Sponges to Be Winners under Near-Future Climate Scenarios

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Sponges are functionally important components of global benthic environments and have been proposed as potential winners under future climate scenarios. We review the evidence to support this hypothesis by examining the individual and combined effects of ocean warming (OW) and ocean acidification (OA) on sponges and comparing sponge responses with tolerance thresholds for other benthic organisms. Although sponges are generally tolerant of OA and may even benefit from elevated partial pressure of carbon dioxide, they are often sensitive to seawater temperatures only a few degrees higher than their normal range. Sponge responses to the combined effects of OA and OW are generally more positive than their response to OW alone. We found that sponges are generally less affected by OW or OA than are a number of currently dominant benthic organisms, such as corals. Therefore, sponges are expected to benefit under near-future climate scenarios, although species-specific differences in tolerance will likely shift the sponge assemblage composition toward more resilient species.

Keywords: Porifera, sponge, ocean acidification, ocean warming, climate change

Present day atmospheric carbon dioxide levels (CO$_{2}$ atm) now exceed 400 parts per million (ppm; NOAA 2016), which is more than 100 ppm higher than the levels prior to the Industrial Revolution. Global CO$_{2}$ atm concentrations are predicted to exceed 1000 ppm by 2100 if no additional efforts are made to reduce greenhouse gas emissions (IPCC 2014). The Earth’s oceans have served as a global sink for at least half of this anthropogenic CO$_{2}$ atm over the past 200 years (Sabine et al. 2004). However, with the partial pressure of CO$_{2}$ (pCO$_{2}$) in seawater increasing, pH in the upper layers of the world’s oceans is predicted to decrease by 0.3–0.5 units by 2100 (IPCC 2014), a phenomenon referred to as ocean acidification (OA). Furthermore, rising CO$_{2}$ atm has increased global surface temperatures by approximately 0.2°C per decade over the past 30 years, with 2011–2015 being the warmest 5-year period on record (WMO 2016). As oceans absorb a significant amount of this excess energy (Hoegh-Guldberg and Bruno 2010), the Intergovernmental Panel on Climate Change (IPCC) predicts that global warming resulting from rising CO$_{2}$ atm, will see mean sea surface temperatures increase a further 1.1°–4.0°C by the end of this century (IPCC 2014). Changing water chemistry and ocean warming (OW) will strongly affect biological processes, resulting in reduced organism fitness and subsequent implications for population survival and species persistence (Hoegh-Guldberg and Bruno 2010).

The effects of OA and OW have been well described for many species, with impacts including reduced calcification rates and mass bleaching events in corals (e.g., Albright et al. 2018) and the disruption of reproduction and larval development (e.g., Albright and Langdon 2011). Although negative effects of OA and OW have been described for many organisms, some organisms appear to have higher tolerance. This has led some authors to suggest there will be winners and losers in response to climate change (e.g., Fabricius et al. 2011, Bell et al. 2013, Peck et al. 2015, 2018). Sponges have been identified as potentially benefiting more than other species from climate change because there is increasing evidence that sponges are generally more tolerant than a number of other benthic groups to OW and OA and may even benefit from changing ocean conditions through increased productivity and reduced spatial competition (Bell et al. 2013, 2018). The aim of this article is to review the individual and combined impacts of OA and OW on sponges and their microbial symbionts (referred to as the holobiont), to compare these responses with those of other dominant benthic groups, and to consider the broader implications of sponge responses to OA and OW for benthic ecosystem function.

Functional significance of sponges
Sponges, the most ancient multicellular animals on Earth, are the exclusive representatives of the phylum Porifera. There are four extant classes—Calcarea, Hexactinellida, Homoscleromorpha, and Demospongiae—and 83% of all known sponge species belong to the Demospongiae (Van Soest et al. 2012). The sponge skeleton is primarily composed of spicules and collagen fibers, but calcareous sponges have spicules made of calcium carbonate (calcite),
and sponges in the other three classes have spicules made of silica (a few demosponges also have aragonite skeletons; see Hartman and Goreau 1975). The sponge body plan comprises three distinct cell layers (Bergquist 1978): the external epithelium (pinacoderm), which is a single-celled layer that isolates the sponge from its external environment; the internal epithelium (choanoderm), which is composed of a single layer of flagellated cells that facilitates water flow through the sponge; and the mesohyl, which is located between the pinacoderm and the choanoderm and which contains the mobile cells and skeletal elements. This simple body plan is specialized for the sponge's sedentary, suspension-feeding lifestyle and has changed very little since early sponge origins (Bergquist 1978). Water enters through many small openings (ostia) on the sponge surface and flows through the canal system, which is lined with choanocyte chambers, using flow created by the beating flagella of the choanocyte cells. The collar filters of sponge choanocytes retain suspended particles (e.g., bacteria and picoplankton) as the inhalant water is drawn through the canal system and out of the sponge's exhalent oscules. Such a simple but effective way of life has likely facilitated sponge persistence through historical mass extinction events, enabling them to prevail today within benthic ecosystems spanning temperate, tropical, and polar habitats (Van Soest et al. 2012).

