Bleaching and recovery of a phototrophic bioeroding sponge

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NOTE

Bleaching and recovery of a phototrophic bioeroding sponge

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Abstract In the Wakatobi region of Indonesia, a prolonged period of elevated water temperature in 2016 caused extensive coral bleaching and mortality. Unusually, bleaching was also observed in the bioeroding sponge *Cliona* aff. *viridis*, with affected sponges expelling 99% of their *Symbiodinium*. Bleaching surveys of *C.* aff. *viridis* were conducted 6 weeks apart, coinciding with a 0.8 °C drop in water temperature. Over this period, bleaching prevalence dropped from 73.9% (± 9.9 SE) to 25.7% (± 5.8 SE), and bleaching severity dropped from 25.95% (± 4.5 SE) to 11.54% (± 1.9 SE) of sponge tissue. Over the same period, monitored bleached sponges showed an 81% drop in bleaching severity, but also a 13% reduction in overall sponge size. Our results show that while the clionaid–*Symbiodinium* relationship is susceptible to break down under thermal stress, rapid recovery can occur, although incurring some partial host mortality.

Keywords Bleaching · *Cliona* · Bioerosion · Climate change

Introduction

The survival of coral reefs across the globe is threatened by ocean warming and acidification as a result of climate change (Hoegh-Guldberg et al. 2007). This has predominantly and most dramatically manifested as global-scale coral bleaching events in 1997–1998, 2010 and 2014–2016, with an associated extensive coral mortality (Hughes et al. 2017). Despite these climate change impacts on corals, other *Symbiodinium*-hosting reef taxa are thought to be more resilient to the impacts of temperature stress. Bioeroding sponges of the Clionaidae family are one such group, many of which harbour *Symbiodinium* (Rützler 1990). For these organisms, bioerosion rates are expected to increase with rising $p\mathrm{CO}_2$, which possibly has an ameliorating effect on temperature stress (e.g. Fang et al. 2013; Wisshak et al. 2013). Furthermore, *Symbiodinium*-containing clionaids have been observed to remain unchanged during thermal events that have resulted in bleaching of corals (Vicente 1990), and bioeroding sponge abundance has increased after some coral bleaching events (Schönberg and Ortiz 2009; Carballo et al. 2013). The apparent thermal resilience of the *Symbiodinium*-sponge association has been attributed to high thermal tolerance of the clade G symbionts associated with many clionaid sponges (Schönberg et al. 2008) and the ability of some sponges to redistribute symbionts into deeper tissues during periods of stress (Schönberg and Suwa 2007). To date, the only reported bleaching of clionaid sponges (outside of ex situ manipulations) occurred in the Florida Keys in 2015, when the mass bleaching of *Cliona varians* was associated with a prolonged period of thermal stress (31–32 °C; Hill et al. 2016).

The Wakatobi region of south-east Sulawesi, Indonesia, harbours highly diverse coral reefs (McMellor and Smith

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2010), and due to large seasonal thermal variation, the region's corals are thought to be relatively resilient to elevated temperature events (Wilson et al. 2012). In the 2010 bleaching event, 65% of the corals were affected, but mortality was estimated at less than 5% (Wilson et al. 2012). During July 2016, we observed widespread coral bleaching on reefs in the Wakatobi. Satellite data from the National Oceanic and Atmospheric Administration's Coral Reef Watch programme (herein: NOAA) showed that previously in early May, sea surface temperature in the Wakatobi had briefly reached (3 d) the regional bleaching threshold of 30.6 °C (1.5 °C above the monthly norm), but by July had dropped to approximately 28.5 °C. The extent of the coral bleaching was not assessed, but was potentially of greater magnitude than the 2010 event; sea surface temperature across Indonesia was about 0.4 °C higher in the peak of the 2016 event than in 2010 (Wouthuyzen et al. 2018). Unusually, this bleaching event not only was restricted to cnidarians but also was also seen in a locally abundant zooxanthellate bioeroding sponge, *Cliona* aff. *viridis*. The primary aim of this study was to determine the prevalence and severity of the sponge bleaching and assess capacity for recovery. Additionally, the hypothesis that *Symbiodinium* retraction can convey bleaching resilience in clionaids (Schönberg and Suwa 2007) was tested.

