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OPINION

Could some coral reefs become sponge reefs as our climate changes?

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Abstract

Coral reefs across the world have been seriously degraded and have a bleak future in response to predicted global warming and ocean acidification (OA). However, this is not the first time that biocalcifying organisms, including corals, have faced the threat of extinction. The end-Triassic mass extinction (200 million years ago) was the most severe biotic crisis experienced by modern marine invertebrates, which selected against biocalcifiers; this was followed by the proliferation of another invertebrate group, sponges. The duration of this sponge-dominated period far surpasses that of alternative stable-ecosystem or phase-shift states reported on modern day coral reefs and, as such, a shift to sponge-dominated reefs warrants serious consideration as one future trajectory of coral reefs. We hypothesise that some coral reefs of today may become sponge reefs in the future, as sponges and corals respond differently to changing ocean chemistry and environmental conditions. To support this hypothesis, we discuss: (i) the presence of sponge reefs in the geological record; (ii) reported shifts from coral- to sponge-dominated systems; and (iii) direct and indirect responses of the sponge holobiont and its constituent parts (host and symbionts) to changes in temperature and pH. Based on this evidence, we propose that sponges may be one group to benefit from projected climate change and ocean acidification scenarios, and that increased sponge abundance represents a possible future trajectory for some coral reefs, which would have important implications for overall reef functioning.

Keywords: climate change, coral reef, microbes, ocean acidification, phase shift, sponge

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Introduction

The primary effects of climate change are a predicted 1.8–4 °C increase in global air temperature by 2100, along with similar rises in sea surface temperature (IPCC, 2007) and a projected rise in atmospheric carbon dioxide (CO_2) concentration from a present day partial pressure (pCO_2) of 400 μatm (IPCC, 2007) to between 730 and 1088 μatm by 2100, depending on the model and assumptions being applied (Meehl *et al*., 2007). Uptake of CO_2 by the ocean changes the seawater carbonate chemistry, causing a reduction in pH and carbonate saturation, and an increase in dissolved inorganic carbon availability (Caldeira & Wickett, 2003; Raven *et al*., 2005). These conditions particularly affect carbonate-accreting reef organisms, as evidenced by reduced calcification of reef-building corals (Schneider & Erez, 2006; Anthony *et al*., 2008) and crustose coralline algae (Anthony *et al*., 2008; Jokiel *et al*., 2008). Ocean acidification (OA) and elevated sea surface temperatures have also been shown to negatively affect reproduction and early developmental stages in calcifying marine invertebrates (Jokiel & Coles, 1990; Albright *et al*., 2010; Heyward & Negri, 2010; Albright, 2011; Albright & Langdon, 2011; Byrne, 2011) and can interfere with the settlement of coral larvae indirectly by modifying the inductive capacity of their preferred settlement substratum (Albright *et al*., 2010; Albright & Langdon, 2011; Webster *et al*., 2011a, 2013a; Doropoulos *et al*., 2012).

Coral reefs across the world have already been seriously degraded (Pandolfi *et al*., 2003; Sweatman *et al*., 2011; De'ath *et al*., 2012) and have a bleak future in response to predicted global warming and OA scenarios, as well as a range of other stressors (Hughes *et al*., 2003; Hoegh-Guldberg *et al*., 2007; Burke *et al*., 2011). Current models (IPCC, 2007) indicate that many coral species will not survive until the end of this century and, as unpalatable as that may be, we have to imagine coral reef ecosystems with significantly reduced levels of coral compared with today. With the decline of calcifying organisms, other potential 'winners' may emerge, including an increase in some of the oldest living

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organisms on reefs - the sponges. Sponges are an important component of coral reef fauna worldwide with a range of important functional roles, from facilitating primary production to filtering large quantities of water and eroding the carbonate reef structure (reviewed in Bell, 2008). They also form a wide range of biological associations with organisms from microbes to vertebrates, which are critical to their success (Ávila *et al.*, 2007; Webster & Taylor, 2012). This diversity of functional roles means that changes to the abundance or composition of sponge assemblages is likely to significantly influence other reef organisms and overall ecosystem functioning (e.g., Peterson *et al.*, 2006). Despite the importance of sponges on reefs, research to date has primarily focused on how corals will respond to stressors associated with global warming and OA (e.g., De'ath *et al.*, 2012), while the responses of other reef invertebrates have been relatively poorly studied (Przeslawski *et al.*, 2008). Considering the predicted declines in coral cover, combined with the possibility that sponges may be one of the 'winners' under future global warming and OA scenarios, a more complete understanding of sponge responses is clearly warranted. We propose that shallow water tropical reefs that are currently dominated by corals could be replaced by sponges that will live on the remaining calcium carbonate structure (hereafter termed sponge reefs).

