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OPINION

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Will coral reef sponges be winners in the Anthropocene?

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Abstract

Recent observations have shown that increases in climate change-related coral mortality cause changes in shallow coral reef community structure through phase shifts to alternative taxa. As a result, sponges have emerged as a potential candidate taxon to become a "winner," and therefore a numerically and functionally dominant member of many coral reef communities. But, in order for this to occur, there must be sufficient trophic resources to support larger populations of these active filter-feeding organisms. Globally, climate change is causing an increase in sea surface temperatures (SSTs) and a decrease in salinity, which can lead to an intensification in the stratification of shallow nearshore waters (0–200 m), that affects both the mixed layer depth (MLD) and the strength and duration of internal waves. Specifically, climate change-driven increases in SSTs for tropical waters are predicted to cause increased stratification, and more stabilized surface waters. This causes a shallowing of the MLD which prevents nutrients from reaching the euphotic zone, and is predicted to decrease net primary production (NPP) up to 20% by the end of the century. Lower NPP would subsequently affect multiple trophic levels, including shallow benthic filter-feeding communities, as the coupling between water column productivity and the benthos weakens. We argue here that sponge populations may actually be constrained, rather than promoted, by climate change due to decreases in their primary trophic resources, caused by bottom-up forcing, secondary to physical changes in the water column (i.e., stratification and changes in the MLD resulting in lower nutrients and NPP). As a result, we predict sponge-dominated tropical reefs will be rare, or short-lived, if they occur at all into the future in the Anthropocene.

KEYWORDS
Anthropocene, coral reefs, mixed layer depth, ocean acidification, phase shifts, sponges, thermal stress, trophic ecology

1 | INTRODUCTION

There has been considerable interest in the causes of worldwide declines in coral cover, phase shifts in coral reef community structure, and the apparent rise in diseases of coral reef organisms (Lesser, 2004). In particular, worldwide coral bleaching events (Hoegh-Guldberg, Poloczanska, Skirving, & Dove, 2017; Hughes et al., 2017) have caused high rates of coral mortality, and phase shifts to dominance by other taxa such as soft corals and sponges (Norström, Nyström, Lokrantz, & Folke, 2009). As a result of these ecological changes, coral reefs have become the "poster child" for ecosystems experiencing profound ecological changes now, and predicted to worsen into the future in the Anthropocene, where high biodiversity coral reefs will probably exist in very few places (Hoegh-Guldberg et al., 2017). Sponges, in particular, have been predicted to become "winners" under these climate change scenarios when phase shifts in community structure occur (Bell, Bennett, Rovellini, & Webster, 2018; Bell, Davy, Jones, Taylor, & Webster, 2013; Bell, Rovellini, et al., 2018). But there is not widespread support for a general increase in sponge populations on shallow reefs; site-specific increases (McMurray, Finelli, & Pawlik, 2015) and decreases (Wulff, 2006) have been reported for sponge populations monitored over extended time periods.

In their hypothesis on climate change and sponge resilience, Bell, Bennett, et al. (2018) and Bell, Rovellini, et al. (2018) correctly note that understanding the ecological impacts of increased sponge populations on coral reefs must address their effects on carbon fluxes, and the potential for food limitation. Here, we describe a scenario where sponge populations may actually be constrained rather than promoted by climate change due to decreases in their primary trophic resources. This would be caused by bottom-up forcing, following oceanographic changes in the water column (see Figure 1 and below). As a result, we argue that sponge-dominated shallow tropical reefs may be rare, if they occur at all, and that predicting which reefs will become dominated by sponges will require long-term studies integrating oceanography with the ecology of coral reefs.

2 | TROPHIC ECOLOGY OF SPONGES

Sponges play a significant role in benthic–pelagic coupling via filtration of large quantities of both dissolved and particulate organic matter (DOM and POM; Lesser, Slattery, & Mobley, 2018). Experimental evidence on shallow reefs has also shown the importance of both POM (Trussell, Lesser, Patterson, & Genovese, 2006) and DOM (de Goeij, Moodley, Houtekamer, Carballeira, & van Duyl, 2008) in the trophic ecology of sponges. While DOM, and specifically dissolved organic carbon (DOC), can contribute up to 97% of a sponge's carbon requirements (reviewed in de Goeij, Lesser, & Pawlik, 2017), dissolved and particulate organic nitrogen (DON and PON) are also important to maintain balanced growth (de Goeij et al., 2017; Lesser, Slattery, et al., 2018). Sponge consumption of large amounts of DOM has been shown to cause the release of cellular debris, primarily choanocytes, that fuel a “sponge loop” detrital pathway of significant importance to higher trophic levels on coral reefs (de Goeij et al., 2013, 2017; Rix et al., 2016, 2018). Additionally, it is now known that the consumption of either particulate organic carbon (POC) and/or DOC can result in the production of sponge detritus (Maldonado, 2015). But while most sponges consume both POC and DOC, not all sponges produce detritus (e.g., McMurray, Stubler, Erwin, Finelli, & Pawlik, 2018). The amount of detritus produced also decreases with increasing depth (Lesser, Slattery, et al., 2019), and may be a result of the decreased availability of DOC, while POC increases, with increasing depth (Lesser, Slattery, Laverick, Macartney, & Bridge, 2019). The general increase in trophic resources, as carbon and nitrogen, with increasing depth (Lesser, Mueller, et al., 2019; Lesser, Slattery, et al., 2019) results in faster growing, and larger, sponges dominating the community on deep, mesophotic, reefs (>30 m: Lesser, 2006; Lesser & Slattery, 2018; Lesser, Slattery, et al., 2018). This occurs because PON, as a component of POM, is

