Review

# The functional roles of marine sponges

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## ABSTRACT

Despite the wide range of functional roles performed by marine sponges they are still poorly represented in many research, monitoring and conservation programmes. The aim of this review is to examine recent developments in our understanding of sponge functional roles in tropical, temperate and polar ecosystems. Functions have been categorised into three areas: (a) impacts on substrate (including bioerosion, reef creation, and substrate stabilisation, consolidation and regeneration); (b) bentho-pelagic coupling (including carbon cycling, silicon cycling, oxygen depletion and nitrogen cycling); and (c) associations with other organisms (facilitating primary production, secondary production, provision of microhabitat, enhanced predation protection, survival success, range expansions and camouflage though association with sponges, sponges as a settlement substrate, disrupting near-boundary and reef level flow regimes, sponges as agents of biological disturbance, sponges as releasers of chemicals and sponges as tools for other organisms). The importance of sponges on substrate, sponge bentho-pelagic coupling, and sponge interactions and associations is described. Although the scientific evidence strongly supports the significance and widespread nature of these functional roles sponges still remain underappreciated in marine systems.

## 1. Introduction

Sponges are an important component of the benthic fauna throughout temperate, tropical and polar habitats (e.g. Lilly et al., 1953; Dayton et al., 1974; Diaz et al., 1990; Barthel et al., 1991; Bell and Barnes, 2000; Bell and Smith, 2004; Bell, 2007), but despite their often numerical abundance, biomass dominance and longevity in many ecosystems, their functional significance still appears to be poorly appreciated. Although sponge ecologists have long since realised the functional significance of sponges in benthic environments (e.g. Rützler, 1975, 1978, 2004; Rützler and MacIntyre, 1978; Diaz and Rützler, 2001; Wulff, 2001, 2006), this information and recognition has not always reached large-scale research, conservation and monitoring programmes. Any exclusion of sponges from monitoring programmes is of considerable concern, particularly since some of the functional roles that sponges play have the potential to exert a major influence on overall ecosystem functioning and potentially more pronounced impacts on marine communities in light of current environmental change (e.g. cascade effects). Given the increased emphasis over the past two decades on understanding the functional diversity in marine ecosystems including its relationship to species diversity, ecosystem functioning and extinction (see Steele, 1991; Petchey and Gaston, 2002a,b; Micheli and Halpern, 2005), there is considerable need to

highlight the roles that sponges play in marine systems, which is the purpose of this review article.

Wulff (2001) and Diaz and Rützler (2001) provided earlier reviews of the functional roles that sponges play on Caribbean coral reefs, although the information is also relevant to other geographic regions. Wulff (2001) highlighted the following important functional roles: enhancing coral survival by binding live corals to the reef frame and preventing access to their skeletons by excavating organisms; mediating regeneration of physically damaged reefs by temporary stabilisation of carbonate rubble; reworking of solid carbonate through bioerosion; nutrient recycling; primary production through microbial symbionts; clearing the water column of prokaryotic plankton; and a food source for other organisms. In spite of the importance of Wulff's paper in highlighting the functional roles of coral reef sponges, according to the ISI Web of Knowledge citation database (accessed 13/02/08) it has only been cited 13 times (representing 7 research groups), all of which are specifically related to different aspects of sponge ecology, rather than broader-scale aspects of coral reef research to which it is highly relevant.

Diaz and Rützler (2001) considered sponges to have at least six functional roles on Caribbean coral reefs including: primary production and nitrification through complex symbioses; chemical and physical adaptation for successful space competition; capability to impact the carbonate framework through calcification, cementation, and bioerosion; and potential to alter the water column and its processes through high water filtering capabilities and

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exhalation of secondary metabolites. The ISI Web of Knowledge citation database (accessed 13/02/08) shows that this paper has been cited 22 times (representing 17 research groups) and that these citations are also restricted exclusively to direct research on sponge ecology, rather than to broader-scale coral reef research. Furthermore, few of the studies citing Wulff (2001) and Diaz and Rützler (2001) are specifically related to functional aspects of sponge ecology. It is noteworthy that citation indices may not fully represent the impact of any specific scientific paper, especially when considering marine monitoring or management, since the information may be assimilated in non-published reports. However, since these earlier review papers are primarily cited by other sponge groups this does suggest that the information they contain has not been fully embraced by the wider scientific community.

Further recent reviews relevant to sponge functional ecology include Wulff (2006), who examined sponge ecological interactions, and Rützler (2004) who further considered selected ecological roles of coral reef sponges. Finally, recent reviews by Taylor et al. (2007) and Webster (2007) highlight microbial communities associated with sponges and sponge diseases, respectively, while McClintock et al. (2005) reviewed the ecology of Antarctic sponges, although it is clear from this final review that our understanding of polar sponge assemblages (and particularly functional roles) still lags considerably behind our knowledge from tropical and temperate regions.

This present review describes all the currently identified functional roles that sponges perform specifically focusing on: (1) the advances in our knowledge of tropical ecosystems that have been made since the reviews of Wulff (2001), Diaz and Rützler (2001) and Rützler (2004); (2) the further development of areas discussed by these authors in light of recent research developments (e.g. bentho-pelagic coupling, control volume research and the potential predation by sponges on viruses); (3) a description of all functional roles of sponges (including those not identified in previous reviews) including nitrogen cycling, silicon cycling, viral predation, oxygen depletion, facilitating primary production, secondary production, provision of microhabitat, enhanced predation protection though association with sponges, provision of camouflage, enhancing survival success of other species, causing range expansions, sponges as a settlement substrate, disrupting near-boundary and reef level flow regimes, sponges as agents of biological disturbance, sponges as releasers of chemicals (in relation to other functional roles) and sponge use as tools by other organisms; and (4) the functional roles that sponges play in temperate and polar regions.

## 2. Impacts on substrate

### 2.1. Bioerosion

Sponges are one of the primary bioeroders of coralline structures, particularly coral reefs (Goreau and Hartman, 1963; MacGeachy, 1977) and bioerosion is probably one of the earliest functional roles identified for sponges (Ginsburg, 1957). The importance of boring sponges has been highlighted by previous reviews (Rützler, 1978, 2004; Wilkinson, 1983a; Glynn, 1997; Diaz and Rützler, 2001; Wulff, 2001), and the large number of recent taxonomic papers describing new species of boring sponges further identifies this sponge group as diverse, widespread and abundant (e.g. Rosell and Uriz, 2002; Zea and Weil, 2003; Carballo et al., 2004; Calcinai et al., 2005; Carballo and Cruz-Barraza, 2005; Bautista-Guerrero et al., 2006; Blissett et al., 2006; Schönberg et al., 2006; Carballo et al., 2007). In addition to the role of sponge bioerosion in reef dynamics (for temperate reefs as well) there is also commercial interest in boring sponges, since they infest economically valuable species (e.g. Guida, 1976; Rosell et al., 1999; Fromont et al., 2005).