Sponges fulfill a range of important functional roles in marine systems (Bell 2008). Of particular importance is their ability to process large volumes of water and efficiently remove particulate organic carbon (POC), such as picoplankton and bacteria, as well as dissolved organic carbon (DOC; Perea-Blaquez et al. 2012, McMurray et al. 2017). For example, Perea-Blaquez and colleagues (2012) found that the total POC sponges could consume as a proportion of the total POC available was 0.2%–12.1% for heterotrophic bacteria, 0.4%–21.3% for *Prochlorococcus*, and 0.3%–15.8% for *Synechococcus*, depending on sponge abundance (their range was only 0.1%–5%). Furthermore, the recent discovery of the so-called sponge loop, whereby DOC uptake by cryptic sponges is passed to higher trophic levels through detritus production, has further highlighted the important roles sponges play in water column interactions and in supporting higher trophic levels (De Goeij et al. 2013). However, since the initial discovery of the sponge loop, there has been some debate over the ecological importance of this detritus production. McMurray and colleagues (2018) found little evidence of detrital production in nine Caribbean coral reef sponges, whereas Rix and colleagues (2018) found that Red Sea reef sponges assimilated mucus produced by corals to fuel the sponge loop through detrital production. This apparent discrepancy may reflect different evolutionary histories of sponges in different geographic regions. Sponges also play important roles in substrate consolidation and erosion, in spatial competition, and in providing habitat for other species (Bell 2008). With such a broad range of functional roles, OA and OW impacts on sponges (positive or negative) would have important consequences for ecosystem function and other trophic levels.

Importantly, sponges form intimate associations with diverse microorganisms (Moitinho-Silva et al. 2017). These partnerships are often crucial to sponge health and survival (Webster and Thomas 2016, Pita et al. 2018); therefore, the consortium comprising the sponge host and its associated bacteria, archaea, fungi, protists, and viruses is referred to as the sponge holobiont (Webster and Taylor 2012). Importantly, the abundance and composition of these microbes may play important roles in stress responses of the sponge holobiont (Pita et al. 2018). Although all sponges contain microbes, the holobiont can be categorized into two nutritional types on the basis of the sponge's association with phototrophic symbionts: phototrophic (i.e., less than 50% of energy requirements are acquired from photosynthetically fixed carbon) and heterotrophic (i.e., primarily reliant on suspension feeding for carbon requirements; Cheshire and Wilkinson 1991). This distinction is important because it may influence the way climate change affects sponges (e.g., Bennett et al. 2017).

### Direct impacts of climate change on sponges

To identify general responses of sponges to OW, OA and the combined effects of OW and OA and to compare the overall research effort relative to other benthic groups, we conducted a Scopus literature search ([www.scopus.com](http://www.scopus.com)) including the name of the benthic group and the keywords “climate change,” “ocean warming” and “ocean acidification,” which were searched in titles, abstracts, and keywords. We extracted information for nine abundant groups of sessile benthic organisms: sponges, hard corals, crustose coralline algae (CCA), fleshy macroalgae, octocorals, hydrocorals, ascidians, bryozoans, and brachiopods and summarized the number of climate change–associated studies for each of these benthic groups between 2000 and 2017 (figure 1). The number of studies in which the impacts of climate change on sponges were assessed have increased rapidly over the last decade, which is consistent with the research focus for other benthic groups (figure 1). Because OA and OW occur concurrently, there has also been an increase in studies in which the authors attempt to define those factors’ combined effects. However, in comparison with the large body of literature assessing how corals and macroalgae respond to the individual and combined effects of OA and OW, the impacts of climate change on sponges have been explored in relatively few studies (figure 1). Organisms with calcium carbonate skeletal elements are expected to be particularly sensitive to OA because of a reduced ability to calcify. In contrast, with the exception of the 8% of extant sponges in the class Calcarea that have calcium carbonate skeletons and the few demosponges with aragonite exoskeletons (Van Soest et al. 2012), the impact of OA on sponge skeletal development is expected to be minimal (see Vicente et al. 2016). However, although OA is not expected to affect the siliceous or collagen skeletal elements of most species, just one cell layer separates a sponge from the external environment.
Bergquist (1978), so changes to ambient water temperature and chemistry could potentially have a large impact on cellular processes (Pörtner and Farrell 2008). In addition, although there have been minimal reports of sponge bleaching to date (but see Bell et al. 2017, Marlow et al. 2018), the risk of sponge bleaching may increase with further OW (Ramsby et al. 2018). Importantly, non-phototrophic microorganisms also play a significant role in sponge fitness via host defense and nutrient transformations (Taylor et al. 2007, Webster and Thomas 2016), and these symbionts can be disrupted under OW, ultimately resulting in the destabilization of the sponge holobiont and eventual host mortality (Fan et al. 2013).

Sponge responses to OA. Of the 25 sponge species that have been experimentally exposed to OA alone, 17 have shown either neutral or positive responses, whereas the other species have been adversely affected (figure 2a). There appears to be no obvious correlation between tolerance and sponge taxonomy. The clear positive responses include increased bioerosion rates and cyanobacterial density, whereas abundance, microbial community composition, and growth are affected more variably (figure 2a).

