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Sponges structure water-column characteristics in shallow tropical coastal ecosystems

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ABSTRACT: Sponges can have powerful effects on ecosystem processes in shallow tropical marine ecosystems. They drive benthic–pelagic coupling by filtering dissolved and particulate organic matter from the water column, alter water chemistry in association with their symbiotic microorganisms, and increase habitat structural complexity. Anthropogenic degradation of coastal waters is widespread and can reduce the density and diversity of foundation species such as sponges, potentially diminishing their contributions to ecosystem processes. We used a novel mesocosm design that minimized artifacts associated with traditional single-species and closed-system filtration experiments to examine the effects of water turnover and sponge biomass on water-column properties. Using a 3-factor, fully-crossed design, we manipulated water turnover and the biomass of 10 sponge species common in Florida Bay, Florida (USA), and measured the effects of their feeding on concentrations of nutrients (nitrogen, carbon, and phosphorus) and plankton (measured as chl *a* and bacterioplankton). High sponge biomass and low water turnover greatly reduced chl *a,* ammonium, and dissolved organic carbon (DOC) in the water and increased concentrations of nitrites, nitrates, and phosphates. Sponge species identity had idiosyncratic effects on water-column constituents, especially with respect to the influence of sponges on chl *a*, DOC, and ammonium. This study demonstrates the importance of sponge biomass and species-specific filtration on nutrient cycling and highlights how changes in the abundance and diversity of sponges in coastal ecosystems can drastically alter water-column properties.

KEY WORDS: Community · Density · Ecosystem function · Florida Bay · Sponge · Flow regime

1. INTRODUCTION

In many coastal ecosystems, benthic suspension feeders control the rates of biogeochemical cycling and the strength of benthic–pelagic coupling via removal of dissolved and particulate organic matter (DOM and POM) (Gili & Coma 1998, Petersen 2004, Jiménez & Ribes 2007). These influential suspension feeders (e.g. bivalves, ascidians, bryozoans, polychaetes, cnidarians, echinoderms, and sponges) also alter turbidity, oxygen concentration, and sedimentation levels in a wide range of ecosystems, from tropical waters to Antarctica (Grebmeier & Barry 1991, Barnes & Clarke 1995, Orejas et al. 2000, Jonsson et al. 2005). When sufficiently dense, aggregations of suspension feeders exert strong top-down control of pelagic plankton communities and sometimes experience density-dependent regulation (i.e. competition) due to depletion of limiting water-column resources (Hily 1991, Newell 2004, Dame & Olenin 2005, Wulff 2017).

Sponges are important filter feeders in many marine ecosystems (Riisgård & Larsen 2010), but until recently there have been few studies of density-dependent and species-specific effects of sponge communities on water-column filtration (Reiswig 1974). Contemporary studies of sponge feeding show that they can have stronger effects on nutrient processes than bivalves, especially in shallow subtropical and tropical ecosystems (Lesser 2006, Bell 2008,

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Alexander et al. 2014, McMurray et al. 2014, Easson et al. 2015). Sponges consume a diverse array of suspended picoplankton including bacteria and viruses in sizes ranging mainly from 0.5 to 50 µm, and their filtration efficiencies (i.e. particle removal) typically exceed 75% (Reiswig 1971, Pile et al. 1997, Ribes et al. 1999, Hadas et al. 2009). Where abundant, sponges form an important benthic–pelagic link (Diaz & Ward 1997) by altering organic and inorganic matter acquired from the water column into forms (i.e. chemical states, organic particles) that are used by other benthic organisms (Diaz & Rützler 2001, Webster & Taylor 2012, de Goeij et al. 2013).

Much of the nutrient conversion efficiency of sponges is attributable to their multifaceted relationships with symbiotic bacteria, archaea, and some eukaryotes (fungi and microalgae) living within the interstices of their tissues (Weisz et al. 2007, Webster & Taylor 2012, Thomas et al. 2016). For this reason, sponges have been categorized into one of 2 broad functional groups based on their microbial communities. The bacteriosponges (Reiswig 1981) harbor diverse and abundant microbial communities and are referred to as high microbial abundance (HMA) sponges (Hentschel et al. 2003). HMA sponges often have dense tissues that contain large anaerobic areas and microbial biomass that can comprise up to 40% of their volume (Webster & Taylor 2012). They also have low pumping/clearance rates, cycle dissolved organic carbon (DOC), and fix nitrogen; thus, most of their energetic requirements are hypothesized to be provided by symbiotic microbial constituents (Taylor et al. 2007, Weisz et al. 2007). In contrast, low microbial abundance (LMA) sponges (Hentschel et al. 2003) harbor comparatively depauperate microbial communities and are thought to rely on the filtration of POM from the water column to meet their nutritional needs (Reiswig 1974). However, recent studies (Morganti et al. 2017, Rix et al. 2017) have shown that some LMA sponges also feed on DOM. Because of the unique, species-specific differences in microbial community composition among sponge species (Lee et al. 2011), the effect of each species on water-column parameters is likely to be idiosyncratic and environmentally dependent.

To date, studies of the effects of sponges and their associated symbionts on nutrient cycling have relied on the use of either incubator-based or *in situ* measurements on individual sponges. Incubator-based measurements may overestimate nutrient cycling and particle filtration (e.g. Pile et al. 2003, Jiménez & Ribes 2007) if sponges filter the same water repeatedly. Alternatively, if oxygen and nutrient availability decline and wastes build up unnaturally within the incubator, then sponge filtration is likely to be suppressed (Hadas et al. 2009, Maldonado et al. 2012). *In situ* measurements of changes in water-column constituents are made by comparing water entering and leaving the incurrent and excurrent canals of a sponge (Yahel et al. 2003, Maldonado et al. 2012); these provide a more natural approximation of a sponge's effect on the water column. But such results are based on single-specimen measurements and are usually short in duration. Thus, they do not capture variability in feeding rates and cannot be easily manipulated to measure the effects of intra- or interspecific competition (Patterson et al. 1997). Moreover, the possible synergistic or inhibitory effects of multiple individuals or species on filtration cannot be ascertained from single individual experiments, whether measured in incubators or *in situ*. These experimental drawbacks limit the extrapolation of filtration to community or ecosystem scales or to estimates of the effect of changes in filter feeder abundance or diversity due to natural or anthropogenic perturbation. Although some investigators have scaled up measurements made on individuals to communities based on total sponge biomass (see McMurray et al. 2014, 2017), this does not account for potential interactions and emergent effects among individuals in sponge communities. Most studies of sponge filtration have also been conducted on coral reefs or rocky bottoms in water that is several to tens of meters deep, but extrapolating the effects of sponge filtration on water-column characteristics in those environments is likely to underestimate their effects in shallow water habitats, where sponges filter a larger fraction of the water column.

In the shallow waters surrounding the Florida Keys, Florida (USA), including portions of Florida Bay, sponge communities are threatened by the persistent effects of a multitude of stressors including recurrent cyanobacteria blooms, highly variable temperature and salinity regimes, and, to a much lesser extent, commercial sponge fishing (Cropper & DiResta 1999, Stevely et al. 2011, Kearney et al. 2015, Butler et al. 2017). Repeated cyanobacteria blooms, first documented in 1991 (Butler et al. 1995, Boyer et al. 1999), have had the most dramatic impact on sponge communities. Each has triggered sponge die-offs over large areas (up to 500 km^2) in south-central Florida Bay, where sponge densities and diversity have been reduced by 90% or more (Herrnkind et al. 1997, Torres et al. 2006, Stevely et al. 2011). The large-scale losses of sponges are

thought to have dramatic consequences for water-column geochemistry and plankton community composition (Lynch & Phlips 2000, Peterson et al. 2006, Weisz et al. 2007), but those conclusions are based on experiments that did not take into account intra- and interspecies interactions that may occur in dense sponge communities.

The aim of our study was to determine potential effects of the loss of sponge biomass and species composition on the structure of planktonic communities and nutrient cycling in the shallow water Florida Keys ecosystem. To do so, we conducted experiments in flow-through mesocosms uniquely designed to quantify the effects of changes in sponge community biomass and species identity on water-column properties at ecologically relevant water velocities.

2. MATERIALS AND METHODS

2.1. Origin and preparation of sponges

To assess the effects of species-specific sponge loss on water-column constituents and nutrient concentration, we conducted a series of experiments in custom-made flow-through mesocosms using 10 species of sponges common in Florida Bay and representing both major functional groups (mostly HMA and some LMA) (see Table 2) (Weisz et al. 2008, Hardoim et al. 2009, Gloeckner et al. 2014). Some species have not been categorized as HMA or LMA sponges, so we assumed classifications based on other species within the same genus. To procure the large numbers of sponges needed to conduct these experiments, individual sponges of each species were collected from the seafloor and cut into multiple smaller pieces (~300 cm^3). Sufficient tissue (~2 cm thick) from each individual source sponge was left attached to the seafloor to facilitate regrowth (Stevely 1985). The experimental sponge cuttings were then attached with plastic cable ties to individually tagged concrete brick baseplates and returned to the seafloor for a few months to heal, adhere to the baseplate, and grow. An equivalent number of brick baseplates without sponges were placed for an equivalent period of time on the seafloor for use as experimental controls to account for the potential effects of fouling microorganisms on the bricks used to anchor sponges.