Bioerosion by sponges, where solid carbonate is processed into smaller fragments and fine sediments, is a destructive process performed by sponges that also contributes to the production of reef sediment and affects the structural integrity of coral (Rützler, 1975). On coral reefs the balance between erosion and accretion is crucial since it influences the development and sustainability of reef ecosystems; on healthy reefs bioerosion and accretion rates are approximately equal (Hein and Risk, 1975). Although tropical bioerosion research has predominately focused on coral reef structures, a bioeroding sponge has also recently been reported from a sabellariid worm reef in Florida, USA (see Schönberg, 2002a). On most temperate and polar reefs bioerosion is considered less significant (with some notable exceptions); in fact bioerosion by sponges has not yet been reported in the polar seas, which has been explained by the scarcity of calcareous structures (Cerrano et al., 2001). Unsurprisingly, most bioerosion research has focused on tropical coral reef ecosystems given the nature of the calcareous substrate, but bioerosion is also important on temperate deep water reefs and in the Mediterranean. Beuck et al. (2007) reported several species of bioeroding sponge associated with deep water *Lophelia pertusa* reefs, which are thought to influence the structural integrity of the coral.

Both past and more recent research has focused on the factors that influence bioerosion rates including nutrient availability and input, food abundance, type of substratum, sponge physiological state and light (Rützler, 1975; Rose and Risk, 1985; Risk et al., 1995; Hill, 1996; Holmes, 1997, 2000; Schönberg, 2002b; Ward-Paige et al., 2005). One of the particularly interesting factors that can increase sponge bioerosion rates is eutrophication (e.g. Rose and Risk, 1985; Muricy, 1991), illustrating how anthropogenic impacts have the potential to disrupt the balance between reef erosion and accretion. Ward-Paige et al. (2005) found that the greatest boring sponge size and cover occurred in areas where total nitrogen, ammonium and $\delta^{15}N$ were highest in Florida, indicating that bioeroding sponges dominate in the areas subjected to the highest nutrient levels (from land-based pollution). These authors were also able to correlate the greatest increases in bioeroding sponge abundance with the greatest decreases in stony coral abundance over a 5-year period in the same region of Florida. Such results raise concerns given the widespread decline in coral abundance across the globe, since the reduction of the organisms primarily involved in reef accretion, may be replaced by a greater number of those organisms (e.g. sponges) that are involved in reef erosion, possibly resulting in a positive bioerosion feedback loop and cascade effects (e.g. see Butler et al., 1995; Cebrian and Uriz, 2006).

In the Mediterranean bioeroding sponges are common on photophilic seaweed biocoenosis habitats, and *Cliona viridis* is the most common bioeroding sponge (Rosell and Uriz, 1992). Cebrian and Uriz (2006) have reported positive correlations between the abundance of the excavating sponge *Cliona viridis* and grazing urchin abundance, and a negative correlation with fleshy algae abundance in the western Mediterranean. These authors propose that increased light as a result of algal grazing enhances the growth rate of *C. viridis* accounting for its greater abundance in the absence of fleshy algae. Furthermore, these authors have suggested that increased fishing effort (or past over-exploitation) may have potential cascading effects resulting in the increased abundance of *C. viridis* and therefore the weakening of calcareous structures. The study by Cebrian and Uriz (2006) shows how abiotic and biotic effects may not be independent of each other and bioerosion rates may be multifaceted and particularly influenced by changes in overall community structure. Other bioeroders have been reported from red coral (*Corallium rubrum*) in the Mediterranean, and the sponge assemblages are thought to show selectivity to this species and not to other local calcareous substrates (Corriero et al., 1997).

Most temperate bioerosion research has focused on the effects of bioeroders on commercial bivalves (e.g. Guida, 1976; Krakatitsa and Kaminskaya, 1979; Schleyer, 1991), while more recent studies have highlighted the negative impacts of boring sponges on the gastropod *Littorina littorea* (Stefaniak et al., 2005) and the deep sea coral *Lophelia pertusa* (Beuck et al., 2007). In the studies of *L. littorea* and *L. pertusa*, the sponge erosion has negative effects, causing the weakening of calcareous structures in the case of the coral. For *L. littorea*, its internal shell volume is reduced as the snail tries to combat the erosion by laying down additional internal calcareous layers. Therefore, this bioerosion is likely to result in an increased energetic cost for the gastropod, and reduced space for the gastropod to grow (which may also have reproduction implications). The infestation of commercial oysters by eroding sponges has a range of effects, most of which result in decreased condition and an energetic cost for the oysters (Fromont et al., 2005) and is therefore of considerable economic importance.

Light has also been considered an important factor influencing excavation rates in a number of previous studies (e.g. Hill, 1996; Schönberg et al., 2005) since many bioeroding sponges form symbiotic relationships with zooxanthellae. The relationship between many bioeroding sponges and zooxanthellae should be of interest to coral reef ecologists, since they may also be susceptible to bleaching (see Hill and Wilcox, 1998) in a similar way to coral. Although most research has hypothesised that environmental change will result in higher bioerosion rates on coral reefs, there is also the potential for erosion rates to decrease. López-Victoria and Zea (2004) reported an increase in abundance of some important excavating sponges over the past 25–30 years in some parts of the Caribbean, particularly in areas where *Acropora palmata* was heavily bleached during the 1980s. Increased dead coral substrate may increase the abundance of bioeroding sponges, since available substrate is increased and competition with corals reduced. In addition to the destruction from direct excavation of carbonate reefs, many excavating species also encrust the substrate as they grow (see below for discussion of this activity as a separate functional role) and compete for space with other reef organisms (Glynn, 1997; Schönberg and Wilkinson, 2001; Rützler, 2002). Interestingly, recent research by López-Victoria et al. (2006) has identified the importance of angle of engagement between excavating sponges and competitors as an important determinant in the successful lateral advancement of sponges.

Currently, the geographic distribution of research on sponge bioerosion is prominently skewed towards Caribbean reefs with a comparative paucity of information from the Pacific and Indian Oceans. Recent work by Bautista-Guerrero et al. (2006, in press) on the Mexican Pacific coast has further highlighted the diversity and abundance of boring sponges in the Pacific. These authors have found that coral infestation rates, biodiversity and abundance of bioeroding sponges are higher in response to increased coral reef degradation and availability of carbonate substrate, which supports previous results from the Caribbean (see above). Further investigation is needed in the Indian Ocean (and Indo-Pacific), where diversity of bioeroding sponges is thought to be high (e.g. Calcinai et al., 2005), but their functional ecology poorly known.

## 2.2. Reef creation, and substrate stabilisation, consolidation and regeneration

Sponges interact with the substrate in other ways than bioerosion, but the role that sponges play in reef creation, stabilisation, consolidation and regeneration has been comparatively poorly studied. Wulff and Buss (1979) were the first to experimentally demonstrate the role that sponges can play in increasing the survival of live coral on Caribbean reefs by binding fragments together, which is expected to increase rates of carbonate accretion. These authors found that coral survival was increased by an order of magnitude by the presence of sponges, compared to areas without sponges. Further research by Wulff (1984) showed that sponges were able to mediate the consolidation of *Porites* rubble until carbonate secreting organisms could grow and consolidate the rubble to the reefs after storms. Rubble was essentially "glued" together, as it was held in place by sponge fragments generated during the same storm that created the rubble; this then provides a stable substrate for the settlement of coral. Wulff (1984) found that when sponge populations were established in experimental rubble piles, the substrate became tightly bound in only 7 months, compared with control areas that were not seeded with sponge fragments. Over the same time scale that consolidation was reported by Wulff (1984), the control experiments, which were not 'seeded' with sponges, had become scattered with little chance of future consolidation. These studies clearly highlighted the role that sponges can play in reef stabilisation, consolidation and regeneration, and although Wulff (2001) further highlighted this important functional role, and more recently Rasser and Riegl (2002) discussed the importance of preliminary sponge binding on Holocene coral reefs, this area has received little further attention despite its potential use in reef restoration.