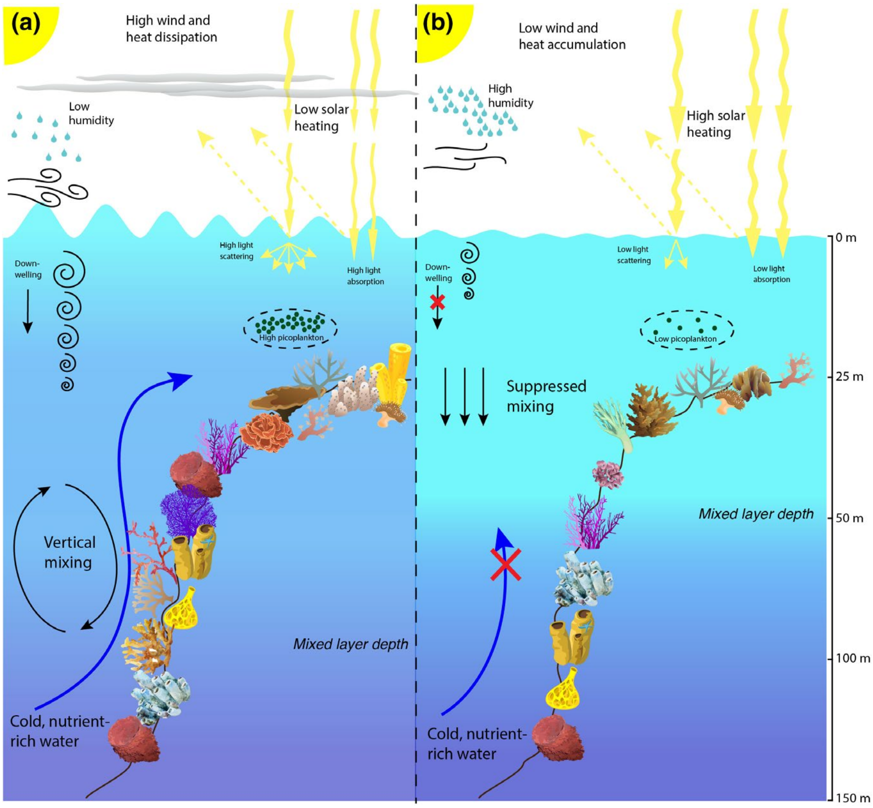

FIGURE 1 Illustration showing (a) the physical oceanography of a contemporary coral reef from shallow (<30 m) to mesophotic (30–150 m) depths down to the mixed layer depth (~100 m), and (b) the same coral reef in 2100 with the changes in physical forcing, productivity, and changes in reef community structure (see text for detailed description). Redrawn from Fordyce et al. (2019) with permission from the authors

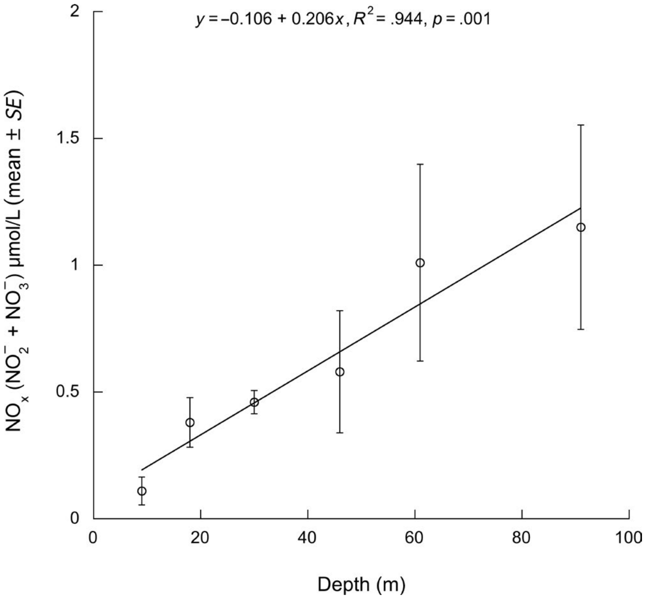

FIGURE 2 Significant effect of depth on NO_x (NO_2^- and NO_3^-) in µmol/L (mean ± *SE*) concentration around Lee Stocking Island (Bock Wall), Bahamas in summer 2009. NOx concentration was reanalyzed from Morrow, Fiore, and Lesser (2016)