2.2. Mesocosms

We constructed 6 flow-through rectangular mesocosms (fiberglass tanks; 25 cm high × 30 cm wide × 2.4 m long) for use in our experiments on Long Key, FL (USA) (Fig. 1). The mesocosms were set up outdoors under a 50% shade cloth canopy. A flume-like design was employed instead of round tanks (Maldonado et al. 2012) to reduce water recirculation during our experiments, thus minimizing the confounding effects of water refiltering by sponges. This design enabled us to standardize flow rate and ensure that possible changes in water quality due to the presence of other organisms (e.g. algae, sediment microbial community) were minimized. We were not attempting to achieve laminar flow in the mesocosms, merely the unidirectional movement of seawater to mimic the natural, tidally driven flow of seawater through a stand of sponges on the seafloor. Unfiltered seawater drawn from Florida Bay (2 m depth) by a 1.5 hp pump was introduced at one end of each mesocosm through three 5 cm diameter pipes that were equipped with valves to adjust flow. The water delivery system was new and custom built for this experiment, so the chemical and biological constituents of the water entering the mesocosms were probably minimally impacted by fouling organisms in the piping system. A honeycomb-like baffle (7.5 cm long pieces of 1.3 cm diameter PVC stacked to the water surface) was installed in each mesocosm

Table 1. Estimated rates of water flow through mesocosms and filtered by sponges at each treatment level based on filtration rates of *Spheciospongia vesparium*. Sponge volume is the estimated liters of sponge per high and low biomass treatments. Mesocosm turnover is the estimated time for mesocosm water volume (180 l) to be completely cycled without sponges present. Sponge turnover is the estimated time sponges would need to turn over the water in the mesocosm with no input of water based on reported sponge filtration rates of 0.09 l s^{-1} l^{-1} sponge biovolume (Wall et al. 2012). Estimated treatment turnover is the projected length of time it would take sponges to clear a mesocosm of water during the experiment; it represents the combined time of sponge turnover of the water column based on treatment volume and tank turnover without sponges. The negative value of the low biomass, high flow treatment indicates that sponges are never able to completely process the mesocosms' water volume

Biomass and flow regime	Sponge volume (l)	Mesocosm turnover (l min^{-1})	Sponge turnover (l min^{-1})	Estimated treatment turnover (min)
High biomass, low flow	6.408	4	34.60	5.88
Low biomass, low flow	2.136	4	11.53	23.89
High biomass, high flow	6.408	16	34.60	9.67
Low biomass, high flow	2.136	16	11.53	–40.32

15 cm from the supply pipes to more evenly disperse the water through the 1.8 m long × 0.3 m wide working area in each mesocosm. A weir was installed at the opposite end of the mesocosm at a 70° angle relative to the bottom to prevent water from striking the rear wall and rebounding through the working area of the mesocosm. Seawater drained behind the weir into a reservoir through two 5 cm drain lines, where a hand-operated valve was used to collect samples from the seawater effluent. Water was not recirculated after passing through the mesocosm. After each trial, the walls of the mesocosms were cleaned of fouling organisms, and seawater was allowed to flow through each mesocosm for at least 12 h without sponges present. To reduce the buildup of fouling organisms in the intake pipes, the system was intermittently drained and left empty.

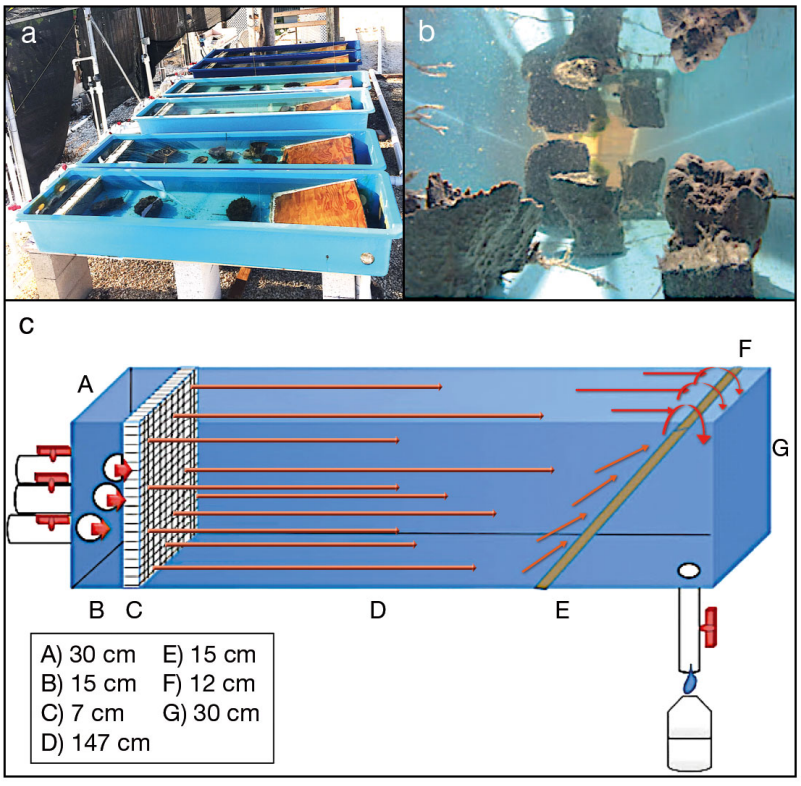

Fig. 1. (a) Six mesocosm flume tanks in operation, (b) underwater view of sponge cuttings within a mesocosm flume tank, and (c) diagram of a mesocosm flume tank showing water movement (depicted by red arrows). Raw seawater enters the mesocosm at left, passes through a baffle to reduce turbulence, flows through the working section of the mesocosm, and then spills over a weir (which reduces backflow) into the drain section, where a subsample of the water is collected in a flask for analysis. The dimensions at various locations around the mesocosm are listed by letters at the bottom left of the diagram

2.3. Experimental treatments

A 3-factor, fully crossed design was used to test for the effects of differences in sponge biomass (high biomass, low biomass, and a sponge-free control), sponge species identity (one of 10 species plus 1 sponge-free control), and flow regime (high, low turnover). This design resulted in a total of 44 treatments, each of which was replicated 7 times.

The sponge biomass levels and the identity of species selected for use in our experiments were based on sponge surveys conducted at sites located throughout the Florida Keys (Butler et al. 2015). Estimates of the volume of individual species derived from those 100 m^2 surveys were scaled to the size of the mesocosms, so that the high and low sponge biomass treatment levels used in our experiments represented the upper and lower quartiles (i.e. 25 and 75%) of the estimated natural sponge biomass in an equivalent water volume. Natural biomass was calculated as the average volumes of sponges (based on height and diameter) based on length, width, and depth of the survey area. Based on these calculations, natural sponge volumes were on average 14 337 cm^3 at 25% and 43 012 cm^3 at 75%. These estimates were scaled to the mesocosm volume, so that experimental sponge volumes were 2136 and 6408 cm^3 in the low and high biomass treatments, respectively. Using this approach, the biomass of each experimental replicate was equivalent in each treatment. Sponge biomass in the 2 treatments was standardized using total volume displacement of all sponges in the mesocosm to control for differences in sizes and shapes of the sponge species selected for use in these trials. To estimate biomass by volume displacement, experimental sponges (attached to brick bases) were submerged in buckets, and the displaced water was measured using a graduated cylinder. To compensate for water displaced by the bricks to which sponges were attached, the volume of control bricks was measured and subtracted from the volume measured for the sponge plus brick replicates. To achieve the treatment biomass, and because the dis-

placement volumes varied greatly among the sponge species, sponge density varied across the treatments.

Flow regimes in our experiments mimicked the range of flows observed during typical tidal changes in Florida Bay (Wang et al. 1994). To better estimate common velocities in nearshore Florida Bay hard-bottom areas, we made a series of vertical velocity profiles at 8 hard-bottom sites (2 to 3 m deep) during spring tides using a WaterMark USGS current meter (Model 6205). Based on those field measurements, mean velocity in the center of the mesocosms was set at 3 cm s^{-1} in the low flow regime treatment and 12 cm s^{-1} in the high flow regime treatment. Water turnover rate through the flume tanks (approximate volume 180 l) without sponges present averaged 4 l min^{-1} (45 min) in the low flow treatments and 16 l min^{-1} (11 min) in the high flow treatments. When sponges are present and there is no replenishment, high biomass treatments can turn over the mesocosm volume at a rate of 34.6 l min^{-1} and low biomass treatments at 11.53 l min^{-1}. The turnover presence of sponges in the 4 treatments (high biomass, low flow [HBLF]; low biomass, low flow [LBLF]; high biomass, high flow [HBHF]; low biomass, high flow [LBHF]) is projected to be 5.88, 23.89, 9.67, and −40.32 min, respectively. In the LBHF treatment, water replenishment exceeded the rate of sponge filtration. The velocity slowed near the walls of the mesocosms; thus, sponges were placed no closer than 5 cm from the sides of each mesocosm and were raised ~5 cm from the bottom because of their attachment to brick baseplates.