Methods

Study site and species

This study was conducted at two reef sites on the fringing reef off Hoga Island in the Wakatobi (Fig. 1). Pak Kasim's is a sloping reef with a mixed composition of complex corals, rubble and sandy areas, while Buoy 3 is a shaded reef wall with high cover of low complexity corals and a high diversity of sponges. A HOBO temperature data logger was deployed at each site for the period of the study. *C.* aff. *viridis* is an encrusting *Symbiodinium*-containing bioeroding sponge that is locally abundant and is most commonly found at approximately 10–15 m depth. Previous work (J. Marlow unpubl. data) has found that this species relocates symbionts deeper into the sponge tissue on a diurnal basis in a similar way to *Cliona orientalis* (Fang et al. 2016).

Bleaching and recovery assessment

An initial assessment of clionaid bleaching prevalence and severity was conducted in early July 2016. Three 50 × 1 m phototransects were conducted at 5, 10 and 15 m depth at each site ($n = 18$), and on each transect, all individuals of *C.* aff. *viridis* were located and photographed next to a scale bar and greyscale colour chart (DeepPro Systems, Bellingham). These surveys were then repeated 39 d later in mid-August to ascertain whether there had been any recovery from bleaching at the population level. Over the same period, eight of the most severely bleached sponges (> 30% severity) were tagged at 10 and 15 m depth at both sites ($n = 32$). As sponge abundance was generally found to be lower at 5 m depth, sponges at this depth were not tagged. Tagged sponges were photographed next to a scale bar and colour chart on a near-weekly basis (d 0, 15, 22, 29 and 36).

Differences in *Symbiodinium* density in bleached and unbleached sponges were determined from tissue samples obtained from seven bleached and seven unbleached sponges at 10 m depth on the Pak Kasim's reef. Columnar cores (7 × 20 mm) were taken from each sponge, ensuring each core contained all sponge tissue layers and a small degree of substrate underneath. *Symbiodinium* cells were isolated from the sponge cores using NaOH extraction (Zamoum and Furla 2012), and cell counts were determined using a haemocytometer and standardised to sponge core surface area.

Image and statistical analysis

The surface area of all sponges (both from surveys and those tagged) was measured using the image analysis software ImageJ. Bleaching prevalence, i.e. either bleached or unbleached, was identified by eye. For those bleached individuals, bleaching severity was analysed as surface area bleached as a percentage of total surface area using ImageJ.

All statistical analyses were performed within the SPSS statistical analysis package (version 23). Differences in bleaching prevalence, bleaching severity and sponge size were analysed using generalised linear mixed models (GLMMs) with depth, sites and time as fixed effects and transect as random effect. Bleaching prevalence was assessed using untransformed data and a binary logistic regression, while bleaching severity and sponge size data were log transformed and analysed using a linear model. For the tagged sponges, changes in bleaching severity and sponge size over the observation period were tested using a repeated-measures ANOVA, with time, depth and site as fixed factors. Where data violated the assumption of sphericity, a Greenhouse–Geisser correction was applied.

Results and discussion

Water temperature when the first surveys were conducted (28.4 °C ± 0.008 SE) had dropped considerably since the May temperature maxima of 31 °C, but was still ~ 0.7 °C