The geographic extent of coral rubble stabilisation and binding by sponges is poorly known since information is currently only available from the Caribbean, although Wulff (2001) did report a positive correlation between rubble consolidation and the presence of cryptic sponges in the Pacific. Preliminary unquantified observations from SE Sulawesi in the Indo-Pacific (see Bell and Smith, 2004 for location) by myself suggest that cryptic and encrusting sponges do appear to be stabilising coral substrate in areas where blast fishing has taken place and in many areas the only organisms colonising the broken carbonate fragments are sponges, which are further stabilising the rubble substrate. Although the time since this blast fishing took place is unknown (but is likely to be within the last 5–10 years), there has been little recolonisation of the fragmented rubble by coral, despite its apparent stability.

In the past sponge substrate stabilisation has been considered a reef-based process, but sponges can also act as substrate stabilisers in temperate regions. In many rocky habitats, boulders form an overlying matrix and sponges and other organisms commonly grow between the boulders stabilising the habitat and potentially reducing disturbance levels (see Bell and Barnes, 2003).

Although most sponges are associated with hard substrates some species live buried within sand, such sponges have been termed psammobiontic sponges and have special morphological and ecophysiological adaptations to allow them to survive in these habitats. Rützler (1997) described how the psammobiontic sponge *Speciospongia cuspidifera* helps to consolidate soft carbonate sediment in Caribbean soft sediment habitats. In stabilising the substrate these sponges contribute to reef functioning by consolidating, venting and enriching reef sands and by generating patch-reef communities on sandy bottoms.

## 2.3. Importance of sponges on substrate

The impact of sponges on benthic substrates, both as bioeroders and consolidators/stabilisers are the most important roles that sponges perform in tropical environments, but their effects are far less known in polar and temperate ecosystems, although in some circumstances their effects can also be important in temperate regions (e.g. Cebrian and Uriz, 2006). Despite the extensive research on the impact of sponges on substrate, most tropical research has focused on the Caribbean. Therefore future studies should focus on the Pacific and Indian Ocean reefs. One interesting aspect of sponge–carbonate binding and stabilisation that should be further

explored is the potential for sponges to be used in reef restoration as temporary binders of unconsolidated carbonate (Wulff, 2001), however, the interaction of any 'seeding' sponges with bioeroding sponges would need to be considered, since they also show increased abundance in unconsolidated reef areas.

## 3. Bentho-pelagic coupling

The link between benthic and pelagic environments has received renewed interest in recent years, with the terms 'bentho-pelagic coupling' and 'benthic–pelagic coupling' being used to describe such interactions. Since sponges filter large quantities of water (Reiswig, 1971, 1974; see below) they remove food particles (carbon source) and other nutrients (e.g. oxygen, silicon and nitrogen) from the water column, thereby having the potential to significantly impact pelagic ecosystems. For example, Peterson et al. (2006) explained that increased phytoplankton blooms in Florida Bay are likely to be the result of decimated sponge populations in the region, rather than increased nutrients fuelling the blooms. By estimating particle removal rates and pumping rates these authors found that the historical sponge populations in Florida Bay had the potential to control the phytoplankton blooms. In addition to increased interest in bentho-pelagic coupling, there is also emerging interest in 'control-volume' research (Genin et al., 2002), where net exchange between pelagic and benthic environments (e.g. nutrients and carbon) is measured. Such approaches are likely to be strongly influenced by the presence of sponges given their filtering capability.

### 3.1. Carbon cycling and energy flow

Suspension feeding is one of the most well known impacts of sponges on the pelagic environment (e.g. see Buss and Jackson, 1981) and a number of studies have identified that sponges feed on ultraplankton and picoplankton in shallow waters (Reiswig, 1971; Pile, 1996; Pile et al., 1996, 1997; Ribes et al., 1999), with more recent studies also highlighting the importance of sponge feeding to bentho-pelagic coupling in the deep sea (Pile and Young, 2006). The feeding of sponges on ultraplankton represents an important link between carbon in the water column and the benthos, which may then enable carbon flow to higher trophic levels through predation (Wulff, 2006; see below). Previously, authors have considered the potential that sponges may have to alter the planktonic community over coral reef ecosystems (e.g. Ayukai, 1995), but more recently, several other sources of nutrition to sponges have been identified and quantified. The largest proportion of organic matter in the oceans is found in the dissolved pool and although Diaz and Rützler (2001) identified bulk dissolved organic matter (DOM) uptake by sponges as important, research by Yahel et al. (2003) was the first to demonstrate direct evidence for uptake of DOM by sponges, indicating that the role of sponges (and other metazoans) in DOM cycling may be hugely underestimated. Viruses have also been recently identified as a second new important potential source of nutrition to sponges. Hadas et al. (2006) found the tropical sponge *Negombata magnifica* had high viral particle removal efficiency, with particles being removed by the sponge at an average efficiency of between 23.3% and 62.9%. These authors suggest that significant amounts of nutrients are transported from virus particles to higher trophic levels via sponges. The identification and demonstration of these two new potential nutrient flow pathways illustrates the varied ways that sponges may interact with the water column in order to obtain food. Currently, some care must be taken in the interpretation and extrapolation of the results from these two studies on virus predation and DOC utilisation by sponges, since both were only single species studies, and further

species needed to be examined to confirm the importance of these pathways across the phylum.

### 3.2. Silicon cycling

The deposition of silicon (Si) is a fundamental process in the production of the sponge skeleton, where siliceous spicules are produced by sponges that can interlock, fuse or form three-dimensional structures that are usually connected by spongin (Uriz et al., 2003). Although earlier studies indicated that sponges may play a role in global Si cycling (e.g. Harriss, 1966; Rützler and MacIntyre, 1978), more recent models have considered that photo-autotrophic diatoms are primarily responsible for global Si cycling (e.g. Greenwood et al., 2001; Rickert et al., 2002). However, recent work by Maldonado et al. (2005) has highlighted a potential oversight, and that sponges may indeed be important in global Si cycling. Contrastingly, Whitney et al. (2005) suggested that deep water sponge reefs on the western Canadian continental shelf may only have a small impact on the local Si budget, which may represent geographic variation in the importance of sponges in Si cycling. Maldonado et al. (2005) found that sponge spicules dissolved considerably slower than diatom frustules, which is consistent with earlier studies (see Katamani, 1971), and that given sponges can be very long-lived (e.g. Leys and Lauzon, 1998) compared with diatoms; they concluded that sponges may potentially have an important impact on global Si cycling, particularly as an Si sink. Although in some cases the depletion of Si from the water column by sponges may be somewhat localised to areas of high sponge abundance, the fact that sponges are common (and often dominant) in many areas of the ocean means they do have the potential to be significant Si sinks. In addition to the direct uptake of Si for spicule production, sponges also have the potential to obtain silica from the digestion of diatom frustules, which has been suggested for Antarctic sponges (Cerrano et al., 2004). Furthermore, siliceous spicules may constitute a significant component of reef sediment (Rützler and MacIntyre, 1978), acting as a further Si sink.