a very important source of nitrogen that varies along the shallow to mesophotic depth gradient down to depths of at least 90 m (Lesser, 2006; Lesser, Slattery, et al., 2019). Suspension-feeding sponges filter POM, with its lower C:N ratios compared to DOM (Lesser, Mueller, et al., 2019; Lesser, Slattery, et al., 2018), mostly in the form of picoplankton, with clearance rates of 83%–90% (Lesser, 2006; Slattery & Lesser, 2015).

Additional nutrient and food resources in the form of zooplankton (Andradi-Brown et al., 2017), picoplankton (Lesser, 2006), and inorganic nutrients (Figure 2) on many shallow (<30 m) and mesophotic (~30 to 150 m) coral reefs are provided by upwelling or internal waves (e.g., Leichter & Genovese, 2006; Leichter, Stewart, & Miller, 2003; Lowe & Falter, 2015; Williams et al., 2018). Given this evidence, and the available experimental data, a strong argument can be made for the importance of bottom-up forcing in the ecology of sponges on coral reefs (de Goeij et al., 2017; Lesser, 2006; Lesser & Slattery, 2013; Lesser, Slattery, et al., 2018; Slattery & Lesser, 2015; Wulff, 2017), although there is not universal agreement (e.g., Pawlik, McMurray, Erwin, & Zea, 2015).

3 | EVIDENCE FOR BOTTOM-UP FORCING OF SPONGE POPULATIONS FROM MESOPHOTIC CORAL REEFS

The trophic ecology of sponges describes a large portion of the variability in the population dynamics of sponges on mesophotic coral ecosystems (MCEs; Lesser, Slattery, et al., 2018). Understanding this deep sponge system provides important insights into the potential effects of food limitation, and provides an analog for what may occur on shallow coral reefs structured by climate change-driven decreases in net primary production (NPP). The structure and function of MCEs changes along the mesophotic depth gradient based on the availability of light and trophic resources (Lesser, Mueller, et al., 2019; Lesser & Slattery, 2018; Lesser, Slattery, et al., 2018, 2019). In particular, while corals and macroalgae decrease in abundance with increasing depth into the mesophotic zone due to light limitation (Lesser, Slattery, et al., 2018, 2019), sponges increase in abundance with increasing depth in many coral reef ecosystems (Lesser & Slattery, 2018; Lesser, Slattery, et al., 2018, 2019; Slattery & Lesser, 2012). This change in community composition with depth also affects the availability of DOM, since benthic primary producers are an important source of bioavailable DOM on coral reefs (Haas et al., 2011; Mueller et al., 2014). Additionally, decreasing irradiance reduces DOM production by benthic primary producers (Mueller, den Haan, Visser, Vermeij, & van Duyl, 2016; Mueller et al., 2014), which is consistent with observations that DOM concentrations decrease with increasing depth (Lesser, Mueller, et al., 2019; Lesser, Slattery, et al., 2019; Slattery & Lesser, 2015). In contrast, POM increases with increasing depth into the mesophotic zone as zooplankton and as picoplankton (Lesser, 2006; Lesser, Mueller, et al., 2019; Lesser, Slattery, et al., 2019).

Given this inverse relationship between DOM and POM across a depth gradient, the relative importance of DOM in sponge nutrition may decrease with depth while the importance of POM importance will increase. But, Lesser, Mueller, et al. (2019) show that even though DOM, as both DOC and DON, decreases with increasing depth, its availability is still significantly greater than POM. The C:N ratio of sponge tissues is generally low, suggesting carbon sufficiency across habitats and depths (de Goeij et al., 2017; Lesser, Slattery, et al., 2018). It has been suggested, however, that sponges, and specifically sponge growth and biomass accumulation, may be limited by the availability of nitrogen (de Goeij et al., 2017; Lesser, Slattery, et al., 2018). This is due to the fact that DOM on coral reefs has a high C:N ratio (>10; Ogawa & Tanoue, 2003; Rix et al., 2016; Tanaka et al., 2011). So, if sponges depend on DOM for a large proportion of their carbon, this would result in nitrogen limitation and the need for other sources of nitrogen such as POM (Lesser, Slattery, et al., 2018). Given the lower C:N ratio of POM compared to DOM, one hypothesis is that the balance between new sponge growth, which includes the production of choanocyte chambers, and cell turnover might be shifted in favor of new sponge growth at deeper depths. Again, the value of POM, while a small fraction of the total available carbon for sponges, is significant for its nitrogen content which narrows the C:N ratio of carbon remaining after the maintenance demands associated with respiration have been met, and may contribute to balanced growth for sponge communities in the mesophotic zone compared to shallow reef sponges (Lesser, Mueller, et al., 2019; Lesser, Slattery, et al., 2018).