In several studies, naturally occurring CO$_2$ seeps have been used to assess how sponges might respond to OA. Goodwin and colleagues (2013) surveyed a pH gradient at a CO$_2$ vent in Italy and found a strong negative correlation between pH and sponge cover. They also found an impact of pH on species composition, although these effects were primarily evident when comparing control sites with very-low-pH (6.6) sites (much lower than OA conditions expected by 2100). No significant differences in spicule size or form were evident between sites, and overall, this study suggested a degree of sponge tolerance to OA conditions expected for 2100 but with species-specific sensitivities. Morrow and colleagues (2015) also conducted...
Figure 2. Summary of the number of sponges showing positive (+), negative (−) and neutral (=) effects in response to (a) ocean acidification (OA), (b) ocean warming (OW), and (c) the combined effects of OW and OA. For OA (a) and OW (b), a summary of the main positive (↑) negative (↓) and unchanged (↔) response variables are shown in the right panel (based on measured parameters). For the combined effects of OW and OA (c), the specific responses for each species is shown. Studies were from 2000–2017 inclusive. The interactive effect of OW and OA on Cliona orientalis does not increase growth and bioerosion after exposure to the warmest temperature under RCP 8.5 predictions for 2100.
comparative sponge surveys at natural CO₂ seeps (pH range 7.28–8.01) and adjacent control sites (pH range 7.91–8.09) in Papua New Guinea and found that although Styllissa massa was six times less abundant at the seep, Coelocarteria singaporenisis and Cinachyra sp. were approximately 40 times more abundant at the seep, again highlighting species-specific responses to OA.

In experimental studies in which the effects of OA on sponges were considered, researchers have also reported variable results. For example, exposure of the temperate sponges Tethya bergquistae and Crella incrustans to pH 7.6 (compared with pH 8 controls) adversely affected sponge growth over a 4-week experiment (Bates and Bell 2017). In the only analysis of a calcareous sponge, Peck and colleagues (2015) found that the biofouling community composition on plastic pipes changed considerably when exposed to pH 7.7 for 100 days (compared with pH 7.9 controls). In particular, sponge abundance changed from 4% cover at the start of the experiment to approximately 29% cover by the end of the experiment, possibly because of reduced spatial competition with more pH sensitive species. This apparent pH tolerance was unexpected for a calcareous sponge; however, Leucosolenia complicata spicules are known to have an organic sheath, which may offer protection against the effects of OA (Jones 1955).

Bioeroding sponges have been a major focus of single stressor OA experiments (see Schönberg et al. 2017 for a review). Wisshak and colleagues (2012) were the first to highlight the potential for sponge bioerosion to be facilitated in a high-CO₂ world, finding that experimental exposure of Cliona orientalis to the OA conditions expected in 2100 (approximate pH 7.9 in a 110-day experiment) resulted in a significant increase in the sponge’s bioerosion capacity. However, Wisshak and colleagues (2012) indirectly inferred the OA effects for 2100 from an equation drawn through other pH response data, such that Wisshak and colleagues (2012) predicted a 30.9% increase in bioerosion rates of the OA effects for 2100 from an equation drawn through other pH response data, such that Wisshak and colleagues (2012) predicted a 30.9% increase in bioerosion rates of Cliona orientalis at the year 2100 under the representative concentration pathways scenario RCP8.5. This is consistent with latter studies on the temperate bioeroding sponge Cliona celata (exposed to pH 7.8 at 31°C for 133 days; see Duckworth and Peterson 2013), which is an important eroder of commercially important bivalves and also important for other tropical bioeroding sponges (Enochs et al. 2015).

Few studies have considered the nature of OA effects on sponge-associated microbial communities. At CO₂ seeps in Papua New Guinea (pH range 7.28–8.01), Morrow and colleagues (2015) found that Coelocarteria singaporenisis and Cinachyra spp. hosted a significantly higher relative abundance of the cyanobacteria Synechococcus than did sponges at adjacent control sites (pH range of 7.91–8.09), which was hypothesized to provide a nutritional benefit and enhanced scope for growth under future climate scenarios. Interestingly, the microbial community in Styllissa massa was not significantly different between the seep and control sites, and this sponge was found in lower densities at sites with elevated pCO₂, suggesting that the ability to alter the microbial biome may play an important role in supporting sponge survival in lower pH conditions. More recently, Ribes and colleagues (2016) found that although Mediterranean sponges did not show any variation in overall microbial abundance, richness or diversity in response to experimental exposure to OA (pH 8.10 and 7.82 for the control and treatment conditions, respectively, for 66 days), species differed in their ability to acquire new microbes through horizontal transmission. The ability of the different sponge species to alter their microbial community positively correlated with growth rate, providing further support for a flexible microbial biome being important for sponge tolerance to OA. The role that microbes play in sponge tolerance and the potential for these microbes to enhance the performance of the sponge holobiont under OA require further investigation.

Sponge responses to OW. Forty-four studies have included an examination of how sponges respond to OW alone, assessing the holobiont response at multiple levels and describing effects on host physiology, gene expression, feeding ecology, and microbial symbiosis (figure 2b). Of these studies, only 10 included positive effects, usually as a result of declining competitor abundance; 4 showed no effect; and the remaining studies showed negative effects of OW. The effects of OW include decreased reproductive output, photosynthetic rates, pumping rates, filtration efficiency, choanocyte chamber size and density, and changes to microbial community composition and microbial function. OW also causes increases in necrosis, bleaching, disease, and heat shock protein production, whereas mortality, abundance, and growth are more variable responses (summarized in figure 2b).