Not all corals will respond uniformly to OA and global warming scenarios due to physiological variation between different hosts and their dinoflagellate symbionts (e.g., Anthony *et al.*, 2008; Mieog *et al.*, 2009). We propose that such species-specific sensitivities may also occur in sponges, particularly due to the wide diversity of symbiotic microbes that reside within them (Webster & Taylor, 2012). Whilst sponges hosting photosynthetic cyanobacteria can obtain a source of fixed carbon from their symbionts (Wilkinson & Cheshire, 1990), this is not universal and the importance and stability of these interactions vary greatly across host species (Leong & Pawlik, 2010; Bannister *et al.*, 2011; Freeman & Thacker, 2011; McMurray *et al.*, 2011). Overall, the relative importance of photosymbionts for the provision of food appears to be less than that in the coral–dinoflagellate symbiosis. Nevertheless, sponges supporting phototrophic cyanobacteria may have higher productivity with increased CO_2 availability, consistent with observations reported for free-living cyanobacteria (Fu *et al.*, 2007). Heterotrophic species may also benefit if picoplankton food resources are stimulated (McKinnon *et al.*, 2007), although there is still considerable uncertainty regarding picoplankton responses to climate change in reef environments. Here, we argue that sponge reefs represent a credible future for some current coral reefs, as sponges and corals respond differently to changing ocean chemistry and environmental conditions. To support our hypotheses we present evidence from the geological record, describe recent changes from coral- to sponge-dominated systems, and consider the physiological responses of the sponge holobiont (host and microbial symbionts) to temperature and pH fluctuations. Finally, we consider how a tropical sponge reef might function and how it might influence important processes like nutrient cycling and productivity. We primarily focus on tropical coral reef ecosystems rather than temperate and polar environments where sponge reefs can also be found (Eluik, 1991; Conway *et al.*, 2001; Goodwin *et al.*, 2011; Reveillaud *et al.*, 2011), as very little is known about the ecology of cold water sponge reefs and it is likely that they function very differently from tropical reef systems.

Lessons from the past: sponge reefs in ancient times

The notion of sponges coming to dominate marine areas is not without historical precedent. During the Upper Carboniferous (~300 Mya), algae and sponges were the major frame-building organisms on reefs, with cnidarians, bryozoans, foraminiferans and microorganisms playing a secondary role (West, 1988). Siliceous sponges and benthic microorganisms together formed substantial reef mounds at various stages of the Paleozoic (540–250 Mya) and Mesozoic (250–65 Mya) eras (Brunton & Dixon, 1994). In such reef mounds, both demosponges and hexactinellids were abundant, although there was a change towards dominance by the latter in the Mesozoic. Paleontological evidence suggests that these episodes of reef building by benthic microbes, with siliceous sponges functioning largely as bafflers and binders, each lasted approximately 5–10 Myr (Brunton & Dixon, 1994). A group of calcareous stromatoporoid sponges were also major reef builders in the mid-Paleozoic (Wood, 1999). The stromatoporoids have largely resisted finer taxonomic classification (currently classified as sclerosponges), but do appear to include some demosponges with a secondary calcareous skeleton (Pisera, 2006).

At times, siliceous sponges have been the beneficiaries of significant global events, which have harmed other marine benthic organisms. Most notably, the transition from the Triassic to Jurassic periods, some 200 Mya, was marked by a mass extinction event, with calcifying marine invertebrates (including scleractinian corals) being particularly adversely affected (Kiessling *et al.*, 2009; Kiessling & Simpson, 2011). Paleontological evidence suggests that this event was accompanied by ocean acidification, resulting from a wider disruption of the carbon cycle due to volcanic activity associated with the Central Atlantic Magmatic Province (Schaller *et al.*, 2011; Greene *et al.*, 2012). There is evidence in the geological record that the decimation of biocalcifier communities was followed by the proliferation of siliceous sponges, which appeared to persist over a geologically relevant time scale (millions of years) and be widespread across Europe (Delecat *et al.*, 2011). Changes in sea level and sedimentation processes at this time are thought to have led to the radiation of siliceous sponges from the deep ocean, from which they came to dominate mid-shelf habitats previously occupied by biocalcifiers (Delecat *et al.*, 2011 and references within). Interestingly, it has been suggested that four out of the five global crises to affect reef metazoans in the past 500 Myr were affected, at least in part, by OA and rapid global warming (Kiessling & Simpson, 2011). Moreover, two of the five main mass extinctions exhibit evidence of a link with OA. While some care needs to be exercised when comparing across geological time periods, as local and regional environmental conditions may be different, the available geological evidence clearly supports the persistence of demosponge-dominated assemblages at certain times in geological history.

Changes from coral- to sponge-dominated systems

While there has been considerable interest in rapid changes from coral to non-coral states (so-called phase shifts), most focus has been on shifts towards algal-dominated systems. However, these algal phase shifts have been predominantly reported from the Caribbean, with such widespread shifts less common in other regions, despite coral reef degradation (e.g., Bruno & Selig, 2007; De'ath *et al.*, 2012). This suggests that key drivers of shifts to algal systems may vary regionally, such that algal phase shifts might not occur ubiquitously in response to declines in reef quality. Importantly, there are now reports of reef systems becoming dominated by other organisms (including sponges) as coral cover declines (Norström *et al.*, 2009), although comparing patterns of change across studies and regions can be difficult due to local and regional factors that drive community structure. While the shift to algal systems is often attributed to increased nutrient levels and reduced herbivory (Hughes *et al.*, 2010), changes to non-algal systems are far less understood, but may be related to similar factors (Norström *et al.*, 2009). Interestingly, a recent modelling study by Gonzalez-Rivero *et al.* (2011) highlighted the potential for sponges to actually influence the transition between algal- and coral-dominated systems, by providing an alternative food source for grazing fish, thereby enhancing the shift to algal-dominated systems on Caribbean reefs. This demonstrates the complex interplay between the dominant reef organisms and how changes in sponge abundance may alter other key processes or transitions. It also suggests that sponges and algae might be able to coexist to form sponge-algal reefs, especially as there is no evidence to date that algae are able to competitively eliminate sponges from coral reefs (see Wulff, 2012).