### 3.3. Oxygen depletion

Sponges may also influence the water column by utilising dissolved oxygen for respiration, which in some circumstances may cause localised oxygen depletion. Recent developments in oxygen microelectrodes have allowed accurate, reliable methods to be applied to the measurement of sponge oxygen consumption rates (see Gatti et al., 2002), although these methods have not been used to date to measure oxygen depletion of the surrounding environment. Richter et al. (2001) reported small, but significant oxygen depletion by the large populations of cave and cavity dwelling sponges in the Red Sea, but the degree that oxygen depletion occurs as a result of sponge pumping activity elsewhere remains unknown.

### 3.4. Nitrogen cycling

Like other nutrients the concentration of nitrogen in coral reef waters is very low and most of the available nitrogen is bound into particulate or dissolved organic matter (organic nitrogen). Dissolved inorganic nitrogen must go through a series of microbial transformations before it is available to other reef organisms (Corredor et al., 1988). It appears that nitrogen cycling in sponges and its release to the water column for use by other organisms is primarily undertaken by associated cyanobacteria (Wilkinson and Fay, 1979) and that atmospheric nitrogen that is fixed by cyanobacteria can be utilised by sponges. This was shown by Wilkinson et al. (1999) who was able to demonstrate the incorporation of the stable isotope $^{15}N_2$ into some amino acids of *Callyspongia muricina*.

Earlier studies by Corredor et al. (1988), in the Caribbean, identified the role that sponges may play in reef nitrogen cycling, by measuring the release of nitrate (resulting from the biological conversion of ammonia to nitrite and then to nitrate), which has been subsequently confirmed for other species by Pile (1996) and Diaz and Ward (1997), however, until recently no comparable data existed for temperate regions. Recently, Jiménez and Ribes (2007) highlighted the importance of temperate Mediterranean sponges as a source of dissolved organic nitrogen to pelagic environments and consider that sponges could have a relevant role in the remineralisation of organic nitrogen in oligotrophic marine coastal zones, such as the Mediterranean Sea.

Past studies have also highlighted the importance of bacteria in the nitrification capacity of tropical sponges (Diaz and Ward, 1997), and Jiménez and Ribes (2007) suggest that the consumption of nitrifying bacteria may account for differences between ingested and excreted nitrogen rates. The role of nitrogen excretion has also been considered important in sponge–algal symbiosis (see Davy et al., 2002), where the sponge is thought to supply dissolved inorganic nitrogen to the algae, which has been suggested as an explanation for why there are so many algal–sponge symbioses. Sponges have also been shown to supply mangroves with inorganic nitrogen through stable isotope analysis (Ellison et al., 1996). The importance of sponges in nitrogen cycling should not be underestimated given their abundance in ecosystems (e.g. coral reefs) where nutrient levels in the water column are low. There is currently no information from polar ecosystems on nitrogen cycling.

## 3.5. Importance of sponge bentho-pelagic coupling

The most important aspect related to sponge bentho-pelagic coupling is the high abundance of sponges in many benthic ecosystems. For example: in SE Sulawesi, Indonesia sponges occupy up to 30% of the available substrate (Bell and Smith, 2004); in the Red Sea, although sponge abundance on reefs is low, their abundance in caves, caverns and cavities is thought to be very high (Richter et al., 2001); at Lough Hyne, Ireland sponges can occupy >80% of the available space on subtidal cliffs (Bell, 2001); and in the Caribbean sponges also occupy >40% of the available space (Schmahl, 1990). Yet sponges were one of the dominant organisms in fall out material from submarine cliffs at Lough Hyne, with higher fall out associated with overhanging cliffs than vertical cliffs. This fall out of marine organisms in low current situations is likely to provide an important source of nutrition in close proximity to the cliffs (Bell et al., 2003). The high abundance of sponges in many benthic habitats is likely to result in a significant interaction between sponges and the water column, with sponges being an important link to higher trophic levels. For example, measurements of the pumping rates of the tropical sponge Verongia lacunosa by Gerrodette and Flechsig (1979) found water pumping rates between 1 and 6 l/h for a sponge of volume 500 ml, while Kowalke (2000) reported rates between 0.18 and 0.22 l/h for two Antarctic sponges (for a standardised 1 g ash free dry weight of sponge) and Thomassen and Riisgård (1995) reported a pumping rates of approximately 1 l/h (10 g dry weight of sponge) for the temperate sponge Halichondria panicea. Although estimates of pumping rates indicate considerable amounts of water can be processed for tropical, temperate and polar sponges, comparisons between studies is difficult due to the different standardisation methods used. Thomassen and Riisgård (1995) did suggest that sponge pumping rates may actually be lower than for other suspension feeders, but that they compensate for this by having a higher retention efficiency of small particles (<10 μm).

It is also important to note that bentho-pelagic coupling is a two way process, with material moving both to and from the benthos, and through various processes, sponges are involved in this bidirectional movement of nutrients. Finally, bentho-pelagic coupling may also influence the distribution of sponges. Lesser (2006) and Trussell et al. (2006) have shown that the growth rate and size of some important Caribbean sponges is positively correlated with depth, suggesting that food supply and therefore bottom-up processes influence the distribution and abundance of these sponges. The complex interactions between sponges and the pelagic environment require further investigation, since the links are numerous and changes in sponge populations have the potential to cause cascading ecosystem-level effects (e.g. see Butler et al., 1995).

## 4. Sponge associations with other organisms

Separating the different functional relationships between sponges and their associated fauna is often difficult. A huge range of organisms are associated with sponges, and identifying the functional role that sponges play in such relationships is difficult, but our understanding of the interactions between sponges and other organisms has been enhanced considerably in recent years through developments in the field of chemical ecology. The associations between sponges and other organisms have been recently reviewed, including sponge associated micro-organisms, symbiotic associations, spatial competition, sponges as microhabitats and sponges as a food source by Wulff (2006) and Taylor et al. (2007) and therefore this section only briefly considers these aspects of sponge functional ecology and for more detailed reviews readers are directed to these recent papers. This section examines some functional roles that sponges play when associated with other organisms that have not been previously considered. It is important to note that sponges may fulfil more than one functional role (e.g. providing a microhabitat and predator protection) in the majority associations and determining the relative importance of each role remains a challenging area of research.

Sponges produce a range of chemical compounds and many interactions between sponges and other organisms are mediated through chemical production (Bakus and Green, 1974; Pawlik et al., 1995; Uriz et al., 1996; Becerro et al., 2003; Jones et al., 2005). Past research on the chemical ecology of sponges has focused on predator deterrence, settlement inhibition, spatial competition and advantages to sponge feeders (e.g. from accumulation of metabolites). A single sponge species many contain many different chemicals, which are likely to have multiple ecologically significant functions (Becerro et al., 1997).

