



Photoacclimation to light-limitation in a clonaid sponge; implications for understanding sponge bioerosion on turbid reefs

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ABSTRACT

Watershed-based pollution is a common form of coral reef degradation. Affected reefs are often highly turbid, where light-limitation confines the distribution of photosynthetic benthic taxa and the capacity for photoacclimation is important for survival. We investigated low light photoacclimation in a *Symbiodinium*-hosting bioeroding sponge using *in situ* PAM fluorometry. *Cliona* aff. *viridis* was artificially shaded (70 & 95% ambient light reduction) on a low turbidity Indonesian reef for 25 days, with a subsequent 14-day recovery period. Significant changes in $rETR_{max}$ and qP , and a non-significant but observable decline in E_k , demonstrated that *C. aff. viridis* is able to photoacclimate to conditions of extreme light reduction and recover within a relatively short period of time. The sponge is therefore unlikely to be light limited on even the most turbid reefs. However, other aspects of watershed-pollution such as sedimentation may still limit their distribution in affected coastal waters.

1. Introduction

Coral reefs are generally accepted as being one of the most stressed and threatened ecosystems in the marine environment (e.g. Hoegh-Guldberg and Bruno, 2010; Frieler et al., 2013). In addition to climate change-associated stressors (Hoegh-Guldberg et al., 2007; Normile, 2016), reefs are at risk from local disturbances, which can further exacerbate the negative impacts of climate change (Ateweberhan et al., 2013; Ban et al., 2014; McClanahan et al., 2014). Of growing concern is watershed-based pollution, which is increasing due to anthropogenic changes in land usage such as deforestation, agricultural intensification and coastal urbanisation (Munday, 2004; Bartley et al., 2014; Stender et al., 2014). Watershed-based pollution can expose coral reefs to excessive levels of sedimentation, turbidity, eutrophication and pollutants (see Fabricius, 2005 for review), and is responsible for reef degradation across the globe (e.g. Crabbe and Smith, 2005; Wolanski et al., 2009; Golbuu et al., 2011). In some locations the negative impacts of terrestrial runoff alone could outweigh those of climate change (Maina et al., 2013). In the case of increased turbidity, i.e. increased suspended sediment, associated reductions in ambient light availability can have serious negative consequences for scleractinian corals, as they are reliant on endosymbiotic photosynthetic dinoflagellates of the genus *Symbiodinium* for their nutritional needs. Furthermore, suspended sediment can directly affect coral health by clogging the feeding

apparatus (see Erftemeijer et al., 2012 for review). Corals in turbid environments can display reduced growth rates (Crabbe and Smith, 2005), reduced diversity (De'ath and Fabricius, 2010) and increased disease prevalence (Pollock et al., 2014).

While the impacts of turbidity are relatively well understood for scleractinian corals, few studies have considered how other photosynthetic reef taxa might be affected in these environments. The need for such information is increasing given the trend for regime shifts away from coral dominance towards dominance by other benthic taxa on degraded reefs (McManus and Polsenberg, 2004; Norström et al., 2009; Bell et al., 2013). One important group that has so far been understudied in this respect is bioeroding sponges. Bioeroding sponges are increasing in abundance on degraded reefs (López-Victoria and Zea, 2005; Schönberg and Ortiz, 2009; Carballo et al., 2013), and many species host *Symbiodinium* (Rützler, 1990). As in cnidarians, the relationship is generally assumed to be mutualistic; carbon translocated from symbiont to host enhances bioerosion and growth rates (Hill, 1996; Schönberg, 2006; Weisz et al., 2010), and photosynthetic clonoids are some of the most aggressive spatial competitors on coral reefs (Vicente, 1978; Schönberg and Wilkinson, 2001). Abundance surveys of *Symbiodinium*-hosting clonoids regularly show a preferential occupation of well-lit substrate (López-Victoria and Zea, 2005) and it is presently unclear what acclimatory mechanisms they have (if any) for prolonged exposure to turbid environmental conditions.

