



# The effects of coastal development on sponge abundance, diversity, and community composition on Jamaican coral reefs



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## ABSTRACT

Over the past decade, development along the northern coast of Jamaica has accelerated, resulting in elevated levels of sedimentation on adjacent reefs. To understand the effects of this development on sponge community dynamics, we conducted surveys at three locations with varying degrees of adjacent coastal development to quantify species richness, abundance and diversity at two depths (8–10 m and 15–18 m). Sediment accumulation rate, total suspended solids and other water quality parameters were also quantified. The sponge community at the location with the least coastal development and anthropogenic influence was often significantly different from the other two locations, and exhibited higher sponge abundance, richness, and diversity. Sponge community composition and size distribution were statistically different among locations. This study provides correlative evidence that coastal development affects aspects of sponge community ecology, although the precise mechanisms are still unclear.

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## 1. Introduction

Caribbean reef ecosystems have undergone a series of alterations, both natural and anthropogenic, during the last several decades. Overfishing (Munro, 1983; Hardt, 2008), hurricanes (Woodley et al., 1981; Kjerfve et al., 1986), echinoid disease (Lessios et al., 1984; Hughes et al., 1985; Liddell and Ohlhorst, 1986) and other human activities (Hughes, 1994) have led to large-scale deterioration of nearshore coral reef ecosystems (Goreau, 1992; Liddell and Ohlhorst, 1992; Hughes, 1994). The overall ecosystem health of Caribbean reefs has been substantially reduced during the modern era (Pandolfi et al., 2003) and continues to decline on many reefs due to overfishing and the myriad effects of coastal development.

One third of Caribbean reefs are directly threatened by coastal development and the associated impacts (Burke et al., 2004). For many islands in the Caribbean, long-term growth in the domestic population has contributed to mounting environmental pressure; however, anthropogenic activities directly impacting island resources have risen most recently due to increased tourism. Proximity of the United States and Canada has resulted in dramatically increased tourism to Caribbean nations over the past 30–

40 years. For example, the number of annual visitors to Jamaica was just under 400,000 in 1977 (Alleyne and Boxill, 2003) compared to 3.3 million in 2012 (Jamaica Tourist Board, 2012). The resultant economic boom has fueled large-scale coastal development and alteration, removing important coastal habitats and transforming them into resorts and beaches. While these activities can have a variety of damaging impacts to marine ecosystems, one of the most ubiquitous threats of coastal development is elevated sedimentation resulting from construction, artificial beach creation, and run-off (Fabricius, 2005).

Suspended and settled sediment negatively affects many reef organisms, particularly many coral species. Experimental manipulations have demonstrated that many corals are physiologically distressed by increased sediment deposition and suspension (Riegl and Branch, 1995; Gilmour, 1999; Phillipp and Fabricius, 2003; Weber et al., 2006). High amounts of suspended sediments decrease light availability to the benthos and reduce the photosynthetic yield of zooxanthellae within hermatypic corals (Phillipp and Fabricius, 2003). Shading experiments designed to mimic light attenuation in turbid waters (Rogers, 1979) demonstrated that hard corals experienced bleaching and a decrease in community metabolism after five weeks of limited light. Reduced coral recruitment, changes in the size, diversity and abundance of coral colonies, and reduced community diversity have all been reported as effects of increased run-off and sedimentation (Cortés and Risk, 1985).

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While understanding the effects of sediment deposition on hermatypic corals has been a priority in the past, many modern reef environments are biogenically dominated by non-hermatypic invertebrates, most notably gorgonians and sponges (Norström et al., 2009; González-Rivero et al., 2011; Bell et al., 2013). In the Caribbean, there are >300 known sponge species, compared to approximately 70 hard coral species (Diaz and Rützler, 2001), with growing evidence that sponge population growth may be outpacing corals on Caribbean reefs (McMurray et al., 2010), potentially shifting reefs toward sponge dominance (Bell et al., 2013). Therefore, there is a growing need to understand the impacts of sedimentation on the physiology, ecology and distribution of sponges in the Caribbean (Bell et al., 2015).

Sponges are filter-feeding organisms that rely on processing large volumes of water to obtain the majority of their nutrition (Reiswig, 1971; Southwell et al., 2008). Sponges are able to efficiently retain particles within the size range of 0.3–50 µm (Reiswig, 1971); however, this particle size range partially overlaps with that of silts and clays (<62.5 µm). To prevent their aquiferous system (internal canal network) from becoming congested with unwanted sediment particles, many sponges can temporarily close or reduce the size of their incurrent openings (ostia) during times of increased turbidity (Ilan and Abelson, 1995; Nickel, 2004; Leys and Meech, 2006). Alternatively, sponges may cease to pump water if suspended sediment concentrations become intolerable. Gerrodette and Flechsig (1979) demonstrated that the reef sponge, *Aplysina lacunosa* (formerly known as *Verongia lacunosa*) reduced its pumping rate after just 4 h of exposure to suspended sediment concentrations greater than 11 mg L<sup>-1</sup>, and chronic exposure (4 days) resulted in a continuous decline in pumping rates. Similar effects of sediment exposure on pumping rates were found in glass sponges (Tompkins-MacDonald and Leys, 2008). Settled sediments can also affect sponge feeding by smothering and clogging ostia. Some sponge species are capable of reversing water flow in an effort to expel deposited sediments from their ostia (Nickel, 2004), while others are able to trap settling sediments within a mucus layer that can be discarded (Turon et al., 1999).

For sponges that acquire a portion of their nutrition from photosynthetic symbionts (hereafter referred to as phototrophic sponges), suspended and settled sediments may have negative consequences for both the symbionts and sponge hosts (reviewed by Bell et al., 2015). Light reductions, such as those found in constantly turbid environments, may suppress symbiont photosynthetic rates (Cheshire et al., 1995) and alter the amount of symbiont-derived carbon transferred to host sponges (Freeman and Thacker, 2011). While differences in light availability caused by increased turbidity negatively affect phototrophic sponges, Pineda et al. (2015) showed that exposure to a single pulse of sediments (meant to mimic dredging activity) did not alter the overall microbial assemblages in seven sponge species. Observational studies of phototrophic sponge distributions have shown lower abundances in turbid areas compared to less turbid environments (Wilkinson and Cheshire, 1989; Bannister et al., 2010), providing further evidence that suspended sediments negatively impact phototrophic sponge communities.