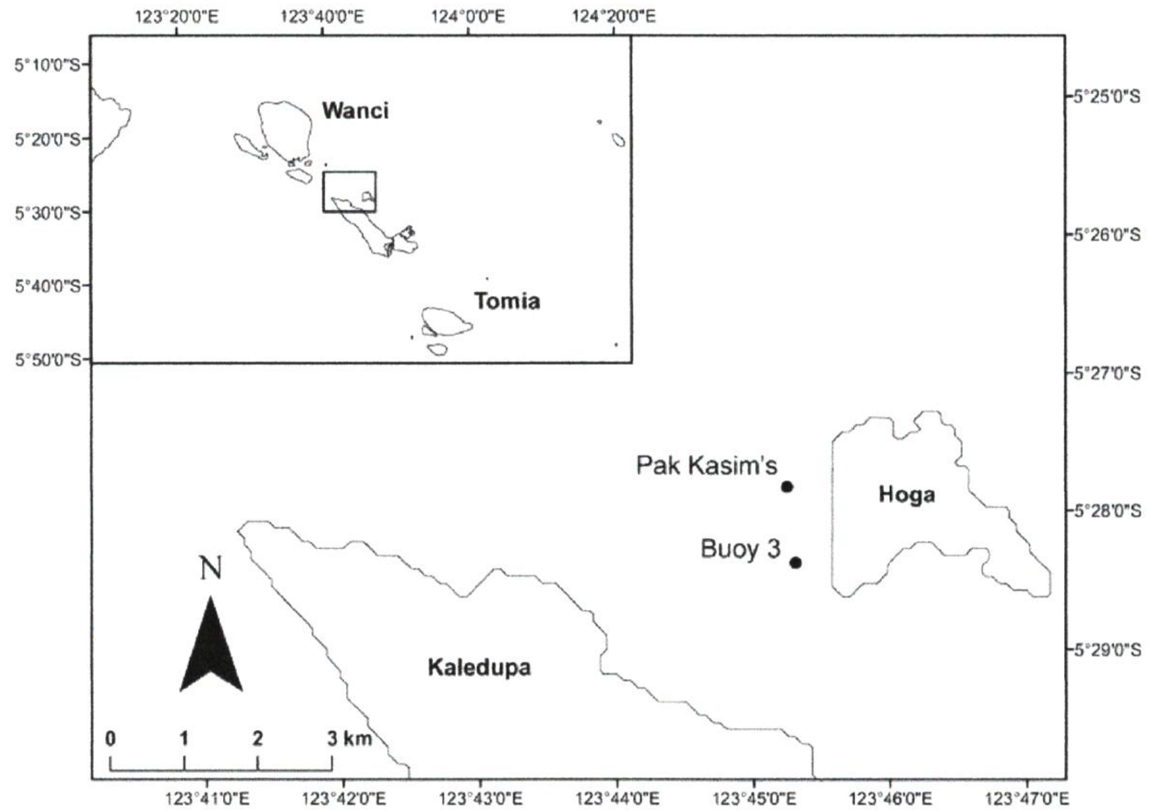


Fig. 1 Location of study area within the Wakatobi (inset black square) and position of reef sites Pak Kasim's and Buoy 3 in relation to the islands of Hoga and Kaledupa

above the monthly average for the region (NOAA). Initial surveys found *C.* aff. *viridis* to be present at all sites and depths (0.12 sponges m^{-2} ± 0.03 SE), and the majority of these sponges (73.9% ± 9.9 SE) were showing signs of bleaching; average bleaching severity in bleached sponges was 25.95% (± 4.5 SE) of sponge tissue (Fig. 2). The 39-d period between the first and second set of surveys (which coincided with a 0.8 °C drop in water temperature) resulted in considerable recovery of *C.* aff. *viridis*. Bleaching prevalence had dropped significantly (GLMM, $F_{(1446)} = 39.650$, $p < 0.001$) to 25.7% (± 5.8 SE), and bleaching severity was also significantly lower (GLMM, $F_{(1194)} = 5.590$, $p = 0.019$) at 11.54% (± 1.9 SE; Fig. 2). The tagged bleached sponges showed a similar significant decline in bleaching severity across the study period (Greenhouse–Geisser, $F_{(1.779,\ 48.567)} = 55.3$, $p < 0.001$) from 37.6% (± 2.6 SE) to 7.2% (± 0.5 SE; Figs. 3, 4). The recovery of these sponges and the fact that our bleaching assessment was conducted nearly 2 months after the highest water temperature period indicate that clionaid bleaching prevalence and severity were likely higher prior to our initial surveys. However, it is not possible to retrospectively extrapolate our observations, as bleaching onset