The high flow regime reduced the residence time of water in the mesocosm, which presumably increased the supply of POM, DOM, and nutrients to sponges and reduced the recycling of water by sponges as it would in nature. Although our mesocosm design reduced the amount of water reprocessed by sponges, differences in sponge biomass in the treatments and filtration rates among species means that some refiltration may have occurred, particularly in the low flow regime treatment. Based on estimates of filtration by *Spheciospongia vesparium* (0.09 l s^{-1} l^{-1} sponge biovolume; Wall et al. 2012), we estimated the possible refiltration of water within mesocosms for each of our treatment groups (Table 1). These estimates are likely to represent an upper bound because *S. vesparium* filters water at a higher rate than is suspected for most of the other species tested. In our HBLF treatment, we estimate that sponges may have filtered the water in the mesocosm at approximately 8 times the rate of replenishment. In the LBLF treatment, they perhaps could have filtered the water twice as fast as it was replenished in the mesocosm. However, in our high flow treatments, we estimate that at high biomass, sponges could possibly filter the water in the mesocosm about twice the rate of its replenishment but less than once in the low biomass treatment.

2.4. Preliminary trials

Preliminary trials were conducted in February to April 2015, using *S. vesparium* and *Ircinia campana* in all combinations of high and low biomass and flow regime to determine the appropriate acclimation period and sampling interval for our experiments. To determine the time needed for sponges to begin filtering, fluorescein dye was injected into the water near the incurrent canals of representative sponges on an hourly basis. We observed that all of the sponge species began filtering within an hour of their placement into the mesocosms.

During preliminary trials, water was collected at the mesocosm outlets at 4 h intervals over 3 consecutive days and the concentrations of nitrite + nitrate (NO_2^- + NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}) analyzed to determine if sponge effects on water chemistry were consistent over time or affected by diel cycles (Patterson et al. 1997). Those results revealed that the most distinct filtration effects occurred during mid-afternoon; minimal differences from controls were detected at night and in the morning. Based on these preliminary results, we used an acclimation period of 24 h and collected water from experimental treatments at 14:00 h. We would have preferred to sample water periodically throughout each experimental trial, but such an approach was cost prohibitive given the large number of treatment combinations and replicates.

2.5. Experimental design

To initiate an experiment, sponge cuttings (Fig. 1) were haphazardly selected from those established earlier and left on the seafloor to grow. Any flora or fauna (e.g. algae or other encrusting sponges) attached to the sponges or to the brick baseplate (including control bricks without sponges) were removed underwater and the sponges then placed in aerated, seawater-filled coolers for transport (~1 h) to the mesocosm facility. Treatments were randomly assigned to each mesocosm before trials began. Sponges were placed in the mesocosms and allowed

to acclimate for 24 h at the determined treatment flow regime. We had 6 mesocosms, so we ran 4 experimental treatments and 2 controls (i.e. seasoned bricks placed in the mesocosms, at high and low flow regimes) simultaneously. Trials were not conducted if rain occurred during the 24 h period preceding trials, or if winds exceeded 30 kph, to minimize the effects of freshwater runoff and wind mixing of sediments on seawater chemistry. After each 24 h trial, 2 l of seawater was collected from the outlet of each mesocosm. At the conclusion of each trial, sponges were returned to their original locations on the seafloor and were not used again for a period of at least 3 wk; over 3000 separate sponge cuttings were used in this experiment.

2.6. Nutrient analysis and plankton counts

All glassware used in this study was acid washed, rinsed with deionized water, and sterilized in a muffle furnace prior to use. Each sample container was rinsed with treatment seawater 3 times before aliquots were collected from the mesocosms. Water collected for nutrient and DOC analysis was filtered through a 0.7 µm GF/F filter and stored at −30°C for no longer than 2 mo before processing. Treatment effects on NO_2^- + NO_3^-, NH_4^+, and total PO_4^{3-} concentrations were documented using a SAN^{++} automated wet chemistry analyzer. For chlorophyll analysis, filters were extracted using 10 ml of acetone for 24 h and then processed using a TD-700 fluorometer (Turner Designs). DOC samples were processed using a Shimadzu total organic carbon analyzer (TOC-V). The instrument was calibrated after each run of 30 samples over 200 runs, standardized from a 1000 ppm standard of potassium biphthalate. The accuracy of each run varied between 0.08 and 0.2 ppm (checked for drift every 5 samples), and individual samples were repeatedly tested until a coefficient of variation (CV) of <2% was reached.

Samples from treatments containing the sponges *S. vesparium, I. campana, Ircinia* sp., *Cinachyrella alloclada,* and *Tectitethya crypta* were selected to assess the extent to which bacteria were removed from the water column by each separate sponge species. To quantify treatment effects on bacterial cells in the water column (Shibata et al. 2006), 10 ml of water was collected from each mesocosm water sample and fixed with 1 ml of filtered formalin (37% formaldehyde). For bacterial analysis, fixed water was filtered onto Whatman™ black Nuclepore filters, and filters were mounted and stained using Vectashield DAPI stain with mounting medium. Slides were sealed with clear nail polish and frozen at −80°C for storage. All slides were analyzed within 1 mo of fixation to minimize sample degradation. We used an epifluorescent microscope and 377 nm cube to count the presence of bacteria; 25 images were haphazardly taken from each prepared slide for bacterial enumeration (Patel et al. 2007).

2.7. Statistical analysis

To test for treatment effects on the multiple dependent variables measured in this study, we used a 3-factor MANOVA using the factors sponge species identity, sponge biomass, and flow regime; the response variables tested were bacterioplankton, DOC, PO_4^{3-}, NO_2^- + NO_3^-, NH_4^+, and chl *a*. Because of the number of treatments and replicates in the study, trials were conducted across multiple months; thus, daily fluctuations in the concentrations of dependent variables were normalized by subtracting dependent variable concentrations from the corresponding daily values in control mesocosms. Therefore, water-column constituent values used in these analyses are based on the differences in water-column parameters measured concurrently in the outflows from control mesocosms and the mesocosms containing sponge treatments. The MANOVA assumptions of normality, homogeneity of variances, and collinearity were tested, and the data were rank transformed because the MANOVA assumption of non-collinearity was not met. An additional MANOVA was performed to test the differences between HMA and LMA sponges for each treatment group. For this, 8 levels were created representing the 4 treatment groups classified as HMA and 4 treatments classified as LMA. An ANCOVA was also performed using control mesocosm water constituent values as covariates to determine the relative effect of ambient conditions on changes to nutrient concentrations attributable to sponge filtration in the 4 treatments (i.e. high and low sponge biomass × high and low water turnover).

When treatment effects were significant ($p < 0.05$), post hoc Tukey's tests were used to examine differences among species and microbial associations (HMA, LMA) across 4 sponge biomass/water turnover treatments: HBHF, HBLF, LBHF, and LBLF. A Bonferroni correction of significant p-values was made to control for experiment-wise error when testing for each response variable, so only Tukey's test p-values < 0.008 were considered significant. Effect sizes and least significant differences (error

bars) were also plotted to inspect for significant relationships among treatments (Williams & Abdi 2010, Hector 2015). To assess whether sponge filtration rates depended on ambient concentrations of water-column constituents, we performed a linear regression analysis for each species and treatment group and separate linear regression analyses for all species and treatments combined (McMurray et al. 2017). All statistical analyses were conducted using SPSS (V.22).

3. RESULTS

The results of the MANOVA conducted on the main effects (species identity, biomass, and water turnover) showed that all treatments significantly ($p < 0.008$) affected the concentrations of water-column constituents with the exception of turnover effects on $NO_2^- + NO_3^-$ ($p = 0.249$) and DOC ($p = 0.148$) and biomass on $NO_2^- + NO_3^-$ ($p = 0.011$) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m608p133_supp.pdf). In general, regardless of sponge species or biomass, concentrations of chl *a*, NH_4^+, DOC, and bacterioplankton were lower (Figs. S1 & S2), whereas $NO_2^- + NO_3^-$ and PO_4^{3-} (Fig. S3) concentrations were higher in mesocosms with sponges relative to control mesocosms. The strength of these effects, however, was heavily dependent on species identity (Table S1, Fig. 2) and a particular response variable. When comparisons of sponge effects were based on functional classification (HMA or LMA), clear differences were detected between the treatments (Fig. 3). HMA sponges removed relatively greater concentrations of chl *a*, NH_4^+, and DOC, whereas LMA sponges produced relatively greater concentrations of $NO_2^- + NO_3^-$ and PO_4^{3-}.

All species effects were pooled to estimate the cumulative effect of a natural multispecies situation, and pairwise comparisons showed the interaction of biomass and water turnover significantly increased the change in concentrations of PO_4^{3-} ($p < 0.008$), $NO_2^- + NO_3^-$ ($p < 0.008$), NH_4^+ ($p < 0.008$), DOC ($p < 0.008$), and chl *a* ($p = 0.003$) (Table S1, Fig. 4). High sponge biomass had a significant positive effect on PO_4^{3-} ($p < 0.008$) but not on $NO_2^- + NO_3^-$ ($p = 0.011$) and a significant negative effect on the concentrations of chl *a* ($p < 0.008$), NH_4^+ ($p < 0.008$), and DOC ($p < 0.008$). The magnitude of each response was generally greater in the low turnover regime treatment than in the high turnover regime treatment. The linear regression analyses showed that there is a positive relationship between ambient water quality conditions and sponge effects on those response variables (Table S2, Fig. 5). The greater the concentration of a nutrient in the control, the greater the change in the response variable.