While various physiological and morphological adaptations allow sponges to cope with short-term increases in suspended or settled sediment (Bell et al., 2015), persistent or intense sediment stress may have severe impacts on sponge health, survival and reproduction. Lohrer et al. (2006) determined that even sponge species adapted to living in environments with elevated suspended sediment loads (e.g. *Aaptos* sp.) were still negatively affected by experimental deposition of terrigenous sediment (77% silts and clays, 23% sands). Three weeks after application of sediment, sponges exhibited reduced clearance rates, decreased oxygen consumption and significantly lower indices of condition in

treatments where sediment was applied (Lohrer et al., 2006). In an experimental manipulation of sediment deposition over a 125-day period, Maldonado et al. (2008) demonstrated that sponge survival was greatly reduced in areas of high sediment accumulation. Bannister et al. (2012) showed that sponges living in environments with higher sedimentation rates do so at a substantial metabolic cost, ultimately reducing reproductive output and growth. And finally, Maughan (2001) differentiated between the effects of light reduction and sedimentation on sponge recruitment by using clear covers over settlement panels; sponge recruitment was lowest on tiles exposed to sediment deposition, regardless of light exposure.

The negative impacts on individual sponge physiology, health, reproduction and survival associated with suspended and settled sediments may translate into broad-scale sponge distribution and community composition changes. As vulnerable species succumb to sediment stress, communities may transform in unexpected ways. Carballo (2006) found that seasonal differences in sedimentation shifted the sponge community from a morphologically (and taxonomically) diverse community to one dominated almost exclusively by low-relief morphologies, such as encrusting and boring sponges. In Indonesia, the distribution, abundance and diversity of sponges were directly related to depth, sedimentation and substrate angle (Bell and Smith, 2004). Also in Indonesia, Powell et al. (2014) found that sponges were consistently the dominant organisms in highly sedimented reefs, yet sponge diversity was lower when compared to sites with less sedimentation. Bannister et al. (2012) found a correlation between the abundance of *Rhopaloeides odorabile* on the Great Barrier Reef and the level of sedimentation; abundance was lower on inshore reefs where terrigenous, fine-grained sedimentation occurred than on outer reefs with less sediment.

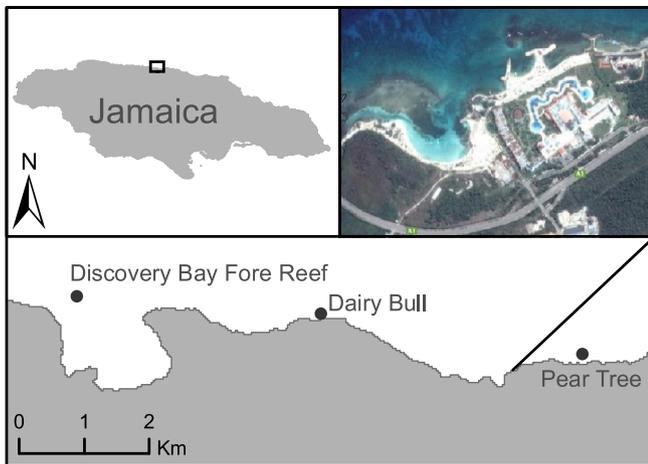
This study aimed to characterize sponge communities at three locations experiencing different stages of coastal development along the northern coast of Jamaica. We sought to understand the effects of sediment deposition that have been linked to development activities (Westfield, 2008) on sponge community metrics. Based on previous studies of sponge community response to sedimentation, we hypothesized that higher rates of sediment deposition would impact the sponge community and result in (1) reduced species richness and abundance, (2) lower diversity, (3) distinct community composition, and (4) differences in the dominant morphology and size distribution of sponges.

## 2. Materials and methods

### 2.1. Study locations

Three study locations along the northern coast of Jamaica, West Indies were chosen, representing different intensities of coastal development and direct shoreline alteration (Westfield, 2008): Dairy Bull (N 18.471, W 77.379), Discovery Bay fore reef (N 18.473, W 77.412), and Pear Tree (N 18.465, W 77.343) (Fig. 1). The Dairy Bull reef location lacks any recent coastal development and the shoreline is composed of hardened Falmouth Limestone (Land, 1973) that has not undergone any anthropogenic alterations. Sediment accumulation occurring at Dairy Bull is primarily autochthonous reef material (e.g. *Halimeda* debris, foraminiferan particles, and sediments from the adjacent sandy groove). Discovery Bay fore reef is located north of the reef crest, just west of the inlet, and experiences low levels of sediment disturbance despite the moderate residential and industrial (bauxite mining and distribution facility) development occurring within the bay.

Pear Tree, the easternmost location, has the most residential and commercial development of the three study reefs. Pear Tree



**Fig. 1.** Upper left inset: The island of Jamaica, West Indies; the small black box indicates the specific region where our surveys took place. Study locations are denoted by circles on the expanded coastal map. Upper right inset: The resort adjacent to our Pear Tree location.

is located adjacent to a large resort that was constructed in 2005 (Fig. 1, inset), despite environmental concerns from the Jamaican government (NEPA Environmental Impact Assessment, 2005). The creation of this resort resulted in a 42% enlargement of the beach area (additional 25,000 m<sup>2</sup>) along less than 2 km of shoreline (Westfield et al., 2008). At the same time that the resort was built, expansion of the main highway, which comes within 50 m of the shoreline, occurred. Using geochemical fingerprinting, Westfield et al. (2008) identified the construction activities associated with the highway and resort construction (e.g. dredging and run-off) and the episodic erosion of the resort's beaches as primary causes of elevated sediment deposition on Pear Tree reefs.

The three locations, which provide a gradient in coastal development intensity, were each divided into two sites, an eastern and western, separated by approximately 500 m to create a level of replication within locations. A depth element was also of interest, as suspended sediment concentration and the amount of sediment deposition are affected by wave energy, distance from shore, and depth of water column. Two distinct depth strata within each site nested within location, 8–10 m and 15–18 m, were used in all surveys and sampling.

## 2.2. Sediment collection and characterization

The study locations were chosen based on a geochemical fingerprinting and sediment source study by Westfield (2008); however, to compare the relative sediment accumulation rate at our survey locations, we deployed sediment traps with a diameter to height ratio of 3:1, as recommended by Gardner (1980) for low flow environments. Sediment traps have been used for decades to measure sedimentation rate on reefs, but there has been some controversy as to whether they effectively estimate the sediment accumulation experienced by the benthos (Storlazzi et al., 2011). Despite their pitfalls (see Storlazzi et al. (2011) for full review), sediment traps are still a relevant and useful method of obtaining relative trap accumulation rates in areas with low flow/horizontal currents (such as our study locations; NEPA Environmental Impact Assessment, 2005), provided that traps are designed correctly and values reported appropriately (Jordan et al., 2010; Storlazzi et al., 2011). Three sediment accumulation traps were placed 20–25 m apart at each site/depth combination ( $n = 36$  total;  $n = 12$  at each location) approximately 0.5 m above the benthos for 5–9 days in August 2010, January 2010, January 2011 and January 2012.