## 4.1. Facilitating primary production

In addition to the assimilation of carbon from feeding on ultraplankton, and possibly viruses and DOM, sponges form associations with a range of photosynthetic organisms, particularly cyanobacteria and to a lesser extent dinoflagellates, providing potential for sponges to assimilate carbon from a range of associated micro-organisms. The degree to which sponges rely on their symbiotic micro-organisms for nutrients is less well studied compared to the relationship between zooxanthellae and corals (but see the review by Taylor et al., 2007). However, multiple studies have demonstrated the extent to which sponges (associated with photosynthetic microorganisms) contribute to coral reef primary production (e.g. Wilkinson, 1983a, 1987; Cheshire and Wilkinson, 1991), but there is contrastingly little data available for temperate or polar sponges. Wilkinson (1983b) found that 6 of the 10 most common sponge species on Davies Reef (Great Barrier Reef) were net primary producers.

Primary production is one of the few functional roles that has been directly compared at an oceanic scale. Sponge assemblages on the Great Barrier Reef are considered to be more dependent on

relationships with photosynthetic organisms than those in the Caribbean (Wilkinson, 1987), highlighting inter-ocean differences in primary production attributed to sponges. Estimates of the amount of photosynthetic productivity from sponge symbiosis in the Coral Sea (Pacific Ocean) indicates that these relationships can provide between 48 and 80% of the sponges' energy requirements, while contributing up to 10% of the overall reef productivity (Wilkinson, 1986). Therefore sponge primary production in some parts of the world may be significant. Wilkinson (1987) also found considerable differences in the proportion of sponge species containing photosynthetic symbionts between near and far shore reef environments; increasing occurrence of symbiont containing sponges was found with increasing distance from the shore. Differences between inner shelf and outer shelf reefs, and between oceans were explained by Wilkinson (1987) to be the result of fundamental differences in the nutrient characteristics of the water column with increasing isolation of reef habitats (from the mainland), and between Caribbean and Pacific reefs.

Although diverse microbial communities have been associated with temperate and polar sponges (see Hentschel et al., 2002; Webster et al., 2004; Taylor et al., 2007), there is still little information on their productivity levels. Cheshire et al. (1995) provided some preliminary data for an Australian temperate sponge suggesting that it may be a net primary producer above 5–11 m, but this depended on the season, however, they considered their results tentative because of their small sample size. There appears to be no further information on the levels of primary production for temperate or polar sponges, although in shallow water temperate regions at least, primary production from sponges is probably insignificant compared with pelagic phytoplankton and benthic macroalgae. Therefore the role of sponges as primary producers may only be important in nutrient-poor tropical waters, particularly in the Caribbean.

In addition to the primary production directly associated with sponge tissues, Soltwedel and Vopel (2001) reported increased bacterial biomass (and hence production) surrounding the deep sea sponge Thenea abyssorum, compared with control sediment. Although an explanation for this situation of increased bacterial biomass surrounding a sponge remains unknown it does demonstrate the ability that sponges have to alter the surrounding environment (see below). Deep sea sponges have also been found to have associations with methanothrophic bacteria surrounding hydrothermal vents and cold seeps. These associations often dominate deep sea communities that depend on chemosynthesis, resulting in locally high densities of invertebrates, which may suggest an important productivity role of the sponges in methane-rich environments (Vacelet et al., 1996).

Although the importance of cyanobacteria to sponge related productivity has been reasonably well described, far less is known about the relationship between sponges and other photosynthetic organisms. One group of sponges of particular interest are the boring sponges, many of which are associated with zooxanthellae (Rützler, 1990; Hill, 1996; Schönberg et al., 2005). This relationship between a sponge whose tissues are mainly hidden from sunlight and a photosynthetic organism appears surprising, but the zooxanthellae are exclusively located in the sponge tissue that is exposed to light (i.e. exhaling and inhaling papillae) and no zooxanthellae inhabit the excavating tissue (Rosell and Uriz, 1991). Indeed bioerosion rates are increased in the presence of light for some bioeroding species containing photosynthetic symbionts (e.g. Hill, 1996), although how widespread this feature is among bioeroding sponges remains unknown. Not all interactions between sponges and photosynthetic organisms are considered beneficial to the sponge. For example, parasitic diatoms have been associated with Antarctic sponges, which are thought to use the metabolic products of the host sponge (Bavestrello et al., 2000).

## 4.2. Secondary production

Sponges are consumed by a range of organisms including fish, opisthobranchs, crustaceans, molluscs and echinoderms (see Wulff, 2006 for a complete review of sponge predation). These sponge predators represent the link between sponges and higher trophic levels and in many cases the link between primary and secondary production. The major sponge predators vary between temperate, tropical and polar ecosystems. In the Antarctic and temperate regions starfish and nudibranchs are thought to be the most important sponge predators (Dayton et al., 1974; McClintock et al., 2005), although Guida (1976) found crabs, shrimps, limpets and sea urchins feeding on Cliona celata inhabiting shells on the North Carolina coast. Antarctic sponge predation, and the associated disturbance, is considered to be very important in structuring benthic communities (Dayton et al., 1974). Fish predation has also been reported in temperate regions (see Battershill and Bergquist, 1990), but is more commonly associated with tropical ecosystems (Randall and Hartman, 1968; Dunlap and Pawlik, 1996, 1998; Wulff, 1997a), along with starfish (e.g. Wulff, 1995), turtles (e.g. Meylan, 1990; Hill, 1998), and nudibranchs (Rogers and Paul, 1991), however, the majority of tropical studies on sponge predation have been conducted in the Caribbean, with far less being known of Indian and Pacific Ocean interactions. Although feeding on sponges has been considered a carnivorous trophic interaction, Becerro et al. (2003) reported that the opisthobranch Tylodina perversa fed preferentially on the sponge Aplysina aerophoba over Aplysina cavernicola in the Mediterranean, with the former sponge containing high concentrations of cyanobacteria compared with the latter. These authors suggest that sponge–predator interactions may actually represent a type of herbivorous interaction, with the organisms contained within the sponge being of greater nutritional importance than the sponge tissue itself.

## 4.3. Provision of microhabitat and sponge associations

Sponges support diverse microbial and macrofaunal communities, which have been the focus of several past (Rützler, 1976) and recent (e.g. Webster et al., 2004; Wulff, 2006; Taylor et al., 2007) reviews and for this reason are not considered extensively in this review, but an overview is given for completeness. Examples of numerous marine phyla have been reported in association with sponges. For example, Ribeiro et al. (2003) reported over 2000 individual organisms associated with the encrusting sponge Mycale microsigmatosa, representing over 70 species and 9 phyla, while Voultsiadou-Koukoura et al. (1987) reported over 100 species associated with the sponge Verongia aerophoba in the North Aegean Sea. Considering many associations have been found to be sponge species specific, sponges have the potential to support a huge biodiversity and their role as microhabitats should not be underestimated. The species specific use of sponges (or within a limited range of species) may make it difficult to generalise patterns of sponge use as microhabitats. The nature of the relationships between sponges and associates varies considerably, for example, some organisms spend their entire life associated with sponges, while others may only utilise sponges as juveniles (e.g. Turon et al., 2000). The provision of protection afforded by sponges is a commonly cited advantage for sponge-associated organisms (see below), although some species also feed directly on the host sponge they inhabit, while others receive feeding advantages (see Wulff, 2006). One of the best described sponge relationships is between a polynoid species, Harmothoe hyalonemae, which has been reported living inside the atrial cavities of deep-water hexactinellid sponges Hyalonema thomsoni, Hyalonema infundibulum, Hyalonema lusitanicum and Hyalonema toxeras; over 85% of sponge specimens at a Mediterranean study site contained the polychaete (Martin

et al., 1992) and the polychaetes receive protection from potential predators from the sponge.