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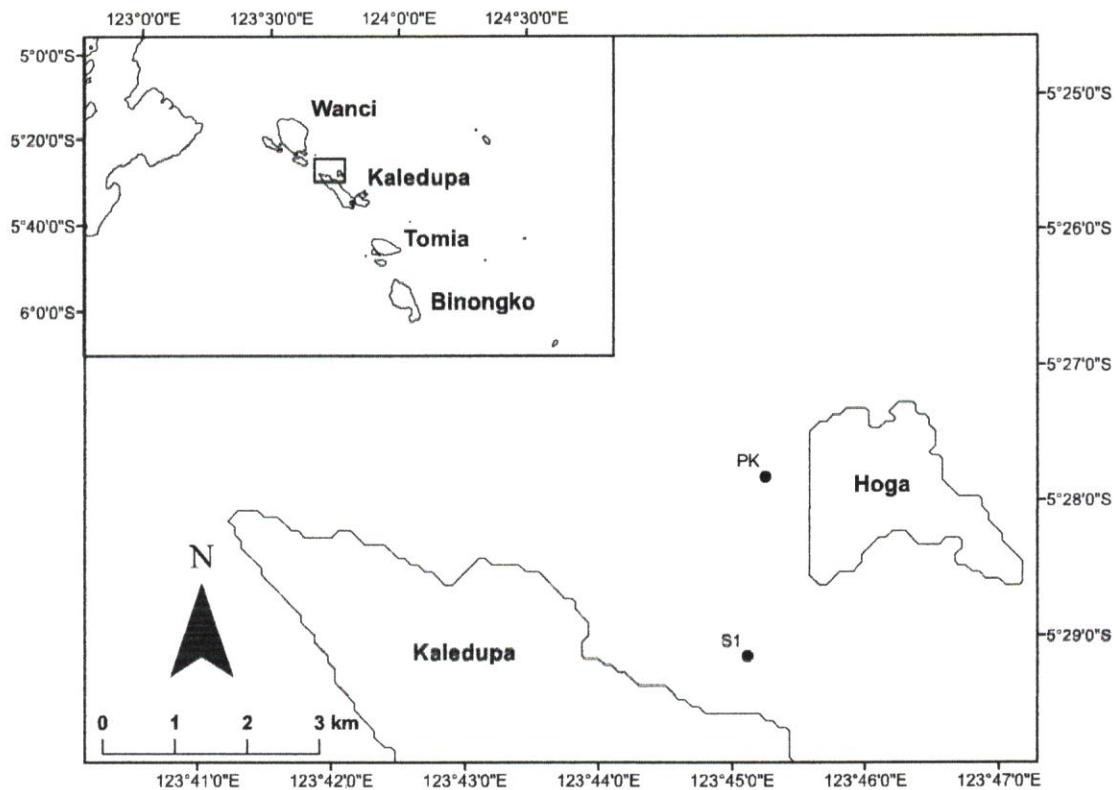


Fig. 1. Location of study area within the Wakatobi (inset black square) and position of reef sites Pak Kasim's and Sampela 1 in relation to the islands of Hoga and Kaledupa. Pak Kasim's and Sampela 1 abbreviated to PK and S1, respectively.

For photosynthetic organisms, maintaining optimal photosynthetic efficiency (and hence photosynthetically derived nutrition) requires a capacity to modify elements of the photophysiological apparatus and overall morphology in response to changing light availability. This is termed “photoacclimation” and for *Symbiodinium*-hosting animals, has predominantly been studied in cnidarians. Some scleractinian corals have a capacity to modify their photophysiology and trophic mode, allowing these animals to live and thrive in highly turbid environments and occupy a broad depth range (Anthony and Fabricius, 2000; Hennige et al., 2008; Morgan et al., 2016). Photoacclimation to low light is possible by adjusting pigmentation within *Symbiodinium* cells (Falkowski and Dubinsky, 1981), by increasing *Symbiodinium* density (Titlyanov et al., 1980), and by changing holobiont (i.e. the whole symbiosis) morphology (Einbinder et al., 2009). In the past, this information was derived from destructive sampling and *ex situ* respirometry analysis in the form of photosynthesis-irradiance curves (MacIntyre et al., 2002). However, the development of portable underwater pulse amplitude-modulated (PAM) fluorometry devices (DIVING-PAM) has allowed for non-destructive *in situ* assessments of photoacclimation by providing rapid collection of a suite of photophysiological data (Maxwell and Johnson, 2000; Ralph and Gademann, 2005). PAM fluorometers measure chlorophyll *a* fluorescence of photosystem (PS) II, providing information on the electron transport rate (ETR; equivalent to photosynthetic activity (Beer et al., 1998)), as well as photochemical and non-photochemical quenching (qP and NPQ, respectively) (Ralph and Gademann, 2005). By plotting ETR (or relative ETR; rETR) against irradiance (photosynthetically active radiation; PAR), rapid light curves (RLCs) can be constructed that allow for not only the determination of current photosynthetic capacity but also responses over a broad range of ambient light conditions (Ralph and Gademann, 2005), i.e. photoacclimatory capability. Of specific interest for investigating photoacclimatory potential is the minimum saturating irradiance (E_k) and maximum photosynthetic capacity (ETR_{max}). E_k is

located on the RLC at the transition from the light limited to the light saturated region (Sakshaug et al., 1997) and can be an accurate reflection of the ambient light levels to which the organisms are acclimated to. ETR_{max} occurs where the RLC plateaus, is a reflection of maximum photosynthetic capacity and is consistent indicator of photoacclimation (Sakshaug et al., 1997; Schreiber, 2004; Ralph and Gademann, 2005). PAM fluorometry has had limited use in *in situ* sponge photophysiological studies but has been used to demonstrate photoacclimation in the *Symbiodinium*-hosting sponge *Pione vastifica* and in the cyanobacteria-hosting sponges *Theonella swinhoei* and *Lamellodysidea herbacea* (Beer and Ilan, 1998; Steindler et al., 2001; Biggerstaff et al., 2015).