After collection, trap sediment was rinsed with distilled water, lyophilized or dried at 60 °C for 36 h and weighed. Sediment mass was standardized to the trap collection area and number of days to calculate trap accumulation rate (g m<sup>-2</sup> day<sup>-1</sup>). Analysis of the grain-size distribution and proportion of insoluble (non-carbonate) sediments was performed for the January 2012 trap samples. Mesh sieves (500 μm and 63 μm) were used to separate coarse sand and gravel (>500 μm) from coarse sand and very fine sand (63–500 μm) and silts and clays (<63 μm) (Krumbein, 1938). After sediments were sieved, sediment fractions were weighed and then digested in 10% HCl following recommended USGS procedures (Poppe et al., 2000) to dissolve the soluble material (e.g. calcium carbonate) from each size class within the samples. The remaining insoluble sediments were rinsed with deionized water 5 times, dried to a constant weight at 60 °C and re-weighed. Additionally, ~20 L of surface seawater was collected at each location in January 2012 and filtered through pre-weighed Millipore® glass fiber filters to quantify total suspended solids ( $n = 5$ ; 4 L per filter). Filters were immediately dried for 24 h at 60 °C and re-weighed.

## 2.3. Environmental parameters

To further characterize the locations, measurements of salinity, temperature and dissolved oxygen were made using a YSI-6600EDS from the surface to 15 m depth over a time period of 30 min at each location in January and August 2010, January 2011 and 2012. An optional chlorophyll sensor was used to measure the relative fluorescence units (RFU) (YSI6025; resolution: 0.1 μg/L or 0.1% RFU). Additionally, at each site and depth combination, HOBO® pendant temperature/light data loggers were secured alongside the sediment traps to stainless steel rods 0.5 m above the seafloor. Data loggers recorded temperature and light every 15 min during the same duration that sediment traps were deployed (i.e. 5–9 days); the analysis of light data was restricted to a 6-h period of peak and direct light intensity (09:30–15:30 h). Data logger light measurements are reported as photometric units (lux = lumens m<sup>-2</sup>). Wind data was obtained from the Sangster International Airport database of atmospheric conditions in Montego Bay, the closest official weather reporting station.

## 2.4. Survey protocol

Sponges were surveyed using 20-m belt transects at two distinct depths, 8–10 m and 15–18 m at each site nested within locations. Five transects were surveyed per site/depth combination for a total of 20 transects at each location ( $n = 10$  in shallow,  $n = 10$  in deep, per location). Transect surveys were performed randomly in August 2009, January 2010 and August 2010 to ensure that each location/depth was sampled at multiple times and seasons. Belt transects were laid out haphazardly by two divers; divers worked from both ends to count and measure sponges (to the nearest 1 cm) found within 1 m of one side of the transect tape (20 m<sup>2</sup>). For all sponges, volume was estimated based on the general morphology of each species. For example, several height, width and length measurements were taken for massive and bulbous sponges, and the volume was modeled by a series of rectangles; branching species were best modeled by a series of cylinders, therefore the length and circumference of each branch was recorded. Due to the difficulty in measuring the interior height and diameter of smaller tube sponges, all tube sponges were modeled as solid cylinders. The giant barrel sponge, *Xestospongia muta*, was best modeled as a semi-hollow frustum of a cone (McMurray et al., 2008). Encrusting sponges that were less than 1 cm in height were measured using surface area alone. The more complex the sponge, the greater the number of measurements taken to create

an appropriate series of geometric models for calculation of volumes. It is important to note that due to the simplicity of geometric shapes used to model sponges (e.g. solid cylinders, spheres, cubes, frustums, etc.), the calculated sponge volumes are not estimates of biomass, and are used only to compare relative sizes across locations and depths within our study.

Divers visually identified and photographed sponges *in situ*. For any unknown sponge, a small sample was collected and analyzed (e.g. through spicule characteristics) to determine its species. Only sponges living exposed on the substrate were surveyed, as it was not possible due to diving limitations to count and measure any cryptic sponges living under or in substrate (e.g. crevices, holes). Sponges were also classified morphologically (Zea et al., 2014) as branching, tube, fan/lobate, massive, encrusting, bushy or spherical to compare abundance and diversity of growth forms among locations.

### 2.5. Data analysis

For all data analyses, no differences between sites (western vs. eastern) were found within each location, therefore site data were combined for each location, and only location and depth were used as factors. All analyses were performed using R 2.15.1 (R Development Core Team, 2008).

Water quality parameters were compared using multiple one-way ANOVAs where the parameter of interest (e.g. salinity, chlorophyll *a* or dissolved oxygen) was compared between locations. To dampen the effects of season and depth, light data from HOBO® loggers were analyzed using depth and sampling period-specific anomalies as a metric (season \* depth specific means were subtracted from the means of each logger over the corresponding sampling period); a one-way ANOVA of anomalies by location was performed for each parameter to determine whether there were differences by location. Trap sediment accumulation rates ( $\text{g m}^{-2} \text{d}^{-1}$ ) from each date were analyzed using a two-way ANOVA on ranked data for differences in location and depth. Sediment grain size proportions and proportion of insoluble material were each analyzed using a two-way ANOVA for differences between location and depths. Total suspended solids (TSS) were analyzed using a one-way ANOVA to evaluate differences among locations. For all ANOVA models run, the Tukey HSD test was used when a significant main effect or interaction term was found to differentiate treatment levels.

Because the assumptions of ANOVA (equal variance and normality) were not met, we fit the over-dispersed abundance data to a quasipoisson-distributed generalized linear model (GLM) to test whether sponge abundance was related to location and depth; an analysis of deviance table was computed for the GLM using the F test. Multiple comparisons for the GLM were calculated using the Tukey HSD test in the *glht* function in the *multcomp* package of R. Proportion of sponges that were phototrophic were analyzed using a two-way ANOVA with depth and location as factors. A two-way ANOVA was used to determine location and depth differences in the proportion of boring sponges (Family Clionaidae), which may be more common on impacted reefs. Differences in species richness due to location and depth were assessed with a two-way ANOVA on ranks (a non-parametric test) after data failed to meet the assumptions of equal variance and normality. Species diversity was calculated using both the Shannon and Simpson's diversity indices and each was analyzed using a two-way ANOVA of diversity with location and depth as factors. To determine whether there were differences in the diversity of sponge morphologies a two-way ANOVA was used to test the main and interactive effects of location and depth on morphological diversity (Shannon index only). Sponge volumes were log-transformed and a two-way ANOVA was used to determine location and depth differences.