Although records of sponge phase shifts are certainly less widespread than algal phase shifts, there are reports from the Caribbean, Atlantic, Indo-Pacific and Pacific reefs (Fig. 1). Within Caribbean reef systems, it is largely increases in bioeroding sponges that have been reported in response to coral declines (Antonius & Ballesteros, 1998; Aronson *et al.*, 2002; Lopez-Victoria & Zea, 2004; Ward-Paige *et al.*, 2005; Maliao *et al.*, 2008;). In such cases, it is usually sponges taking advantage of newly available substrate rather than sponges outcompeting corals for space (see indirect effects section below). For example, the bioeroder *Cliona langae* is thought to have increased in abundance on Puerto Rican reefs in the late 1970s following declines in hard coral cover, resulting from the combined effects of disease, hurricane damage, siltation and eutrophication (>10% cover, although quantitative estimates for predisturbance levels are not available; Williams *et al.*, 1999). However, such changes are not restricted to bioeroding sponges (Zea, 1994; Aronson *et al.*, 2002; Maliao *et al.*, 2008). For example, reefs in Belize experienced large increases in the sponge *Chondrilla nucula* following a thermal anomaly that drove mass coral mortality (from 15 to 43% between 1999 and 2001; Aronson *et al.*, 2002). In the latter example, this shift appears to be persistent, as *C. nucula* was still the dominant reef organism in 2007 (see Norström *et al.*, 2009). While these events in the Caribbean might appear to represent relatively local-scale shifts that are primarily mediated through increases in bioeroding sponges, relative sponge abundance does appear to be increasing and sponge biomass now exceeds coral biomass Caribbean-wide (Diaz & Ruetzler, 2001; Maliao *et al.*, 2008; Pawlik, 2011). Further south, a major reduction in all reef organisms except sponges, following the 1997–1998 El-Niño Southern Oscillation (ENSO) on an Atlantic coral reef in Brazil, resulted in sponges becoming the dominant reef fauna, as they were largely unaffected by this temperature anomaly (Kelmo, 2002).

Within the Indo-Pacific, there has only been one reported shift from a coral- to sponge-dominated system, although these shifts may be more widespread, but unreported. In the Wakatobi Marine National Park (SE Sulawesi, Indonesia), sponges now dominate several once coral-dominated sites. Coral cover has declined from >30% to 8–11% over a 6–7 year period (McMellor, 2007; Powell *et al.*, 2010), while sponge

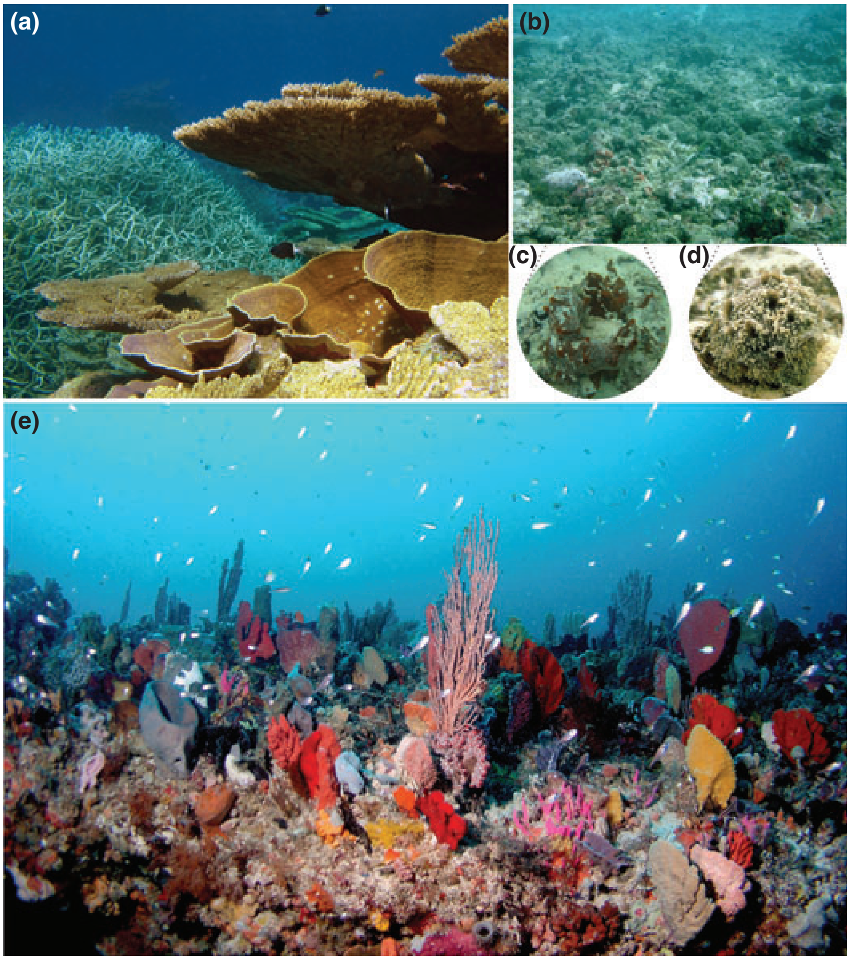

Fig. 1 The likely once coral-dominated (a) lagoon at Palmyra Atoll in the Central Pacific looks devoid of life (b), but on closer inspection the hard surfaces are dominated by sponges (c and d). Sponge-dominated reefs (e) have lower structural complexity than coral-dominated ecosystems (45 m depth, Western Australia).