Arguments have been made against the important role of bottom-up effects in sponge communities, specifically that food is not limiting and top-down effects are more important in structuring sponge populations (Pawlik, Loh, McMurray, & Finelli, 2013; Pawlik et al., 2015). Despite evidence to the contrary (Lesser, 2006; Trussell et al., 2006), and criticisms of the experimental design and analysis of Pawlik et al. (2013) supporting the top-down hypothesis (Lesser & Slattery, 2013), more recent data support the concept of food limitation with its potential influences on the population dynamics of sponges (Wooster, McMurray, Pawlik, Morán, & Berumen, 2019).

4 | SPONGE-LOOP AND VICIOUS CIRCLE HYPOTHESES

Our long-term understanding of how highly productive coral reefs maintain such high biomass and biodiversity under oligotrophic conditions (i.e., "the paradox of the reef") was recently challenged with the discovery of the "sponge loop" pathway (de Goeij et al., 2013). In essence, sponges efficiently transform a proportion of the trophic resources they consume (i.e., DOM and POM) to higher trophic levels via a detritus-based pathway (de Goeij et al., 2017). The sponge loop hypothesis continues to stimulate significant research interest in the coral reef community (Lesser, Mueller, et al., 2019; Maldonado, 2015; Pawlik et al., 2015; Slattery & Lesser, 2015), which has led to a number of recent studies examining where and when the sponge loop is operating on coral reefs (e.g., shallow reef flats: McMurray et al., 2018; mesophotic reefs: Lesser, Mueller, et al., 2019). Soon after the sponge loop hypothesis was proposed, Pawlik, Burkepile, and Thurber (2016) expanded upon the important role of sponges under changing reef conditions (i.e., community phase shifts) to explain the lack of resilience of Caribbean reefs, a hypothesis referred to as the "vicious circle." Here, as coral mortality continues to increase, the increased release of DOC from the expanding populations of macroalgae will result in greater carbon fluxes through the sponge loop, as well as an increase in the fluxes of dissolved inorganic nitrogen (DIN) species to support macroalgal populations in a reciprocal positive interaction that facilitates phase shifts to sponge- and macroalgae-dominated communities at the expense of corals (Pawlik et al., 2016). The vicious circle requires that sponges effectively compete with seawater microbes for DOC (i.e., "microbial loop"), and potentially use more recalcitrant forms of DOC by the sponge directly. Given the kinetics of DOC uptake between most bacteria (higher affinity, lower maximal uptake rate), including those of the sponge microbiome, relative to eukaryotic cells (lower affinity, higher maximal uptake rate), and known concentrations of DOC in coral reef waters, neither sponges, their microbiomes, nor seawater microbes are likely experiencing any kinetic restraints, or carbon limitation, as it relates to DOC. And while a significant amount of attention, and importance, has been placed on benthic macrophytes as a source of DOC on coral reefs (Haas et al., 2011), DOM release from phytoplankton and picoplankton can represent over 50% of the DOM pool (Becker et al., 2014). Important contributions to the DOM pool come from *Synechococcus* and *Prochlorococcus*, both important particulate food sources for sponges as well (Lesser, Slattery, et al., 2018). In fact, planktonically derived DOC has been shown to be an important source of carbon over large spatial and temporal scales for those coral reefs with rapid flushing, and therefore shorter residence times in the overlying water column (e.g., Nelson, Alldredge, McCliment, Amaral-Zettler, & Nelson, 2011). This oceanic DOM has been suggested to be of the more recalcitrant type, and it can also be metabolized by the bacterioplankton communities associated with coral reefs (Nelson et al., 2011). Nonetheless, many aspects of DOM release by phytoplankton and picoplankton under climate change scenarios remain largely unknown (Thornton, 2014).

