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REVIEW

ANNIVERSARY ARTICLE

Ecosystem engineers on tropical reefs in transition: giant barrel sponges in the Anthropocene

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ABSTRACT

Tropical coral reef ecosystems are changing rapidly to an alternative state in which sponges are the dominant living habitat, with giant barrel sponges (GBSs, *Xestospongia* spp.) representing the largest biomass. Unlike other benthic reef organisms, GBSs are ecosystem engineers that pump large volumes of seawater, disrupting the benthic boundary layer and directing flow away from the reef surface and into the water column. The morphology and size of GBSs have made them particularly good experimental subjects to study the hydraulics of sponge pumping and the transformation that occurs as seawater is processed by the sponge holobiont (sponge cells and microbial symbionts). This Review is part of a series marking the 100th birthday of The Company of Biologists, which was founded by marine biologist George Parker Bidder III, who primarily worked on sponges. The Review provides an integrative assessment of research on GBSs with comparisons with what is known about other marine sponges. Recent discoveries suggest that ancient lineages of morphologically indistinguishable GBSs are responding to environmental changes over sub-decadal time periods to rapidly populate reefs stripped of coral cover by climate change. If GBSs remain robust to rising seawater temperatures, they will become the greatest source of habitat complexity on reefs of the future, so knowledge of their biology and physiology will be important to our understanding of these ecosystems.

KEY WORDS: Invertebrate physiology, Sponge biology, Sponge feeding, Coral reef ecology, Aquatic biology, Benthic–pelagic coupling, *Xestospongia*

Introduction

This Review is part of a series that commemorates the 100th anniversary of the founding of The Company of Biologists, an event which saved the British Journal of Experimental Biology (which eventually became Journal of Experimental Biology) from bankruptcy. Instrumental to the founding of the Company was George Parker Bidder III, a marine biologist who, among other interests, studied the biology of sponges and contributed to the literature on sponge pumping. Bidder was among the first zoologists to use dye visualisation to quantify the large volumes of seawater processed by sponges (Bidder, 1923). With Bidder's contributions in mind, here, I review the literature on the biology and physiology of giant barrel sponges (GBSs), arguably the most-studied sponges in the sea. Notably, GBSs may be poised to become the dominant habitat-forming organisms in tropical reef ecosystems of the future, as reef-building coral cover declines as a result of climate change, disease and other anthropogenic effects. Indeed, this is already true on most Caribbean reefs. It is even more important, then, that we understand the physiology of GBSs and the effects that they have on the biological and chemical constituents of the large volumes of seawater that they pump as they feed, excrete, and cycle carbon and nutrients.

The intent of this Review is to provide an integrative and critical assessment of the literature regarding GBSs, with the goal of highlighting interesting and important areas for future research (although it should be noted that this Review is not an exhaustive compendium of research papers on GBSs). The Review begins by discussing growth and age of GBSs, and goes on to consider recent discoveries related to their biodiversity, remarkable pumping ability, impact on seawater chemistry and sources of mortality. The Review closes with a consideration of the role of GBSs on tropical reefs of the future.

Redwoods of the reef

GBSs are among the largest and longest-lived animals on Earth (McClain et al., 2015), with a geographic range that includes tropical reefs of the Western Atlantic, Indian and western Pacific Oceans, and the Red Sea (Fig. 1; de Voogd et al., 2024). GBSs live in benthic hardbottom (reef) habitats at 5–80 m depth and reach sizes of more than 2 m in height and 1 m in diameter (Fig. 2B). The most common form of GBSs is the barrel morph (Fig. 2A), with a barrel-shaped exterior and an interior cavity (atrium) shaped like the frustum of a cone (McMurray et al., 2014). But GBSs are noted for their morphological variability (hence the name 'muta' for the Caribbean species), with other morphologies including highly flattened individuals that resemble a car tire on its side, elongated barrel forms that look like smoke stacks, and very unusual clam and tub morphologies that are common in the southeast Caribbean (Fig. 2C; Pawlik et al., 2021). Similarly, the external surface of GBSs is highly variable: colouration includes white, pink, gray, golden and most often dark reddish-brown; and morphology ranges from nearly smooth to highly rugose (Kerr and Kelly-Borges, 1994; Zea et al., 2024), often with pits and digitate projections and with vertical lamellar ridges that are particularly common in the Indo-Pacific (Fig. 2D). The sponge tissue of GBSs is heavily infused with silicious spicules, giving it a hard but slightly compressible feel, although there is variability in tissue texture as well (Kerr and Kelly-Borges, 1994). There are three described species of GBSs based on distribution and tissue characteristics: *Xestospongia muta* in the Western Atlantic, *X. testudinaria* in the Red Sea, Indian and Pacific east to Taiwan and New Caledonia, and *X. bergquistia* in Northern Australia and New Caledonia (Fig. 1; de Voogd et al., 2024); however, more recent phylogenetic studies have revealed a more complicated story that is discussed below.

Estimates of growth and age are rare for sponges but have been calculated for GBSs. Like all sponges, GBSs do not exhibit an indicator of annual growth in tissue or skeleton, requiring growth

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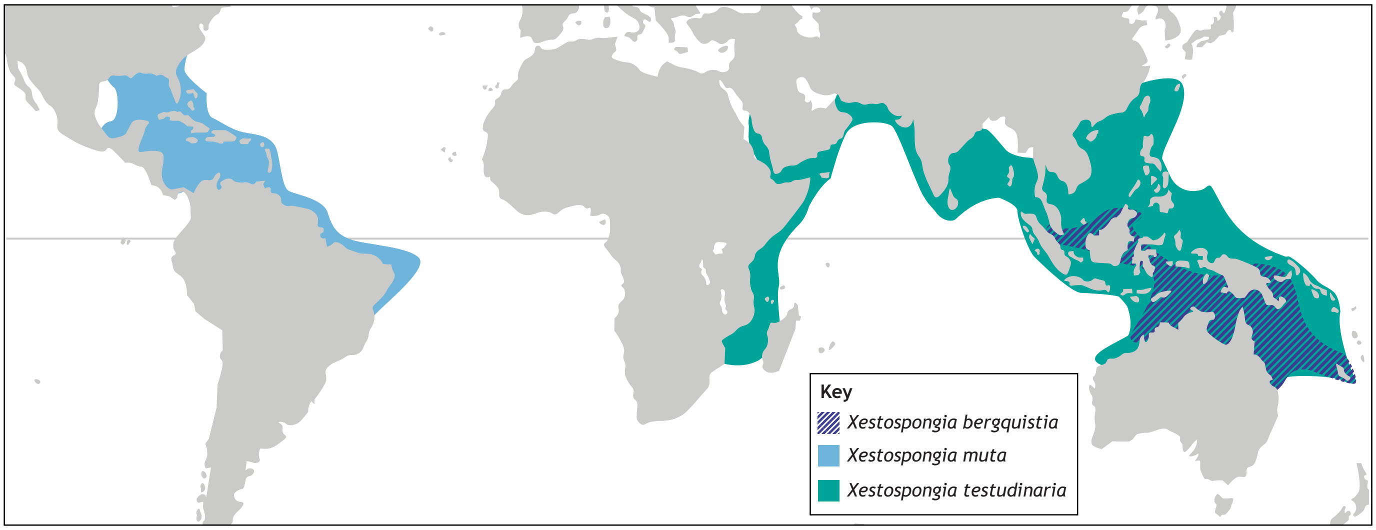