At the sponge population level, numerous mass mortalities have been reported in association with abnormally high seawater temperatures (Vicente 1990, Vacelet 1994, Cerrano et al. 2000, Garrabou et al. 2009, Cebrian et al. 2011, Di Camillo et al. 2013, Rubio-Portillo et al. 2016, Bell et al. 2017), although whether these occurred as a result of exceeding the host’s thermal threshold, because of disruption of functionally important symbiotic partnerships, or because of infection by opportunistic pathogens (reviewed in Luter and Webster 2017) remains to be determined. In contrast to these reports of thermal stress negatively influencing sponges, other studies have shown sponges to be more tolerant to increased temperature than other benthic organisms. For example, Kelmo and colleagues (2013) found that sponge assemblages in Brazil were highly stable before and after the El Niño Southern Oscillation (2°C increase in temperature during the El Niño event), despite massive declines in corals and other benthic organisms.

At the host level, the researchers behind numerous studies have explored the effects of OW on the survival, growth bioerosion, bleaching sensitivity, and feeding efficiency of sponges, and it is clear that tolerance varies considerably among sponge species. For instance, many
Symbiodinium-bearing bioeroding sponges can tolerate temperatures that induce bleaching in sympatric corals (Vicente 1990, Schönberg and Ortiz 2008, Carballo et al. 2013, Fang et al. 2014, 2018, Marlow et al. 2018). Interestingly, in the Caribbean barrel sponge Xestospongia muta, bleaching susceptibility varies across the sponge population but does not result in sponge mortality, suggesting that the cyanobacterial symbionts are not crucial to host health for this species. However, OW has been identified as the primary stressor, inducing bleaching in the bioeroding sponge *C. orientalis* at very extreme OW scenarios (an increase of 2.7°C above the local maximum monthly mean; Achlatis et al. 2017), whereas *Rhopaloeides odorabile* exposed to OW 2°C higher than the average local ambient seawater temperature exhibits significantly reduced flow rates and feeding efficiency (Massaro et al. 2012). Therefore, temperature tolerance appears to vary among sponge species and is also likely to vary with respect to the actual temperature the species is exposed to.

At the molecular level, *X. muta* (exposed to temperatures lower than 30°C for 15 hours), *R. odorabile* (exposed to 31°–32°C for 14 days), and *Haliclona tubifera* (exposed to 32°–34°C for 12 hours) have all been shown to increase expression of heat shock proteins when exposed to OW (López-Legentil et al. 2008, López-Legentil et al. 2010, Pantile and Webster 2011, Guzman and Conaco 2016). In *R. odorabile*, genes involved in important biological functions such as cytoskeletal rearrangement, signal transduction, and protein synthesis or degradation become downregulated under OW (Webster et al. 2013). In *H. tubifera*, OW results in the immediate induction of heat shock proteins, antioxidants, and genes involved in signal transduction and innate immunity pathways, whereas longer exposure to conditions of OW affects the expression of genes involved in cellular repair, apoptosis, signaling, and transcription (Guzman and Conaco 2016).

Much of the research addressing sponge responses to OW has been focused on the microbiome (López-Legentil et al. 2008, Webster et al. 2008, 2011, López-Legentil et al. 2010, Simister et al. 2012, Fan et al. 2013, Strand et al. 2017). Although some species maintain stable microbial communities irrespective of seawater temperature (Webster et al. 2011, Erwin et al. 2012, Strand et al. 2017), and others retain their symbionts until the very late stages of heat stress, when the sponge itself exhibits necrosis (Webster et al. 2008, Luter et al. 2012, Simister et al. 2012), some species experience major shifts in the microbial community that precede visible signs of host stress (Ramsby et al. 2018). For example, changes in the microbial communities of *C. orientalis*, *R. odorabile*, *X. muta*, and *Haliclona bowerbanki* occur under OW (Lemoine et al. 2007, Webster et al. 2008, López-Legentil et al. 2010, Ramsby et al. 2018). Interestingly, although the microbiome of *R. odorabile* is stable at sublethal temperatures (31°C for 21 days; Simister et al. 2012) and although the microbiome of *X. muta* is stable when the sponge undergoes cyclic bleaching (López-Legentil et al. 2010), the microbiome of *C. orientalis* shifts at a temperature lower than the 32°C threshold that induces sponge bleaching, suggesting that changes in the microbiome may play a role in the destabilization of the *C. orientalis* holobiont (Ramsby et al. 2018). OW-induced microbial shifts often involve the disappearance of suspected symbionts from thermally stressed sponges and the appearance of an opportunistic community reflecting that seen in diseased corals (Webster et al. 2008). This shift away from symbiosis has also been observed at the functional level, with a metaproteogenomic study of *R. odorabile* revealing the loss of putatively symbiotic microbial functions and increased opportunistic bacterial functions under OW (32°C for 4 days; Fan et al. 2013). A host gene expression analysis of *R. odorabile* performed in conjunction with a metaproteomic analysis of the symbiont community showed that OW triggers an immediate stress response in both the host and the symbiont community, including a decrease in the expression of functions that mediate the holobiont partnership. OW appears to destabilize the holobiont via disruption to nutritional interdependence and reduced expression of transporters involved in the uptake of sugars, peptides, and other substrates (Fan et al. 2013).