densities also appear to have increased over the same time period (from 60–80 sponges m^{-2} to 100–120 sponges m^{-2}; Bell & Smith, 2004; Powell *et al.*, 2010). Interestingly, these sponge-dominated sites are characterised by a single dominant sponge species (*Lamellodysidea herbacea*) and by high levels of sedimentation and turbid water at certain times of the year, and consequently experience reduced light levels compared with other sites where coral declines have also been reported. Within the Central Pacific, a shift from a coral-dominated state has been reported for the lagoon of Palmyra Atoll (Knapp *et al.*, 2013; Fig. 1). This lagoon was the subject of extensive modifications during WWII, and the hard substratum is now dominated by sponges (16–33% of available hard substrate, <1% coral). Based on anecdotal evidence, comparisons of lagoon and outer-reef sponge assemblages and the presence of nonindigenous sponge species at Palmyra, it seems that this site has undergone a change from a coral- to sponge-dominated community as a result of environmental degradation and the introduction of exotic sponge species. Given that the initial site degradation occurred over 60 years ago, this sponge state appears stable. Interestingly, like the sponge-dominated reefs in the Wakatobi Marine National Park, the lagoon environment at Palmyra is highly turbid with low light penetration (Knapp *et al.*, 2013), which perhaps aids in sponge proliferation as it prevents colonisation by algae. Many reefs have experienced increased levels of sedimentation within the Indo-Pacific region, and it is possible that such sites also support abundant sponge assemblages that have not yet been reported. Also within the Pacific, there have been multiple reports of 'outbreaks' of the cyanobacteriosponge *Terpios hoshinota* (Rűtzler & Muzik, 1993). This sponge can very rapidly increase in abundance (>90% cover) in response to environmental perturbations and devastate coral communities. For example, Schils (2012) reported a sudden transition from a coral- to a cyanobacteria-dominated community, including *T. hoshinota*, in the Northern Mariana Islands between 2009 and 2010, as a result of nutrient enrichment from volcanic ash. However, while the outbreaks of *T. hoshinota* can be locally devastating, they generally appear to be short-lived and therefore do not represent stable states (Reimer *et al*., 2010).

While there is increasing evidence of higher sponge abundance in response to declines in corals, it is important to note that there have also been reports of concomitant declines in sponge assemblages and biomass as coral cover is lost. For example, Wulff (2006a) reported a large decline in a localised Caribbean sponge assemblage in Panama, with the loss of >50% of sponge species and >40% of biomass over a 14-year period (1984–1998). However, these declines could not be correlated with any specific abiotic or biotic factors, although disease was proposed as a possible cause. Whilst some sponge disease outbreaks have correlated with elevated seawater temperature, others appear to be unrelated to environmental factors (reviewed in Webster, 2007) and, overall, reports of sponge disease are much less prevalent than the massive reductions in coral cover due to disease events (Bourne *et al*., 2009). While there are other sporadic reports of sponge loss (Cerrano *et al*., 2000), there are also frequent reports of increasing sponge biomass. For example, one of the most ecologically important sponge species in the Caribbean, *Xestospongia muta*, has increased by almost 50% since 2000 on some reefs (McMurray *et al*., 2010). Population models have also indicated that these sponges will continue to increase in abundance as large pulses of new recruits and high sponge survival support this population growth (McMurray *et al*., 2010). This contrasts with findings for Caribbean corals where significant population declines have, at least in part, been attributed to recruitment failure (Hughes & Tanner, 2000). Interestingly, Colvard & Edmunds (2010) also reported increases in sponge abundance between 1992 and 2007 on shallow reefs of St. John, US Virgin Islands, although the increases were independent of coral cover that remained at approximately 5% over the study period.

Changes in sponge abundance across natural CO_2 gradients have also been reported. Price *et al.* (2012) studied natural temporal variation in temperature and pH from three reef systems in the Central Pacific, and examined how these changes correlated with community development. They found that in areas where daily pH ranges were high, noncalcifying benthic organisms dominated the space; this included a higher abundance of sponges. Sponges have also been reported at CO_2 vent systems in Papua New Guinea, demonstrating their tolerance to higher $p\mathrm{CO}_2$ (see Fabricius *et al*., 2011), although their overall abundance was higher at ‘control’ areas away from the CO_2 seeps.