3.1. Chl *a*

We observed a mean decrease in the concentration of chl *a* across all species and treatments of 0.23 ± 0.01 µg l^{-1} (mean ± SE), an approximately 41% decrease from the control treatments (Table 2). In the HBHF treatment, the mean decrease was 0.21 ± 0.01 µg l^{-1}, in the HBLF treatment it was 0.28 ± 0.02 µg l^{-1}, in the LBHF treatment it was 0.17 ± 0.01 µg l^{-1}, and in the LBLF treatment it was 0.25 ± 0.01 µg l^{-1}. Pairwise comparisons showed that the decrease of chl *a* was significantly greater ($p < 0.008$) in the HBLF treatment than in any of the other treatments, whereas the smallest decrease was documented in the LBHF treatment. HMA sponges decreased chl *a* concentration about 0.26 ± 0.01 µg l^{-1} and LMA sponges about 0.20 ± 0.01 µg l^{-1}, a statistically significant difference ($p < 0.008$). All LMA sponges were statistically similar in their effects on chl *a*; *Hippospongia lachne* had the greatest ($p < 0.008$) effect on chl *a*, and *Ircinia campana, Niphates erecta, Spheciospongia vesparium, and Cinachyrella alloclada* had the least.

3.2. Ammonium

The mean decrease of NH_4^+ across all species and treatments was 1.82 ± 0.07 µM, a value approximately 51% lower than that measured in the controls. In the HBHF treatment, the mean decrease was 1.54 ± 0.12 µM, in the HBLF treatment it was 2.73 ± 0.23 µM, in the LBHF treatment it was 1.34 ± 0.06 µM, and in the LBLF treatment it was 1.75 ± 0.08 µM. Pairwise comparisons showed that the decrease of NH_4^+ was significantly greater in the HBLF treatment than in any of the other treatments ($p < 0.008$). No other significant differences among the remaining treatments were detected. The mean decrease of NH_4^+ across HMA sponges was 2.48 ± 0.12 µM as compared to 1.23 ± 0.05 µM in LMA sponges. HMA sponges had a significantly greater effect on NH_4^+ decrease than LMA sponges ($p < 0.008$). Of the 10 sponges tested in this study, *H. lachne* had the greatest ($p < 0.008$) effect on NH_4^+ decrease and *N. erecta* the least.

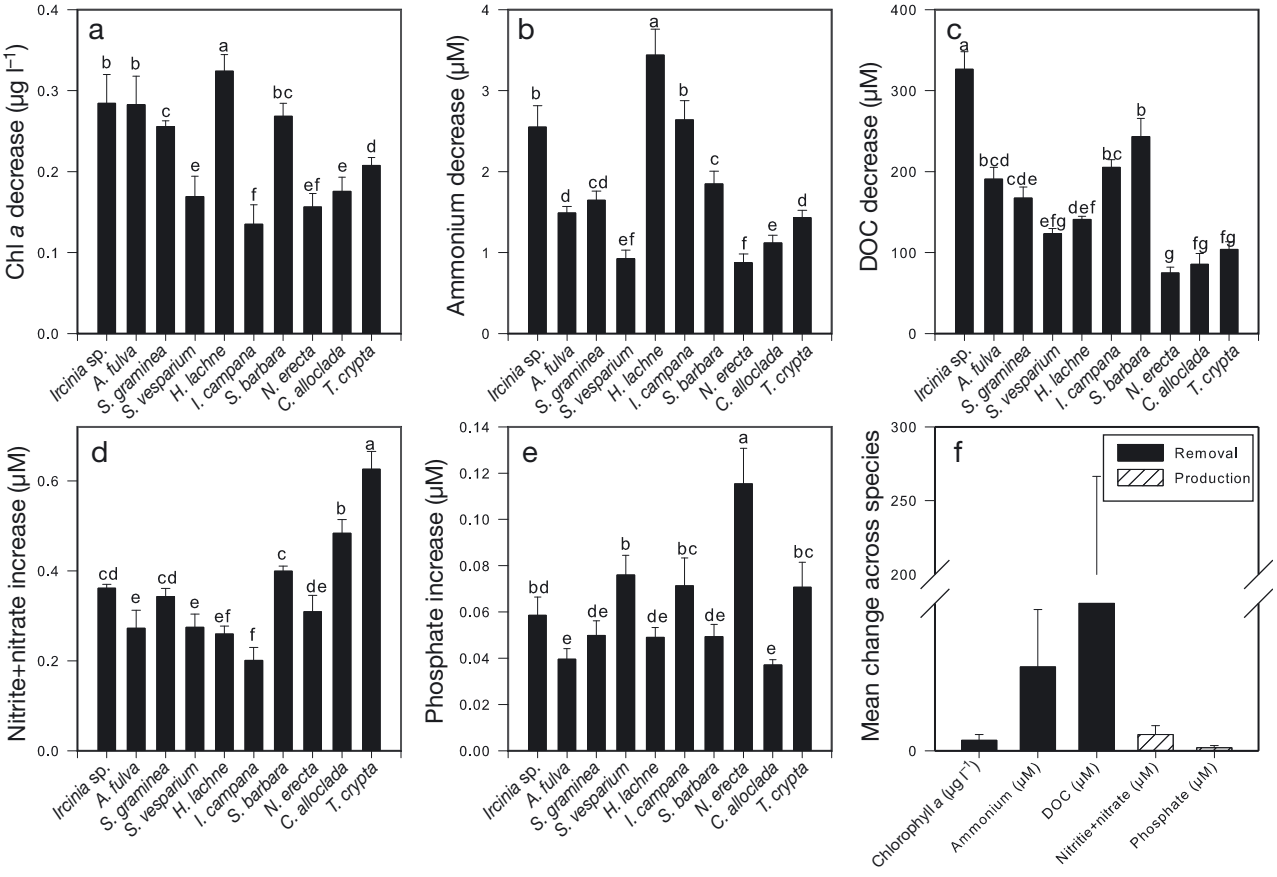

Fig. 2. Species-specific effects of sponge biomass and flow on the mean decrease or increase of the water quality constituents (a) chl *a*, (b) ammonium, (c) dissolved organic carbon (DOC), (d) nitrite + nitrate, and (e) phosphate, and (f) mean across all species. Values represent the mean (±1 SE) change of each variable in comparison to controls. Lower case letters represent statistically significant differences among treatments ($p < 0.008$). Full species names are in Table 2

Table 2. Mean percent change (±1 SD) in chl *a* and nutrients (NO_2^- + NO_3^-; NH_4^+; PO_4^{3-}; DOC) in seawater exiting mesocosms containing sponges compared to that in control treatments with no sponges. The top portion of the table presents species-specific data depicted by the scientific and common names of sponges along with their microbial associations (HMA: high microbial abundance; LMA: low microbial abundance). The bottom portion of the table summarizes data by biomass and water flow treatments

Grouping	Common name	Microbial association	Chl *a*	NO_2^- + NO_3^-	NH_4^+	PO_4^{3-}	DOC
Species							
Spheciospongia vesparium[a,b]	Loggerhead	HMA	−30.00 ± 25.60	90.51 ± 118.81	−26.14 ± 17.15	115.18 ± 147.20	−34.09 ± 15.14
Ircinia campana[a,c]	Vase	HMA	−22.75 ± 24.22	55.54 ± 65.81	−63.30 ± 14.21	88.20 ± 85.76	−49.10 ± 20.47
Spongia barbara[d]	Yellow	HMA	−48.01 ± 16.16	86.28 ± 47.64	−42.29 ± 24.27	48.57 ± 33.99	−56.10 ± 23.51
Hippospongia lachne[d]	Sheepswool	HMA	−51.33 ± 20.83	55.82 ± 72.32	−62.39 ± 22.88	47.40 ± 37.77	−35.37 ± 12.29
Ircinia sp.[a,b]	Brown branching	HMA	−47.26 ± 33.29	106.97 ± 101.55	−61.40 ± 16.95	66.01 ± 53.03	−70.80 ± 24.83
Spongia graminea[d]	Glove sponge	HMA	−45.44 ± 17.00	84.73 ± 82.97	−51.67 ± 25.19	59.73 ± 72.43	−43.59 ± 21.70
Niphates erecta[b]	Lavender rope	LMA	−27.25 ± 18.98	64.99 ± 50.14	−23.52 ± 16.65	172.82 ± 238.01	−19.90 ± 11.91
Cinachyrella alloclada[a,b]	Golf ball	LMA	−28.26 ± 17.29	93.81 ± 68.14	−37.10 ± 18.15	44.89 ± 33.95	−22.02 ± 20.36
Tectitethya crypta[a,e]	Green volcano	LMA	−39.78 ± 17.53	130.02 ± 78.97	−38.50 ± 14.62	103.03 ± 138.58	−28.98 ± 17.96
Aplysina fulva[f]	Yellow rope	HMA	−46.53 ± 20.29	62.30 ± 55.49	−32.50 ± 14.03	36.38 ± 27.65	−44.91 ± 15.47
Treatment							
High biomass, high flow			−37.04 ± 22.51	99.28 ± 89.66	−44.76 ± 27.50	112.98 ± 175.50	−42.06 ± 24.45
Low biomass, high flow			−30.16 ± 21.26	99.15 ± 88.73	−36.08 ± 15.88	58.01 ± 69.25	−36.92 ± 27.67
High biomass, low flow			−46.56 ± 24.51	64.75 ± 50.08	−46.33 ± 27.34	109.87 ± 115.33	−40.71 ± 21.43
Low biomass, low flow			−41.56 ± 23.96	71.00 ± 82.48	−51.04 ± 19.93	40.01 ± 29.26	−41.85 ± 21.50