Fig. 1. Estimated range of the three described species of giant barrel sponge (GBS) based on entries in the World Register of Marine Species (www.marinespecies.org). Phylogenetic studies have since revealed a pan-global complex of up to nine cryptic species (see text).

estimates based on size changes over time. For *X. muta* on Florida reefs, the change in volume of 104 tagged sponges over 4.5 years has been estimated using digital images, and the specific growth rate ranges from 2% to 404% per year, with a mean of 52% per year (McMurray et al., 2008). Growth is best described by von Bertalanffy and Tanaka growth curves (see 'An enigmatic complex of cryptic species' below), with the largest sponge measured in the survey (~1 m height and diameter) estimated to be 127 years old. Based on the growth curves, the age estimate from a photograph of a very large (~2.5 m diameter) sponge (now dead) from Curaçao is 2300 years (McMurray et al., 2008; Nagelkerken et al., 2000), although the authors made it clear that

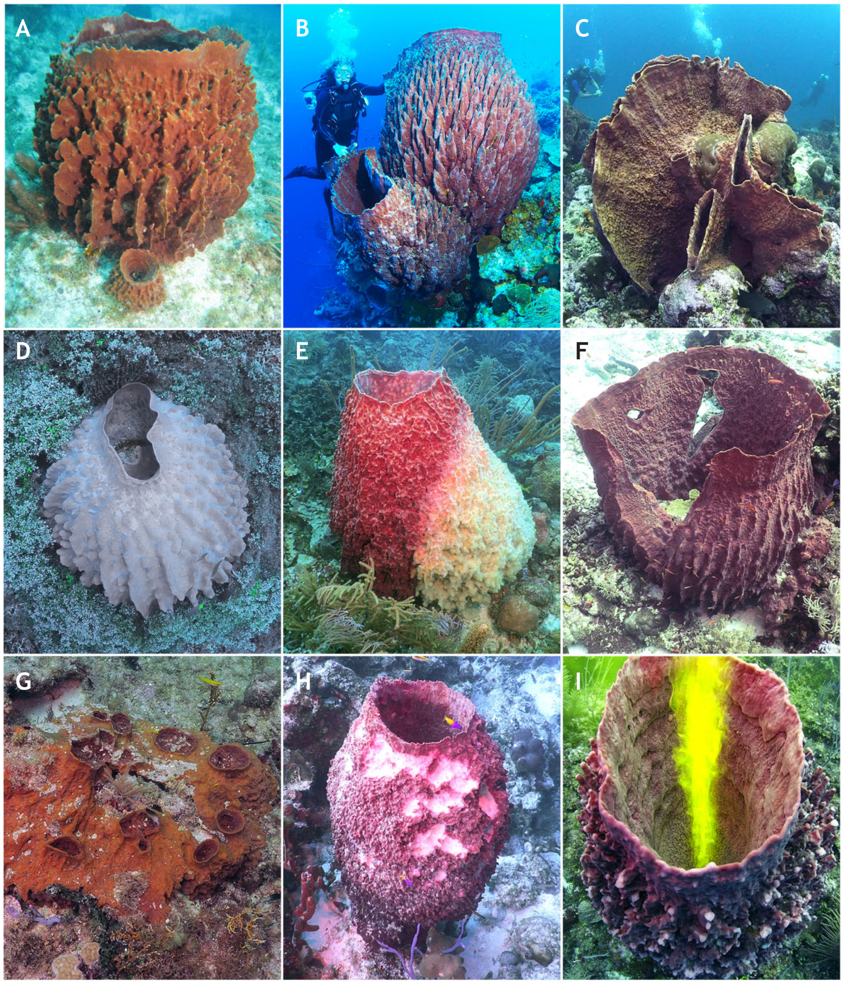

Fig. 2. Photos of GBSs illustrating concepts covered in this Review. (A) Relative height of two GBSs that differ in size, Florida Keys, 2012. (B) Large GBSs on an offshore island reef, Mayaguana, Bahamas, 2013. (C) Unusual GBS morphology that is common in the SE Caribbean, Tobago, 2015. (D) Non-fatal or cyclic bleaching, Solomons, 2024. (E) Fatal bleaching, Roatan, 2021. (F) Survivor of recent 'fatal' bleaching, Philippines, 2022. (G) Recovery of sponge base after storm damage, Florida Keys, 2019. (H) Predation by hawksbill turtle, Turks and Caicos, 2023. (I) Visualization of excurrent stream using fluorescein dye, Belize, 2015. Photo credits: J. R. Pawlik.

extrapolations for very large sponges are subject to considerable error. Similar growth analyses were conducted for GBSs in Wakatobi, Indonesia, revealing specific growth rates that ranged from −12% to 624% and a mean of 47% per year (McGrath et al., 2019). Despite the lower mean specific growth rate, the authors of this study concluded that GBSs from Wakatobi grow twice as fast as those from Florida, based on growth models. This difference between studies may be attributed to several factors, including the 2-fold greater growth interval for the Florida study, or the removal of sponges with negative specific growth rates from the growth models in the Wakatobi study. What is striking is the similarity in mean specific growth rates of ∼50% per year and the very large intra-site variation in growth rates among GBSs in both studies.

There are limited data to compare growth rates of GBSs with those of other sponge species. A recent study used direct volume determination or digital imagery and 3D photogrammetry of sponges that had grown on shipwrecks of known age to derive specific growth rates for 16 Caribbean sponge species (Olinger et al., 2019). Specific growth rates were higher than determined previously for GBSs, likely reflecting both different methods and different growth models. Additionally, there were higher specific growth rates among sponge species that are known to lack chemical defenses, such as *Callyspongia fallax* (∼150% per year), *Desmapsamma anchorata* (∼115%) and *Geodia neptuni* (∼100%; Olinger et al., 2019), the last of which is the closest in size and shape to GBSs. Sponges with known chemical defenses grow more slowly; for example, *Aiolochroia crassa* (∼97% per year), *Ircinia felix* (∼96%) and *Smenospongia conulosa* (∼90%; Olinger et al., 2019).