The present study was conducted in the UNESCO Wakatobi Biosphere Reserve in Southeast Sulawesi Indonesia. Surveys of bioeroding sponges in the region has found that a regionally common *Symbiodinium*-hosting clonoid, *C. aff. viridis*, is not present at a local turbid and sedimented reef, ‘Sampela 1’, despite abundant habitat availability (Marlow et al., 2018). This absence suggests that the species is either unable to acclimate and survive in light-limited conditions or directly physiologically impacted by high levels of suspended or settled sediment, or a combination of all three. The aim of this study was to address the first of these hypotheses: to determine whether *C. aff. viridis* is light limited on turbid reefs or capable of photoacclimating in conditions of moderate to extreme ambient light reduction. Individuals of *C. aff. viridis* were artificially shaded for prolonged periods on a low turbidity reef and *in situ* PAM fluorometry was used to detect photoacclimatory changes in *Symbiodinium* PSII. In addition, photographic analysis was used to infer changes in holobiont health.

2. Methods

2.1. Study area

This study was conducted within the Wakatobi region of Southeast Sulawesi, Indonesia in July–August 2015. The photophysiological acclimatory capabilities of *C. aff. viridis* were assessed *in situ* at a reef site known locally as Pak Kasim's (Fig. 1). Pak Kasim's is a section of the sloping fringing reef on the western side of Hoga Island and a location where *C. aff. viridis* is abundant. At this site (and within the wider Wakatobi), *C. aff. viridis* encrusts dead calcareous substrate and is most abundant at 10–14 m depth. Measurements of light attenuation were taken at the turbid reef, Sampela 1 (Fig. 1), to provide ecological relevance to the light limitation treatments. Bioeroding sponge abundance surveys in 2014 found *C. aff. viridis* (therein referred to as *C. aff. viridis* sp. A) to be absent at this site (Marlow et al., 2018) which is considered to be highly degraded. Adjacent to the Bajau village of Sampela, the reef is subject to excessive levels of suspended and settled sediments, and reduced light availability, thought to be due to mangrove removal, untreated local sewage discharge and seasonal changes in currents (Crabbe and Smith, 2005; Hennige et al., 2010; Salinas-de-Leon et al., 2013; Biggerstaff et al., 2015, 2017).

2.2. Chlorophyll fluorometry

All chlorophyll fluorometry was conducted using a red-light DIVING-PAM (Walz, Iffeltrich Germany) and rapid light curves (RLCs). Prior to treatments, trial RLCs were performed on haphazardly selected sponges at Pak Kasim's to identify a suitable dark adaption period, RLC-PAR width and RLC-PAR intensities. Full dark adaption was found to take approximately 30 min, which was logistically unachievable for collecting data from multiple sponges on a single dive. Instead the initial fluorescence measurement (in the absence of actinic light) was collected after a period of 10 s of quasi-darkness was applied (Ralph and Gademann, 2005). This was followed by increasing actinic light steps of 270, 382, 510, 724, 954, 1399, 1957 and 2762 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, each for a duration of 10 s. For all fluorometry measurements, the fibre optic cable was placed in the centre of the sponge, taking care to avoid patches of necrosis or algal growth. To maintain consistency in the distance to the sponge surface, a 1 cm spacer was attached to the end of the fibre optic cable.

Maximum electron transport rates (ETR_{max}), light saturation coefficients (E_k), light-limited photosynthetic efficiency (α), effective quantum yield (Φ_{PSII}), photochemical quenching (qP) and minimum fluorescence yield (F_0) were calculated in the software package WinControl (version 3.25). Equal PAR absorption between photosystems I & II and an absorption coefficient of 0.84 was assumed (Schreiber et al., 1994). However, as these were not directly measured, ETR and ETR_{max} are considered relative (rETR & rETR_{max}).

2.3. Shading experiment

Twenty individuals of *C. aff. viridis* were located and tagged at 10 m depth at Pak Kasim's. Sponges were selected based on organism size (10–60 cm^2), upwards orientation (to minimise self-shading) and minimal shading by other reef topographical features. Tagged sponges were randomly allocated treatments of control, procedural control, 70% light reduction and 95% ambient light reduction ($n = 5$ per treatment). Control sponges were left uncovered for the duration of the experiment, while procedural controls had the same transparent polymethyl methacrylate (Plexiglas GS Clear 0F00, Evonik Industries, Morrinsville NZ) suspended above the sponge as were used in the 70% and 90% shading experiments. A light reduction of 70% was achieved by attaching shade-cloth (Redpath, Palmerston North NZ) to the underside of the Plexiglas and a 95% reduction was achieved by painting both sides of the Plexiglas with marine paint. Shade and procedural control cover

dimensions were $15 \times 15 \times 0.3 \text{ cm}$, and were suspended approximately 5 cm above sponges using cable ties and masonry nails embedded into adjacent dead substrate. Shades and procedural controls were cleaned every other day to clear algal growth and settled sediment. RLCs were performed on days 0 (just prior to treatment application), 5, 11, 18 and 25, after which the treatments were removed. Final RLCs were performed to each sponge 14 days post-treatment removal (recovery). All RLCs were performed between 11 am and 12 noon to minimise the influence of circadian rhythms.