5 | CLIMATE CHANGE-RELATED EFFECTS ON THE PHYSICAL OCEANOGRAPHY OF CORAL REEFS

The ecological effects of climate change stressors are routinely interpreted from organismal level studies relative to predicted changes in ocean acidification and/or warming (Doney et al., 2012). But climate change effects on organismal performance occur simultaneously with changes in the abiotic and biotic properties of the surrounding water. In particular, the distribution, productivity, and phenology of phytoplankton in the oceans are primarily driven by autotrophic phytoplankton and picoplankton regulated by the availability of light. However, nutrients (i.e., nitrogen), which are themselves affected by oceanic circulation patterns (Behrenfeld et al., 2006), are also crucial resources for phytoplankton communities. In contrast to the deep permanent thermocline, thermoclines and mixed layer depth (MLD) in tropical locations vary between 60 and 125 m (Figure 1a; Montégut, Madec, Fisher, Lazar, & Iudicone, 2004). This variability is seasonal in nature and shows a deepening of the MLD during the winter and a shallowing during the summer in tropical waters (Kara, Rochford, & Hurlburt, 2003; Tai, Wong, & Pan, 2017). Climate change-related increases in sea surface temperature (SST), and reduced winds, will increase and intensify the stratification of shallow nearshore tropical waters (0–200 m), resulting in widespread shoaling of the MLD (Alexander et al., 2018; Behrenfeld et al., 2006; Capotondi, Alexander, Bond, Curchister, & Scott, 2012; Gittings, Raitsos, Krokos, & Hoteit, 2018; Signorini, Franz, & McClain, 2015). The shallowest MLDs are already observed during the maximum mean monthly seawater temperatures on coral reefs from around the world and range in depth from 16 to 53 m (Wyatt et al., 2019). This is caused by the increase in solar insolation during the summer months, and results in a strong density gradient at the bottom of the MLD that prevents the mixing of nutrient-rich waters within the shallow euphotic zone creating a zone of nutrient limitation above the MLD and light limitation below the MLD for phyto- and icoplankton (Figure 1b). Regional changes in the physical oceanography of tropical oceans can also contribute to the increasing occurrence of local perturbations such as marine heatwave hotspots which have similar oceanographic features; increased heat absorbed in shallow waters, increased stratification, and a decrease in the MLD (Fordyce, Ainsworth, Heron, & Leggat, 2019). The depths observed for the maximum MLD overlap with the maximum depths of the euphotic zone (i.e., 1% of downwelling irradiance [E_d]) observed on many coral reefs from 58 to 102 m (Lesser, Slattery, et al., 2018). For Lee Stocking Island, Bahamas, the bottom of the euphotic zone is at 81 m (Lesser et al., 2010), and the depth of the MLD in August is ~32 m (Wyatt et al., 2019). The depth-dependent distribution of nutrients at this same location (Figure 2) during the summer shows NOx concentrations of <0.5 µmol/L at depths less than 30 m and significantly increasing concentrations of NOx (>1 µmol/L) with increasing depth. The source of these nutrients is the transport of sub-thermocline water masses by transient internal waves, which occurs on many coral reefs in the Caribbean and Pacific (Leichter, Helmuth, & Fischer, 2006; Reid et al., 2019), or the mineralization of DOM and POM by the sponge holobiont resulting in the release of dissolved inorganic nutrients (DIN; Fiore, Baker, & Lesser, 2013). In addition, the pattern of increasing nutrient concentration with depth also correlates with the depth-dependent increase in autotrophic picoplankton (i.e., low-light adapted prochlorophytes) and heterotrophic picoplankton with increasing depth (Lesser, 2006; Lesser, Mueller, et al., 2019).

Given the temperature-driven projected changes in MLDs for tropical waters based on global general circulation models, the magnitude of changes in the MLD is dependent on the rate of SST warming, but in all model outputs, an increase in stratification and shallowing of the MLD with SST increases is predicted (Yeh, Yim, Noh, & Dewitte, 2009). The observed pattern of shallow and stable MLDs, caused by seasonal warming, will likely become a longer, potentially permanent, feature of shallow waters surrounding coral reefs under projected climate change scenarios (Figure 1b). As described above, a shallow MLD around many of the worlds coral reefs would likely reduce deep-water nutrients from reaching the upper euphotic zone, with predicted decreases in NPP of up to 20% by the end of the century realized on coral reefs (Capotondi et al., 2012; Fu, Randerson, & Moore, 2016; Steinacher et al., 2010). In the Mediterranean, warming-enhanced stratification has already been demonstrated and experiments predict that reduced food supplies will create energetic constraints and mass mortalities of benthic invertebrate communities in the future (Coma et al., 2009). Modeling, using long-term data at specific locations, rather than synoptic coverage of temperature, light, and chl *a* biomass, has suggested that the coupling between increases in SST and shallowing of the MLD is not as consistent or strong as suggested (Somavilla, González-Pola, & Fernández-Diaz, 2017), but the main finding of this study was that winter deepening of the MLD has been occurring over decadal timescales. Additionally, nutrient and food subsidies contained in deeper waters below the tropical thermocline normally transported upslope to shallow coral reefs by vertical mixing caused by internal waves, will be affected by increasing SSTs, stratification, and decreases in wind velocities which cause both weakened internal waves and a decrease in the vertical deliveries of these subsidies by upwelling (Figure 1b; Woodson, 2018). However, increases in internal wave activity and strength have also been observed at unique locations such as Luzon Strait, Philippines, where some of the largest amplitude internal waves in the ocean occur when SSTs increase, and stratification increases (DeCarlo, Karnauskas, Davis, & Wong, 2015). This points out that there will undoubtedly be reef to reef variability in the MLD of tropical oceans due to a large number of variables such as season, wind forcing, tides, current shear, etc., but the large-scale modeling projections predict a shallowing of MLDs driven primarily by increased solar insolation in surface waters and subsequent stratification in the world's oceans (Alexander et al., 2018; Behrenfeld et al., 2006; Capotondi et al., 2012; Gittings et al., 2018; Signorini et al., 2015).