Aside from large intra-site variation in specific growth rates for GBSs, there are other reasons why accurate estimates of growth and age are difficult to obtain. As modular organisms, GBSs can regenerate after tissue loss, whether minor, as from predation events (Fig. 2H; Dunlap and Pawlik, 1998), or major, as from storm events or necrosis. GBSs can be fatally detached from the reef by storm surges – during which monofilament fishing line is dragged by debris and can detach sponges (McMurray and Pawlik, 2009) – or by earthquake events (Foster et al., 2010), leaving behind a patch of living tissue as the former sponge base (McMurray et al., 2015). Regeneration of the sponge base begins as a ring of atrial openings that could be mistaken for multiple individual sponges (Fig. 2G); these openings then merge into a single sponge with several atrial openings, and finally to a single sponge with one opening. Growth rates of sponges recovering from tissue loss are generally greater than those of sponges that have not experienced damage, with overall growth rates decreasing for the largest sponges (McMurray et al., 2008). It is conceivable that some large GBS individuals are the product of multiple rounds of loss and regeneration, greatly increasing their true age relative to estimates based on the application of growth curves to their current size.

In addition to their size and age, GBSs dominate the living biomass on many tropical reefs. Loh et al. (2014) performed cross-Caribbean transect surveys from 69 fore-reef sites and reported that mean cover of sponges was 15.9% of reef surface area, whereas that of hard coral was 16.2%, with GBSs comprising the second most common sponge in their surveys (behind the branching species *Aplysina cauliformis*). In a time-series study of GBSs on reefs off the Florida Keys at depths of 15–30 m, McMurray et al. (2015) reported mean densities of GBSs in 2012 ranging from 0.23 to 0.37 individuals m^{-2}, representing ∼0.5–1.3% cover of the reef surface and biomass (sponge volume) of ∼800–3200 $\mathrm{cm}^3\ \mathrm{m}^{-2}$. Similar densities of GBSs were reported from Saba Bank (de Bakker et al., 2016), with lower densities reported for studies from East Kalimantan and Sulawesi in Indonesia (Bell et al., 2013; de Voogd et al., 2009). Considering the biomass difference between GBSs and all but a few other sponge species (e.g. some *Agelas* spp., *Geodia neptuni*, *Verongula gigantea*), it is not difficult to conclude that GBSs are the dominant benthic animal on many tropical reefs, particularly in the Caribbean; as such, it is clearly important to better understand the physiological impacts of GBSs on their environment.

An enigmatic complex of cryptic species

The application of phylogenetics to GBSs has resulted in surprising discoveries. A global study of GBS tissue samples from 395 sponges across 17 locations revealed that: (1) existing species designations are invalid, (2) there are at least eight cryptic (i.e. morphologically indistinguishable) species, with several distributed sympatrically, and (3) cryptic species complexes in the Western Atlantic and Indo-Pacific are not separate monophyletic lineages (Fig. 1; Swierts et al., 2017). The last of these discoveries was perhaps the most surprising, because it suggests that the reproductively isolated cryptic species of GBSs were already established before the most recent geographic separation of the Western Atlantic and Indo-Pacific Oceans. However, rather than suggesting separation on a time scale of ∼3 million years with the formation of the Isthmus of Panama, the most likely explanation for the genetic pattern is that the global population of GBSs was split with the closure of the Tethys Seaway during the Miocene, ∼15 million years ago (Swierts et al., 2017).

The cryptic diversity of GBSs may provide an explanation for some puzzling past observations. For example, in the rare cases in which spawning by GBSs has been observed, it is notable that only some of the individuals on the reef are engaged in producing either eggs or sperm (Neely and Butler, 2020). Species boundaries among GBSs might be maintained through reproductive isolation as cryptic sponge species respond to different environmental or chemical cues to coordinate spawning at different times. GBSs are dioecious and are presumed to maintain their sexual identity throughout their lives, but this has yet to be established empirically. Further, the lack of a clear pattern to the timing of spawning makes it difficult to sample tissue of spawning individuals for sequencing. Tracking the same individuals over time and sampling over successive spawning events would allow us to determine both the frequency of reproduction and whether GBSs change sex.

Cryptic diversity is also likely to explain the results of past studies that attempted to parse GBS species boundaries based on morphological or chemical characteristics (Kerr and Kelly-Borges, 1994). For example, in one such study, *X. bergquistia* was differentiated from *X. testudinaria* ‘almost exclusively on the basis of skeletal characters, with the latter species having enhanced spongin fibre development’ (Fromont, 1991). In another study, Caribbean individuals of *X. muta* were split into three groups based on either tissue sterol composition or external morphology, with the authors having found no pattern to differences in tissue texture or spicule variation (Kerr and Kelly-Borges, 1994). It remains to be seen whether any morphological or chemical differences among individual GBSs correspond to genetic differences. The idea that differences in surface morphologies have a genetic basis was subsequently contradicted: repeated photographs of individual sponges show that surface morphologies can change over time (Evans et al., 2021). Future studies of morphological plasticity in GBSs would benefit from time-series studies of individual sponges under different abiotic and biotic conditions (flow regimens, depth, food availability), with digital images and 3D photogrammetry used to document changes in surface morphology (Olinger et al., 2019).

GBSs as ecosystem engineers – a jet-like sponge pump

Few sponge species reach the size and biomass of GBSs, and none are as abundant across tropical reefs worldwide. Unlike other common benthic reef organisms, such as corals, gorgonians and seaweeds, GBSs actively pump seawater through their bodies, disrupting the boundary layer next to the reef and transporting seawater out into the water column (Fig. 2I). As the seawater is pumped, GBSs remove particles and alter seawater chemistry by absorbing some metabolites and releasing others (see below). These functions are shared to a lesser degree by smaller sponge species (Reiswig, 1974), and although sea squirts (tunicates) and some bivalves (Tridacninae, Chamidae) also pump water, their incurrent and excurrent siphons are discrete, relatively close together, and generally held above the boundary layer of the reef. Unlike most other sponge species, the movement of seawater through a GBS is unidirectional and predictable, entering pores on the exterior sponge surface, proceeding through the sponge tissue and exiting pores that line the central cavity (atrium or spongocoel), with the mass flow of water moving inward from the boundary layer and sides of the cylindrical sponge and rapidly jetting outward away from the reef (Fig. 3).