Changes in sponge surface area and colouration were monitored through the use of *in situ* images taken on day 0 and immediately after treatment on day 25. At each time point, photos were taken of each sponge adjacent to a scale bar and colour chart. Images were subsequently analysed with the software package ImageJ to assess any changes in the visible surface area of each sponge before and after treatment. Changes in tissue colour were judged by eye in relation to the colour chart.

2.4. PAR assessment

Daily ambient PAR at Pak Kasim's and Sampela 1 was quantified using three separate 24-h deployments of an ODYSSEY PAR logger (Dataflow Systems, Christchurch NZ) at 10 m depth, at each site. The logger was set to record every minute and data averaged over daylight hours.

Average PAR levels for individual sponges used in the treatments were measured using an external PAR sensor on the PAM. This was done to assess not only the effect of treatment but also differences in PAR reaching individual sponges due to shading by reef topography and sponge orientation. PAR measurements were taken once from the middle of the sponge surface and then immediately after in the water column at the same depth. This was repeated once for each sponge at 12 noon pre-treatment and for each sponge at 8 am, 12 noon and 4 pm during the treatment period (on non-cloudy days). Sponge PAR was calculated as a percentage of ambient light levels in the water column.

2.5. Statistical analysis

All statistical analyses were performed within the SPSS statistical analysis package (version 23). Any data that did not meet the assumptions of variance, normality for the relevant analysis were square root, fourth root or log-transformed.

Differences in ambient PAR among sponge treatment groups were tested using a One-Way Analysis of Variance (ANOVA) on log-transformed data, with Tukey's *post hoc* test where necessary. Differences in sponge surface area between days 0 and 25 were tested using paired *t*-tests on un-transformed data.

Differences in rETR_{max} (square transformed), E_k , α , Φ_{PSII} , F_0 and average qP (all un-transformed) among the different treatment groups over time were tested using a Repeated Measures ANOVA, with time and treatment as fixed factors, and with *post hoc* Bonferroni adjusted pairwise tests. Where data violated the assumption of sphericity, the Huynh-Feldt correction was applied.

3. Results

3.1. PAR and treatments

Average daily PAR at 10 m depth during the experimental period was $116 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (± 20 standard error (SE)) at Sampela and $188 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (± 29 SE) at Pak Kasim's. This equated to daily light integrals (DLI) of 4.94 and 8.01 $\text{mol photons m}^{-2} \text{d}^{-1}$ respectively, an almost 60% difference and justifying the use of the 70% light reduction treatment. At Pak Kasim's, midday water column PAR at 10 m depth was $216 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (± 7 SE). Shading by reef topography and differences in sponge orientation meant that average

sponge surface PAR (pre-treatment) was less, at $170 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (± 18 SE). However, there were no significant differences in pre-treatment sponge surface PAR between treatment groups. Following application of the treatments, the average amount of PAR reaching each treatment group across a day (from 8 am, 12 noon and 4 pm readings) was $87 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (± 24 SE) for controls, $80 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (± 20 SE) for procedural controls, $25 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (± 6 SE) for 70% treatments and $3 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (± 1 SE) for 95% treatments. This equated to respective DLIs of 3.71, 3.41, 1.06 and $0.13 \text{ mol photons m}^{-2} \text{ d}^{-1}$. These differences were significant (ANOVA, $F_{(3,56)} = 29.066$, $p < 0.001$), with *post hoc* tests revealing differences between the 95% treatment and all other treatments ($p < 0.001$), between the 70% treatment and all other the treatments ($p < 0.001$ for 95% treatments, $p = 0.02$ for controls, and $p = 0.08$ for procedural controls), and no differences between the controls and procedural controls.

3.2. Sponge photophysiology

There was a significant difference in $r\text{ETR}_{\text{max}}$ across time (Huynh-Feldt, $F_{(5,80)} = 44.366$, $p < 0.001$), and an interaction with time and treatment (Huynh-Feldt, $F_{(15,80)} = 6.983$, $p < 0.001$) (Fig. 2). Pairwise comparisons showed that on days 11, 18 and 25, average $r\text{ETR}_{\text{max}}$ across all treatments and controls was significantly lower than on days 0 and 5, or after recovery ($p < 0.001$ for all). After the recovery period, average $r\text{ETR}_{\text{max}}$ was not significantly different from on days 0 and 5. Differences were primarily caused by a drop in the $r\text{ETR}_{\text{max}}$ in the 95% treatment group; by day 11, average $r\text{ETR}_{\text{max}}$ was significantly lower than in the controls ($p = 0.010$), procedural controls ($p = 0.001$) and 70% treatment ($p = 0.011$). This trend continued on days 18 and 25 ($p < 0.001$ for all). There were no other significant differences in $r\text{ETR}_{\text{max}}$ between any of the other treatment groups on any of the measured days, and after recovery no differences existed between any of the treatments. When examining differences across time within