Sponge size frequency distributions were compared among locations using a two-sample Kolmogorov–Smirnov test.

Prior to ordination by non-metric multidimensional scaling (NMDS), species community composition data (species counts) were  $\log(x + 1)$  transformed to reduce the importance of rare species. The Bray–Curtis dissimilarity matrices of sponge communities were analyzed against 999 null permutations with the *ADONIS* function in the R package *vegan*, to test the effects of location and depth. The *ADONIS* function is a non-parametric multivariate analysis of variance (MANOVA) using distance matrices, which is considered more robust than an analysis of similarity (ANOSIM) (Anderson, 2001).

## 3. Results

### 3.1. Sediment accumulation and water quality

Overall sediment trap accumulation rates varied significantly by collection date ( $F_{(2,115)} = 76.397$ ;  $P < 0.001$ ). Tukey HSD post hoc analysis showed that January 2010 and 2012 traps were not statistically different from one another and had significantly higher rates of trap sediment accumulation ( $\text{g m}^{-2} \text{day}^{-1}$ ) than August 2010 and January 2011. To simplify subsequent analyses, these two time points—January 2010 and January 2012—were combined and analyzed together. Traps deployed during these two periods, January 2010 and 2012 captured sediment accumulation during high-wind events; the weather database from Sangster International Airport in Montego Bay reported that the highest sustained wind speed in 2010 occurred in January ( $13.4 \text{ m s}^{-1}$ ) and January 2012 experienced sustained winds between 8 and  $10.3 \text{ m s}^{-1}$  during trap deployment (Table 1). The January 2010 and 2012 trap accumulation rates were significantly different by location ( $F_{(2,36)} = 10.551$ ,  $P < 0.001$ ), however, depth was not significant ( $F_{(1,36)} = 3.645$ ,  $P = 0.06$ ) and no significant interaction term was found. During these collection periods, overall mean trap accumulation rates ( $\pm 1\text{SD}$ ;  $\text{g m}^{-2} \text{d}^{-1}$ ) at Pear Tree were an order of magnitude higher than the other two locations (Pear Tree:  $139.6 \pm 180.5$ , Discovery Bay:  $11.0 \pm 6.6$ , Dairy Bull:  $9.9 \pm 5.3$ ). Trap accumulation rates for the other time-points, August 2010 and January 2011, were not statistically different by location or depth. Mean sediment accumulation for the January 2011 and August 2010 sampling periods did not exceed  $3.0 \text{ g m}^{-2} \text{d}^{-1}$  at any of the locations or depths (Table 1).

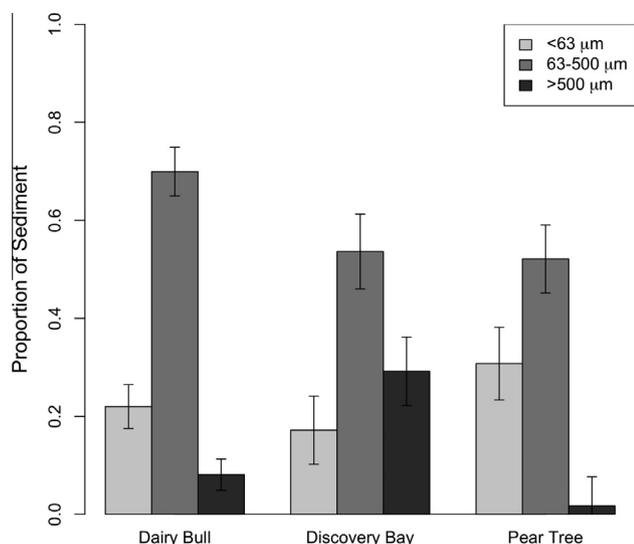
Grain size analysis from January 2012 traps revealed that Pear Tree sediments had a significantly higher proportion of silts and clays ( $< 63 \mu\text{m}$ ) than both Dairy Bull and Discovery Bay ( $F_{(2,21)} = 8.207$ ,  $P = 0.002$ ); depth was not a significant factor. Within the  $< 63 \mu\text{m}$  size class, the mean proportion of insoluble material was significantly higher at Pear Tree ( $F_{(2,24)} = 12.4$ ,  $P < 0.001$ ) than at the other locations. Proportion of sediments classified as sand ( $63\text{--}500 \mu\text{m}$ ) were significantly different by location ( $F_{(2,21)} = 6.136$ ,  $P = 0.008$ ), but not depth. Dairy Bull had the highest proportion of sediments that fell between 63 and  $500 \mu\text{m}$  (70%; Fig. 2) and was significantly different than Pear Tree (Tukey HSD:  $P = 0.006$ ) but not Discovery Bay. Sediments that were over  $500 \mu\text{m}$  were not statistically analyzed, since they were likely autochthonous reef debris (*Halimeda*, foraminiferans, etc.) that were too large to negatively impact sponges. The mean ratio of insoluble to soluble sediment collected in traps at Pear Tree was 0.153 for  $63 \mu\text{m}$  and 0.135 for  $63\text{--}500 \mu\text{m}$  size classes; ratios were 0.033 and 0.08 for Discovery Bay and 0.088 and 0.071 at Dairy Bull, respectively for the same size classes.

No differences in salinity, dissolved oxygen or chlorophyll *a* were found between locations. Mean water temperature in August was  $30.1 \pm 0.2 \text{ }^\circ\text{C}$  and January  $27.0 \pm 0.6 \text{ }^\circ\text{C}$ ; no statistical

**Table 1**

Trap accumulation rates ( $\text{g m}^{-2} \text{d}^{-1}$ ) over four collection periods from January 2010–January 2012 at all locations and depths. Mean total suspended solids (TSS;  $\text{mg L}^{-1}$ ), collected in January 2012 from the surface of the water, are reported for each location. Wind speeds ( $\text{m s}^{-1}$ ) were obtained from weather records at Sangster International Airport in Montego Bay, Jamaica. All values are means; standard deviations are denoted where applicable.