The morphology of barrel-shaped GBSs has important advantages when studying physiology, feeding or excretion, because (1) the seawater in the atrium has been fully processed by the sponge and is easily sampled, (2) the flow of seawater from the atrium outward is the product of the whole sponge and is easily estimated, and (3) the volume of the whole sponge body can be estimated, allowing population-level estimates of water-column transport rates. Additionally, because GBSs have perhaps the greatest range in size of all sponge species, they are good choices for studies of size-specific changes in pumping and feeding (McMurray et al., 2017). Except for a few other solitary vase-shaped species (e.g. *Verongula gigantea*, *Niphates digitalis*), most sponge species have more complex morphologies with diffuse incurrent ostia and excurrent osculae (Fig. 3), sometimes intermingled, making studies of sponge pumping much more difficult.

Comparative studies of sponge pumping were pioneered by Bidder (1923), followed by Henry Reiswig (Reiswig, 1971, 1974), but have recently experienced a surge in interest (e.g. Morganti et al., 2021) along with several recent reviews (e.g. Riisgård and Larsen, 2022, 2024). Repetition of much of that information is therefore unnecessary here, except to mention that generalizations of pumping rates across sponge species may not be valid because (1) sponges include thousands of species that are phylogenetically highly diverse, (2) comparative studies often use different techniques for assessing flow, and (3) some studies have focused on small sponges with multiple oscules (see previous paragraph).

Regarding GBSs, McMurray et al. (2014) examined pumping as a function of morphology and size, measuring the velocity of seawater emerging from the atrial openings of 274 individual sponges on reefs in the Florida Keys and Bahamas. One of the most important outcomes of this study was the determination that the pumping rate could be simply determined from measurements of sponge size, allowing relatively easy estimates of site-specific seawater turnover by GBSs (McMurray et al., 2014). Excurrent seawater velocities are highest in the center of the atrial opening and decrease toward the sponge lip, with overall mean flow rates of $0.06\pm0.04\ \mathrm{l\ s^{-1}\ l^{-1}}$ sponge tissue. These values can be compared with those for other vase-shaped sponges: 0.005 to $0.034\ \mathrm{l\ s^{-1}\ l^{-1}}$ sponge tissue for *Aplysina lacunosa* and $0.578\ \mathrm{l\ s^{-1}\ l^{-1}}$ sponge tissue for *Callyspongia vaginalis* (Weisz et al., 2008). Direct comparisons of pumping by nine species of tube-, vase- and barrel-shaped sponges using the same techniques and in two different locations (Florida Keys, Belizean Barrier Reef) yields mean pumping rates as high as $0.13\ \mathrm{l\ s^{-1}\ l^{-1}}$ sponge tissue for *Niphates digitalis* and as low as $0.001\ \mathrm{l\ s^{-1}\ l^{-1}}$ sponge tissue for *Verongula gigantea* (McMurray et al., 2018). For GBSs, the volume of seawater pumped increases isometrically with increasing sponge

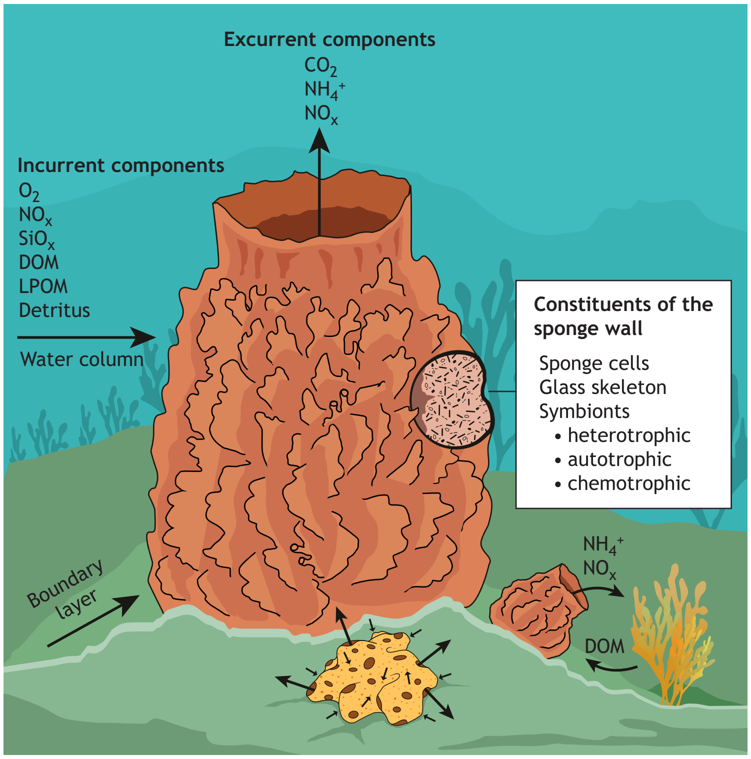

Fig. 3. Schematic of seawater processing by GBSs. The schematic shows chemical and dietary components in the water column and in the boundary layer being drawn into the sponge (left side), excurrent components (top), and constituents of the sponge wall (right side). Symbiont categories include those that derive nutrition from dissolved organic matter (DOM; heterotrophic), photosynthetic cyanobacteria (autotrophic), and those that derive energy from chemical reactions (chemotrophic). The 'vicious circle' feedback loop between GBSs and macroalgae is shown in the lower right. A typical non-GBS sponge is shown in the foreground to contrast the diffuse water flow through this common multi-oscular morphology. LPOM, live particulate organic matter.

tissue volume, although the very largest GBSs have reduced relative flow rates (McMurray et al., 2014). In the study by McMurray et al. (2014), excurrent velocities ranged from 0.03 to 13.66 cm s^{-1} and increased linearly as a function of sponge volume to the area of the atrial opening. The time required for a sponge to pump a volume of seawater equivalent to its body volume (i.e. cycle time) was determined to be 30±33 s. For GBS populations at various sites in the Florida Keys and Bahamas, water-column transport rates were calculated as the product of the mean sponge biomass per unit area and the mean sponge-induced flow, then the time for these populations to turn over a water column 30 m deep was estimated: for the Florida Keys, the estimated turnover rate was 2.8–6.0 days, versus 2.3 days for a site off San Salvador and 18.0 days for a site off Sweetings Cay in the Bahamas (McMurray et al., 2015b).