treatment groups, controls and procedural controls had a lower $r\text{ETR}_{\text{max}}$ on day 18 than after recovery ($p = 0.05$ & 0.016 , respectively). However, the main differences occurred for the 70 and 95% treatments; by day 11, $r\text{ETR}_{\text{max}}$ was significantly lower in these groups than it was on day 0 within the same groups ($p = 0.018$ & $p < 0.001$, respectively). On day 25, $r\text{ETR}_{\text{max}}$ was at its lowest for the 70% and 95% treatments, and significantly lower than in the same treatments on days 0 ($p < 0.001$ for both) and 5 ($p = 0.003$ & $p < 0.001$, respectively), and after recovery ($p = 0.011$ & $p < 0.001$, respectively). After the recovery period, $r\text{ETR}_{\text{max}}$ was not significantly different from that on day 0 within each group.

There was a significant difference in E_k across time (Huynh-Feldt, $F_{(5,80)} = 5.917$, $p < 0.001$) but no significant interaction with time and treatment (Fig. 3). Across all sponges, mean E_k on day 11 ($308.3 \mu\text{mol photons m}^{-2} \text{s}^{-1} \pm 18.6$ SE) was significant lower ($p = 0.009$) than on day 0 ($387.6 \mu\text{mol photons m}^{-2} \text{s}^{-1} \pm 20.2$ SE). Mean E_k was also significantly lower on days 11 and 18 ($332.4 \mu\text{mol photons m}^{-2} \text{s}^{-1} \pm 18.5$ SE) than after the recovery period ($417.9 \mu\text{mol photons m}^{-2} \text{s}^{-1} \pm 25.7$ SE; $p = 0.003$ & 0.005 , respectively). On day 25, E_k appeared lower in the 70% and 95% treatment groups than in both control groups (Fig. 3), and lower than within the same treatments on day 0 and after recovery. However, the lack of significant interaction between time and treatment fails to demonstrate this, probably due to the large amounts of within-treatment variation in E_k .

Light-limited photosynthetic efficiency (α) (Fig. 4) changed significantly with time (Huynh-Feldt, $F_{(5,80)} = 6.294$, $p < 0.001$): at day 25, α was significantly lower than on days 0 and 5 ($p = 0.41$ & 0.34 respectively), but was not significantly different from any other day, including after the recovery period ($p = 0.062$). Changes in α also occurred in an interaction between time and treatment (Huynh-Feldt, $F_{(15,80)} = 2.074$, $p = 0.020$) (Fig. 4). By day 11, α was significantly lower in the 95% treatment group than the controls and procedural controls ($p = 0.05$ & 0.017), however after day 11 no significant

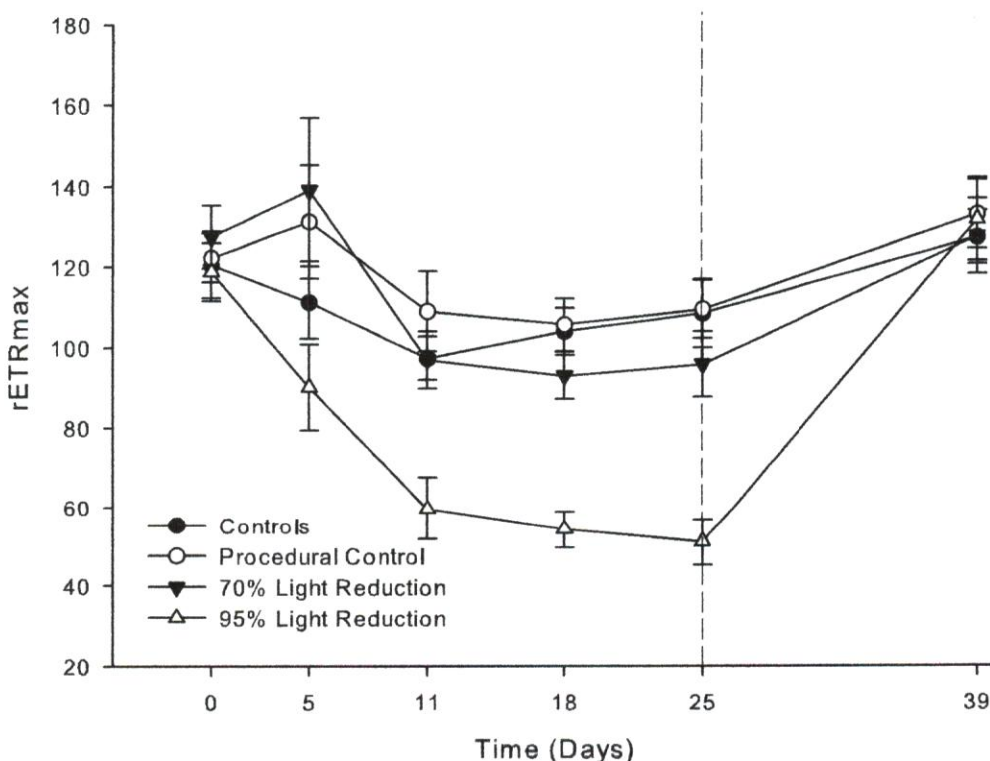


Fig. 2. Mean $r\text{ETR}_{\text{max}}$ (\pm SE) of controls (filled circles), procedural controls (open circles), 70% light reduction (filled triangle), and 95% light reduction (open triangle) treatments over time ($n = 5$ for each). The vertical dashed line represents the time when shades were removed.