Adult sponges have been the primary focus of OW studies, but in the only study to have assessed responses to OW across life history stages for the same species (see below for a discussion of combined stressor impacts on larvae), the larval response to temperature was different from that of adults (Webster et al. 2011, 2013). In *R. odorabile*, larvae exhibited a markedly higher thermal tolerance, with adverse health effects, alterations in gene expression, and accompanying microbial shifts not occurring until 36°C. These distinct thermal tolerances across life history stages highlight that additional research across ontogenetic stages is required to better predict the long-term consequences of climate change for sponge population dynamics and to understand the mechanisms by which larvae are better able to deal with higher temperatures than adults.

**Sponge responses to the combined effects of OA and OW.** The interactive effects of OW and OA have been explored for 15 sponge species. Only three of these sponge species exhibited negative effects (figure 2c); nine showed little or no response, whereas three showed positive responses. For those species showing negative responses, survival and photosynthetic rates decreased, whereas necrosis and bleaching increased. Species that appeared unaffected by combined OA and OW treatments showed no change in survival, necrosis, growth, spicule production, respiration, or secondary metabolite production (figure 2c). The main positive effects of combined treatments were increased bioerosion rates and growth.

The primary focus of combined stressor research has been the response of bioeroding sponge species—*C. celata* (Duckworth and Peterson 2013), *C. orientalis* (Wisshak et al. 2012, Fang et al. 2013), and *Cliona varians* (Stubler et al. 2015)—and, more specifically, the effects on sponge
Figure 3. The positive (+), negative (−) and neutral (=) responses shown by major groups of benthic organisms in response to the individual and combined effects of ocean warming (OW) and acidification (OA). Studies were included from 2000–2017, inclusive.
bioerosion rates (figure 3). Sponge bioerosion rates increased under future OW and OA scenarios for C. celata and C. orientalis but not for C. varians (Wisshak et al. 2012, Duckworth and Peterson 2013, Fang et al. 2013, for details of the experimental conditions, see the supplemental material, but they were exposed to at least 2100 RCP8.5 conditions). However, Achlatis and colleagues (2017) suggested that after longer-term exposure to OA, acidification effects were somewhat decoupled from erosion enhancement because of heterotrophic losses under the RCP8.5 conditions predicted for 2100.

Combined OW and OA studies on nonbioeroding sponges also suggest a degree of sponge tolerance to the effects of a changing climate (Duckworth et al. 2012, Vicente et al. 2016, Lesser et al. 2016, Bennett et al. 2017). Research exposing six sponge species to OW and OA (31°C, pH 7.8) showed no impact on growth, survival, or secondary metabolite biosynthesis (Duckworth et al. 2012). Furthermore, despite slight negative effects of elevated pCO2 on spicule biomineralization, OW and OA (3°C higher than current ambient, pH 7.8) had little effect on overall survival or growth rates of Mycale grandis (Vicente et al. 2016). The productivity of cyanobacterial symbionts in the giant barrel sponge (X. muta) declined with exposure to elevated temperature and pCO2, although no evidence of bleaching or associated host stress was reported, despite a reduction in holobiont carbohydrate levels and reduced stability of the sponge microbiome (2100 conditions under an A2 climate model, pCO2 of approximately 800 ppm and 2°C to 5.4°C temperature increase above ambient; Lesser et al. 2016). Species-specific sensitivities were observed in four Great Barrier Reef sponge species exposed to OW and OA levels predicted for 2100 under two CO2 RCPs (Bennett et al. 2017, 2018). Although all species were generally tolerant of climate change scenarios predicted under the RCP6.0 conditions (30°C, pH 7.8), significant adverse effects were evident in response to RCP8.5 conditions (31.5°C, pH 7.6). OW effects were much stronger than OA effects for all species; however, phototrophic and heterotrophic species responded differently to OA. Interestingly, elevated pCO2 exacerbated temperature stress in heterotrophic sponges but somewhat ameliorated thermal stress in phototrophic species (Bennett et al. 2017). Membrane lipids and fatty acids were shown to play a major role in the sponge stress response to OW and OA (Bennett et al. 2018). Specifically, sponges altered their membrane lipids in response to OW, and additional CO2 appeared to facilitate the resistance of phototrophic sponges to OW by increasing synthesis of membrane-stabilizing sterols (Bennett et al. 2018). An increase in fatty acid unsaturation in phototrophic sponges, but a decrease in heterotrophic species provided support for a difference in the thermal response pathway between the sponge host and the associated photosymbionts (Bennett et al. 2018).