McMurray et al. (2014) also examined changes in pumping, along with parameters such as seawater temperature, turbidity, dissolved oxygen and pH, for 29 GBSs over periods of 15–60 h. Pumping over a span of time was relatively constant for most individuals, but rapid decreases and total cessation of pumping were observed in some, with pumping cessation lasting 100–230 min for three sponges. No clear correlations were found between variations in pumping and environmental parameters (McMurray et al., 2014), indicating that much remains to be learned about GBS pumping behavior. However, it is known that symbiotic zoanthid cnidarians, which are common on the inhalant outer surface of many species of tropical reef sponges, reduce GBS pumping rates by 75% and appear to alter sponge morphology (Lewis and Finelli, 2015). Similarly, the build-up of sediment on the outer surface of GBSs increases sponge respiration, presumably because the sponge needs to expend greater energy pumping against clogged incurrent ostia (McGrath et al., 2017). Research on pumping by GBSs pre-dates the discovery that GBSs include several cryptic species, but it seems likely that the full variability in sponge pumping has been captured, considering that the most divergent taxa among GBSs occur side-by-side in the Caribbean, and over 270 individual sponges were studied between sites in the Florida Keys and the Bahamas (McMurray et al., 2014). Nevertheless, it remains to be determined whether there are significant differences in pumping rates among the cryptic taxa of GBSs, and the reasons for GBS pumping variability are ripe for future research.

The sponge holobiont

It has long been understood that the tissue of some sponge species is packed with microbial symbionts, whereas others are relatively free of microbes. Originally called ‘bacteriosponges’ (Reiswig, 1981), species with high microbial biomass are now termed ‘high microbial abundance’ (HMA) sponges in contrast to ‘low microbial abundance’ (LMA) sponges (Gloeckner, et al., 2014). Rather than falling into two discrete groups, the large diversity of demosponge species falls into a spectrum from HMA to LMA. Within this symbiotic spectrum, GBSs clearly belong in the HMA group (Gloeckner et al., 2014), and like most of the topics explored in this Review, there has arguably been more replicated research done on the microbial symbionts of GBSs than any other sponge species. Again, some of this research pre-dates the discovery of cryptic speciation among GBSs and may consequently be more difficult to interpret, but more recent studies have investigated patterns of microbial symbiosis associated with GBS diversity. For example, Evans et al. (2021) used next-generation sequencing to characterize the symbiont communities of GBSs in the Florida Keys representing the two most distantly separated GBS cryptic species (genetic clusters 1 and 2). The symbiotic microbial communities of both clusters are highly diverse, with 12,185 total operational taxonomic units (OTUs) representing 38 bacterial and 3 archaeal phyla, and the two clusters are significantly different in microbial community structure and diversity, further supporting their designation as distinct species. More recently, 24 GBSs from reefs around Singapore were studied for both their relationships within the cryptic species complex and microbiome differentiation (Deignan et al., 2023), with results strikingly similar to those for Caribbean GBSs linking sponge haplotype with microbiome composition.

Among the microbial symbionts of GBSs are host-specific photosynthetic cyanobacteria that impart the variable red-brown colour and that are found at greatest density in surface tissues of the sponge (Fig. 2; Erwin and Thacker, 2007). Although some sponge species are dependent on their photosymbionts for nutrition – particularly Indo-Pacific phototrophic phyllosponges (Abdul Wahab et al., 2021) – this is not the case for GBSs, as they can be found bone-white in dark locations such as caves and deep in the mesophotic zone. In the lab (pers. obs.), the facultative nature of the association between GBSs and cyanobacteria was evident when fist-sized GBSs were kept in dark aquaria and rapidly lost their pigmentation, changing from dark brown to light pink to white over the course of a few weeks. This colour transition can also be seen in a cross-section of the sponge tissue, indicating the limited ability of light to pass through the sponge, although glass spicules may enhance light penetrance. Further evidence of the non-obligatory nature of the symbiosis between cyanobacteria and GBSs are the observed bleaching events that have been described among sponge populations (Fig. 2D), with individuals developing white patches or turning entirely white or gray-white over the course of several weeks, then returning to darker colours thereafter, with this process repeating erratically over time and space (García-Hernández et al., 2021; López-Legentil et al., 2008; McMurray et al., 2011). Unlike coral bleaching, bleaching of GBSs is not associated with sponge mortality, and although there is some evidence that sponge bleaching is correlated with warm seawater temperatures, this does not fully explain the phenomenon (McMurray et al., 2011). Variability in sponge bleaching is likely to be linked to the more recent discovery of cryptic species of GBS with distinct microbial symbiont populations living side-by-side, although testing this hypothesis would require time-series observations of tagged and identified individuals through several years of bleaching events. Although GBSs can grow in the absence of cyanobacterial symbionts, some evidence suggests that sponges can derive nutrition from these microbes (Morrow et al., 2016), expanding the potential nutritional sources that GBSs may rely upon to avoid food limitation. The relative role of cyanobacterial symbionts in the nutritional budget of GBSs is a topic ripe for research and could involve reciprocal transplantation of GBSs (McMurray and Pawlik, 2009) to different light regimens, followed by 3D photogrammetry to track sponge growth (Olinger et al., 2019).

Transfer of carbon and nutrients

As discussed above, GBSs dominate the living biomass of many tropical reefs, and their capacity to pump large volumes of water in a jet-like manner from the reef surface into the water column is unsurpassed. The combination of these factors greatly enhances the impact of GBSs on the cycling of carbon and nutrients from benthic to pelagic habitats as seawater is transformed by the sponge holobiont, particularly for the largest GBSs (Fig. 3). Living and dead particles (microbes, detritus) along with dissolved organic matter (DOM) are processed as they travel through the high surface area of the aquiferous system, with the excurrent jet containing a transformed mixture, primarily of dissolved waste products. In the

Caribbean, *X. muta* has been estimated to overturn a 30-m water column on the fore-reef every 2.3–18 days (McMurray et al., 2014), with carbon flux estimates of 1575 mg C day^{-1} m^{-2} (McMurray et al., 2017). Dissolved organic carbon (DOC) comprises ∼70% of the sponge diet, followed by detritus (∼20%), with living microbes making up only ∼10% of dietary metabolic needs (McMurray et al., 2016). Within the sponge tissue, the relative contributions of microbes and sponge cells to seawater transformation are largely unknown, and most studies approach seawater processing by the sponge holobiont as a ‘black box’, although new isotopic tracer techniques that use nanoscale secondary ion mass spectrometry permit the visualization of seawater constituents at the subcellular level for species such as *Plakortis angulospiculatus* and *Halisarca caerulea* (Hudspith et al., 2021). Here, I consider our current understanding of the changes to the constituents in seawater before and after it passes through the aquiferous system of a GBS.