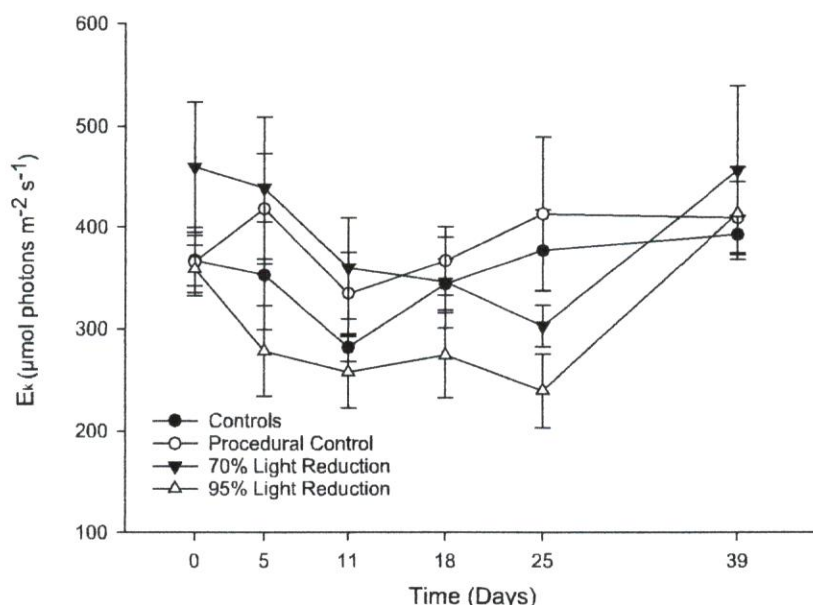


Fig. 3. Mean E_k (\pm SE) of controls (filled circles), procedural controls (open circles), 70% light reduction (filled triangle) and 95% light reduction (open triangle) treatments over time ($n = 5$ for each). The vertical dashed line represents the time when shades were removed.

differences between treatments existed. Within treatment groups, the only change in α across time was in the 95% group, which by day 11 was significantly lower than on day 0 and after recovery ($p = 0.001$ for both), and remained so on days 18 ($p = 0.039$ & 0.018 , respectively) and 25 ($p = 0.016$ for both).

Effective quantum yield (Φ_{PSII}) across all treatment groups did not change significantly over time, however a significant interaction between time and treatment existed (Huynh-Feldt, $F_{(15,80)} = 2.004$, $p = 0.025$). Pairwise comparisons showed that this interaction was driven by changes in the Φ_{PSII} of the 70% treatment (Fig. 5); Φ_{PSII} was significantly greater on day 18 than on day 0 and after recovery ($p = 0.017$ & 0.016 , respectively). On day 25, Φ_{PSII} in the 70% was also higher than after recovery ($p = 0.048$), but not significantly higher

than on day 0 ($p = 0.055$).

F_0 declined significantly across time (Huynh-Feldt, $F_{(5,80)} = 36.511$, $p < 0.001$) but there was no significant interaction with time and treatment (Fig. 6).

Mean qP changed significantly with time (Huynh-Feldt, $F_{(2,32)} = 113.071$, $p < 0.001$) and there was an interaction with treatment (Huynh-Feldt, $F_{(2,32)} = 2.686$, $p < 0.001$). Mean qP dropped significantly from day 0 to day 25 in the 70% and 95% treatment groups ($p < 0.001$ for both), and increased again after 14 days of recovery for both of these treatment groups (70%: $p = 0.001$; 95%: $p < 0.001$) and controls ($p = 0.024$) (Table 1).