Although there are numerous studies of the actual fauna and flora that use sponges as microhabitats, there has been less study on the sponge features that make them a good habitat. For example, siliquariid molluscs are obligate commensals of sponges, and although the associations are not thought to be species specific, they are thought to be limited in the sponges that they can colonise by the nature of the specific sponge's skeletal architecture (Pansini et al., 1999). There may be many examples where the association between sponges and other organisms is limited by the skeletal or morphological nature (internal or external) of the sponge. Koukouras et al. (1992) found that the total number of associated organisms found in four sponge species in the Aegean Sea could be related to sponge volume, but not sponge complexity (measured as surface area to biomass ratio), with larger sponges (by volume) supporting more species (supporting island biogeography models). There is a considerable paucity of information on the use of sponges as microhabitats in Antarctic regions, compared with tropical and temperate regions. Research in the Mediterranean by Gherardi et al. (2001) described the epibiontic and endobiontic polychaetes of *Geodia cydonium* and found that internal sponge structure was important in determining the differences in the polychaete assemblages; these authors also reported an increase in abundance and density with increasing sponge size, contrasting with the results of Koukouras et al. (1992). Sponges are certainly important in the provision of habitats to arrange of organisms that have a diverse range of associations with sponges.

In addition to the habitat provision by individual sponges, they can also form sponge reefs, such examples are currently known from the Canadian Continental Shelf, which represent "living fossil reefs" and are likely to be over 9000 years old (Conway et al., 2001). Siliceous hexactinellid sponges form reefs, which provide settlement surfaces for other sponges, which in turn form a network that is subsequently filled with sediment, eventually creating mounds over 18 m high (Leys et al., 2004). These reefs support diverse deep sea communities that appear to be particularly vulnerable to deep sea fishing activities, particularly trawling.

### 4.4. Enhanced predation protection, survival success, range expansions and camouflage though association with sponges

Inter-phyletic sponge interactions appear to offer numerous advantages to the associated organisms, and in a number of cases specific predation protection has been reported. One of the best studied systems is that between bivalves and sponges (Bloom, 1975; Forester, 1979; Chernoff, 1987; Pitcher and Butler, 1987; Pond, 1992; Marin and Belluga, 2005), where reduced bivalve mortality from starfish predation has been correlated with the presence of sponges on their valves; both manipulation ability and chemical/tactile defences have been implicated. In addition to these relationships (protecting the scallops from predation), in some cases sponges are also thought to benefit from the association. Forester (1979) found that *Halichondria panicea* had increased feeding efficiency while encrusting the shells of scallops, while more recently Burns and Bingham (2002) highlighted how the encrusting sponges *Mycale adhaerens* and *Myxilla incrustans* suffer reduced mortality when encrusting the valves of live scallops in low energy environments, as sediment settlement on the sponges is reduced as the scallops move. Irrespective of whether protection is provided by sponge associations with scallops or enhanced sponge survival, there appears to be little energetic cost to the bivalves as a result of the association (Donovan et al., 2002). There has also been some suggestion that the encrusting of calcareous surfaces, particularly bivalve shells, by massive encrusting sponges reduces and prevents bioerosion by boring sponges (Pitcher and

Butler, 1987; Corriero et al., 1991). Even though the relationship between scallops and sponges has received considerable attention and is well described, sponges do not always afford effective protection to bivalves, as reported by Laudien and Wahl (1999) when examining the effect of sea star predation on blue mussels that were biofouled by *Halichondria panicea*.

Other protective interactions have been recorded. For example, Uriz et al. (1992) suggested that the association between horny sponges and the scyphozoan *Nausitoë punctata* may provide protection for the scyphozoan, although experimental evidence is not available. These authors also suggest that there may be energetic costs for the sponge due to the nature of the relationship, which contrasts with the sponge–scallop interaction. The sponge *Geodia corticostylifera* is thought to provide protection for the brittle star *Ophiactis savignyi* on the Brazilian coast (Clavico et al., 2006). Interestingly, in this study the bioactive compounds that are thought to protect the sponge (and the associated brittle star) from predation and inhibit settlement, were also chemically recognised by the symbiotic ophiuroids, highlighting the multiple roles that sponge natural products may play. There have been numerous other studies suggesting that sponges confer protective advantages (also see Magnino et al., 1999; Calcinai et al., 2004) to associated organisms, but very few of these studies (with the exception of the sponge–scallop symbioses) have experimentally shown this advantage.

Sponges have also been considered to provide camouflage to a range of other organisms (McClay, 1983), although specific attention has predominantly focused on the sponge fauna of crab carapaces. There has been some discussion (see Woods and Page, 1999) on the factors that are important in the selection and growth of sponges on crab carapaces including the nutritional quality of the sponge (then utilised as a food source), longevity of the sponge, decay rate, structural integrity and presence of secondary metabolites (to deter predators), although a number of studies have found correlations between the dominate local sponges and those found on crab carapaces. Schejter and Spivak (2005) found that sponges were the most abundant organisms on the carapace of the crab *Libidodaea granaria*, and since the sponge fauna matched that found on the bivalve beds (*Zygochlamys patagonica*) from where the crabs were collected, they concluded that the sponges provide camouflage for this crab species, although this camouflage was more pronounced on larger crabs, than smaller ones because of the frequency of moulting. The decorator spider crab, *Inachus phalangium*, in the Adriatic Sea, uses sponges as an important source of decoration material (Martinelli et al., 2006). These authors recorded 14 species of sponge on this crab and aquarium observations showed that crabs actively cut sponges and place fragments on their exoskeleton. Comparisons between the sponges present in the local environment with those observed on crab carapaces indicated that *I. phalangium* generally uses the most common sponges present, which probably provides the crab with the most effective camouflage in its specific habitat. Research in the temperate waters of New Zealand by Woods and Page (1999) also showed that spider crabs are more likely to select abundant sponges as masking agents than those that are less common. In some cases sponges are only used for camouflage by crabs when preferential material is not available, for example, Stachowicz and Hay (2000) found that *Libinia dubia* preferentially decorates with the protective algae, but when this is unavailable it will use the sponge *Hymeniacidon heliophila*, which like the algae is unpalatable to fish, thereby providing protection when the algae becomes seasonally unavailable. Differences have also been found between the sponges associated with the sexes and sizes of crabs. Maldonado and Uriz (1992) found differences between sponge fauna on the carapaces of male and female *Inachus aguiarii* in the Mediterranean. Percentage cover of sponges was only related to size in males crabs, and was

independent of size for female crabs (which always had high sponge cover). This difference was attributed to the long resting periods undertaken by female crabs in sponge rich habitats. Despite the extensive observations of sponge material on the carapace of crabs, experimental data is still needed to support the use of sponges as a source of camouflage.