What’s going into the sponge?

As indicated previously, the size and morphology of GBSs allow for discrete field sampling of seawater before and after sponge processing. In addition to changes owing to respiration, the constituents of ambient seawater that are transformed include DOM and particulate organic matter (POM). These two components can be further subdivided: DOM includes a spectrum of compounds that can be categorized by size (small to large fully dissolved metabolites to colloids), consisting of carbon, oxygen and hydrogen, but also including nitrogen, phosphorus, halides and other elements. Additionally, DOM is categorized on a spectrum of availability to cellular metabolism, from labile (primary metabolites such as sugars and amino acids) to recalcitrant or refractory (e.g. tannins). Although labile DOM is likely to be rapidly consumed by seawater microbes, recalcitrant DOM is not, and it ultimately makes up the largest pool of DOM in seawater (Hedges, 1992). *In situ* field experiments have demonstrated that DOM represents a primary component (>60%) of the diet of GBSs (Hoer et al., 2018; McMurray et al., 2018; Wooster et al., 2019), and that the threshold level of DOM in seawater is ∼80 µmol C l^{-1}, with little or no uptake of DOM by sponge processing below this concentration, likely because all of the labile compounds in the DOM mixture have been removed, leaving only refractory DOM (Wooster et al., 2019). This limitation in DOM uptake has been documented for other sponge species as well (e.g. Ribes et al., 2023). The labile DOM on which most GBSs rely for much of their diet is likely to be spatially and temporally transient and is produced primarily by benthic macroalgae and secondarily by corals and other soft-bodied invertebrates, decomposition processes associated with benthic sediments, and microbial cellular lysis occurring in the water column. As analytical techniques become more sophisticated, much remains to be explored regarding the constituent molecules of DOM that are processed by the GBS holobiont. There is already evidence that GBSs can take up halogenated compounds, some of which may be produced by cyanobacterial mats on the reef (Olinger et al., 2021, 2025). This suggests that GBSs may have the capacity to consume DOM constituents that are less bioavailable to other filter-feeding metazoans or to seawater microbes.

Nutritional studies of GBSs across oceans have done much to address the debate on whether tropical sponges are food-limited (Pawlik et al., 2015). Using identical techniques in the Caribbean (McMurray et al., 2016) and the Red Sea (Wooster et al., 2019), GBSs were found to be food-limited only on highly oligotrophic offshore reefs of the Red Sea, corroborating past studies of sponge communities on reefs of the Caribbean and Australia (Wilkinson and Cheshire, 1990). Further, GBSs on offshore reefs of the Red Sea exhibit greater oxygen demand than onshore or Caribbean GBSs, suggesting that food-limited sponges may increase pumping rates to capture more food particles when DOM concentrations are low (Wooster et al., 2019). Considering feeding and growth together, GBSs have remarkable flexibility to handle food limitation, including selective feeding on particulate versus dissolved resources, facultative reliance on photosymbionts, greater pumping when faced with lower food availability, and reduced or negative growth (McMurray et al., 2008; Wooster et al., 2019).

As GBSs dominate the benthos on many tropical reefs, they also represent the primary sink for silicon in the form of their glass skeletons. GBSs are densely perfused with glass spicules, which make up ∼92 mg ml^{-1} of sponge tissue (Chanas and Pawlik, 1996), despite growing under conditions of chronic silicon limitation. Ambient concentrations of dissolved silicic acid on shallow reefs are estimated at one to two orders of magnitude below levels of maximum efficiency of silicon uptake (López-Acosta et al., 2018). It would be expected that silicon limitation would promote the growth of sponge species without glass spicules over species such as GBSs, but there is no evidence for this, a paradox called the ‘silicon enigma’ (Pawlik and McMurray, 2020). Additionally, there is no evidence that glass spicules play a role in the defense of GBSs against potential predators (Chanas and Pawlik, 1996). The same field techniques used to study the processing of carbon and nitrogen by GBSs could be used to gain insights into their uptake of silicon on reefs in the tropics, as was done for five species of Mediterranean sponges (Morganti et al., 2017).

What is coming out of the sponge?

It has long been known that most of the particles in seawater that pass through the aquiferous system of a sponge are removed, but more recently, the ‘sponge loop hypothesis’ proposed that sponges produce large quantities of shed sponge cells as detritus particles in the excurrent flow (de Goeij et al., 2013). Although detritus production remains a subject of debate for other sponge species, and was originally proposed based on work with encrusting species such as *Halisarca caerulea* and *Chondrilla caribensis*, it has been definitively tested for GBSs. No significant net production of detritus by GBSs has been observed in field studies across a large number of replicate sponges in the Florida Keys, Bahamas and Red Sea (McMurray et al., 2018; Wooster et al., 2019). Using detritus production estimates based on the sponge loop hypothesis (de Goeij et al., 2013), an average-sized GBS would be expected to produce approximately 1800 g of detritus each day (Pawlik and McMurray, 2020), a value that is three orders of magnitude larger than that measured by McMurray et al. (2018).

Detritus aside, analyses of the removal of living microbes and DOM by GBSs and sponge species with similar morphologies and using similar techniques have revealed differences that largely correspond to the abundance of microbial symbionts in their tissues (McMurray et al., 2018). Common Caribbean LMA species such as *Callyspongia plicifera*, *Mycale laxissima* and *Niphates digitalis* do not take up DOM, and have relatively higher specific filtration rates for picophytoplankton, whereas HMA species have relatively lower specific filtration rates for picophytoplankton, but take up DOM to different degrees, with the specific filtration rates of DOM for GBSs similar to those of *Agelas tubulata* and *Ircinia strobilina*, but ∼2- to 5-fold lower than those of *Verongula gigantea* (McMurray et al., 2018).