[a]Species selected for the study of bacterioplankton concentrations; [b]Microbial associations from Gloeckner et al. (2014); [c]Microbial associations from Marino et al. (2017); [d]Unpublished microbial associations; [e]Microbial associations from Reiswig (1974); [f]Microbial associations from Weisz et al. (2007)

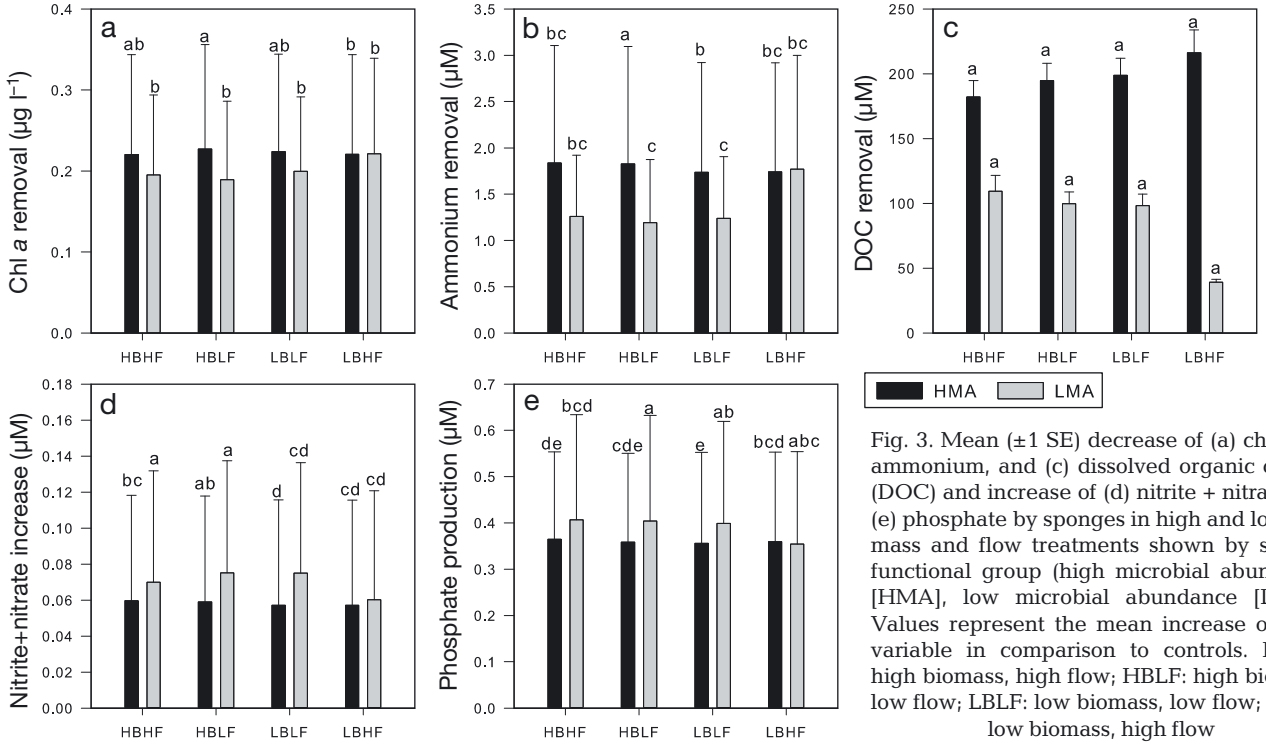

Fig. 3. Mean (±1 SE) decrease of (a) chl *a*, (b) ammonium, and (c) dissolved organic carbon (DOC) and increase of (d) nitrite + nitrate and (e) phosphate by sponges in high and low biomass and flow treatments shown by sponge functional group (high microbial abundance [HMA], low microbial abundance [LMA]). Values represent the mean increase of each variable in comparison to controls. HBHF: high biomass, high flow; HBLF: high biomass, low flow; LBLF: low biomass, low flow; LBHF: low biomass, high flow

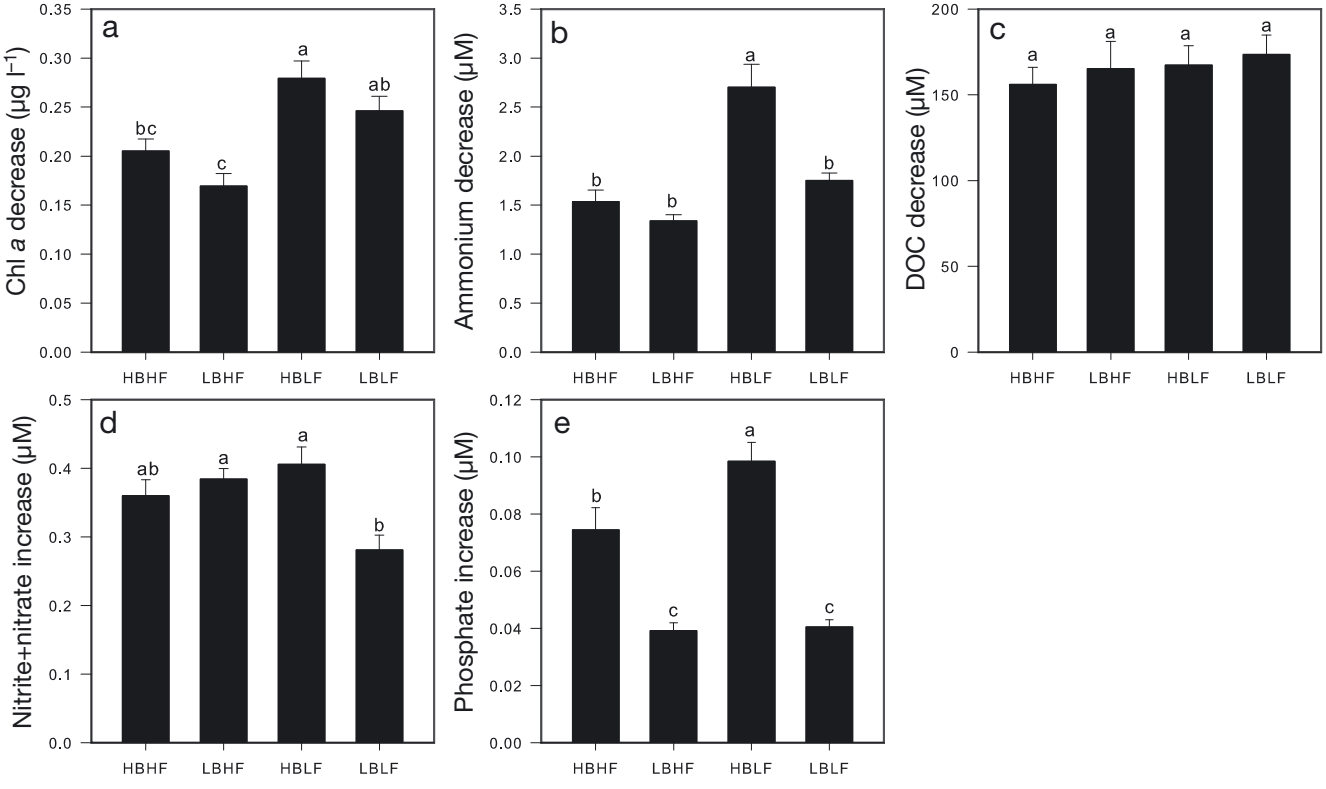

Fig. 4. Mean (±1 SE) effects of sponge biomass and water flow on the response variables (a) chl *a*, (b) ammonium, and (c) dissolved organic carbon (DOC) and increase of (d) nitrite + nitrate and (e) phosphate for all flow and biomass treatments. Values represent the mean increase of each variable in comparison to controls. Letters represent statistical significance ($p < 0.008$). HBHF: high biomass, high flow; LBHF: low biomass, high flow; HBLF: high biomass, low flow; LBLF: low biomass, low flow