The response of early life history stages to OW and OA has been explored in the abundant phototrophic GBR sponge Cartierospongia foliacea (Bennett et al. 2017). Larval survival and settlement success was unaffected by OW and OA treatments (control 28.5°C, pH 8.1 and treatment 31.5°C, pH 7.6, fully crossed), and juvenile sponges exhibited greater tolerance than their adult counterparts. Consistent with adult C. foliacea, OA actually reduced OW stress for these early life stages. The survival of early life stages is fundamental for population persistence, so an improved understanding of species-specific differences in larval and juvenile sponge responses to climate change is crucial.

**Overview Article**

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**Indirect impacts of climate change on sponges**

Other effects of climate change that may affect sponges include increased intensity or frequency of storms and extreme weather events, including changes in rainfall patterns (Fischer and Knutti 2014), changes in ocean circulation and upwelling patterns (Harley et al. 2006), increased frequency of ice scour from icebergs as a result of sea ice melt (Barnes et al. 2014), and species range expansions and contractions (Doney et al. 2010).

Although much uncertainty remains, climate change is expected to alter rainfall patterns such that more rain falls in some locations and less in others, and the intensity of rainfall and the frequency of more extreme rainfall events is also expected to increase (Fischer and Knutti 2014). Little is known about how sponges respond to salinity changes associated with extreme weather events (Bell et al. 2015a); however, increased sediment and nutrient loads in coastal waters associated with terrestrial runoff can negatively influence sponges by smothering and clogging their feeding apparatus and reducing the light available for photosynthesis (Bell et al. 2015b). A short-term elevation in suspended sediment concentrations showed a decrease in sponge pumping by up to 90% and high suspended sediment concentrations for extended periods can reduce survival, increase necrosis, and deplete energy reserves in some species, although sediment concentrations lower than 10 milligrams per liter generally have negligible effects (Pineda et al. 2017). Similar to OW and OA, sponge responses to sediments vary considerably among species, which can likely be attributed to the species-specific mechanisms for sediment rejection and sediment clearance (Strehlow et al. 2017). Increased storm activity in shallow waters, such as hurricanes and cyclones, can also have devastating impacts on shallow-water reef areas, although Wulff and Buss (1979) found that cyclones were actually important in fragmenting sponges and in facilitating asexual reproduction.

Climate change is also expected to drive variation in major currents and in the strength of upwelling. Because upwelling drives plankton productivity (Kudela et al. 2008), it has the potential to indirectly affect sponges. Changes in ocean circulation and upwelling might also alter water oxygen levels and chemical makeup, particularly in coastal and shelf regions. For example, although the Hexactinellid (glass sponge) reefs off the coast of North America are not expected to be affected by localized ocean warming, they may be susceptible to increasing hypoxia associated with
increased ocean stratification and upwelling (Conway et al. 2017). However, because sponges are the first known multicellular organisms in Earth’s history and because all extant sponges are the descendants of lineages that have survived drastic changes in climate and ocean conditions throughout Earth’s history, they may be expected to possess mechanisms that confer some level of tolerance to various stressors.

Scour from icebergs contacting hard substrate is known to be an important source of physical disturbance to subtidal polar and subpolar benthic ecosystems. With the breakdown of the polar ice sheets as a result of OW, increased iceberg-generated disturbance has been reported (Barnes et al. 2014). Sponges are a major component of benthic polar ecosystems, with a number of higher trophic levels directly reliant on sponges as a food source (see McClintock et al. 2005). If scour from icebergs increases, polar subtidal benthic communities could become dominated by fast-growing k-strategists, which would have major implications for ecosystem dynamics, including trophic pathways. The loss of sea ice may also indirectly influence sponge assemblages. For example, Fillinger and colleagues (2013) reported a two- to threefold increase in Hexactinellids 12 years after the disintegration of the Larsen A ice shelf in Antarctica, likely as a result of increased local primary production.

Climate driven range expansions to new areas and contractions from historical ranges have already been reported for a number of taxa, including fish, algae, and coral (Lenoir and Svenning 2015). Although warmer water sponge species may increase their ranges poleward, the generally limited dispersal ability of sponges (Maldonado and Reisgo 2008) means that their rates of range expansion might be slower than benthic groups with longer-lived pelagic larvae. To our knowledge, there has been no climate change–related range expansion described for sponges, although invasion of benthic habitats by sponges has been reported as a result of human-mediated transport (e.g., Knapp et al. 2015).

**Comparative analysis with other benthic groups**

In order to compare sponge responses to OW, OA, and both OW and OA with those of other benthic groups, we used the Scopus search (described above) to collate information on the responses of the nine groups of sessile benthic organisms: sponges, hard corals, CCA, fleshy macroalgae, octocorals, hydrocorals, ascidians, bryozoans, and brachiopods. For each study, the response of the organisms to the stressor was evaluated as positive, negative, or neutral (figure 3). A positive response was assigned if the stressor had a positive effect on the organism’s physiology, improved organismal fitness, or provided a competitive advantage over other organisms. Multiple responses were reported for those studies in which different taxa showed heterogeneous responses to a common stressor or for studies in which a stressor had mixed effects on one organism depending on the duration and intensity of the exposure. Our assessment included all studies in which organisms were either naturally or experimentally exposed to OA, OW, and both OA and OW, irrespective of the strength of the stressor. However, when multiple responses were reported, we included all responses of the benthic groups to varying stressor levels.