Direct impacts of OA and temperature on the sponge holobiont and component parts

Whether the decline of reef-building corals has generated additional space on the reef for sponges to colonise, or whether sponges are just less susceptible to climate change and environmental degradation, remains uncertain. While OA may be expected to primarily affect sponges with calcareous skeletons (<3% of all sponge species), it is also likely to impact those more dominant species with siliceous skeletons, because the sponge body plan is based around a system of water canals that leaves all cells in close contact with seawater. There are a number of ways that OA and elevated sea surface temperatures may impact sponges, including changes to cellular and physiological processes, disruption to acid base physiology, metabolic suppression and loss of function by the symbiotic microbial community. For example, seawater temperature experimentally raised to 30 °C caused an increased expression of heat shock protein 70 in the Caribbean sponge *Xestospongia muta* (López-Legentil *et al*., 2008) and temperatures of 32 °C induce stress responses in the holobiont of the Great Barrier Reef sponge *Rhopaloeides odorabile* (Webster *et al*., 2008, 2013b; Pantile & Webster, 2011; Fan *et al*., 2013). In *R. odorabile*, expression profiling of the host and symbiont community, in conjunction with analysis of the phylogenetic and functional structure of the microbial community, indicated that elevated temperature caused an immediate stress response in all components of the holobiont. Disruption to nutritional interdependence and molecular interactions between the members of the holobiont further destabilised the sponge, ultimately leading to the loss of archetypal symbionts and eventual mortality (Fan *et al*., 2013). In contrast to these studies, other recent publications have indicated that the ecological roles, physiological processes and larval dynamics of coral reef sponges across a range of taxa are unaffected by water temperature and pH conditions predicted for the end of this century (Whalan *et al*., 2008; Webster *et al*., 2011b; Duckworth *et al*., 2012). For example, growth and survival of six ecologically important Caribbean sponge species was similar between treatments consistent with present day conditions (28 °C; pH = 8.1) and those predicted for 2100 (31 °C; pH = 7.8). Interestingly, gene expression in the larvae of *R. odorabile* is also not significantly affected by temperatures under 36 °C, although adults of the same species undergo a molecular shutdown at 32 °C (Webster *et al*., 2013). This indicates that, at least in this species, environmental adaptation may occur via the tolerant larval stage acting as a thermally resistant vector for geographic range expansion. In addition, bioerosion of reef substratum by sponges can dramatically accelerate at lower pH (Duckworth & Peterson, 2012) and elevated *p*CO2 (Wisshak *et al.*, 2012), suggesting that bioerosion by sponges will be greater under future environmental scenarios. Wisshak *et al.* (2012) proposed that this increase in bioerosion rate in response to elevated $p\mathrm{CO_2}$ is due to an enhanced efficiency of the sponge bioerosion process, as lowered pH results in a shallower dissolution gradient between the environment and the sponge's etching site. In particular, eroding clionid sponges (which are one of the major groups of reef bioeroders) appear to take advantage of the higher dissolution rates in the more acidic environment and erode more substrate rather than lowering their metabolic rates, although more research is needed to fully understand these mechanisms. In addition to these eroders having direct impacts on dead substrate, they also have the potential to weaken coral heads and therefore increase mortality rates of living corals (Schönberg & Wilkinson, 2001).

In contrast to corals, photosymbiont-containing sponges appear to be particularly resistant to bleaching events, with no widespread bleaching episodes recorded to date. Minor bleaching of some species was observed in the 1998 global coral bleaching event (Fromont & Garson, 1999) and bleaching of *Xestospongia muta* has been reported from the Caribbean (López-Legentil *et al.*, 2008), although no correlation has been found between bleaching and temperature anomalies (McMurray *et al.*, 2011). In sponges, symbiosis with dinoflagellates of the genus *Symbiodinium* (zooxanthellae) is largely restricted to members of the bioeroding Clionaidae, which have been shown to have higher bleaching resistance than other coral reef organisms that host zooxanthellae (Vicente, 1990; Hill & Wilcox, 1998; Schönberg & Suwa, 2007; Schönberg *et al.*, 2008). This is possibly due to differences in the *Symbiodinium* types they host or protection provided by their physical location deep within the host tissue (Schönberg & Suwa, 2007). In contrast to corals, cyanobacteria are the dominant photosymbionts in sponges and they can potentially avoid photoinhibition by moving phycobilisomes around on the thylakoid membrane (Joshua & Mullineaux, 2004), which allows them to maximise their use of available energy, and reduce photodamage to Photosystem II by absorbing excess energy. This capability also likely contributes to the reduced incidence of bleaching in cyanobacteria-containing sponges compared with corals harbouring zooxanthellae. Interestingly, cyclically bleached Caribbean barrel sponges do not increase expression of heat shock proteins (although fatally bleached sponges do), indicating that when cyclic bleaching occurs, it is not a sign of sponge stress, but rather a response by cyanobacterial symbionts that likely has no negative effect on their host sponge (López-Legentil *et al.*, 2008).

Cyanobacteria such as *Synechococcus spongiarum* are common and abundant symbionts of sponges globally (Simister *et al.*, 2012), and recent research has indicated that *Synechococcus* cells increase photosynthetic rates under the synergistic effects of elevated temperature and $p\mathrm{CO_2}$ (Fu *et al.*, 2007). Considering this stimulatory effect, sponges that rely on photosynthetically fixed carbon for nutrition may have increased scope for growth under the climate conditions expected to occur in the coming century. Increased scope for growth under elevated $p\mathrm{CO_2}$ was recently demonstrated in *Anemonia viridis*, a sea anemone that occurs along a naturally occurring $\mathrm{CO_2}$ gradient in the Mediterranean (Suggett *et al.*, 2012). Photosynthesis and respiration in this species, which hosts zooxanthellae, increased at elevated $p\mathrm{CO_2}$, indicating that the increased growth was at least partially due to $\mathrm{CO_2}$ stimulation of metabolism. Enhanced productivity with elevated $p\mathrm{CO_2}$ would likely increase overall host fitness and potentially enable noncalcifying organisms, such as sponges, to thrive under predicted climate change conditions.

Indirect effects of global warming and OA on sponges

The complex ecological interactions that sponges have with other organisms (Wulff, 2006b) mean that there are likely to be considerable indirect effects (both positive and negative) of changing sponge abundance.

