera, ocean warming). The *chart* shows the proportion of studies by topic between 1989 and 2016

those single stressor studies on sponges considering climate change, the majority have focused on temperature, with far fewer on ocean acidification.

The small number of sponge species studied to date limits the extent that responses can be generalised. We need to increase not only the number of species being examined but also the taxonomic spread of species to encompass more genre and families. Of particular concern is that there have still been no studies on the impacts of OA on any calcareous sponge species or hexactinellids. While calcareous species only represent less 5% of all sponge species (still 400+ species), they are most likely to be impacted by pH changes since they rely on calcareous spicules for skeletal support. While calcareous sponges are not generally as ecologically important as demosponges, they can still be very abundant in some locations and habitats, such as caves. Finally, the typical duration of experimental OW/OA studies on sponges is around 2–3 months, and to fully understand sponge responses, we need to conduct longer experiments and try to cover the entire life cycle from settlement through to reproductive maturity.

We also need to broaden the geographic spread of the studies on sponge OA/OW impacts. There has been a predominant focus on tropical sponges to date, with very little information, particularly on OA, for temperate sponges, and virtually no information for polar sponges. This focus on tropical regions is perhaps not surprising given the severe negative impacts identified for corals (see Hoegh-Guldberg et al. 2007) and the fact that organisms living on coral reefs are likely to have less tolerance to increases in temperature given they already live at high temperature. Obtaining information from a greater range of locations, environments and habitats will allow a more general assessment of climate change impacts on sponges.

11.2 Mechanisms of Acclimation

The majority of OA/OW studies on sponges to date have measured responses of sponges to various pH/temperature combinations broadly in line with those predicted by the International Panel on Climate Change (IPCC) Relative Concentration Pathways (RCP) (IPCC 2014). This has included measurements of physiological processes (e.g. respiration), population/individual parameters (e.g. growth and reproduction) and changes in microbial communities. While we only have this information for a few species, given there is evidence of resilience, we need to shift some of our focus to understanding the mechanisms supporting these responses. Our knowledge of these mechanisms significantly lags behind what is known for other groups, such as coral and molluscs. There are a number of potential ways in which these mechanisms could be studied, but there should be a particular focus on molecular/cellular level responses including transcriptomic, metabolomic, proteomic and epigenetic studies. It would also be useful to gain a better understanding of how sponges are interacting with their associated microbial communities and any mechanisms by which microbes are contributing to or reducing resilience in sponges. Finally, it will also be important to investigate sponge responses to natural levels of pH variation as considerable diurnal and seasonal variation has been reported (e.g. Price et al. 2012); this might provide insight into mechanisms allowing tolerance to future OA conditions.

11.3 Potential for Adaptation

While short-term acclimation responses are relatively easy to study, it is much harder to study the evolutionary potential of sponges to show longer-term adaptation to projected changes in OA and OW. However, for OA at least the presence of sponges at shallow water CO_2 seeps, such as those found in Papua New Guinea (Morrow et al. 2015) and in the Mediterranean (Goodwin et al. 2014), may provide some insights in sponge evolutionary potential. This does depend on how such populations at vents are maintained; if they are simply the result of influxes of larvae from non-vent areas, which then show acclimation responses, they are unlikely to be experiencing local adaptation. In contrast, if sponge populations are being maintained by locally produced larvae, then such vent sites may provide research opportunities to study evolutionary responses to OA and local adaptation. The application of newly available molecular markers such as single nucleotide polymorphisms (SNPs) as a result of advances in next-generation sequencing may provide initial means for investigating gene-level differences in sponges at these sites.

11.4 Multiple Stressor Interactions

While studies of the individual effects of OA and temperature are still useful, especially those of temperature because OA generally appears to have limited negative effects on sponges, studies should try where possible to conduct multiple stressor experiments. This is particularly important as one of the most recent combined OA/OW studies on sponges by Bennett et al. (2016) found interactive effects of OA/OW, with OA mitigating temperature stress in a phototrophic sponge. This demonstrates what's been found for other organisms, that responses to OW and OA individually may not be the same as when they are applied at the same time. Furthermore, since sponges will be experiencing both these stressors at the same time in the future, it makes sense to conduct combined stressor experiments.

Unfortunately, OA and OW are not the only stressors that sponges are likely to experience in the future; they will likely experience a range of other anthropogenic stressors as well, such as changes in nutrient and sedimentation levels. Conducting multi-stressor experiments is logistically challenging, and assuming adequate replication, they can quickly become unmanageable with two or more factors, especially when we might want to consider a number of levels for each factor corresponding to different climate change scenarios. There are an increasing number of facilities worldwide that are able to undertake such experiments (such as the National Sea Simulator at the Australian Institute of Marine Science), although the number of stressors possible is still limited. In the future, we will need to look for innovative experimental and statistical designs to address these issues, such as the collapsed multi-stressor experimental design described by Boyd et al. (2016).

11.5 Ecosystem Impacts of Changing Sponge Abundance and Diversity

We also need to begin to think beyond just direct impacts of OA and OW on sponges, and we need to also consider the interactions sponges have with other organisms and the way that changes in their abundance or diversity (either increases or decreases) may have other ecosystem impacts. Globally, there are many research groups building different types of ecosystem and trophic models to explore the impact of different environmental stressors on marine ecosystems. However, despite the functional significance of sponges, particularly through their feeding/pumping activities, nutrient recycling and bioerosion, they are rarely included in such models, particularly for coral reef systems. As sponge researchers, we need to work with these research groups to ensure sponges are represented in such models and their functional significance is recognised. Consideration also needs to be given to how coral reefs might function if sponge declines/impacts are less severe than what is being reported for corals or if overall sponge diversity is reduced to only a few tolerant species.

11.6 Geological Perspectives

The intermittent fossil record and a propensity for researchers to concentrate on specific geological time periods where fossils are abundant have limited general interpretations of the response of sponges to climatic changes at geological scales. Our understanding is also influenced by the lack of preservation of some sponge groups, particularly Keratosan sponges that are not preserved in the fossil record. Further examination of existing fossil material and new material as it becomes available will hopefully increase our knowledge of how sponge diversity has changed over geological time and whether there are any climatic drivers at geological scales.

11.7 Final Thoughts

There appears to be little doubt that marine ecosystems will be heavily impacted in the future by ocean warning and acidification, and there is considerable need to understand how species will respond and if they have the potential to acclimate and adapt. For sponges we are already building a picture of how they respond to climate change-related stress, and we need to continue to build on this understanding in the future. Since there is evidence that sponges may be tolerant to ocean acidification, and to a lesser extent ocean warming, we need to understand the limits of these tolerances and the mechanisms providing resilience. This is likely to be challenging and will require multidisciplinary research approaches and extensive funding support. We urge research groups to work together and pool resources to face these challenges.

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