The lowering of NPP would affect multiple trophic levels, including shallow benthic filter-feeding communities such as sponges, as the coupling between water column productivity and the benthos weakens (Fu et al., 2016; Steinacher et al., 2010). The decrease of NPP has been predicted to have significant impacts in some of the least productive waters globally, including many coral reef ecosystems (e.g., tropical North Atlantic: Polovina, Howell, & Abecassis, 2008). While phytoplankton biomass declines with decreasing NPP, autotrophic picoplankton have been predicted to increase (Flombaum et al., 2013). Picoplankton are important trophic resources for sponges, particularly on deep reefs where POC concentrations exceed those of shallow reefs (Lesser, 2006; Lesser & Slattery, 2013), so increases in this resource should select for sponges as "winners" under predicted changes in climate (Bell, Bennett, et al., 2018; Bell, Rovellini, et al., 2018). But a recent holistic model of autotrophic picoplankton abundances, incorporating temperature, chlorophyll biomass, nutrients, and irradiance (photosynthetically active radiation [PAR] and UVR), predicts that *Synechococcus*, *Prochloroccocus*, and picoeukaryote abundances will actually decline by 32%, 18%, and 42%, respectively, with a 2°C increase in ocean warming, subsequent stratification, and the associated decrease in nutrient delivery (Agusti, Lubían, Moreno-Ostos, Estrada, & Duarte, 2019). This should also cause changes to the optical properties of the water column (i.e., scattering and absorption) that might lead to increased penetration of solar irradiance, both its visible and ultraviolet components (Figure 1b), which might further depress low-light adapted picoplankton production (Agusti et al., 2019). A decrease in NPP will also result in a decrease in the amount of DOM released by the phytoplankton community, and subsequently the abundance of heterotrophic picoplankton available as a food resource for sponges (de Goeij et al., 2017; Lesser & Slattery, 2013). This climate change-mediated scenario predicts that diminishing trophic resources for sponges will have significant effects on the distribution, growth, and abundance of sponge populations, which will ultimately affect their functional role on coral reefs relative to nutrient cycling and the sponge loop pathway (e.g., Bell, Rovellini, et al., 2018; de Goeij et al., 2017).

6 | BIOGEOGRAPHICAL DIFFERENCES: THE PACIFIC VERSUS THE CARIBBEAN

When comparing shallow reef sponge population dynamics between the Pacific and the Caribbean, there appears to be consistent differences in abundance and cover for emergent, open reef, sponges.

Caribbean reefs consistently average ~16% higher open reef sponge cover compared to most of the Pacific where sponge cover is typically <1.5%, although sponge cover can be as high as 29% on some reefs in Indonesia (Pawlik et al., 2016). When examining sponge cover at mesophotic depths, however, no significant differences were detected at a depth range of 60–90 m water depth between two Caribbean and four Indo-Pacific reefs (Slattery & Lesser, 2012). But in that study, Indo-Pacific MCE sponge biomass was significantly lower than that of Caribbean MCEs, since cover was dominated by encrusting sponges in the Indo-Pacific compared to massive growth forms on Caribbean reefs (Slattery & Lesser, 2012).