Sponges are important spatial competitors in coral reef systems (Hill, 1998; Rűtzler, 2002; Pawlik *et al.*, 2007) and, given that space is generally limiting on healthy reefs, spatial competition has a major influence on community structure (Jackson, 1977). While we do not expect direct competition to be a primary mechanism by which sponges are 'winners' over corals, there are likely to be indirect effects as a result of decreased coral abundance. Given the expected decline in corals and other calcifying groups (including molluscs, bryozoans and crustose coralline algae) in response to OA and global warming, sponges would likely have greater access to hard substrata and potentially need to devote fewer resources to defend the space already occupied or to prevent overgrowth. Extensive research from the Caribbean has shown that sponges produce an array of chemicals that are important in structuring sponge assemblages through both competitive and predation effects (Porter & Targett, 1988; Engel & Pawlik, 2000; Pawlik, 2011). While there have been many reports of eroding species having negative effects on corals (e.g., Hill, 1998; Rűtzler, 2002), there are relatively few reports of direct coral overgrowth by epilithic sponges (Wulff, 2006a). However, numerous studies have shown negative effects on neighbouring corals through the production of toxic sponge compounds. For example, in the Indo-Pacific, de Voogd *et al.* (2004) found a large number of sponge–coral interactions that resulted in necrosis of coral tissue due to the bioactivity of the sponges. In the Caribbean, Pawlik *et al.* (2007) showed that sponge extracts had negative effects on corals and even caused coral bleaching in some cases, while more recently, Hoeksema & de Voogd (2012) found that the free-living mushroom coral *Heliofungia fralinae* moved away when placed in close proximity to fragments of the toxic sponge *Callyspongia (Euplacella) biru*. Whether allelopathic chemicals are actually used by sponges to aggressively gain space or are more important in retaining already occupied space remains debatable (Wulff, 2006b), but further reductions in coral abundance would likely reduce the need for investment in toxic compounds. Toxic chemical production is expected to be energetically costly, so a reduction in the use of such chemicals means that energy could be devoted to other processes, including growth and reproduction. Given the potentially negative effects of sponges on live coral tissue (see above), changes to sponge abundance or species composition also have the potential to further negatively influence corals.

The effects of OA and temperature on sponge predators [including echinoderms, fish and turtles (Wulff, 2006b)] are largely unknown and currently difficult to predict. Increased sponge biomass would be expected to support an increased abundance of sponge predators with likely flow-on effects for higher trophic levels (Fig. 2). However, the effect of these different predators may not be uniform across species, with research from the Caribbean showing the importance of chemical defence in trophic interactions. Pawlik (2011) proposed that fish predators have differential effects across three categories of sponges: preferred species are removed from the reef, they graze on palatable species and have little impact on defended species. Whilst it is still unclear how such complex relationships might play out with increased sponge abundance (particularly in areas outside the Caribbean where far less is known about sponge predation), if sponge assemblages are structured by top-down processes then increases in sponge biomass may be restricted due to consumption by fish at higher trophic levels.

While changes in the abundance of sponges in response to global warming and OA are the primary focus of this article, reductions in coral abundance could also be accompanied by increases in the abundance of other animal groups (see Przeslawski *et al.*, 2008); this is likely to have effects on sponges and therefore requires consideration. Norström *et al.* (2009) reported changes from coral- to corallimorpharian/soft coral-, and to a lesser degree ascidian-dominated states. The primary ways that these organisms interact with sponges is through competition for food and space, and the potential for sponges to be released from predation if they become a less preferred food source. However, these interacting effects are extremely difficult to predict, especially as the responses of these other groups of animals to OA and global warming are so poorly understood. Corallimorphs, anemones, soft corals and ascidians are generally fast growing and short lived compared with most sponge species (e.g., Shenkar *et al.*, 2008; Work *et al.*, 2008), yet changes to sponge-dominated systems appear more common than phase shifts to other invertebrate states (see Norström *et al.*, 2009). Research examining ecological interactions between sponges and other organisms on coral reefs is rare (see Wulff, 2006b), yet understanding these ecological interactions is an urgent research priority if we are to accurately predict how reefs will respond to warming seas and OA. Finally, it is also important to note that variation in sponge life-history strategies (e.g., *r*- vs. *k*-strategists) will influence all these interactions and as a result there is likely to be some variation in the ecological interactions for different sponge species

How would a sponge reef function?

Given the complexity of reef systems, it is difficult to accurately predict how a reef might function if sponges become the dominant fauna (Fig. 2). Moreover, many transformations may actually arise from coral loss rather than sponge domination *per se*. However, increased sponge abundance is likely to directly influence some key processes. Bioerosion and water filtering (including nutrient cycling) are the most important functional roles of sponges on reefs (Bell, 2008), and both are likely to increase in sponge-dominated systems. Sponges pump large quantities of water (thousands of litres of water per kg biomass per day) and have a significant impact on the water column by removing a large proportion of the available food, particularly picoplankton (e.g., Perea-Blázquez *et al.*, 2012a) and dissolved organic carbon (DOC) (de Goeij *et al.*, 2008), but also possibly viruses (Hadas *et al.*, 2006). A large increase in sponge biomass would therefore have a considerable impact on the surrounding water column through these trophic interactions. Sponges rely heavily on DOC as a food source (Yahel *et al.*, 2003), so an increase in sponge abundance would likely require an increased supply of DOC relative to a coral-dominated reef system. This may in fact be a

