



## Adaptive mechanisms and physiological effects of suspended and settled sediment on barrel sponges



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### ABSTRACT

Coral reefs across the Indo-Pacific are among the most diverse in the world but like reefs globally, they remain vulnerable to a multitude of stressors, including coastal development and the resultant sedimentation. In the Wakatobi Marine National Park, Indonesia, some degraded reefs are characterised by high levels of sedimentation and low coral cover, but support large populations of the ecologically important giant barrel sponge *Xestospongia testudinaria* (Lamarck 1815). Barrel sponges can have a strong influence on water characteristics, yet tolerance and responses to sedimentation are unknown. This study examined the physiological effects of short-term exposure of *X. testudinaria* to suspended sediment. Respiration rates increased compared to controls when sponges were exposed to environmentally relevant suspended sedimentation concentrations of 75 and 150 mg l<sup>-1</sup>. Sponge mucus production was observed as a mechanism to remove settled sediment for the first time and sediment clearance was filmed *in situ* over the course of 24 h. Sponges produced mucus in response to sediment addition, with a mean clearance rate of 10.82 ± 2.04% h<sup>-1</sup> (sediment size fractions 63–250 μm). Mucus production is an effective, but slow mechanism supporting barrel sponge survival in habitats experiencing high levels of sedimentation. Our results show that there are likely to be energetic consequences for sponges living in sedimented environments, which may influence the energy available for other demographic processes, and therefore have implications for barrel sponge population sustainability.

### 1. Introduction

It is widely recognized that coral reefs are among the most highly productive and biologically diverse ecosystems on Earth, providing ecosystem goods and services vital to tropical and subtropical nations (Moberg and Folke, 1999). Despite their value, over half of coral reefs worldwide are considered under threat (Burke et al., 2011), and the multitude of natural and anthropogenic pressures associated with global coral reef decline have been well documented (Wilkinson, 1999; Hoegh-Guldberg et al., 2007; Wild et al., 2011; Perry et al., 2013). Unsustainable land conversion practices such as urbanization, deforestation, and increased agricultural pressures result in runoff and erosion (Airoldi, 2003; McLaughlin et al., 2003; Syvitski et al., 2005), increasing terrigenous sediment loads that may reach near shore waters (Thrush et al., 2004; Bannister et al., 2012; Stender et al., 2014). The impacts of sedimentation are diverse and have been shown to be deleterious to scleractinian corals (see Fabricius, 2005 for a review), but its impact on other reefs organisms is less clear.

Despite sponges being important components of corals reefs, we

have a much poorer understanding of how they are impacted by sedimentation compared to corals (see Bell et al., 2015 for review). Although some sponge species are able to tolerate and even thrive in highly sedimented habitats, there is strong evidence that sedimentation is often deleterious to sponges at the individual and population level (see Bell et al., 2015 for a review). Settled sediment can directly affect sponges via burial or smothering (Wulff, 1997), while sediment can cause tissue scour/abrasion when carried in suspension (Rogers, 1990; Ilan and Abelson, 1995), resulting in partial mortality and reduced survival (Wulff, 1997; Maldonado et al., 2008). Sponges are obligate filter feeders and the experimental addition of fine suspended sediments has been shown to reduce or arrest pumping rates in several sponge species (Gerrodette and Flechsig, 1979; Leys et al., 1999; Tompkins-MacDonald and Leys, 2008; Bannister et al., 2012). As pumping is required to feed, clogging by fine sediment may reduce feeding efficiency and particle retention (Lohrer et al., 2006), as well as respiration (Gerrodette and Flechsig, 1979).

Although sedimentation is generally considered to have negative impacts on sponges, high sponge diversity (e.g. Bell and Smith, 2004;

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Knapp et al., 2013) and abundance (Powell et al., 2014) have been reported from some sedimented sites. For example, in Indonesia, sponge densities have increased over the last decade at some highly sedimented sites (Bell and Smith, 2004; Powell et al., 2010, 2014), while habitat quality and coral cover have simultaneously decreased (Powell et al., 2010). Some sponge species appear to tolerate sedimentation and turbid conditions, and demonstrate specific adaptations that allow them to persist in conditions classically considered sub-optimal for suspension feeders. Active and passive responses are employed by sponges to rid the sponge surface of settled sediment or prevent it from settling (Bell, 2004). Active responses to sedimentation include an alteration or cessation of pumping rates (Gerrodette and Flechsig, 1979; Tompkins-MacDonald and Leys, 2008), physically moving away from sedimented areas in the case of larvae (Maldonado and Uriz, 1999), and the production of mucus (Turon et al., 1999; Bannister et al., 2012). Passive responses include macro-morphological and skeletal-level structural modifications (Barthel and Tendal, 1993; Bell et al., 2002; McDonald et al., 2002; Bell, 2004; de Voogd and Cleary, 2007; Schönberg, 2014), and positioning of the inhaled ostia and osculum to prevent sediment from settling (Bell, 2004).

Changes in respiration rates in response to sediment addition have been examined in a number of sponge species with contrasting results. Following exposure to sediment, sponge respiration rates have been shown to both increase (Bannister et al., 2012) and decrease (Lohrer et al., 2006; Tjensvoll et al., 2013). Increased respiration rates may reflect the energetic requirements of sediment clearance mechanisms, such as mucus production following short term exposure, whereas respiration rates may decrease due to a reduction in pumping rate to prevent sediment ingestion (Bell et al., 2015). Sediment size, mineralogy (Bannister et al., 2012), and concentration (Tjensvoll et al., 2013) may influence these responses. The energetic costs of producing a sediment response is expected to incur additional metabolic costs to the sponge, presumably at the expense of other demographic processes such as growth and reproduction (Reiswig, 1971; Roberts et al., 2006; Whalan et al., 2007; Bannister et al., 2012). Other benthic organisms, such as corals, have been reported to produce energetically costly mucus as a sediment removal mechanism (Riegl and Branch, 1995). The production of mucus as a sediment clearing mechanism has also been observed in several sponge species (Gerrodette and Flechsig, 1979; Turon et al., 1999; Kowalke, 2000; Bannister et al., 2012), though the energetic costs have yet to be determined.