	Maximum sustained wind speed ( $\text{m s}^{-1}$ )	Mean wind speed ( $\text{m s}^{-1}$ )	Pear Tree		Discovery Bay		Dairy Bull	
			Shallow ( $\text{g m}^{-2} \text{d}^{-1}$ )	Deep ( $\text{g m}^{-2} \text{d}^{-1}$ )	Shallow ( $\text{g m}^{-2} \text{d}^{-1}$ )	Deep ( $\text{g m}^{-2} \text{d}^{-1}$ )	Shallow ( $\text{g m}^{-2} \text{d}^{-1}$ )	Deep ( $\text{g m}^{-2} \text{d}^{-1}$ )
January 2010	13.4	$4.18 \pm 1.51$	$365.8 \pm 132.5$	$323.2 \pm 173.9$	$16.9 \pm 4.7$	$11.4 \pm 6.1$	–	–
August 2010	9.0	$2.33 \pm 0.63$	$0.8 \pm 0.8$	$2.2 \pm 1.8$	$1.2 \pm 1.0$	$0.9 \pm 0.5$	$0.8 \pm 0.2$	$0.7 \pm 0.4$
January 2011	9.3	$3.25 \pm 1.02$	$1.5 \pm 1.6$	$2.0 \pm 2.2$	$0.9 \pm 0.4$	$2.2 \pm 2.7$	$2.6 \pm 2.2$	$1.1 \pm 0.3$
January 2012	10.3	$4.22 \pm 1.15$	$30.6 \pm 22.8$	$14.5 \pm 4.7$	$10.2 \pm 7.4$	$4.8 \pm 3.0$	$11.4 \pm 4.9$	$7.0 \pm 5.8$
TSS ( $\text{mg L}^{-1}$ )	–	–	$9.2 \pm 2.7$ (surface)		$6.6 \pm 2.4$ (surface)		$7.7 \pm 2.0$ (surface)	



**Fig. 2.** Mean proportion of sediments ( $\pm$  standard error) within each size class measured ( $>500 \mu\text{m}$ ,  $63\text{--}500 \mu\text{m}$  and  $<63 \mu\text{m}$ ).

differences among locations were found. No statistical differences in light ( $\text{lumens m}^{-2}$ ) were found among locations; however, overall Pear Tree light values were 18% lower than Dairy Bull and Discovery Bay in the shallow depth strata. At the deeper depth strata, overall light reaching the bottom at Pear Tree was 8% lower than Dairy Bull and 32% lower than Discovery Bay. Total suspended solids (TSS;  $\text{mg L}^{-1}$ ) measurements at the surface of the water ranged from 3.5 to 13.5  $\text{mg L}^{-1}$ ; mean TSS was highest at Pear Tree ( $9.23 \pm 2.73 \text{ mg L}^{-1}$ ) compared to Discovery Bay ( $6.63 \pm 2.41 \text{ mg L}^{-1}$ ) and Dairy Bull ( $7.65 \pm 1.99 \text{ mg L}^{-1}$ ) (Table 1). Total suspended solids (TSS;  $\text{mg L}^{-1}$ ) were statistically different by location ( $F_{(2,43)} = 4.99$ ;  $P = 0.01$ ); Pear Tree differed significantly from Discovery Bay (Tukey HSD:  $P = 0.01$ ) but no pairwise differences were found between Discovery Bay and Dairy Bull or Pear Tree and Dairy Bull.

### 3.2. Sponge abundance, species richness, diversity and size distribution

A total of 4046 sponges were sampled throughout the 60 surveys, representing 67 species, belonging to 27 families (Supp. Materials Table 1). An overall species accumulation curve was constructed and a distinct asymptote was reached, suggesting that further surveys were not warranted (Supp. Materials Fig. 1). Of the total number of sponges encountered during the surveys, 63% (2555 individuals) were found at Dairy Bull, while Pear Tree and Discovery Bay had only 16% and 21% of the total sponges, respectively. Overall sponge abundance and density were significantly higher in the deep than in the shallow strata ( $F_{(1,56)} = 15.36$ ;

$P < 0.001$ , Table 3D). Mean ( $\pm$  1SD) sponges densities ( $\text{m}^{-2}$ ) at the deep depth of all locations were  $1.82 \pm 0.60$ ,  $2.65 \pm 1.3$  and  $7.04 \pm 0.75$  for Pear Tree, Discovery Bay and Dairy Bull, respectively (see Table 2 for full abundance summaries). Mean sponge density in the shallows was slightly less: Pear Tree:  $1.34 \pm 0.53$ , Discovery Bay:  $1.91 \pm 0.54$  and Dairy Bull:  $5.49 \pm 1.12$ . Abundance was also significantly different among locations ( $F_{(2,57)} = 142.99$ ,  $P < 0.001$ ; Table 3D), with lower mean abundance found at Pear Tree and Discovery Bay; no significant interaction between location and depth was found (Table 3). No significant differences in the proportion abundance of either boring sponges (clonoids) or phototrophic sponges were found between locations or depths.

Mean and cumulative species richness were lower at Pear Tree and Discovery Bay than at Dairy Bull (Table 2). While species richness was consistently higher at the 15–18 m depth, this was not statistically significant; however, location was significant ( $F_{(2,54)} = 125.646$ ,  $P < 0.001$ , Table 3C) with the highest species richness recorded at Dairy Bull. Sponge diversity, calculated using both the Simpson's and Shannon indices (Table 2), was significantly higher at Dairy Bull regardless of which indices the two-way ANOVA was run on (Simpson's:  $F_{(2,54)} = 9.353$ ,  $P < 0.001$  and Shannon:  $F_{(2,54)} = 26.039$ ,  $P < 0.001$ ; see Table 2 for full summary of diversity values and Table 3A and B for statistical summary). The main effect of location was significant for the analysis of Shannon morphological diversity ( $F_{(2,54)} = 4.164$ ,  $P = 0.02$ ), although Tukey post hoc pairwise comparisons revealed that only Dairy Bull and Discovery Bay were significantly different (Tukey HSD adjusted  $P = 0.02$ ). The largest morphological contributors at Discovery Bay were massive (29%), encrusting (19%) and branching (18%) sponges. Dairy Bull was dominated by branching (27.5%) and massive sponges (25%), and Pear Tree was dominated by encrusting (27%) and massive (25%) morphologies (see Table 4 for depth-specific morphological breakdown).