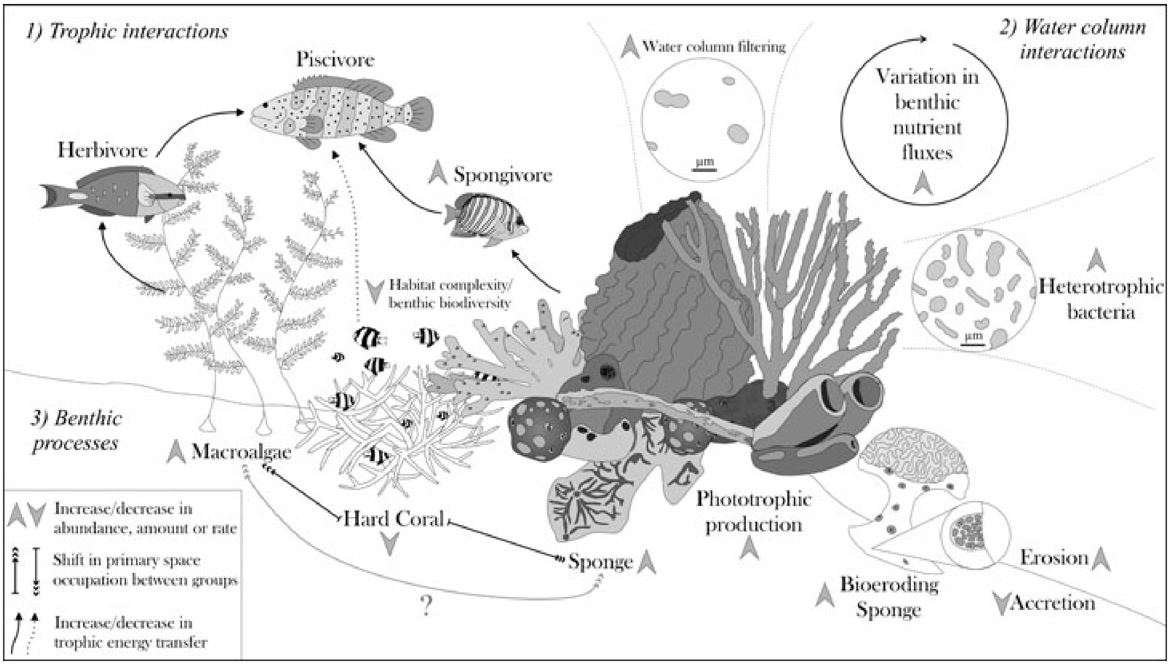

Fig. 2 How would a sponge reef function? There are three ecosystem components that are most likely to be affected if sponge abundance increases relative to corals. (1) *Trophic interactions* – increased sponge abundance/biomass has the potential to support a greater abundance of spongivorous fish, which may support higher trophic levels. Herbivorous fish abundance might also be increased if algal abundance increases as corals decline, but it is unclear how spatial relationships between sponges and algae might play out. (2) *Water column filtering* – greater sponge biomass will result in larger volumes of water being filtered by sponges and therefore a greater flux of nutrients between the benthos and the water column. Higher benthic sponge biomass will likely be supported by greater heterotrophic bacterial abundance, which is predicted to increase in response to predicted OA and temperature scenarios. (3) *Benthic processes* – overall habitat complexity is likely to be reduced with sponges as the dominant organisms as the three-dimensional nature of the environment is reduced, and while photosynthetic production will decline from corals, phototrophic production by some sponges will likely increase. Bioeroding sponge abundance is expected to increase, resulting in increased erosion, while the declining abundance of calcifying organisms will result in an overall decrease in accretion.

constraint on the development of a sponge reef, given that corals are thought to produce a large amount of DOC (Ferrier-Pagès' *et al.*, 1998), which is currently available to sponges for food. However, as sponges already dominate some reefs, it seems that this is unlikely to be a primary limiting factor. If food is a limiting factor for heterotrophic sponges on reefs, then the response of bacterioplankton to nutrient upwelling associated with more severe weather events and changing reef temperatures (see above) will be critical. It is also important to note that the different components of the sponge diet may respond differently to the various climate change variables. For example, heterotrophic bacterial abundance is expected to increase in nutrient-rich warm coastal seawater (McKinnon *et al.*, 2007), whereas cyanobacterial abundance on reefs is likely to be unaffected by OA due to the large microscale and diurnal pH variations that occur naturally across reefs (Price *et al.*, 2012). Increased heterotrophic bacterial abundance would provide an increased level of carbon to support greater sponge productivity, given that it is such an important component of the sponge diet (e.g., Perea-Blázquez *et al.*, 2012a).

A shift towards sponge-dominated reef systems would also alter the balance between accretion and erosion, especially considering evidence that both abundance of bioeroding sponges and bioerosion rates increase at higher $p\mathrm{CO}_2$ (see above). This will have considerable implications for reef structure and likely increase overall reef deterioration. However, while some sponges are eroders, others are known to bind reef fragments (Wulff & Buss, 1979), possibly mitigating some of these impacts. While sponge reefs might still provide some three-dimensional habitat, the overall complexity will be considerably less than for most coral-dominated systems (see supplementary material), which may reduce biodiversity as a result of reduced niche availability. Reef fish assemblages would also be affected, considering that a higher abundance of spongivorous fish may occur at the expense of corallivores. Generally, only a few fish species feed on sponges (Randall & Hartman, 1968), resulting in an overall reduced diversity of fish on sponge-dominated reefs. For example, sponge-dominated reefs in the Wakatobi Marine National Park have reduced levels of overall fish abundance and diversity, but higher levels of spongivorous fish (Powell, 2012). This probable reduction in reef complexity and diversity in sponge-dominated systems may also affect the stability of the ecosystem, with reduced functional redundancy and overall resilience (Hughes *et al*., 2003; Pittman & Brown, 2011).