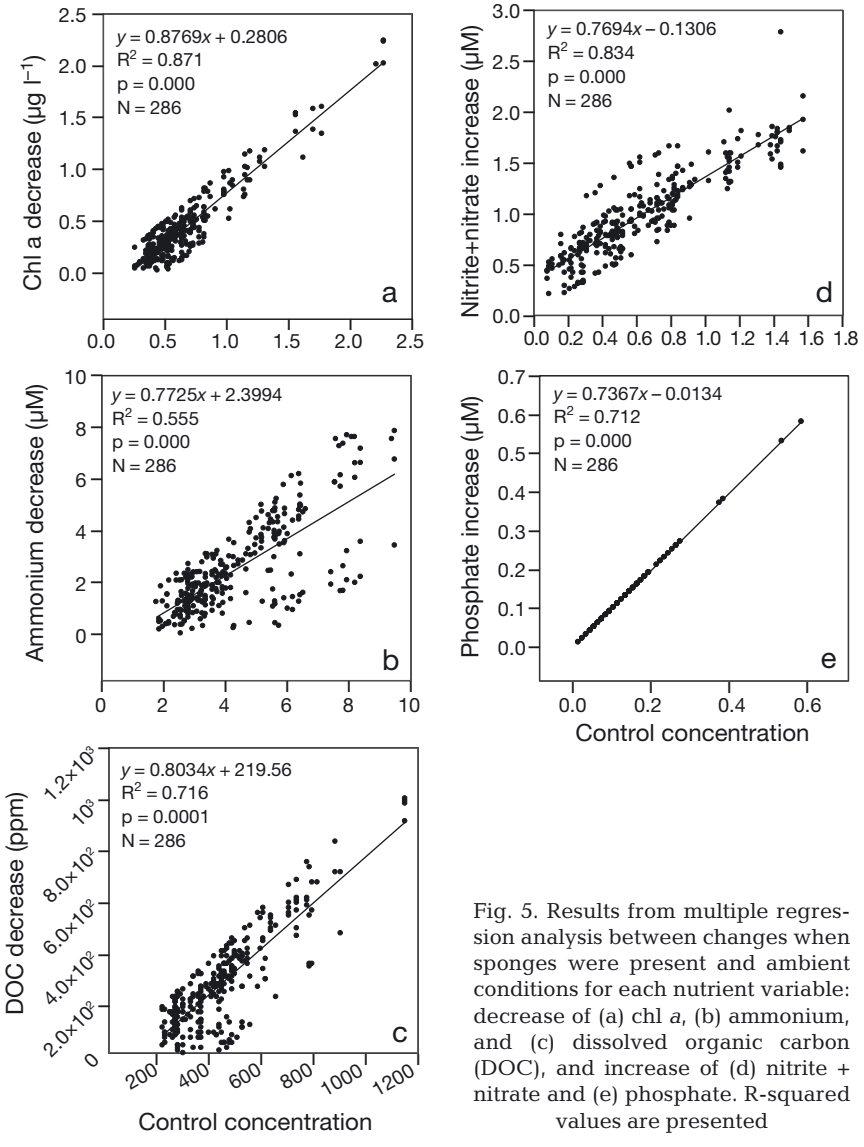

Fig. 5. Results from multiple regression analysis between changes when sponges were present and ambient conditions for each nutrient variable: decrease of (a) chl *a*, (b) ammonium, and (c) dissolved organic carbon (DOC), and increase of (d) nitrite + nitrate and (e) phosphate. R-squared values are presented

3.3. Dissolved organic carbon

The mean decrease in DOC across all species and treatments was 165 ± 101 µM, a concentration that was approximately 40% lower than that measured in the controls. The decrease in the HBHF treatment was 156 ± 9.90 µM, in the HBLF treatment it was 167 ± 9.28 µM, in the LBHF treatment it was 165 ± 15.91 µM, and in the LBLF treatment it was 173 ± 11.22 µM. There was no statistically significant difference between treatment combination effects on DOC decrease. HMA sponges decreased DOC by an average of 197 ± 7.08 µM, approximately double that of LMA sponges, 89 ± 5.72 µM, which was a significant effect ($p < 0.000$). Of the 10 species, *Ircinia* sp. and *Spongia barbara* had the largest effect on DOC decrease and *N. erecta* the least.

3.4. Nitrite + nitrate

Sponges increased nitrogen (NO_2^- + NO_3^-) concentrations across all species and treatments (0.36 ± 0.01 µM, mean ± SE), an approximately 43% increase over controls. In the HBHF treatment the mean increase was 0.36 ± 0.02 µM, in the HBLF treatment it was 0.41 ± 0.03 µM, in the LBHF treatment it was 0.38 ± 0.02 µM, and in the LBLF treatment it was the lowest, at 0.28 ± 0.02 µM. Among treatments, HBLF and LBHF had a larger but non-significant effect on NO_2^- + NO_3^- concentration. LMA sponges had a significantly greater effect on NO_2^- + NO_3^- concentration ($p < 0.008$) increase than HMA sponges, registering a mean value of 0.41 ± 0.02 µM compared to 0.30 ± 0.01 µM in HMA sponges. *Tectitethya crypta* had the greatest ($p < 0.008$) effect on NO_2^- + NO_3^- increase and *I. campana* the least.

3.5. Phosphate

Across all species and treatments, sponges increased PO_4^{3-} concentrations by 43% (0.06 ± 0.003 µM, mean ± SE). Concentration increases in PO_4^{3-} were greatest ($p < 0.05$) in the HBLF (0.10 ± 0.01 µM) and HBHF (0.07 ± 0.01 µM) treatments as compared to those in both the LBHF and LBLF treatments (both averaged 0.04 ± 0.002 µM). The LMA sponges created a significantly ($p < 0.008$) greater increase on PO_4^{3-} (0.07 ± 0.004 µM) than did HMA sponges (0.05 ± 0.003 µM). *N. erecta* had the greatest ($p < 0.008$) effect on PO_4^{3-} concentrations, whereas *Aplysina fulva* had the least.

3.6. Bacterioplankton

Sponge identity, biomass, and water turnover each had significant independent effects ($p < 0.001$) in decreasing bacterioplankton concentrations in the mesocosms in comparison to the controls, but the 2-way interactions between species and biomass ($p = 0.064$) and the 3-way interaction of species × biomass × turnover ($p = 0.553$) were non-significant. How-

ever, when water turnover was crossed with either biomass or species, there was a significant effect on bacterioplankton reduction ($p = 0.003$ and $p < 0.001$, respectively). In general, *T. crypta* and *C. alloclada* were the most efficient filterers of bacterioplankton, whereas *I. campana* had the least effect on bacterioplankton concentrations.

4. DISCUSSION

Our results show that sponge species identity, functional group (i.e. HMA vs. LMA), and biomass interacted in complex ways with rates of water turnover to control biogeochemical cycling and the concentrations of water-column constituents. In general, the strength of the effects of sponges on response variables was greatest when sponge biomass was high and water turnover low, the latter mimicking conditions during slack tides in Florida Keys hard-bottom areas. That said, the effects varied greatly from species to species and among dependent variables. No one species of sponge had consistently strong effects on all response variables. This demonstrates the complex effect of sponge community structure (i.e. species biomass, identity, and functional group) and its interaction with water residence time on the biochemical character of the water column. Therefore, the effect of sponges on the water column will likely be context dependent and vary with location, but in ways that can be predicted from community structure and water flow. Moreover, our results highlight the important biochemical cycling function of sponges that is lost when sponge communities are eradicated or when their diversity is diminished by harmful algal blooms (HABs).

We observed a net decrease in the presence of NH_4^+ in comparison to our controls, and similar to results reported by Morganti et al. (2017), there was a larger decrease in nitrogenous waste products when HMA sponges were present relative to LMA sponges. However, other incubation studies (Southwell et al. 2008) of similar sponge species (*Ircinia campana* and *Niphates erecta*) found an increase in NH_4^+ in contrast to our findings. We also observed much lower concentrations of $NO_2^- + NO_3^-$ after filtration by *I. campana* but higher concentrations after filtration by *N. erecta* (0.201 and 0.309 µM l^{-1} s^{-1}, respectively) in comparison to incubation studies (0.833 and 0.014 µM l^{-1} s^{-1}, respectively) (Southwell et al. 2008). In incubation experiments, *Spheciospongia vesparium* reduced chl *a* by 0.2 to 0.3 µg l^{-1} over a 60 min period (Peterson et al. 2006), whereas we recorded 0.17 µg l^{-1} s^{-1}. If we extrapolated our data to an hourly scale, the rate would have been 10.2 µg l^{-1} h^{-1}, much higher than that documented in Peterson et al. (2006). Peterson et al. (2006) indicated that this plateau in chl *a* reduction was likely due to food concentrations falling below a threshold density, and our results confirm that such a mechanism exists.

Common attributes of ecosystem structure and function can be altered or lost when the density and diversity of suspension feeders are reduced, often resulting in cascades through an ecosystem (Ellison et al. 2005, Hooper et al. 2005). It is clear from our results that sponges (and their microbial symbionts) likely play an important role in mediating the nitrogen cycle (particularly nitrification) in the shallow waters surrounding the Florida Keys. Sponge filter feeding also profoundly reduced concentrations of DOC, chl *a*, and bacterioplankton in our mesocosms. Individual species strongly affected just a single response variable. For example, *I. campana* — a large vase sponge that is highly sensitive to HABs — dramatically reduced water-column concentrations of NH_4^+ but had a negligible effect on chl *a* in comparison with other species. In contrast, the presence of the hardy sponge *Tectitethya crypta* elevated concentrations of $NO_2^- + NO_3^-$ but had little effect on DOC compared to other species,

The variable effects of sponge species on nutrient concentrations observed in our experiments were likely driven by distinct microbial constituents associated with sponge species. We cannot yet separate the confounding effects of sponge genotype from the unique microbial symbionts associated with each individual sponge. But our inability to differentiate host versus microbial effects does not diminish the significance of species-specific ecosystem effects, especially since sponge–microbial community associations are often stable over time (Erwin et al. 2012). Our results also highlight the interactive influence of water flow and turnover on the effects of sponge filtration.

Our experiments show that sponge effects on water quality properties were harder to detect when the rate of water turnover was high. When turnover was low, the filtration signal was more pronounced, indicating that sponges were actively depleting the water column of resources at a rate that exceeded replenishment. These data suggest that the shallow water sponges we studied may be better adapted and more efficient filterers at low rates of water turnover. However, we did not address feeding efficiency of individual sponges in this experiment; thus, we must attribute some of the greater depletion in low flow treatments to refiltration. Other studies have found

that increased water velocity or turnover has inconsistent effects on the rates of filtration by suspension feeders (Peterson & Black 1987, Ackerman 1999). For example, Lassen et al. (2006) reported that at low water velocities, when turnover is limited, concentrations of phytoplankton are diminished, and in response, bivalves maintain high rates of filtration to maximize uptake of particulate organic matter. Our results indicate that sponge filtration rates generally increased with increasing concentrations of the response variables, which further complicate the interactive effects of sponge abundance, water flow, and food availability on rates of filtration. Previous studies have also found a positive relationship between the concentration of available resources and sponge filtration and retention rates (Archer et al. 2017, McMurray et al. 2017).