Where sponge cover is high in the Pacific, it has been reported to be dominated by foliose species that are primarily photoautotrophic (Wilkinson & Cheshire, 1990) because of their symbionts (i.e., cyanobacteria). Sponges harboring cyanobacterial symbionts would appear to be at a distinct advantage given the observed resistance to thermal stress experimentally demonstrated for photoautotrophic sponges from the Great Barrier Reef (GBR; Bennett et al., 2017). Studies on the presence of cyanobacteria in Caribbean sponges suggest that many species, in fact, harbor cyanobacterial symbionts (Erwin & Thacker, 2007), and therefore, the potential for photoautotrophy to contribute to overall carbon metabolism and potential resistance to thermal stress. Previous work by Wilkinson and Cheshire (1990) described the Caribbean basin as selecting for heterotrophic sponges due to a greater abundance and utilization of planktonic food, whereas the Indo-Pacific, specifically the GBR, appeared to favor photoautotrophic sponges due to enhanced light transparency under oligotrophic conditions. They reported no photoautotrophic sponges at their Caribbean location (i.e., reefs around Carrie Bow Cay, Belize) based on ratios (<1.5) of short-term productivity to respiration measurements. However, their physiological measurements were based on lower irradiances than at the sponge collection sites, and are in contrast with multiple reports of symbiotic cyanobacteria in over a third of the Caribbean sponge fauna (Thacker & Freeman, 2012; Usher, 2008). Additionally, as it relates to any biogeographic differences in food supply, the POM on Pacific coral reefs (Charpy, Rodier, Fournier, Langlade, & Gaertner-Mazouni, 2012) is comparable to that of the Caribbean (Lesser, 2006; Lesser & Slattery, 2013) and is actively grazed by a diverse number of suspension feeders including sponges (Houlbreque, Delesalle, Blanchot, Montel, & Ferrier-Pagès, 2006; Lesser, 2006; Lesser & Slattery, 2013; Ribes, Coma, Atkinson, & Kinzie III, 2003, 2005). Similarly, DOM concentrations, both DOC and DON, as well as DIN (i.e., NO_x), does not differ significantly between Pacific (GBR and Hawaii) and Caribbean (Curaçao) shallow coral reefs (Lesser, Morrow, & Pankey, 2019; Lesser, Morrow, et al., 2018). Lastly, the underwater light environment does not differ significantly between these regions as the irradiances of PAR (400–700 nm) and downwelling attenuation coefficients (K_d/m) on Caribbean reefs are similar (Lesser, 2000; Lesser, Slattery, & Leichter, 2009; Lesser et al., 2010) to those of offshore reefs of the GBR (Wilkinson, 1983; Wilkinson & Trott, 1985) and other locations in the Pacific (Lesser, Slattery, et al., 2018). This suggests that POM and DOM, as well as light, are not strong drivers regulating the population dynamics of photoautotrophic versus heterotrophic sponges between the two regions, and that the dominance of photoautotrophic sponges in the Pacific has not been clearly shown. In fact, recent molecular data show that many sponges in both the Pacific and Caribbean harbor cyanobacterial symbionts (Erwin & Thacker, 2007; Konstantinou, Gerovasileiou, Voultsiadou, & Gkelis, 2018; Usher, 2008) with their inherent potential for photoautotrophy.

Is it even possible that a decline in NPP would significantly affect the trophic biology of shallow coral reef sponge populations? A simple “back of the envelope” calculation for the sponge, *Callyspongia vaginalis*, a low microbial abundance (LMA) sponge, from the Caribbean, is presented to illustrate the potential effects of declining NPP for sponges. LMA sponges have been reported to be less dependent on DOM, and recent data show that only 4% of the total carbon intake for this sponge is from DOM, while the remainder is from POM, both detritus and live POC (McMurray et al., 2018). Given this, the following calculation is based solely on climate change-related predictions for declines in the phytoplankton and picoplankton communities, or live POM, as discussed above. First, we took the *C. vaginalis* feeding data from Belize (Lesser & Slattery, 2013) at 7.5, 15, 23, 30, and 46 m, and used an MLD of 30 m for Belize (Wyatt et al., 2019, table S1). Within that mixed layer, we then assumed a decrease of 20% in NPP at depths equal to or less than 30 m, and we recalculated the amount of energy acquired in J/day without changing the values at 46 m, which would be below the MLD. Then, using the sponge respiration data from Trussell et al. (2006) for 12 and 23 m, converted to J/day as energetic costs, we conducted a linear regression of that data which showed a significant decrease in energetic costs with increasing depth ($y = 1{,}030.7–20.77x$, $R^2 = .413$, $p = .045$), and calculated individual costs in J/day for sponges across the depth range described above. We did not include any thermal

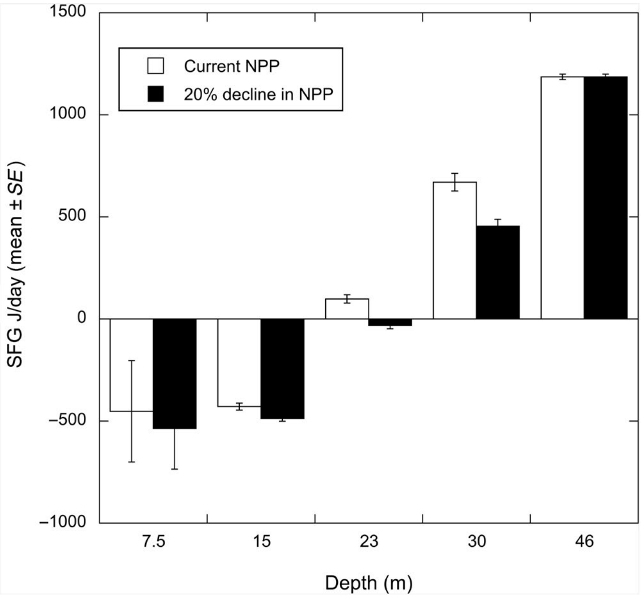

FIGURE 3 Scope for growth (J/day) for the sponge *Callyspongia vaginalis* before and after a predicted 20% decrease in net primary productivity assuming constant feeding