Increased sponge abundance and productivity are also likely to alter the release and consumption of other essential nutrients across the reef. Marine sponges form symbiotic associations with a diverse range of microorganisms, which can comprise up to 35% of total holobiont volume (Vacelet, 1975; Hentschel *et al*., 2012). Collectively, these microbes carry out a range of nutrient transformations, including key steps of the nitrogen cycle, such as nitrogen fixation and nitrification (Fiore *et al*., 2010; Webster & Taylor, 2012). Nitrification involves the oxidation of ammonia ultimately to nitrate, with sponges serving as either nitrate sinks or sources (Bayer *et al*., 2008; Perea-Blázquez *et al*., 2012b). Increased fixation of nitrogen by sponge-associated cyanobacteria could also result in an enhanced input of bioavailable nitrogen into the reef ecosystem. Interestingly, Slattery *et al*. (2013) recently showed that sponges in tropical coral reef caves enhance the biodiversity and health of surrounding areas by providing nitrogen to corals and algae. However, it is difficult to interpret these results in the context of increased sponge abundance as, while elevated nitrogen might enhance coral health, the stimulation of algal growth may negatively affect corals. Sulphur cycling is yet another process that is likely to differ between sponge and coral reefs; zooxanthellae within corals are significant producers of dimethylsulfoniopropionate (DMSP), which in turn is degraded by coral-associated bacteria to dimethylsulfide (DMS) (Raina *et al*., 2010), a key compound in climate regulation due to its role in cloud formation. The relative paucity of zooxanthellate sponges suggests that benthic DMSP production may be reduced in a sponge-dominated ecosystem, as cyanobacteria are thought to produce negligible amounts of DMSP (Yoch, 2002). Further experimental and genomic data about both sponge- and coral-associated microbes should greatly enhance our understanding of the functional potential of these organisms, and allow for better-informed speculation about the differences between nutrient fluxes on sponge- and coral-dominated reefs.

Finally, further investigation of tropical mesophotic reefs (30–150 m depth) may also provide additional insight into how a tropical sponge reef might function. As coral and algal abundances decline in response to decreased light availability in these deeper water reefs, sponges begin to dominate, particularly in the Caribbean where sponges also tend to be larger than in shallower waters (e.g., Slattery & Lesser, 2012). It seems likely that the increased abundance of sponges below 30 m is a direct response to the reduced competition with corals, and it is possible that the sponge species that are typical of mesophotic reefs may invade shallower waters as corals and other calcifiers decline. Interestingly, there is often considerable uncolonised space in these deep water environments (Kahng & Kelley, 2007), suggesting that space is not limiting. These systems are thought to be more dependent on heterotrophy than phototrophy (Kahng *et al*., 2010), and therefore food availability may be the primary limiting factor.

While the focus here has been coral reef sponge assemblages, it is also important to note that sponge-dominated reefs are already common in many temperate, polar and deep-sea regions, particularly below the photic zone (e.g., Bell & Barnes, 2000; Krautter *et al*., 2001; Heyward *et al*., 2010; Goodwin *et al*., 2011; Reveillaud *et al*., 2011). Such reefs are found across the world and in the case of shallow water systems demonstrate how in the absence of coral, but often in the presence of algae, sponges can be one of the dominant benthic organisms. Of particular relevance to our argument is the presence of deep water hexactinellid sponge reefs on the Canadian continental shelf (Conway *et al*., 2001). These reefs are considered to be living fossils and appear to have persisted for over 9000 years, providing an important example of sponge reef persistence. There are also reports of extant siliceous reefs in the Arctic (Eluik, 1991), although very little is known of their ecology. However, while these habitats provide support for the persistence of sponge reefs, the environments in which they are found are very different from shallow water tropical systems, so they might function very differently from coral reef sponge-dominated analogues.

It is important to note that while sponges may increase in abundance as coral abundance declines, their ultimate long-term future (more than hundreds of years) depends on having primary substrate for attachment and excavation. OA is expected to not only reduce the potential for corals to produce calcium carbonate, but also to cause dissolution of the existing reef structure (Andersson & Gledhill, 2012). While sponges can bind rubble and hold reefs together (e.g., Wulff & Buss, 1979), it seems unlikely that this capability would be sufficient to prevent the eventual breakdown of reef structures. It is currently unknown whether the cover of carbonate by sponge tissue would reduce carbonate dissolution, but this will ultimately determine the composition and structure of sponge assemblages (encrusting vs. erect vs. bioeroding species). Finally, despite the perceived need for primary carbonate structure by sponges, the fossil record does demonstrate that sponges can persist (and accrete) in the absence of calcifying organisms (see paleo section). Whether this is still possible on modern reefs is currently unknown.

Summary

While shifts to algal-dominated systems following environmental disturbance are well publicised (e.g., Hughes *et al.*, 2010), these changes are not ubiquitous across reefs. Sponges, which generally appear to show low sensitivity to elevated sea temperatures and OA, will likely benefit from further coral reductions, or at least remain after corals have declined. However, sponges may not be the only organisms to benefit as coral abundance declines, and groups such as ascidians and soft corals may compete with sponges for the newly available space. It is possible that sponges and algae may coexist, as has been reported for some reefs in the Caribbean (e.g., Colvard & Edmunds, 2010), and it is possible that such coexistence may be common on reefs, but masked by the heavy focus on the abundance of corals and algae. We suggest that future research should focus on the competitive relationships between sponges and algae to understand the dynamics behind sponge–algal coexistence. It will also be important to understand how other sources of environmental degradation influence sponges (e.g., sedimentation) and how this might interact with increased sea surface temperature and OA. Finally, even if corals are able to adapt to rapidly changing conditions, the functional importance of sponges in coral reef ecosystems means that research on the physiological and ecological consequences of temperature and pH change is urgently required. Here, we have provided a credible scenario for some reef systems becoming dominated by sponges under conditions predicted for our future oceans.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Video S1. A sponge-dominated reef from Western Australia.