Our study included only high and low water flow regimes meant to bracket the common tidally driven flow present in the shallow water habitats of the Florida Keys. Further testing across a broader range of tidal flows is needed to more fully characterize the effect of flow regime and turnover on species-specific sponge filtration efficiencies. Data on tidal regime and species-specific response to flow versus turnover will permit more accurate projections of filtration rates of sponges at ecosystem scales, dynamics that are now ignored when estimating the effects of sponge filtration over large spatial scales. When we created a low flow environment that mimicked shallow water, slack tide conditions, there was likely refiltration of water by sponges, especially at high biomass. Refiltration by sponges was probably minimal in our high flow treatments, especially when sponge biomass was low. Although our mesocosms were designed to minimize container effects and back eddies, our apparatus likely did not exclude such effects in their entirety. To overcome any limitations posed by experimental containers, we are now conducting similar experiments *in situ*, to better emulate the effect of ambient conditions on sponge community ecosystem effects.

Although it is clear that local hydrodynamics play an important role in determining the effects of sponges on water-column constituents, the effects of species identity and sponge biomass are even more pronounced. As resource-rich water passes over a sessile filter-feeding community, the organisms that first encounter the water mass experience minimal refiltration, whereas those located downstream in the community will receive water depleted of some resources (O'riordan et al. 1995, Jones et al. 2011). Therefore, in high biomass communities, as the water mass is cleared of food particles and usable nutrients are fixed into other forms, resource availability could become a limiting factor to growth and reproduction. Indeed, we have evidence from field experiments that sponge growth in Florida Bay is strongly dependent on the local density of this rather enclosed sponge community. However, the notion that sponge growth can be limited by planktonic resource availability runs counter to the prevailing paradigm that sponges on deeper coral reefs are generally not nutrient limited (Pawlik et al. 2015).

The species richness of shallow hard-bottom sponge communities in the Florida Keys (Stevely et al. 2011) is far lower than that on nearby coral reefs (Pawlik 2011), but it is nonetheless highly variable among locations (2 to >25 species per site) as is sponge density (CV = 172). Those communities can also change rapidly and dramatically over time. In the past 30 yr, sponge communities have been devastated in areas of persistent environmental degradation (e.g. HAB-induced sponge die-offs) or when subject to hurricanes and, to a lesser extent, commercial harvest (Stevely et al. 2011, Butler et al. 2017). Although HAB-associated mortality is relatively uniform among sponge species, commercial harvest alters the relative abundances of sponges because fishers target just a few species (e.g. *Hippospongia lachne, Spongia barbara, S. graminea*). These spatiotemporal fluctuations in sponge community composition and density will thus be reflected in species-specific effects on water-column properties. In short, because sponges are not equal in their effect on ecosystem processes, neither are the implications of community assembly or sponge loss.

Our experiments also show that commercially targeted sponges, such as *H. lachne,* decrease the concentration of NH_4^+ and chl *a* more than any other sponge species. The commercially valuable sponge species are also among those most sensitive to destruction by HABs (Butler et al. 2015, 2017). In contrast, some widespread sponge species of no commercial importance and which are resistant to HABs (e.g. *Cinachyrella alloclada*) had minimal effects on water-column nutrients in our mesocosms. Thus, reductions in the natural diversity as well as the density of these important filter feeders significantly alter biogeochemical cycling and thus benthic–pelagic linkages (Peterson et al. 2006). Management and restoration of sponge communities after HAB-associated die-offs should consider the implications of species-dependent effects and perhaps focus on finding and restoring those that are most resilient and beneficial to ecosystem processes.

In summary, our study established that sponge species identity and biomass along with water flow influence a range of water-column properties, including nitrogen and carbon cycles. Extrapolating our mesocosm-based results to natural sponge communities suggests that differences in sponge community assemblages as well as the loss of sponges due to environmental change are likely to trigger idiosyncratic shifts in plankton communities and nutrient concentrations. We only tested 1 species at a time in this set of mesocosm experiments, each at 2 different biomass and flow regime treatments. What remains to be documented is whether the ecosystem effects of sponge filtration and nutrient conversion differ across the range of naturally occurring sponge communities, that is, between diverse communities and the monospecific communities that we explored here. In essence, the question is not only whether sponge diversity matters but also whether more diverse communities interact in synergistic or inhibitory ways that affect ecosystem function. We explored that question in another study, the results of which will soon follow.

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LITERATURE CITED

Ackerman JD (1999) Effect of velocity on the filter feeding of dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*): implications for trophic dynamics. Can J Fish Aquat Sci 56:1551–1561

Archer SK, Stevens JL, Rossi RE, Matterson KO, Layman CA (2017) Abiotic conditions drive significant variability in nutrient processing by a common Caribbean sponge, *Ircinia felix*. Limnol Oceanogr 62:1783–1793

Alexander BE, Liebrand K, Osinga R, van der Geest HG and others (2014) Cell turnover and detritus production in marine sponges from tropical and temperate benthic ecosystems. PLOS ONE 9:e109486

Barnes DK, Clarke A (1995) Seasonality of feeding activity in Antarctic suspension feeders. Polar Biol 15:335–340

Bell JJ (2008) The functional roles of marine sponges. Estuar Coast Shelf Sci 79:341–353

Boyer JN, Fourqurean JW, Jones RD (1999) Seasonal and long-term trends in the water quality of Florida Bay (1989–1997). Estuaries 22:417–430

Butler MJ IV, Hunt JH, Herrnkind WF, Childress MJ and others (1995) Cascading disturbances in Florida Bay, USA: cyanobacteria blooms, sponge mortality, and implications for juvenile spiny lobsters *Panulirus argus*. Mar Ecol Prog Ser 129:119–125

Butler MJ IV, Behringer DC Jr, Dolan TW III, Moss J, Shields JD (2015) Behavioral immunity suppresses an epizootic in Caribbean spiny lobsters. PLOS ONE 10:e0126374

Butler MJ, Behringer DC, Valentine MM (2017) Commercial sponge fishery impacts on the population dynamics of sponges in the Florida Keys, FL (USA). Fish Res 190: 113–121

Cropper WP, DiResta D (1999) Simulation of a Biscayne Bay, Florida commercial sponge population: effects of harvesting after Hurricane Andrew. Ecol Modell 118:1–15

Dame RF, Olenin S (eds) (2005) The comparative roles of suspension-feeders in ecosystems: proceedings of the NATO advanced research workshop on the comparative roles of suspension-feeders in ecosystems, Nida, Lithuania, 4–9 October 2003. NATO Science Series: IV. Springer, Dordrecht

de Goeij JM, van Oevelen D, Vermeij MJ, Osinga R, Middelburg JJ, de Goeij AF, Admiraal W (2013) Surviving in a marine desert: the sponge loop retains resources within coral reefs. Science 342:108–110

Diaz MC, Rützler K (2001) Sponges: an essential component of Caribbean coral reefs. Bull Mar Sci 69:535–546

Diaz MC, Ward BB (1997) Sponge-mediated nitrification in tropical benthic communities. Mar Ecol Prog Ser 156: 97–107

Easson CG, Matterson KO, Freeman CJ, Archer SK, Thacker RW (2015) Variation in species diversity and functional traits of sponge communities near human populations in Bocas del Toro, Panama. PeerJ 3:e1385

Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Mohan J (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ 3:479–486

Erwin PM, Pita L, López-Legentil S, Turon X (2012) Stability of sponge-associated bacteria over large seasonal shifts in temperature and irradiance. Appl Environ Microbiol 78:7358–7368

Gili JM, Coma R (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol Evol 13:316–321

Gloeckner V, Wehrl M, Moitinho-Silva L, Gernert C and others (2014) The HMA–LMA dichotomy revisited: an electron microscopical survey of 56 sponge species. Biol Bull 227:78–88

Grebmeier JM, Barry JP (1991) The influence of oceanographic processes on pelagic–benthic coupling in polar regions: a benthic perspective. J Mar Syst 2:495–518

Hadas E, Shpigel M, Ilan M (2009) Particulate organic matter as a food source for a coral reef sponge. J Exp Biol 212:3643–3650

Hardoim CCP, Costa R, Araujo FV, Hajdu E and others (2009) Diversity of bacteria in the marine sponge *Aplysina fulva* in Brazilian coastal waters. Appl Environ Microbiol 75:3331–3343

Hector A (2015) The new statistics with R. Oxford Press, Oxford

Hentschel U, Fieseler L, Wehrl M, Gernert C, Steinert M, Hacker J, Horn M (2003) Microbial diversity of marine sponges. In: Müller WEG (ed) Sponges (Porifera). Springer, Berlin, p 59–88

Herrnkind WH, Butler MJ IV, Hunt JH, Childress M (1997)

The role of physical refugia: implications from a mass sponge die-off in a lobster nursery. Mar Freshw Res 48: 759–770