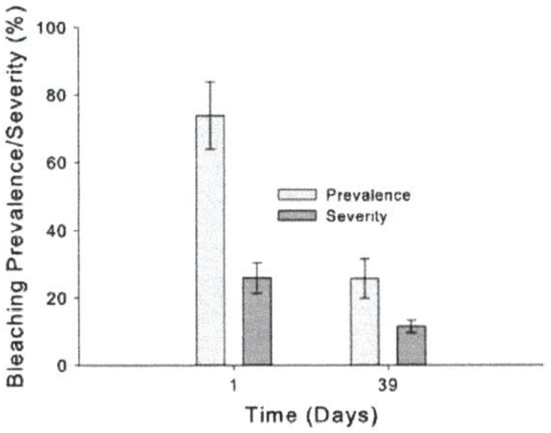
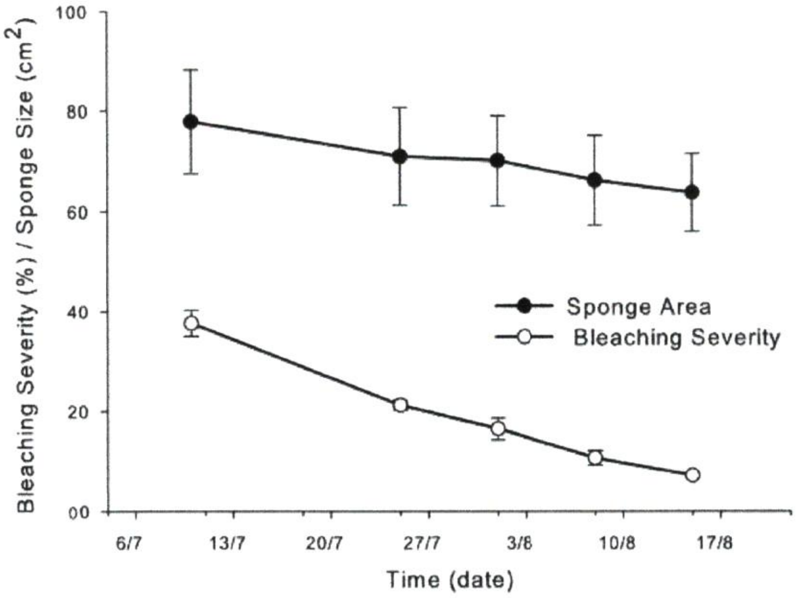


Fig. 2 Average (± SE) bleaching prevalence and severity (n = 34 and 30 transects, respectively) in surveyed *Cliona* aff. *viridis* in early July 2016 and 39 d later in mid-August

Fig. 3 Average (± SE) bleaching severity and sponge size in tagged *Cliona* aff. *viridis* across time ($n = 32$ sponges)



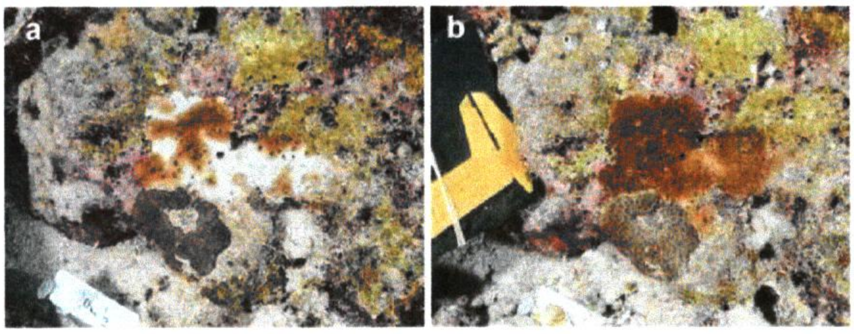


Fig. 4 Example images of a tagged *Cliona* aff. *viridis* in early July 2016 (**a**) and 39 d later in mid-August (**b**)

and recovery timescales are likely species-specific (as in corals; Baird and Marshall 2002).