The results varied among the different groups, although it is important to note that some taxa have only been the subject of a small number of studies (see also figure 1). A largely negative response to OW was observed for most benthic groups, with the exception of ascidians and bryozoans. OA generally had negative effects on corals, brachiopods, bryozoans, and CCA, whereas octocorals, macroalgae, and sponges generally exhibited positive or no response to OA. Although there were fewer data for the interactions between OW and OA (and no data for ascidians), the responses were largely negative for most groups. A higher proportion of sponge studies showed positive responses to both OW and OA stress than to only OW. For corals, the proportion of negative, positive, and neutral responses were similar and were, overall, mostly negative for individual and combined OW and OA stressors. For macroalgae, although individual OA studies showed a high proportion of positive responses, a similar number of positive and negative responses have been reported for the combined effects of OA and OW. In contrast, CCA showed more positive responses when exposed to the combined effects of OA and OW than when exposed to a single stressor. Given that marine organisms will experience the combined effects of OW and OA in the future, our analysis suggests that sponges, octocorals, and macroalgae are more likely to be winners in benthic environments by the end of the century than are corals, brachiopods, bryozoans, and CCA, although not all species of these winning groups will respond positively.

**Ecological consequences of sponge responses to OA and OW**

Changing sponge dominance, either through an increase in absolute abundance or a relative increase in abundance as other organisms decline, will likely alter the functional ecology of reef environments (Bell et al. 2013, Pawlik et al. 2016, de Goeji et al. 2017, 2018). This is particularly the case for coral reefs, given the generally greater susceptibility of corals to climate change effects and the potential for sponge abundance to increase as they are released from competition with corals. For temperate and polar systems, where sponges are generally not competing to the same extent with calcareous species for space as they are on coral reefs, the ecosystem level impacts are likely to be harder to predict.

**Sponge feeding and trophic interactions.** Increasing absolute sponge abundance would need to be supported by increased POC and DOC for heterotrophic species. Although food is not thought to be currently limiting to most benthic suspension feeders in tropical, temperate, or polar systems, this has the potential to change if absolute sponge abundance increases. For instance, in the Caribbean, McMurray and colleagues (2017) showed that X. muta has a higher carbon flux rate than other reef species, and this rate has increased...
over recent years as the abundance of *X. muta* has increased. It is currently unclear what the wider ecosystem impacts of increased consumption ofpicoplankton and DOC would be, particularly in generally oligotrophic environments such as coral reefs (but see de Goeij et al. 2017 for some discussion). However, this resource could potentially become limiting. Because sponges are such efficient suspension feeders, processing large volumes of water, they may remove food currently being used by other organisms and limit those species’ success.

There is also some support for coral reef sponges potentially increasing productivity under more acidified conditions as a result of higher photosynthetic capacity by associated symbionts. For instance, the fortyfold greater abundance of *C. singaporensis* and *Cinachyra* spp. found at the natural CO$_2$ seep site (pH range 7.28–8.01) by Morrow and colleagues (2015) hosted a significantly higher relative abundance of photosynthetic cyanobacterial symbionts than sponges at control sites. However, translocation of photosynthetic products to the sponge host was not demonstrated, so it is still uncertain whether the host sponge can use any additional carbon produced by its photosymbionts. In temperate and polar systems, sponges are generally not phototrophic, likely because of the more limited light penetration in these waters. Any increased productivity by phototrophic sponges could enable sponge abundance to increase, independent of the need for greater consumption of DOC and POM.

As well as sponges feeding on a range of planktonic organisms, they are a direct food source for a number of higher organisms, including fish and turtles (Bell 2008). Therefore any changes in sponge abundance due to climate change (either increases or decreases) will have consequences for these trophic relationships (Bell et al. 2018). Of particular interest is the recently described sponge loop, whereby sponges take up DOC (de Goeij et al. 2013) or POC (Rix et al. 2018) and, via turnover of their choanocyte cells, produce detritus that can be taken up by higher trophic levels. Changes in sponge abundance would alter the availability of this detritus, although McMurray and colleagues (2018) recently suggested that the sponge loop may be restricted to specific habitats and species, because they found no evidence for detritus production in a number of species from the Caribbean. It is also possible that DOC uptake is used for sponge growth and biomass and that this is subsequently transferred through trophic levels by direct grazing from fish and turtles. A key question is whether fish and turtles feeding on sponges are constrained by the abundance of their food source. In the case of turtles, this seems unlikely, because turtle populations are likely to have been much greater in the past (see Pawlik, Loh and McMurray 2018 for a discussion). If fish are constrained by the abundance of their sponge food source, increased sponge abundance could flow through to higher trophic levels directly rather than via the sponge loop.