Beyond the removal of particles and DOM as seawater is processed by sponges, GBSs are important sources of dissolved inorganic nitrogen (DIN) as a product of sponge cellular digestion or microbial transformation. DIN production is likely to be tied primarily to the digestion of particulate organic nitrogen (PON) in the form of picoplankton rather than food sources that have lower C:N ratios (detritus, DOM). Although GBSs are most likely to excrete metabolic waste in the form of ammonium (NH_4^+), large quantities of nitrate and nitrite (NO_x) have also been observed in excurrent flow (Southwell et al., 2008). Ambient NH_4^+ concentrations have been directly correlated with the release of NO_x for other sponge species (Archer et al., 2017), and GBSs have been reported to be both a net source and a net sink of NO_x and NH_4^+ (Fiore et al., 2013; Southwell et al., 2008), which is likely a consequence of the diverse nitrogen metabolic pathways within the microbial community of the sponge holobiont or relative differences in nitrogen content of the food sources available in ambient seawater (McMurray et al., 2016). It has been proposed that the feedback loop of sponges consuming DOM derived from reef macroalgae and producing inorganic nutrients that encourage the growth of macroalgae acts to inhibit the recruitment or growth of hard corals through the occupation of space both by growing sponges and macroalgal populations, a hypothesis called the ‘vicious circle’ (Fig. 3; Pawlik et al., 2016). As GBSs represent the largest sponge biomass on tropical reefs, their impact on this feedback loop is likely to be greatest compared with that of other sponges; indeed, for the sponge community on Conch Reef in the Florida Keys, GBSs represent 73% of the total flux of DIN (Southwell et al., 2008). The largest GBSs are likely to pump inorganic nutrients away from the reef, potentially enhancing the growth of water-column phytoplankton, whereas smaller GBSs are more likely to fertilize macroalgae near the reef surface (Figs 2A, 3).

Chemical defenses against predators

A database search of the scientific literature using ‘*Xestospongia*’ with any of the species names associated with GBSs will return a preponderance of citations describing unusual secondary metabolites from the tissues of these sponges and their effects in various pharmacological bioassays (e.g. Patil et al., 1992). In particular, GBSs contain high concentrations of unusual sterols (e.g. Luu et al., 2024), which, prior to the advent of phylogenetics, were considered to be a potential chemotaxonomic indicator (Fromont et al., 1994; Kerr and Kelly-Borges, 1994). The ecological function of any of these secondary metabolites remains unclear, but it has been suggested that they might act as chemical defenses, particularly against predators (Pawlik, 2011). Caribbean GBSs have been studied to determine whether they are chemically defended against fish predators (Chanas and Pawlik, 1997; Pawlik et al., 1995), with ambiguous results, leading to the designation of *X. muta* as a ‘variably defended’ species (Loh and Pawlik, 2014). This designation needs to be revisited considering new discoveries of cryptic speciation among GBSs to see whether higher levels of chemical defenses are associated with specific GBS haplotypes and their distinct microbiomes (Evans et al., 2021). There is already some evidence that different cryptic species of GBSs have different depth-dependent tissue concentrations of lysophosphatidylcholine lipids (Bayona et al., 2020). However, when defensive chemistry is present, it is associated with more polar constituents in the crude extract of the sponge tissue and not the non-polar sterol fraction (Chanas and Pawlik, 1997).

Despite some evidence for defensive tissue chemistry, GBSs are subject to grazing by fishes and turtles. Casual surveys of GBSs on Caribbean reefs reveal common superficial bite marks from parrotfishes and less frequent deep bites that are likely to be attributable to hawksbill turtles (Fig. 2H; Dunlap and Pawlik, 1998; García-Hernández et al., 2021). Grazing is often highly discriminate, with some GBSs untouched while adjacent individuals appear eroded from excessive grazing. Parrotfish grazing on GBSs on Florida Keys reefs favor specimens that are in a bleached state (Dunlap and Pawlik, 1998), although chemical defense is not linked to the presence of cyanobacteria in the tissue (Chanas and Pawlik, 1997).

The growing abundance of GBSs on tropical reefs, particularly in the Caribbean, may be more of a consequence of release from sponge predation rather than a competitive effect brought on by greater availability of space for recruitment as hard corals have died from increased seawater temperatures and disease. Centuries ago, spongivory by hawksbill turtles was likely to be intense before overfishing drove turtle populations to a tiny fraction of their former number (reviewed in Pawlik et al., 2018). As a consequence of turtle grazing, GBSs on reefs of the past may have had a refuge in the mesophotic zone, just out of reach of their most consequential air-breathing predators.

Mortality from fatal bleaching

Since the 1990s, there have been reports of the bleaching, rapid deterioration and death of individual GBSs in the Florida Keys (Cowart et al., 2006). Unlike non-fatal bleaching, which involves the cyclic loss of cyanobacterial symbionts from sponge tissue (McMurray et al., 2011), fatal bleaching begins as a discolored patch on the exterior surface of the sponge, often (but not always) with a bright orange or pink perimeter surrounding necrotic tissue; hence the term ‘sponge orange band’ (Fig. 2E; Cowart et al., 2006). Fatal bleaching has since been parsed into multiple categories based on appearance (García-Hernández et al., 2021), all of which are likely to be the same condition affecting individual GBSs with different skeletal densities or at different stages of necrosis. Despite considerable study, no agent of disease has been discovered, nor can the condition be passed by transfection, indicating that the initiation of necrosis is not caused by a pathogenic virus or microbial agent (Angermeier et al., 2011). Outbreaks of fatal bleaching have been described from the Florida Keys in 2005 (Cowart et al., 2006), from the Gulf of Thailand in 2015–2016 (Mueller et al., 2023) and from Puerto Rico in 2019 (García-Hernández et al., 2021). For some sponges, the necrotic progression ceases, and the dead skeleton falls away, leaving a gap in the sponge wall that is repaired over several months (Fig. 2F), with no subsequent visible evidence of the former condition.

It is likely that fatal bleaching is not a disease caused by specific pathogens, but rather develops when a GBS, affected by some environmental stressor, stops pumping long enough for some portion of sponge tissue to become anoxic, the normal microbiome is disrupted, and necrosis begins and spreads across the sponge. In support of this hypothesis, pumping cessation by GBSs for as long as 230 min has been observed (McMurray et al., 2014). Further, fatal bleaching usually affects only a low percentage of GBSs on a reef (García-Hernández et al., 2021) and seems to target larger sponges with thicker walls that may be more prone to anoxic tissue development. Despite dire reports, fatal bleaching does not seem to be greatly affecting GBS populations. In the Florida Keys, where individual GBSs were monitored for over a decade, GBS populations increased by 122% on Conch Reef and 44% on Pickles Reef despite regular observations of fatal bleaching throughout the monitoring period and an outbreak in 2005 (McMurray et al., 2015). However, there are clearly limits to the ability of GBSs to survive environmental stressors, as illustrated by the localized mortality event from an unknown cause (possibly a harmful algal bloom) documented in 2015–2016 in the lower Gulf of Thailand (Mueller et al., 2023). In this instance, the loss of 80–98% of GBSs in shallow water (4–6 m) was specific to more onshore reefs, with no impact on GBSs ∼30 km away. Long-term time-series studies of GBS populations would be helpful in explaining the causes of fatal bleaching, particularly if *in situ* electronic sensors are used to record environmental conditions and changes in sponge pumping.