Median and mean sponge volumes found along the surveys were calculated (Table 2). Mean sponge volume can be greatly skewed by a few extremely large (e.g. *X. muta*) or small individuals, therefore in a sponge community where sizes can range several orders of magnitude, median sponge volume may be a more appropriate descriptor of the size distribution. Median sponge volumes were under or around  $200 \text{ cm}^3$ , and Dairy Bull consistently had the lowest median volume at each depth (Table 2). Volume differences among location and depth combinations were analyzed using a two-way ANOVA on log-transformed data to reduce the influence of extremely large or small individuals; there was a main effect of location on volume ( $F_{(2,4160)} = 47.059$ ,  $P < 0.001$ ), but not depth, with a significant interaction term ( $F_{(2,4160)} = 16.731$ ,  $P < 0.001$ ). The volume of sponges was significantly different among locations according to Tukey HSD post hoc tests (Discovery Bay vs. Dairy Bull:  $P < 0.001$ ; Discovery Bay vs. Pear Tree:  $P = 0.02$ ; Dairy Bull vs. Pear Tree:  $P < 0.001$ ). Although Dairy Bull had the highest abundance of sponges, these sponges were also the least voluminous, on average.

**Table 2**  
Mean sponge density, abundance, richness, diversity and volumes (median is also presented) at each location and depth. Reported values are per transect (20 m<sup>-2</sup>) unless otherwise stated and are reported as mean (or median) ±1 standard deviation where applicable.

	Pear Tree (8–10 m)	Pear Tree (15–18 m)	Discovery Bay (8–10 m)	Discovery Bay (15–18 m)	Dairy Bull (8–10 m)	Dairy Bull (15–18 m)
Sponge density (m <sup>-2</sup> )	1.34 ± 0.53	1.82 ± 0.60	1.91 ± 0.54	2.65 ± 1.3	5.49 ± 1.12	7.04 ± 0.75
Sponge abundance (20 m <sup>-2</sup> )	26.7 ± 10.6	36.4 ± 11.9	38.1 ± 10.7	52.9 ± 25.9	109.7 ± 22.3	140.8 ± 15.0
Species richness	13 ± 3.1	15 ± 3.7	14.3 ± 2.7	17.8 ± 5.3	26.5 ± 2.3	28.1 ± 2.2
Cumulative species richness	38	42	41	50	53	56
Shannon Diversity (H')	2.24 ± 0.28	2.35 ± 0.26	2.26 ± 0.23	2.56 ± 0.32	2.83 ± 0.16	2.79 ± 0.12
Simpson's Diversity	0.87 ± 0.04	0.88 ± 0.03	0.87 ± 0.04	0.90 ± 0.04	0.92 ± 0.02	0.91 ± 0.02
Morphological diversity (H')	1.65 ± 0.19	1.70 ± 0.20	1.59 ± 0.20	1.71 ± 0.10	1.8 ± 0.13	1.73 ± 0.09
Mean sponge volume (cm <sup>3</sup> )	958.5 ± 3473.3	1541.1 ± 5888.3	3012.3 ± 21109.2	1406.2 ± 15598.3	404.1 ± 3256.5	1492.3 ± 29868.2
Median sponge volume (cm <sup>3</sup> )	67.3	112.7	201.1	108.0	57.5	72.0

**Table 3**  
Results of a two-way ANOVA testing the effects of location and depth on (a) the Shannon diversity (H'), (b) the Simpson's diversity, (c) and ranked species richness of sponges. Abundance data was fitted to a quasi-poisson distributed generalized linear model (GLM) and an analysis of deviance table was computed for the GLM using the F-test (d).

A	ANOVA	df	SS	MS	F-value	P	
<i>Diversity (Shannon Index, H')</i>							
Location		2	2.937	1.468	26.039	<0.001	
Depth		1	0.218	0.218	3.869	0.0543	
Location * Depth		2	0.300	0.150	2.664	0.0789	
Residuals		54	3.045	0.056	–	–	
<b>B</b>							
<i>Diversity (Simpson's Index)</i>							
Location		2	0.0203	0.0102	9.353	0.0003	
Depth		1	0.0031	0.0031	2.853	0.097	
Location * Depth		2	0.006	0.003	2.762	0.072	
Residuals		54	0.0587	0.0012	–	–	
<b>C</b>							
<i>Richness</i>							
Location		2	2034.5	1017.3	125.65	<0.001	
Depth		1	6.7	6.7	0.823	0.368	
Location * Depth		2	13.3	6.7	0.823	0.444	
Residuals		54	437.2	8.1	–	–	
<b>D</b>							
<i>Abundance</i>							
Location	GLM	2	1427.44	57	360.14	143.0	<0.001
Depth		1	76.65	56	283.5	15.36	0.0003
Location * Depth		2	1.21	54	282.28	0.121	0.886
Residuals		–	–	59	1787.6	–	–

**Table 4**  
Depth-specific morphological classifications at each location; values are the total percent of sponges classified by morphology at each location/depth.

Morphology	Dairy Bull (8–10 m) (%)	Dairy Bull (15–18 m) (%)	Discovery Bay (8–10 m) (%)	Discovery Bay (15–18 m) (%)	Pear Tree (8–10 m) (%)	Pear Tree (15–18 m) (%)
Branching	22	33	18	17	14	22
Bushy	2	1	0.7	3	3	2
Encrusting	19	13	17	20.5	29.5	24
Lobate	12	10	19	8	13	4.5
Massive	24	27	25	35	23	27
Spherical	7	4	1.5	1	7	5.5
Tube	15	12	17.5	15	10	12
Unknown	<0.1	<0.1	0.5	<0.1	0	2.7

Pairwise comparisons of size frequency distributions compared between the three locations using the Kolmogorov–Smirnov test were significant, indicating that size distribution was different at each location (Dairy Bull vs. Pear Tree:  $D = 0.08$ ,  $P < 0.001$ ; Dairy Bull vs. Discovery Bay:  $D = 0.15$ ,  $P < 0.001$ ; Discovery Bay vs. Pear Tree:  $D = 0.095$ ,  $P = 0.002$ ); refer to Fig. 3 for log-transformed size distributions. Untransformed size distributions at Pear Tree and

Discovery Bay were both negatively skewed, with a greater number of large individuals, whereas Dairy Bull was positively skewed, with many small individuals. Dairy Bull had the largest range of sizes represented; the largest individual sponge volume recorded in any of the surveys at Pear Tree was only 86,016 cm<sup>3</sup>, whereas the largest individuals at Discovery Bay and Dairy Bull were 372,738 cm<sup>3</sup> and 1,113,425 cm<sup>3</sup>, respectively.