**Competitive interactions.** Although there is some suggestion that sponge scope for growth might be enhanced in response to OA, particularly as a result of increased symbiont abundance or productivity, the proliferation of sponges would depend on their ability to compete with other benthic groups. In tropical regions, climate change is expected to have negative impacts on corals (Hoegh-Guldberg and Bruno 2010), which are the major sponge competitors on reefs. However, declines in coral often leads to regime shifts, whereby coral is rapidly replaced by fast-growing macroalgae (Graham et al. 2015). Therefore, more information is needed about the competitive interactions between sponges and macroalgae (but see González-Rivero et al. 2011, 2012, 2016). In shallow temperate waters (less than 30 meters) macro and turf algae are typically important spatial competitors with sponges (Cárdenas et al. 2016), although this relationship is complex (see Preciado and Maldonado 2005). Although the presence of large macroalgae may have positive consequences for sponge richness and abundance by providing secondary space (Cárdenas et al. 2016), it is unclear how the generally positive response of OA and OW on macroalgae will play out for sponges. In deeper water, where light cannot support photosynthesis, competition for space may be less important. These communities are typically dominated by sponges, octocorals, hydrocorals, and ascidians (e.g., Kahng et al. 2010) and given our analyses (figure 3) show these groups have similar susceptibility to OA and OW as sponges, deeper water coral reef ecosystems may remain comparatively stable under climate change.

**Reef erosion and complexity.** Although chemical bioerosion by sponges could increase under conditions of OA (e.g., Wisshak et al. 2012), when considered in the context of concurrent OW, sponge bioerosion seems unlikely to increase, particularly for photosymbiotic bioeroding species that respond negatively to increased temperature (Achlatis et al. 2017, Ramsby et al. 2018). Also given that bioerosion is most important in tropical regions and that corals that are the primary calcifiers are negatively affected by OA, any increase in bioerosion may result in a long-term negative carbon budget for coral reefs (Glynn and Manzello 2015), which will affect the longer-term (decadal) persistence of the overall coral reef structure. Ultimately, however, this would also lead to a decline in bioeroding sponge abundance, because substrate availability would decline with reduced calcification. Chaves-Fonnegra and colleagues (2018) recently considered transitions from coral to bioeroding sponge-dominated reefs using a model to explore the impacts of coral bleaching events on the potential for transitions to bioeroding-sponge-dominated states. Model simulations showed that the success of bioeroding sponges depended on the severity of the bleaching and rates of coral recruitment and that future reefs could likely be dominated by macroalgae and bioeroding sponges. This again demonstrates the need for a greater understanding of the interactions between sponges and macroalgae.

A general consequence of the increased erosion or destruction of coral reefs is a loss of habitat complexity,
which generally results in a decrease in biodiversity and productivity (Rogers et al. 2014). Sponges do exhibit a wide range of morphologies, which can sometimes create extensive 3D habitat that might be suitable as refuges for fish and other organisms. However, this is not likely to create the same refuges as a healthy coral reef, and therefore shifts to sponge-dominated reefs as a result of climate change are unlikely to have overall positive effects on diversity or productivity.

**Climate change scenarios and sponge responses**

For most organisms, the magnitude of their response to changing environmental conditions depends on the strength of the stressor and its duration. Although treatment conditions varied among the different climate change studies summarized in the present article (see the supplemental material), most included exposure of sponges to the most extreme scenarios predicted for 2100 as relevant to each specific geographic region. Therefore, although a range of experimental conditions were employed, the differential between control and treatment levels was generally consistent. Overall, most studies showed sponge tolerance to OA but described rapid negative impacts of OW only a few degrees higher than the current temperature maxima. Although Bennett and colleagues (2017) highlighted an interactive effect of OW and OA on two tropical phototrophic species (see above), most cumulative stressor studies did not describe any interactive, synergistic, or antagonistic effects. Importantly, however, in few studies were the responses of the same sponge species to both individual and combined stressors compared (but see Achlatis et al. 2017). In addition, in very few sponge studies have specific tolerance thresholds to OW and OA been defined (but see Webster et al. 2008, 2011, Ramsby et al. 2018), and most studies have been conducted over short time frames (from days to months). Response relationships and deriving sponge tolerance thresholds to longer-term exposure will provide a more comprehensive understanding of how climate change will affect sponge populations at any given location. In addition, future studies should employ environmentally relevant diurnal and seasonal fluctuations within the experimental manipulations to capture the natural fluctuations in temperature and $pCO_2$ that occur on coral reefs.

**Conclusions**

In summary, although OW generally has a negative impact on sponges, OA has much less impact. Furthermore, the combined effects of OW and OA appear much less pronounced for sponges than for many other benthic groups, particularly those with calcium carbonate skeletons. Also important is the differential tolerance of sponge larvae compared with adult conspecifics. The mechanisms supporting such resistant early life stages clearly warrants further investigation, because this topic has the potential to underpin sponge population persistence under OW conditions predicted for 2100. It is also becoming increasingly clear that sponge microbes play an important role in sponge stress responses, and the interaction between the sponge host and its associated microbiome therefore needs to be fully elucidated. Finally, there is still a paucity of studies from some geographical areas, particularly for polar species and for some sponge classes. Despite clear gaps in our understanding of combined OA and OW effects on sponges and the need to consider the responses of many more species, our review highlights the importance of species-specific differences in sponge tolerance to both OW and OA. Therefore, although sponges could be considered potential winners under future climate change, species-specific sensitivities will likely alter population structures with concomitant consequences for ecosystem function.

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**Supplemental material**

Supplemental data are available at BIOSCI online.

**References cited**


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