(i.e., Q_{10}) effects for predicted temperature increases in respiration which would have resulted in increased energetic costs, and then calculated the instantaneous scope for growth (SFG) for all sponges. Prior to the 20% decline in NPP, sponges at 7.5 and 15 m were already exhibiting a negative SFG (Figure 3), similar to values observed for shallow populations of *C. vaginalis* on Conch Reef, Florida (Trussell et al., 2006). After the 20% decrease in NPP, all sponge populations at depths <30 m exhibited negative SFG. Sponges at 30 m saw a ~32% drop in energy available for growth, whereas sponges below the MLD were still in positive SFG (Figure 3). So, for shallow sponge communities, a 20% decrease in food is likely to have profound effects on sponge populations based on this scenario, and given similar levels of POM and DOM in the Pacific, similar effects could potentially occur on those reefs as well.

7 | CONCLUSIONS

Taken together, if climate change proceeds as predicted up to, and beyond, the year 2100, the physical oceanography of coral reefs are likely to change in profound ways (Figure 1) that will affect NPP, and the trophic resources that sponges require on shallow reefs in particular (Figure 3). This portends that rather than seeing an increase in population size (Bell, Bennett, et al., 2018; Bell et al., 2013), sponge populations may actually decrease on shallow reefs as food becomes limiting. Supporting evidence for this comes from the depth-dependent changes in sponge populations as food resources change with depth; MCE sponge density is greatest where food resources are most abundant (Lesser & Slattery, 2018; Lesser, Slattery, et al., 2018, 2019) and the differences between POC and PON availability at 50 m are ~30% and ~50% greater than for sponges at shallow depths (Lesser, Slattery, et al., 2019). While sponge population dynamics can be influenced by predation (Pawlik, 1998) and competition (Wulff, 2017), ultimately their ecology is more strongly influenced by bottom-up forcing, or food, as both DOM and POM (de Goeij et al., 2017; Lesser & Slattery, 2013; Lesser, Slattery, et al., 2018; Wulff, 2017). Given that both the “sponge loop” and “vicious circle” nutrient and energy pathways are dependent on the consumption of POM and DOM resources in the water column by sponges, these pathways are likely to be significantly altered, if not uncoupled from the ecology of sponges in the future. Additionally, recent experimental data reveal that predicted levels of ocean acidification and thermal stress under the IPCC A2 model (i.e., equivalent to RCP 6.0) could have significant effects on the microbiome of sponges causing community level destabilization and a decrease in potential primary productivity (Lesser, Fiore, Slattery, & Zaneveld, 2016). Experiments using levels of ocean acidification and temperature stress equivalent to RCP 8.5 model predictions revealed multiple, negative, effects on different life-history phases of sponges that were different for photoautotrophic versus heterotrophic sponges, and the negative temperature effects (i.e., tissue necrosis, mortality, and elevated respiration) on adult heterotrophic sponges were exacerbated by exposure to ocean acidification (Bennett et al., 2017). Taken together, the combined organismal effects and the predicted changes in the physical environment described above do not support predictions of sponge-dominated coral reefs in the future.

Bell, Rovellini, et al. (2018) describe five specific questions that should be answered to better understand how sponge-dominated reefs would occur, function, and be maintained. We agree with the directions for future research on sponge ecology proposed by Bell, Rovellini, et al. (2018), and encourage the inclusion of novel approaches consistent with the anthropogenic-based changes we are now faced with (e.g., Williams et al., 2019). In particular, we suggest that it is essential to understand the physical and optical oceanography of coral reefs generally because sponge populations are not the only taxa to utilize picoplankton on coral reefs (Houlbréque et al., 2006; Ribes, Coma, Atkinson, & Kinzie III, 2003, 2005). The inherent variability in the physical and optical attributes of individual coral reefs (Freeman, Miller, Norris, & Smith, 2012; Leichter et al., 2013) must be understood in order to contextualize the trophic ecology of sponges related to food resource availability, as well as carbon, nitrogen, and energy fluxes at the organismal and reef scales. These bottom-up processes, along with a robust experimental approach examining the roles of competition and predation, will ultimately determine the dynamics of sponge populations under climate change-related forcing of the physical environment. Sponges may yet survive the Anthropocene, but a closer look at predicted environmental changes across coral reefs as a whole suggest the likelihood of more varied, and potentially negative responses by this taxon to climate change.

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