Hily C (1991) Is the activity of benthic suspension feeders a factor controlling water quality in the Bay of Brest? Mar Ecol Prog Ser 69:179–188

Hooper DU, Chapin FS, Ewel JJ, Hector A and others (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Jiménez E, Ribes M (2007) Sponges as a source of dissolved inorganic nitrogen: nitrification mediated by temperate sponges. Limnol Oceanogr 52:948–958

Jones HF, Pilditch CA, Bryan KR, Hamilton DP (2011) Effects of infaunal bivalve density and flow velocity on clearance rates and near-bed hydrodynamics. J Exp Mar Biol Ecol 401:20–28

Jonsson PR, Petersen JK, Karlsson Ö, Loo LO, Nilsson S (2005) Particle depletion above experimental bivalve beds: *in situ* measurements and numerical modelling of bivalve filtration in the boundary layer. Limnol Oceanogr 50:1989–1998

Kearney KA, Butler M, Glazer R, Kelble CR, Serafy JE, Stabenau E (2015) Quantifying Florida Bay habitat suitability for fishes and invertebrates under climate change scenarios. Environ Manag 55:836–856

Lassen J, Kortegård M, Riisgård HU, Friedrichs M, Graf G, Larsen PS (2006) Down-mixing of phytoplankton above filter-feeding mussels—interplay between water flow and biomixing. Mar Ecol Prog Ser 314:77–88

Lee OO, Wang Y, Yang J, Lafi FF, Al-Suwailem A, Qian PY (2011) Pyrosequencing reveals highly diverse and species-specific microbial communities in sponges from the Red Sea. ISME J 5:650–664

Lesser MP (2006) Benthic–pelagic coupling on coral reefs: feeding and growth of Caribbean sponges. J Exp Mar Biol Ecol 328:277–288

Lynch TC, Phlips EJ (2000) Filtration of the bloom-forming cyanobacteria *Synechococcus* by three sponge species from Florida Bay, USA. Bull Mar Sci 67:923–936

Maldonado M, Ribes M, van Duyl FC (2012) Nutrient fluxes through sponges: biology, budgets, and ecological implications. Adv Mar Biol 62:113–182

Marino CM, Pawlik JR, López-Legentil S, Erwin PM (2017) Latitudinal variation in the microbiome of the sponge *Ircinia campana* correlates with host haplotype but not anti-predatory chemical defense. Mar Ecol Prog Ser 565: 53–66

McMurray SE, Pawlik JR, Finelli CM (2014) Trait-mediated ecosystem impacts: how morphology and size affect pumping rates of the Caribbean giant barrel sponge. Aquat Biol 23:1–13

McMurray SE, Pawlik JR, Finelli CM (2017) Demography alters carbon flux for a dominant benthic suspension feeder. Funct Ecol 31:2188–2198

Morganti T, Coma R, Yahel G, Ribes M (2017) Trophic niche separation that facilitates co existence of high and low microbial abundance sponges is revealed by *in situ* study of carbon and nitrogen fluxes. Limnol Oceanogr 62: 1963–1983

Newell RI (2004) Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. J Shellfish Res 23:51–62

O'riordan CA, Monismith SG, Koseff JR (1995) The effect of bivalve excurrent jet dynamics on mass transfer in a benthic boundary layer. Limnol Oceanogr 40:330–344

Orejas C, Gili JM, Arntz W, Ros JD, López P, Teixidó N, Filipe P (2000) Benthic suspension feeders, key players in Antarctic marine ecosystems? Contrib Sci 1:299–311

Patel A, Noble RT, Steele JA, Schwalbach MS, Hewson I, Fuhrman JA (2007) Virus and prokaryote enumeration from planktonic aquatic environments by epifluorescence microscopy with SYBR Green I. Nat Protoc 2: 269–276

Patterson MR, Chernykh VI, Fialkov VA, Savarese M (1997) Trophic effects of sponge feeding within Lake Baikal's littoral zone. 1. *In situ* pumping rates. Limnol Oceanogr 42:171–178

Pawlik J (2011) The chemical ecology of sponges on Caribbean reefs: natural products shape natural systems. BioScience 61:888–898

Pawlik JR, McMurray SE, Erwin P, Zea S (2015) A review of evidence for food limitation of sponges on Caribbean reefs. Mar Ecol Prog Ser 519:265–283

Petersen JK (2004) Grazing on pelagic primary producers — the role of benthic suspension feeders in estuaries. In: Nielsen SL, Banta GT, Pedersen MF (eds) Estuarine nutrient cycling: the influence of primary producers. Kluwer, Dordrecht, p 129–152

Peterson CH, Black R (1987) Resource depletion by active suspension feeders on tidal flats: influence of local density and tidal elevation. Limnol Oceanogr 32:143–166

Peterson BJ, Chester CM, Jochem FJ, Fourqurean JW (2006) Potential role of sponge communities in controlling phytoplankton blooms in Florida Bay. Mar Ecol Prog Ser 328:93–103

Pile AJ, Patterson MR, Savarese M, Chernykh VI, Fialkov VA (1997) Trophic effects of sponge feeding within Lake Baikal's littoral zone. 2. Sponge abundance, diet, feeding efficiency, and carbon flux. Limnol Oceanogr 42:178–184

Pile AJ, Grant A, Hinde R, Borowitzka MA (2003) Heterotrophy on ultraplankton communities is an important source of nitrogen for a sponge–rhodophyte symbiosis. J Exp Biol 206:4533–4538

Reiswig HM (1971) Particle feeding in natural populations of three marine demosponges. Biol Bull 141:568–591

Reiswig HM (1974) Water transport, respiration and energetics of three tropical marine sponges. J Exp Mar Biol Ecol 14:231–249

Reiswig HM (1981) Partial carbon and energy budgets of the bacteriosponge *Verohgia fistularis* (Porifera: Demospongiae) in Barbados. Mar Ecol 2:273–293

Ribes M, Coma R, Gili JM (1999) Natural diet and grazing rate of the temperate sponge *Dysidea avara* (Demospongiae, Dendroceratida) throughout an annual cycle. Mar Ecol Prog Ser 176:179–190

Riisgård HU, Larsen PS (2010) Particle capture mechanisms in suspension-feeding invertebrates. Mar Ecol Prog Ser 418:255–293

Rix L, de Goeij JM, van Oevelen D, Struck U, Al Horani FA, Wild C, Naumann MS (2017) Differential recycling of coral and algal dissolved organic matter via the sponge loop. Funct Ecol 31:778–789

Shibata A, Goto Y, Saito H, Kikuchi T, Toda T, Taguchi S (2006) Comparison of SYBR Green I and SYBR Gold stains for enumerating bacteria and viruses by epifluoresence microscopy. Aquat Microb Ecol 43:223–231

Southwell MW, Weisz JB, Martens CS, Lindquist N (2008) *In situ* fluxes of dissolved inorganic nitrogen from the sponge community on Conch Reef, Key Largo, Florida. Limnol Oceanogr 53:986–996

Stevely JM, Sweat D (1985) Survival and growth of cut vs hooked commercial sponges in the Florida Keys. Tech Pap No. 38, Florida Sea Grant College, Gainesville, FL

Stevely JM, Sweat DE, Bert TM, Sim-Smith C, Kelly M (2011) Sponge mortality at Marathon and Long Key, Florida: patterns of species response and population recovery. Proc Gulf Caribb Fish Inst 63:384–400

Taylor MW, Radax R, Steger D, Wagner M (2007) Sponge-associated microorganisms: evolution, ecology, and biotechnological potential. Microbiol Mol Biol Rev 71: 295–347

Thomas T, Moitinho-Silva L, Lurgi M, Bjork JR and others (2016) Diversity, structure and convergent evolution of the global sponge microbiome. Nat Commun 7:11870

Torres RC, Butler MJ, Shellito B (2006) A GIS-based characterization of commercial sponge populations in the Florida Keys, FL (USA). Proc Gulf Caribb Fish Inst 57: 1043–1044

Wall CC, Rodgers BS, Gobler CJ, Peterson BJ (2012) Responses of loggerhead sponges *Spechiospongia vesparium* during harmful cyanobacterial blooms in a subtropical lagoon. Mar Ecol Prog Ser 451:31–43

Wang JD, van de Kreeke J, Krishnan N, Smith D (1994) Wind and tide response in Florida Bay. Bull Mar Sci 54: 579–601

Webster NS, Taylor MW (2012) Marine sponges and their microbial symbionts: love and other relationships. Environ Microbiol 14:335–346

Weisz JB, Hentschel U, Lindquist N, Martens CS (2007) Linking abundance and diversity of sponge-associated microbial communities to metabolic differences in host sponges. Mar Biol 152:475–483

Weisz JB, Lindquist N, Martens CS (2008) Do associated microbial abundances impact marine demosponge pumping rates and tissue densities? Oecologia 155: 367–376

Williams LJ, Abdi H (2010) Fisher's least significant difference (LSD) test. In: Salkind N (ed) Encyclopedia of research design. Sage, Thousand Oaks, CA, p 840–853

Wulff J (2017) Bottom up and top down controls on coral reef sponges: disentangling within habitat and between habitat processes. Ecology 98:1130–1139

Yahel G, Sharp JH, Marie D, Häse C, Genin A (2003) *In situ* feeding and element removal in the symbiont bearing sponge *Theonella swinhoei*: bulk DOC is the major source for carbon. Limnol Oceanogr 48:141–149

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