Some of the most conspicuous sponges on coral reefs fall into the genus *Xestospongia*, which include the giant barrel sponges. *Xestospongia* species can grow up to several meters in diameter and live to be hundreds or possibly even thousands of years old (McMurray et al., 2008; McClain et al., 2015). The Caribbean species *X. muta* has been thoroughly studied and found to be ecologically important on coral reefs, largely due to its ability to modify water quality characteristics (e.g. López-Legentil and Pawlik, 2008; López-Legentil et al., 2008; McMurray et al., 2008, 2010, 2015; Southwell, 2008; McClain et al., 2015). Indo-Pacific *Xestospongia* species, however, have received far less attention, despite their abundance and likely similar function in reef ecosystems (but see Fromont and Bergquist, 1994; Swierts et al., 2013; Bell et al., 2014). Sponges, including *Xestospongia* spp., play a variety of functional roles that mediate water column processes (Bell, 2008; Maldonado et al., 2012), including highly efficient removal of picoplankton and bacteria (Pile et al., 1997; Perea-Blazquez et al., 2012) and nutrient cycling (Southwell, 2008; de Goeij et al., 2013; Fiore et al., 2013). In addition, *Xestospongia* spp. are phototrophic and contain a dense microbial community (Montalvo and Hill, 2011), so also contribute to primary production on reefs. Due to their size, ability to pump vast quantities of water (McMurray et al., 2014), and influence biogeochemical processes, changes in *Xestospongia* productivity and abundance could have significant impacts on reef function, particularly in systems impacted by reduced water quality.

Previous research on *Xestospongia* spp. populations in the Indo-

Pacific has demonstrated that this species has high levels of self-recruitment, small population sizes, and low larval dispersal rates (Bell et al., 2014). These characteristics, in addition to the slow growth rates reported for their Caribbean congener *X. muta*, suggest that these populations should be susceptible to environmental disturbance (Bell et al., 2014). However, Bell et al. (2014) reported that *Xestospongia* spp. were very abundant at sites experiencing high levels of sedimentation and habitat degradation. These factors, in conjunction with the presence of large and likely old individuals in these habitats, support the hypothesis that barrel sponges likely possess physiological traits enabling them to tolerate high-sediment environments (Bell et al., 2014).

Given the current trends in coastal development and resultant sedimentation expected to reach coral reefs, it is important to understand the effects that sedimentation may have on *Xestospongia* spp. In this study we aimed to: 1) quantify settled and suspended sediment on a degraded reef dominated by *Xestospongia testudinaria*, enabling environmentally relevant sediment addition experiments; 2) observe the occurrence, location, and rate of sediment accumulation on *X. testudinaria* individuals; 3) observe and measure *X. testudinaria* mucus production as a settled sediment removal mechanism; 4) examine the effects of sedimentation on *in situ* sponge respiration rates for different suspended sediment treatments.

## 2. Methods

### 2.1. Study site

This study was conducted in the Wakatobi Marine National Park (WMNP; 05°29.6S, 123°45.26E; Fig. 1). The WMNP, located in south-east Sulawesi, Indonesia, is the most populated marine national park in Indonesia (Clifton and Unsworth, 2010). Located in the coral triangle, the WMNP contains some of the highest marine diversity in the world, yet is heavily impacted by a local population of over 100,000 people that are reliant on the reef as a resource (Cullen, 2010). Hard coral cover in the WMNP has declined substantially over the last decade; surveys conducted from 2000 to 2007 revealed that coral cover decreased an average of 45% across six sites over that time (McMellor and Smith, 2010). Using microsatellite analyses and external morphological examination, Bell et al. (2014) revealed that barrel sponges in the WMNP are comprised of a species complex, likely including *Xestospongia testudinaria*, *X. bergquistia*, and one undescribed species. As such, only individuals corresponding to the *X. testudinaria* morphology, as previously determined by Bell et al. (2014), were chosen for this study.

Hoga Reef is a shallow sloping reef on the southwest corner of Hoga Island in the centre of the WMNP (Fig. 1), and was the collection site of barrel sponges for our experiments. This site has moderate coral cover (30–40% cover), and low turbidity and sedimentation rates. Sampela 1 has low environmental quality due to close proximity (< 1 km) to the large populations of Sampela Village and Kaledupa Island. The site has high sedimentation rates, low (and decreasing) coral cover and low fish abundance compared to other sites in the vicinity (Crabbe and Smith, 2002; Curtis-Quick, 2013; Bell et al., 2014). Due to the limited availability of suitably small sponges for use in our *in situ* respiration chamber at Sampela 1, sponges used in the respiration experiment were harvested from Hoga Reef and moved the short distance (approx. 100 m) to a single location at Sampela 1. While the sedimentation and turbidity rates differ between the sites, the flow rates are low at both sites (approx 5 cm<sup>-1</sup>; see Powell et al., 2014). The sponges were left to acclimate to the new conditions for two weeks and inspected prior to experimentation for any signs of tissue necrosis. Sediment data were collected in May–July 2015 and 2016, *in situ* respiration experiments were performed from June to August 2015, and mucus clearance experiments were conducted from June to August 2014 and 2015. All statistical analyses were performed by SPSS v. 22 and plotted with SigmaPlot v. 11.0. Data were tested for normality and homogeneity of variance and met the assumptions of the statistical analyses that we

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