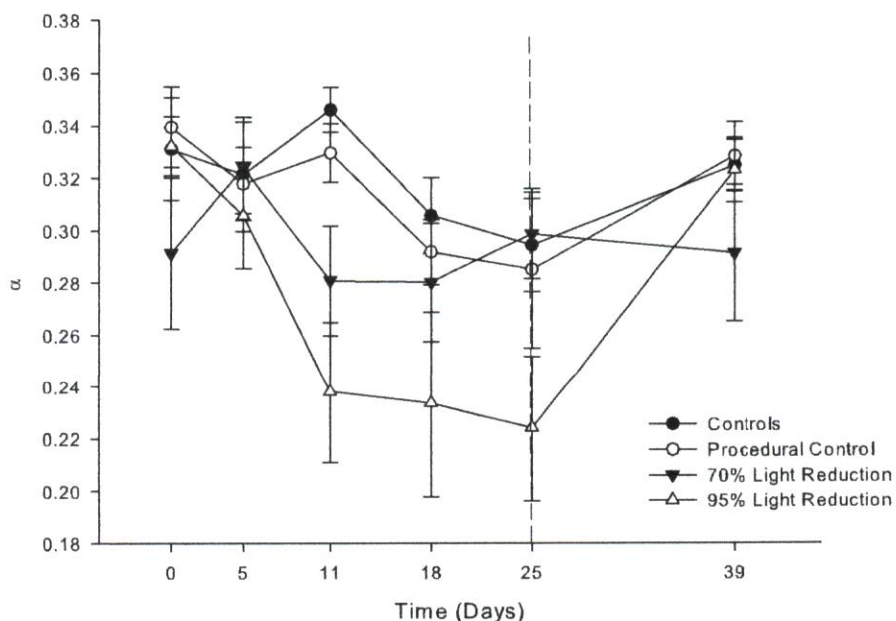


Fig. 4. Mean α (\pm SE) of controls (filled circles), procedural controls (open circles), 70% light reduction (filled triangle), and 95% light reduction (open triangle) treatments over time ($n = 5$ for each). The vertical dashed line represents the time when shades were removed.

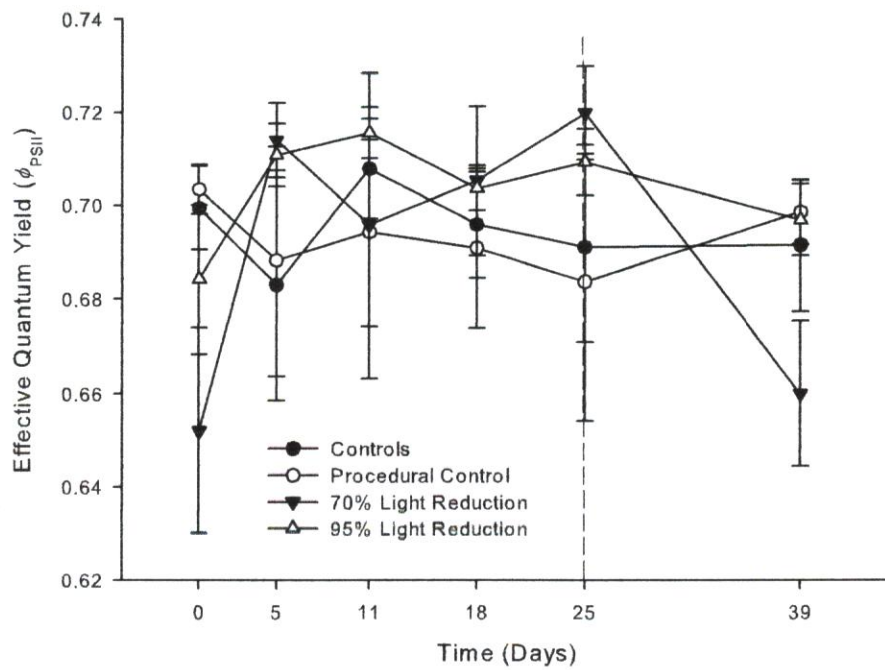


Fig. 5. Mean ϕ_{PSII} (\pm SE) of controls (filled circles), procedural controls (open circles), 70% light reduction (filled triangle), and 95% light reduction (open triangle) treatments over time ($n = 5$ for each). The vertical dashed line represents the time when shades were removed.

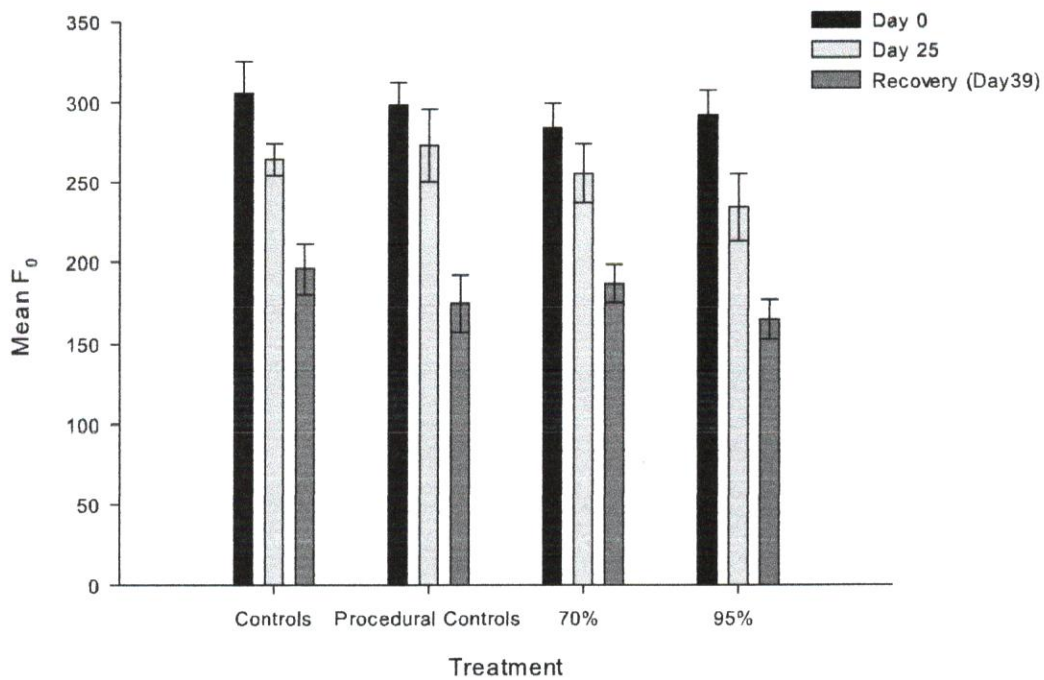


Fig. 6. Mean F_0 (\pm SE) across time in different treatment groups ($n = 5$ for each).