Will GBSs dominate tropical reefs of the future?

There is little question that tropical reefs are transitioning from benthic dominance by hard corals to dominance by other taxa, including seaweeds, octocorals and sponges (Edmunds, 2024a; Mumby and Steneck, 2018; Pawlik et al., 2016). It has been proposed that coral reefs will transition to sponge reefs, assuming that sponges are less affected by the stressors killing reef-building corals (Bell et al., 2013). This transition may be difficult to measure because of the lack of long-term or broad-scale benthic monitoring studies of tropical reefs (Edmunds, 2024b). Survey and time-series studies of coral reef benthos, mostly done in the Caribbean, have been focused on hard corals and algae, with sponges often listed among 'other invertebrates'. The few long-term studies that have included or focused on sponge populations have ceased providing updates or are no longer funded. Nevertheless, data from these studies suggest that sponge abundance is increasing (de Bakker et al., 2017; McMurray et al., 2015). For GBSs on reefs of the Florida Keys, McMurray et al. (2015) tracked more than 1500 individual GBSs over 12 years (ending 2012) at three depths (15, 20 and 30 m), and found that sponge density increased by 122% and biomass increased by 39% over this period, with accelerating population growth. Further, a careful analysis of GBS distribution as a function of size revealed no negative density dependence in survivorship, indicating that further population growth is not inhibited by increasing numbers of GBSs (Deignan and Pawlik, 2015).

As tropical reefs transition away from coral dominance, sponges may play an increasing role in the provision of habitat for fishes and invertebrates that previously relied on corals (Coppock et al., 2024). It has long been known that sponges serve as facultative and obligate habitat for many invertebrates (e.g. Henkel and Pawlik, 2011; Pawlik, 1983) and fishes (Rocha et al., 2000), but the large size of GBSs affords a level of habitat complexity upon which large fishes (e.g. grunts, snappers) and invertebrates (lobsters) can rely. Although GBSs do not contribute to reef growth through limestone deposition, they provide complex habitat and effectively cover the reef on which they grow, preventing erosion of their holdfast area by grazers and sponge and invertebrate borers.

Anecdotal information suggests that GBSs may be more resilient to high seawater temperature events than reef-building corals. For example, the Caribbean experienced an unprecedented El Niño–Southern Oscillation-driven heatwave during the summer of 2023 (Reimer et al., 2024), with sea surface temperatures in the Florida Keys exceeding 30°C for several weeks. Coral restoration sites on Looe Key reef experienced near 100% mortality of corals on both shallow and deep-water reefs. The author surveyed Looe Key reef in March and December 2024 and observed a very high density of healthy GBSs, mostly 25–50 cm in height, at 20–30 m depth growing on dead coral colonies (Fig. 4). There were also a surprising number of similarly sized, healthy GBSs on very shallow spur and groove reef at only 5 m depth, also surrounded by dead coral skeletons.

There is evidence that GBS populations are adapting to the rapid anthropogenic changes affecting Caribbean reefs. Using time-series survey sites in the Florida Keys in which each GBS individual was monitored over 12 years, Deignan et al. (2018) investigated the genetic structuring of the population over time and determined that there were two distinct GBS populations, genetic clusters 1 and 2 (as discussed above). Interestingly, virtually all of the recent recruitment had taken place among cluster 2 sponges, which were

Fig. 4. A GBS-dominated tropical reef. Looe Key reef, 20 m depth, Florida Keys, 6 December 2024. GBSs cover skeletons of hard corals killed by warm-water events, most recently the unprecedented high temperatures of summer 2023. GBSs shown here are in the same size class as the rapidly recruiting genetic cluster 2 sponges that are known to be taking over the GBS population on nearby Conch Reef, Florida Keys (Deignan et al., 2018). Photo credit: J. R. Pawlik.

also absent among the very largest individuals in the population (Deignan et al., 2018). This was striking, because larger sponges should have greater fecundity, but the smaller, cluster 2 sponges were rapidly taking over the reef. Subsequent research confirmed this population divergence and determined that clusters 1 and 2 are the two most divergent cryptic species haplotypes among GBSs across the global network of GBS cryptic diversity (Evans et al., 2021). Most of the microbial community dissimilarity between the two clusters is due to variation among a relatively small number of OTUs, raising the possibility that these lineage-specific symbiont differences may be tied to the rapid population rise of GBSs in cluster 2. These results suggest that ancient lineages of morphologically indistinguishable GBSs and their symbionts are responding to environmental changes over sub-decadal time periods to rapidly populate reefs stripped of coral cover by climate change. Future tropical reefs are therefore likely to be dominated by smaller size classes of GBSs, with larger and older individuals restricted to the refuges of oceanic and mesophotic reefs. This prediction is already evident with the loss of large size-class sponges in the Florida Keys from storm-induced sedimentation from Florida Bay and high seawater temperatures followed by fatal bleaching, while larger sponges persist on better insulated offshore reefs in the Bahamas (Fig. 2B).

Conclusions and future directions

Tropical reef ecosystems have been rapidly transitioning to an alternative state under the influence of anthropogenic climate change. To date, GBSs appear to be resilient to these changes, with some evidence of selective recruitment of genotypes that are better adapted to the altered environment. Considering recent discoveries of cryptic diversity among GBSs, future studies will require monitoring and sampling populations of individually tagged GBSs over time to answer basic questions about these ecosystem engineers as they become more dominant on tropical reefs. As mentioned previously, some of the questions that these time-series studies could answer include whether: (1) GBSs are dioecious or sequential hermaphrodites, (2) timing of spawning is responsible for maintaining cryptic species boundaries, (3) there is variation in pumping and feeding across cryptic species, (4) there is variation in growth across cryptic species with the goal of developing better growth models, (5) variation in sponge chemical defenses is attributable to sponge haplotype or microbiome, and (6) variation in non-fatal (cyclic) bleaching is attributable to sponge haplotype or microbiome. Additionally, ongoing advances in analytical techniques can be brought to bear on identifying the constituents of DOM and POM that are used by GBSs as food and identifying the waste products that are exported to the water column (for large GBSs) or back to the reef (for small GBSs). Clearly, much remains to be discovered about the role of GBSs on tropical reefs as these ecosystems undergo fundamental transformations in the years ahead.

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