Sponge bleaching prevalence and severity did not vary significantly between depths. However, bleaching prevalence among sponges at Buoy 3 was almost 50% higher than at Pak Kasim's (GLMM, $F_{(1446)} = 12.304$, $p < 0.001$). Wall sites such as Buoy 3 have been shown to offer refuge from thermal stress in corals (Hoogenboom et al. 2017), but this appears not to be the case for *C.* aff. *viridis* at our study sites. Differences in other environmental factors such as water flow, which is generally higher at Pak Kasim's then at Buoy 3 (Marlow et al. 2018), may have counteracted any refuge offered by shading (Nakamura and van Woesik 2001). The recovery of tagged bleached sponges also showed no significant differences between sites and depths in terms of bleaching severity.

It has been suggested that clionaid sponges that diurnally vertically relocate their *Symbiodinium* (e.g. *C.* aff. *viridis* and *C. orientalis*) may be able to do so as a protective mechanism when stressed, providing bleaching resilience (Schönberg and Suwa 2007). However, *Symbiodinium* density in *C.* aff. *viridis* was 99.4% lower in bleached sponges (9.2×10^3 cell cm^{-2} ± 3.5 SE) than in unbleached sponges (1.5×10^6 cell cm^{-2} ± 0.4 SE). Consequently, the capacity of *C.* aff. *viridis* to retract symbionts appears to have offered to little bleaching resilience. This relocation capacity may be only sustainable over short periods of thermal stress as it is thought that retracted symbionts survive through parasitism of the host (Fang et al. 2017).

The sponge population appeared to incur no significant mortality from bleaching and subsequent recovery as transect data showed no significant change in sponge density. Among the tagged sponges, all survived the observation period, but there was evidence of partial mortality: sponge size dropped significantly (Greenhouse–Geisser, $F_{(2.296,\ 61.981)} = 3.318$, $p = 0.037$), from 77.8 cm^2 (± 10.4 SE) to 63.7 cm^2 (± 7.7 SE; Figs. 2, 3), a 13% decrease that was seen similarly across sites and depths. However, partial mortality was not detected across the entire population as transect data showed no significant change in sponge size between the two time points. A lower occurrence of bleaching among the transect sponges (in comparison with the tagged sponges) and high sponge size variation made detection of partial mortality in these sponges difficult. Partial mortality could be assumed to be considerably less than 13% at the population level.

High bleaching survivability could reflect a low nutritional dependence on photosymbionts, as has been suggested as an explanation for low mortality in bleached cyanobacteria-harbouring *Xestospongia muta* (McMurray et al. 2011). However, phototrophic clionaids derive significant amounts of their nutrition from their *Symbiodinium* (Weisz et al. 2010; Fang et al. 2016) and the recovery of even the most severely bleached sponges demonstrates a capacity to survive during prolonged periods when nutrition from this source is unavailable. Evidence from experimentally bleached *C. orientalis* has shown that heterotrophy is not significantly increased during these periods, suggesting that survival and recovery are dependent upon substantial but limited lipid stores (Fang et al. 2014; Pineda et al. 2017). The extent of these lipid stores is likely to be species dependent, but evidence from *C. varians* has shown that these sponges are able to survive for months at a time in the absence of phototrophically derived nutrition (Riesgo et al. 2014). Bleached sponge survival is therefore likely dependent upon initial bleaching severity, the magnitude of these lipid stores and the duration of the heating event.

Our study has demonstrated that the symbiosis between bioeroding sponges and *Symbiodinium* is susceptible to disassociation under thermal stress. This is consistent with a recent observation of bleaching in *C. varians* in the Florida Keys (Hill et al. 2016), but is the first to document the recovery of these bleached sponges. Our observations suggest that their capacity for rapid recovery, while incurring only minimal mortality, could put these sponges at spatially competitive advantage following mass coral bleaching events, as has been previously suggested by other authors (Schönberg and Ortiz 2009; Carballo et al. 2013; Chaves-Fonnegra et al. 2018). Future research would benefit from a greater understanding of the physiological mechanisms behind the stress response and recovery.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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