In addition to the protection provided by sponges acting as microhabitats, preventing predation and providing camouflage there have been several other reports of associations with sponges that result in increased survival of the association organism. For example, Goreau and Hartman (1966) found that growth of coral species from the genus *Montastrea* can be enhanced when growing in association with the sponge *Mycale laevis* in the Caribbean. As the corals grow, they create more space for the sponge, which the sponge utilises, and subsequently prevents excavating species from colonising the undersides and bases of the corals. The importance of this relationship was demonstrated by Wulff and Buss (1979) who found that the removal of all non-excavating sponges from reefs in the Caribbean resulted in the loss of nearly half the coral colonies within 6 months of sponge removal. Sponges growing on mangrove roots have also been shown to reduce the infestation rates of boring isopods with sponges being considered to indirectly facilitate root growth (Ellison and Farnsworth, 1990), thereby increasing the success of the red mangrove *Rhizophora mangel*.

Sponge associations have also been responsible for increasing the distribution range of some species. For example, Carballo et al. (2006) found that the red alga *Jania adherens* grows independently of its symbiotic sponge *Haliclona caerulea* in the intertidal zone on the Pacific Mexican coast, which is beyond the distributional range of the association, but *Jania adherens* has spread and increased its range below 1 m due to its association with the sponge.

### 4.5. Sponge as a settlement substrate

Although there has been a lot of discussion with respect to the prevention of settlement of different organisms on sponges through bioactive chemical production (e.g. Davis et al., 1991; Becerro et al., 1997; Hellio et al., 2005; Lee et al., 2006), there is also the potential for sponges to act as an additional settlement surface for other organisms, since some organisms do settle on sponges. Space is limiting in many benthic environments, which results in spatial competition for the available resources. However, in environments where sponges dominate they represent an additional settlement surface. For example, *Agelas clathrodes*, which is a relatively common sponge in the Indo-Pacific, is commonly encrusted by a large number of species including serpulid worms, colonial ascidians, other sponges, calcareous algae and bryozoans (Bell, unpublished data). These species are not exclusively found on the sponge and commonly occur on the reef structure itself. At Lough Hyne Marine Nature Reserve, I have observed several species seasonally settling on *Cliona celata* including red algae and the hydroid *Tubularia indivisa*, which can be locally abundant, but do not exclusively settle on the sponge. Furthermore, in New Zealand crustose calcareous algae can be found growing on the surface of *Tethya* spp. (Bell, personal observation). Despite the research examining the effect of sponge extracts in preventing settlement on sponges, there does appear to be some species that can settle on sponges and take advantage of this settlement surface. Although the importance of sponges as an additional settlement surface may be sponge species and location specific it may increase biodiversity locally and should not be ignored. Many sponge interactions have been considered as mutualistic associations (e.g. Rützler, 1970; Wulff, 1997b; see Wulff, 2006), and it is possible that some of these settlement associations may be species specific and/or mutualistic, providing important advantages to those involved in the relationship.

### 4.6. Disrupting near-boundary and reef level flow regimes

Sponges are a morphologically diverse group (Boury-Esnault and Rützler, 1997), with many morphologies being three-dimensional, protruding from the substrate, often extending further away from the substrate than surrounding corals, gorgonians and algae. For example, barrel sponges (*Xestospongia* spp.) in the Indo-Pacific commonly extend more than 1.5 m from the substrate (Bell and Smith, 2004). Although there is huge potential for the extension of sponges into the water column to alter local-scale flow regimes, influence near-boundary current depletion (Hiscock, 1983) and aid in the food supply to other organisms, this functional role has not yet been investigated for sponges. Changes in flow regimes, as a result of gross morphology/size, has the potential to enhance the feeding in other parts of the same sponge, as has been reported for bryozoans (Okamura, 1985; Okamura and Partridge, 1999; Pratt, 2005) or alter local-scale flow regimes in the vicinity of the sponge and enhance the feeding of other organisms. Although sponge morphological variation has been considered by many authors as a mechanism of environmental adaptation (Palumbi, 1984, 1986; Gaino et al., 1995; Bell et al., 2002), there is also the possibility that species-specific variations are related to feeding advantages. This would explain the results of Bell (2002) who found that *Cliona celata* showed very fast regeneration rates, despite growth rates being considered to be very slow for this species, such that individual sponges recovered their original shape very rapidly. With the increasing availability and sensitivity of acoustic current Doppler profiling (ACDP) techniques, it should be possible to investigate the flow regimes around sponges, and their influence on other organisms in the future.

### 4.7. Sponges as agents of biological disturbance

The competitive interactions between sponges have recently been reviewed by Wulff (2006) and were also considered an important functional role by Diaz and Rützler (2001) and Rützler (2004), although there is one further functional aspect of inter- and intra-phyletic competitive interactions that should be highlighted that has not been previously considered. Sponges are considered one of the top spatial competitors, particularly in temperate regions (Bell and Barnes, 2003), where hermatypic corals (which are important sponge competitors on coral reefs) are absent. However, in addition to sponges being top spatial competitors, many also go through seasonal tissue regression as a result of reduced availability of nutrients and water temperature (see Stone, 1970; Fell, 1978; Thomassen and Riisgård, 1995). This leads to the potential for sponges to kill/outcompete organisms during growing periods, but then the space that they have acquired being available again to other organisms during periods of sponge tissue retraction. In the NE Atlantic two species that show marked seasonal contraction and expansion of tissues are *Halichondria panicea* and *Hymeniacidon perlevis*, which are common intertidal and shallow subtidal sponges (Stone, 1970; Thomassen and Riisgård, 1995). In a study on the Welsh coast (Bell, unpublished data) the patch size of these two species increased during the spring and summer months (April to September), when they are both aggressive spatial competitors overgrowing other sessile organisms including encrusting calcareous algae, bryozoans, hydroids, barnacles and tube worms as they grow. However, patch size of both these species then decreased during winter months (consistent with other previous studies) leaving bare rock around the remaining patches. Interestingly, the direction of growth varied between years and growth was not equal in all directions, so space created in one year was not necessarily re-occupied during subsequent years by the same sponge, which allowed competitively inferior species to occupy the newly created space (particularly barnacles). There is still relatively little data on

temporal variability in sponge assemblages, compared with spatial variability and there does seem to be some differing reports with regard to the level of stability and variability in sponge assemblages (see Pansini and Pronzato, 1990; Wulff, 2001, 2006; Bell et al., 2006; Roberts et al., 2006). If many sponges do go through expansion and contraction patterns (perhaps seasonally) then they are likely to be more important in the release of space to other organisms than previously thought. At present the widespread extent of this functional role remains unknown, but it may be significant in temperate and polar ecosystems where there is large seasonal variation in nutrients resulting in a reduction in sponge patch size/ volume during lowered nutrient periods.