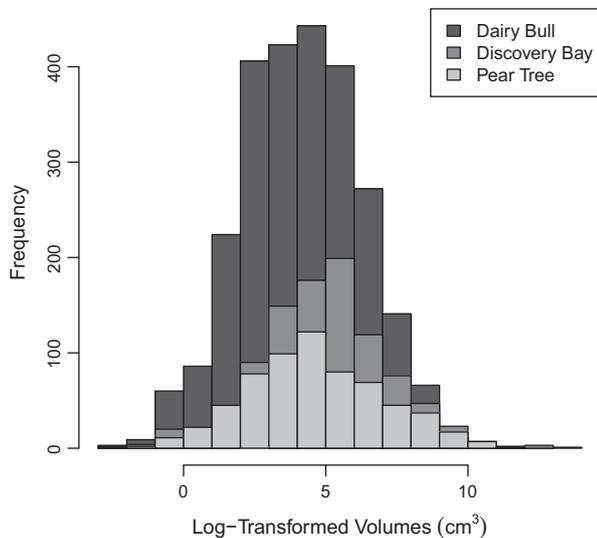


Fig. 3. Frequency distribution of log-transformed sponge volumes at each location.

### 3.3. Community composition

Species community composition patterns were visualized using an nMDS ordination (Supp. Materials Fig. 2); however, the stress level was high ( $>.20$ ), indicating that the 2D-plot was not an accurate portrayal of the data in high-dimensional space. The ADONIS analysis, which runs in high dimensional space and is therefore able to statistically interpret the non-metric dimensional scaling, indicated that there were significant differences in community composition between locations and depths. The ADONIS output indicated that clustering was significant; although the relative contribution of the location and depth factors were generally low – location explained just 19% ( $F = 6.908$ ,  $R^2 = 0.1902$ ,  $P = 0.001$ ) of the variation and depth 4.3% ( $F = 3.091$ ,  $R^2 = 0.0426$ ,  $P = 0.002$ ).

## 4. Discussion

### 4.1. Sedimentation

Our study compared the relative sedimentation rates at three locations with different intensities of coastal development along the north coast of Jamaica and found that sediment accumulation was variable and influenced by wind events. During four periods of sediment monitoring, January 2010, August 2010, January 2011, and January 2012, we were able to capture two wind and wave energy events (January 2010 and January 2012, Table 1) and it was only during these times that Pear Tree, the most developed study location, had statistically higher rates of gross sediment deposition than the other two locations. Sediment deposition at Pear Tree was highest when mean wind speeds were  $>3.5 \text{ m s}^{-1}$  and maximum sustained wind speed exceeded  $10 \text{ m s}^{-1}$ ; these conditions occurred 184 times between 2008 and 2014, an average of  $26.1 \pm 21.6$  occasions  $\text{year}^{-1}$ , indicating that sediment deposition at Pear Tree is primarily wind-driven, and therefore a chronic, yet episodic event.

The mean trap accumulation rates at Pear Tree during the wind events in January 2010 and 2012 were an order of magnitude higher than the accumulation rates at Discovery Bay and Dairy Bull (Table 1). While caution should be used when comparing sedimentation studies using different methods/trap designs (Storlazzi et al., 2011), the overall sediment accumulation rates at Discovery Bay and Dairy Bull remained at or below the range of sediment accumulation previously reported as typical or ‘natural’

( $<10 \text{ g m}^{-2} \text{ day}^{-1}$ ) on reefs not subjected to stress (Rogers, 1990) even when they experienced high wind energy. Mean trap accumulation rates at Pear Tree exceeded this  $10 \text{ g m}^{-2} \text{ day}^{-1}$  threshold during periods of high wave activity, and therefore would be categorized as experiencing periodically ‘high’ levels of sedimentation by Rogers (1990). It is important to note that this threshold (Rogers, 1990) may not be an accurate measure of whether sedimentation is ‘high’ on reefs, as it was based on various sedimentation studies using multiple trap designs (Storlazzi et al., 2011). Previous work in the Discovery Bay lagoon by Dodge et al. (1974) reported trap accumulation rates ranging from  $0.5$  to  $1.1 \text{ g m}^{-2} \text{ day}^{-1}$ , which are comparable to the accumulation rates found in this study during periods of low wind.

Not only is the rate of sediment accumulation higher at Pear Tree, but there is also a significant difference in the proportion of sediments that are classified as silts and clays ( $<63 \mu\text{m}$ ); see Fig. 3. Additionally, the amount of insoluble silts and clays was significantly higher at Pear Tree than at the other two locations. Westfield (2008) found that sediments collected from Pear Tree exhibited a higher proportion of smaller grain sizes and insoluble sediments than Dairy Bull and Discovery Bay, and attributed the increase in insoluble residue to the runoff from the construction of the resort and expansion of the Queen’s Highway in 2005–2007.

Westfield (2008) found no geochemical evidence that the Pear Tree Bottom River, which discharges into an embayment approximately 2 km west of Pear Tree, contributed to the sediments found at the Pear Tree location. Due to the easterly long-shore currents, this small river does not typically influence our study locations. During the January 2012 wind event, we found a gradient of TSS (e.g. silts and clays) from east to west, which suggests that the river may alter the amount of suspended material during wind/wave events at our locations. No differences in surface salinity were found among the locations at any time; however, the fluvial signal may have been lost in January 2012 due to heavy wind mixing. An alternative explanation for the elevated suspended solids and sediment accumulation may be the wind and wave-driven erosion of a small dry canal filled with terrigenous sediment that is located approximately 500 m east of the Pear Tree location (Westfield, 2008). This may be a more likely explanation of the elevated TSS and higher levels of insoluble silts and clays found at Pear Tree than the river, given the easterly long-shore currents and lack of salinity differences found.

### 4.2. Sponge community

Several differences in the sponge communities were found among the three locations, although in many ways Dairy Bull, the location with the least coastal development, was the atypical location. Sponge abundance was significantly different among locations, with the number of sponges found at Dairy Bull an order of magnitude higher than at Discovery Bay and Pear Tree. Dairy Bull also had significantly higher sponge species richness and diversity than Discovery Bay and Pear Tree. While size distributions of sponges were statistically distinct among all locations, Dairy Bull had the smallest mean and median sponge volume of the three locations.