### 4.8. Sponges as releasers of chemicals

A number of the function roles described above are the result of the diverse array of secondary metabolites that are produced by sponges. Of particular relevance are spatial competition, predator defence, settlement inhibition and provision of defence mechanisms to other organisms. Many authors have demonstrated the role of secondary metabolites in tropical sponge predation defence (e.g. Bakus and Green, 1974; Green, 1977; Pawlik et al., 1995; Uriz et al., 1996; Becerro et al., 2003; Jones et al., 2005), although the use of chemicals is not ubiquitous to all sponge species (Pawlik et al., 1995). Fewer studies have investigated the role of chemicals in sponge predation in temperate and polar regions, but Hill et al. (2005) suggested chemical defences, in combination with spicules, are probably responsible for protection of some NE Atlantic sponges from hermit crabs. Furthermore, sponge chemical defence from predation is also thought to be important for Antarctic sponges (McClintock et al., 2005). In addition to the protection afforded directly to sponges from chemicals there have also been reports that organisms that feed on sponges may be able to accumulate sponge secondary metabolites and utilise them in defence from their own predators. For example, Becerro et al. (2006) found that two species of gastropterid molluscs found on sponges shared polybrominated diphenyl ethers (BDEs) with their host sponge *Dysidea granulosa*; the molluscs accumulate BDE in the mantle at approximately the same concentration as in the sponge, and concentrate it in their parapodia at over twice the sponge concentration. These authors thereby suggest the molluscs are sharing the same chemical defence strategy as the sponge by utilising the products produced by sponges.

There has been considerable focus on the spatial interactions between sponges and other organisms (for a recent complete review see Wulff, 2006), particularly on coral reefs as space is usually limited (Pawlik et al., 2007). The use of secondary metabolites by sponges in spatial competition has been long realised, but ecologically relevant tests of allelopathy have been difficult in the past (Pawlik et al., 2007). There has been some discussion on the importance of chemicals in overgrowth activity (occupying more space) versus preventing overgrowth of sponges by other species of sponge, with chemicals being considered most important in the latter (Engel and Pawlik, 2005). The inter-phyletic spatial interactions of sponges may be more complex than intra-phyletic interactions given the different evolutionary histories of phyla and of particular interest is the interaction between corals and sponges. Although there are few reports of sponges overgrowing/outcompeting corals (e.g. Aerts and Van Soest, 1997; Wulff, 2006), compared with 'stand-off' interactions, recent research by Pawlik et al. (2007) using pulse amplified modulated (PAM) fluorometry was able to demonstrate that some sponge chemicals can negatively influence coral–algal photosynthetic potential and also cause bleaching. There appears to be heavy reliance on chemical production by sponges in their interactions with other organisms, although the evidence to date suggests these chemicals are more

important in preventing overgrowth by other organisms, rather than increasing their spatial occupation.

Sponge chemical production is also likely to play a role in the prevention of settlement of organisms on sponge surfaces, thereby keeping sponge surfaces clear of organisms that may potentially smother the sponge or reduce local feeding efficiency. Most of the studies on sponge chemicals have examined the effects of crude extracts on the settlement of other species (e.g. Davis et al., 1991; Becerro et al., 1997; Hellio et al., 2005; Lee et al., 2006), and in most cases sponge extracts have been very successful in preventing the inhibition of a wide range of larvae. More recently, research has been focusing on the ability of sponges to produce bioactive compounds to modulate the bacterial communities on their surfaces to protect the sponge from settlement of other organisms. Lee et al. (2006) provided evidence that sponges can indeed produce bioactive compounds to prevent settlement of larvae through modulation of their associated bacterial communities. The mechanisms of chemical defence by sponges (and other organisms) are of particular commercial interest in the development of natural antifouling compounds.

### 4.9. Sponges as tools

It is noteworthy and novel to mention a very specific functional role of sponges identified in Shark Bay Australia, even though it may be of limited interest beyond the local-scale. During long-term research of bottlenose dolphins, individuals have been observed to carry sponges (*Echinodictyum mesenterinum*) on their rostra (Smolker et al., 1997). Three hypotheses regarding the proposed function of sponge carrying were proposed by Smolker et al. (1997): (1) dolphins are playing with the sponges; (2) the sponges contain some compound of use to the dolphins (e.g. for medicinal purposes); and (3) the sponges were used as a tool to aid in foraging. The foraging tool hypothesis is best supported from observations of the dolphins, although the way in which sponges are used is still not fully understood. More recent molecular investigations have shown a high degree of recent co-ancestry between dolphins that use sponges (since not all dolphins use sponges) suggesting cultural transmission is responsible for the small group of dolphins that use sponges in this way (Krützen et al., 2005). Currently, this use of sponges has not been reported from elsewhere by dolphins.

### 4.10. Importance of sponge interactions and associations

Sponges interact in a variety of ways with a huge diversity of organisms. It is important to realise that although sponges perform many functional roles with respect to these associations, many are not one-sided and sponges may also benefit from the relationship (see Wulff, 2006). It appears that only a very small number of the interactions between sponges and other organisms have been described, and with such huge diversity associated with sponges, and such a range of potential interactions, it is likely to be some time before the full functional relationships between sponges and other organisms are known. The majority of information on these relationships is from tropical and temperate regions, with far less information being known about polar sponge relationships.

## 5. Conclusions

Sponges clearly fulfil a number of important functional roles across temperate, tropical and polar ecosystems. Interestingly, a number of additional important functional roles of sponges have been further developed and identified since the earlier studies of Wulff (2001) and Diaz and Rützler (2001), further highlighting the importance of sponges to ecosystem functioning. One aspect of sponge functional ecology currently considered beyond the scope

of this review, because there is currently insufficient information, is the relative importance of these different functional roles. Determining or ranking the functional roles is difficult, but it is important, since some roles that sponges fulfil will almost certainly be more important than others, and this may vary spatially or temporally. There is also some considerable inequality in the geographic regions where the functional roles of sponges have been studied, particularly for coral reef sponges, where the majority of studies relating to functional aspects of sponge ecology have been conducted in the Caribbean, with little information available from Indian and Pacific Ocean reefs. Given the differences in the evolutionary history of these different biomes it is possible that the importance and prevalence of functional roles differs. It is strikingly apparent from the literature that there is little information on the functional roles of sponges in polar ecosystems, although they are thought to be very important in benthic communities (Dayton et al., 1974). In Antarctica, sponges often dominate benthic environments and will therefore be important in bentho-pelagic coupling, as microhabitat providers and as a food source for a range of organisms (McClintock et al., 2005).

Wulff (2001) suggested a number of reasons why sponges are often overlooked in conservation programmes, highlighting problems in identifying sponges and measuring sponge abundance, but their functional importance means these problems must be overcome. Sponges are not the easiest of organisms to work with but their widespread distribution, often biomass dominance, and important functional roles means their contribution to ecosystem functioning must not be overlooked and sponge monitoring must be fully integrated into all current and future monitoring programmes. Furthermore, care must be taken when including sponges in functional assessments of marine communities since classifying them on the basis of trophic level (e.g. trophic group analysis see Bremner et al., 2003) clearly under-represents the important role they play.

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