The literature is replete with studies focused on the ecological (biotic) and physical (abiotic) factors influencing sponge abundance, richness and diversity. Ecologically, patterns are attributed to factors such as predation (Wulff, 2000; Pawlik, 1998) and food availability (Lesser, 2006; Lesser and Slattery, 2013; Pawlik et al., 2013). Major sponge predators in the Caribbean include spongivorous fish, (Pawlik, 1995), the Hawksbill sea turtle (Meylan, 1988), and sea stars (Wulff, 2000). While previous studies have suggested that spongivory structures tropical sponge assemblages (Pawlik, 1995), it is unlikely that predation resulted in the sponge

distribution patterns observed in this study. No sponge tissue damage or predation scars indicative of sea turtle or fish predation were recorded in our surveys; additionally, spongivorous fish are almost completely absent along the north coast of Jamaica (Loh and Pawlik, 2014) due to heavy fishing pressure.

Whether Caribbean sponges are, or can be, food limited has been hotly contested (e.g. Lesser and Slattery, 2013; Pawlik et al., 2013), yet growing evidence suggests that bottom-up processes on reefs do not limit sponge abundance or distribution (see review by Pawlik et al., 2015). Regardless, we found no evidence that chlorophyll *a* concentrations varied among our study locations, suggesting that phytoplankton abundance is not contributing to the observed differences in sponge communities. Further, recent evidence suggests that sponges are able to utilize DOM and DOC (de Goeij et al., 2013; Mueller et al., 2014) and are unlikely to be limited by phytoplankton abundance. Additionally, many of the species in our surveys are known to contain high abundances of photosynthetic symbionts (Erwin and Thacker, 2007) and would therefore not depend solely on allochthonous food sources in the water column for nutrition and growth. In their review of the evidence of food limitation in sponges, Pawlik et al. (2015) proposed that phototrophic sponges should dominate Caribbean communities, as they do in the Great Barrier Reef, if food availability were a problem. We found no significant differences in the proportion of phototrophic sponges among locations or depths further supporting our assumption that food availability or light did not structure sponge communities at our locations.

Abiotic, or physical, factors affecting sponge distribution are more numerous and complex; environmental factors such as light/depth (Wilkinson and Cheshire, 1989), water flow (Bell and Barnes, 2000a,b), water quality (Rose and Risk, 1985; Holmes, 2000), and sedimentation (Bell and Smith, 2004) have all been credited with structuring sponge communities. Among our three locations we found no statistical difference in light; water flow, although not measured, qualitatively did not differ between locations. Water quality—specifically, the concentration of nutrients—was not assessed directly; however, chlorophyll *a* concentration, an indicator of water quality sensitive to nutrient loading (Boyer et al., 2009), did not differ among locations, suggesting that nutrient differences were either minimal or not exploited by the phytoplankton.

Evidence that Caribbean sponge distributions can be affected by eutrophication is largely limited to boring sponges, with significant increases in clionaid infestation found at sites with elevated land-based nutrients (Ward-Paige et al., 2005), organic pollution (Rose and Risk, 1985) and eutrophication (Holmes, 2000). Interestingly, the abundance of boring sponges was not significantly different between our locations. The analysis of clionaid abundance indicated that the proportion of this bioeroding sponge family was higher at Pear Tree (13%) than at either Discovery Bay or Dairy Bull (7% each), yet these differences were not significant ( $P = 0.08$ ).

Sediment stress has previously been implicated in structuring the species composition and size distributions of sponges. Carballo (2006) found that tropical sponge assemblages in the Mexican Pacific were significantly impacted by seasonal changes in sediment accumulation, both in terms of abundance and distribution, but also size. When sediment disturbance was highest, a shift from large-bodied to small-bodied species occurred (Carballo, 2006), reducing the overall sponge biomass. Volumetric response at our study locations displayed no obvious pattern that corresponded with sedimentation. Although size distributions were statistically distinct among all locations, Pear Tree and Discovery Bay had negatively skewed sponge size distributions, while Dairy Bull had a positively skewed population. The negatively skewed distributions at Discovery Bay and Pear Tree

suggest that recruitment rates are low and/or mortality of small individuals is high. The positively skewed sponge distribution and wide range of sponge sizes at Dairy Bull indicates a healthy population with high recruitment, which has been shown in coral and sponge populations (Meesters et al., 2001; Duckworth et al., 2009).

Sediment deposition was found to negatively affect the overall sponge community assemblages in several studies (Carballo, 2006; Nava and Carballo, 2013; Bell and Smith, 2004). This study found differences in the multivariate community composition among locations and depths (Supp. Materials Fig. 2). There were several noticeable differences in sponge species found within the communities (Supp. Materials Table 1), such as the absence of *Chondrilla caribensis* at Dairy Bull. *C. caribensis* (formerly referred to as *Chondrilla nucula*) is gaining notoriety as an indicator of degraded systems. *C. caribensis* has been reported rapidly colonizing areas where corals have been damaged and, in areas, becoming the dominant component of the benthos (Aronson et al., 2002; Norström et al., 2009). Several other common reef species were conspicuously absent from the Pear Tree surveys, such as *X. muta*, *Ectyoplasia ferox*, *Mycale laxissima* and *Verongula gigantea*, all of which are large, long-lived species. Nineteen species were found at either Discovery Bay or Dairy Bull, but were absent from Pear Tree, whereas the number of species absent at Dairy Bull but found elsewhere was only six (Supp. Materials Table 1). Although many of these species may make up a much smaller (in terms of abundance and biomass) proportion of the community, there is still a notable absence of commonly occurring species at Pear Tree.

Overall, there seem to be no distinct patterns that implicate sedimentation as the driver of sponge community differences among locations. Accounts of sponge abundance and species composition (both qualitative and quantitative) through the 1990s suggest that these sponge communities were once very similar (Lehnert and Fischer, 1999; Lehnert and van Soest, 1998). However, since this time few studies of sponge community structure have been published (but see Loh and Pawlik, 2014). Therefore, the exact timeline of sponge community divergence between these locations is unknown. During our surveys, there were subtle differences between some, but not all, of these locations. Discovery Bay was most similar to Pear Tree (diversity, species richness), while Dairy Bull was distinct, or all locations were statistically different from each other (abundance, community composition, size distribution). Our inability to attribute these differences between communities to one particular environmental factor may have been limited because the differences between the sponge communities were subtle enough that eliciting a statistical difference between all three locations was not possible.

While we are beginning to recognize the importance of sponges in coral reef ecosystems, the impacts of coastal development are still largely unknown for sponges. Overall, we observed that Dairy Bull, the location with no coastal development, had higher sponge abundance, diversity and a wider range of size distributions than the other two locations. Although the exact mechanism is unclear, our study provides correlative evidence that coastal development is influencing sponge communities on reefs along the northern coast of Jamaica.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.marpolbul.2015.05.014>.

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