Table 1

Mean qP (\pm SE) for all controls and treatments at days 0 and 25, and after 14 days recovery.

Treatment	Mean qP		
	Day 0	Day 25	14 days Recovery
Control	0.48 ± 0.02	0.44 ± 0.04	0.51 ± 0.03
Procedural control	0.49 ± 0.01	0.44 ± 0.03	0.50 ± 0.02
70% light reduction treatment	0.51 ± 0.02	0.39 ± 0.03	0.49 ± 0.02
95% light reduction treatment	0.48 ± 0.03	0.22 ± 0.02	0.50 ± 0.02

Table 2

Mean sponge surface area (\pm SE) for all controls and treatments at days 0 and 25.

Treatment	Sponge surface area (cm^2)	
	Day 0	Day 25
Control	18.4 ± 5	17.5 ± 2.9
Procedural control	20 ± 9.1	20 ± 10.4
70% light reduction treatment	15.4 ± 4.8	17 ± 5.3
95% light reduction treatment	17.8 ± 2.2	15.4 ± 4.5

3.3. Sponge surface area

Sponge surface area for all controls and treatments was not significantly different between days 0 and 25 (Table 2), and no necrosis was observed in any sponge. Sixty percent of sponges within the 95% reduction group were notably paler on day 25 than within the same group on day 0. No other group displayed obvious paling.

4. Discussion

In the context of reef degradation and stressor resilience, research on bioeroding sponges has primarily focused on resilience to global stressors such as increased water temperature and ocean acidification (e.g. Schönberg and Suwa, 2007; Wisshak et al., 2012, 2013). Regional and local stressors (with the exception of nutrient enrichment, e.g. Ward-Paige et al., 2005) have been largely overlooked. This is the first study to specifically focus on bioeroding sponge acclimation to low light on turbid reefs using *in situ* PAM fluorometry. We demonstrate that *C. aff. viridis* is capable of rapidly photoacclimating to extreme changes in ambient light availability and furthermore, is capable of surviving for short periods in near darkness without any visible signs of necrosis. This resilience to a regionally common form of reef stress is important given that bioeroding sponges of the *C. viridis* spp. complex frequently increase in abundance on degraded reefs (Rützler, 2002; López-Victoria and Zea, 2005; Ward-Paige et al., 2005).

4.1. Photoacclimation of *C. aff. viridis*

Pertinent characteristics of *Symbiodinium* PSII in *C. aff. viridis* demonstrated altered states in response to shading that are consistent with photoacclimation. The most significant of these was the decline in $rETR_{max}$ and subsequent recovery. Numerous studies have shown a positive correlation between ETR_{max} and light availability in *Symbiodinium* (Steindler et al., 2001; Hennige et al., 2008; Ziegler et al., 2015). In high light environments, high ETR_{max} allows *Symbiodinium* to capitalise on the elevated light availability by increasing photosynthetic rate (Ralph and Gademann, 2005). Reduced ETR_{max} in low light environments appears paradoxical to the increases in photosynthetic ‘units’ that are usually associated with low light acclimation (Falkowski, 1980; Richardson et al., 1983; Ramus, 1990). This is thought to be due to increased light attenuation by accumulation of pigments, resulting in less light reaching the reaction centres and saturating photosynthesis (Falkowski and Raven, 2013). If the observation of tissue paling in the 95% treatment were interpreted as “bleaching” (complete or partial expulsion of symbionts), reductions in $rETR_{max}$ in the treatment could also be a function of a decrease in *Symbiodinium* density (Fine et al., 2004). However, bleaching is unlikely to have occurred given that initial F_0 values, which are proportional to PSII reaction centre density (Ryan et al., 2009), were not significantly lower in the 95% treatment than the controls at day 25. The observed paling is likely due to the retraction of symbionts, which occurs on a diurnal basis in *C. aff. viridis* (J. Marlow pers. obs) and has been documented in light-deprived *Cliona orientalis* (Fang et al., 2017). The drop and subsequent recovery of photochemical quenching (qP) in the shade treatments is also consistent with light-limited photoacclimation (Ralph and Gademann, 2005; Biggerstaff et al., 2015; Harrison et al., 2015). The association between qP capacity and *in situ* light conditions is a reflection of the photochemical operating efficiency of PSII, and hence photosynthetic organisms that display higher qP demonstrate a higher PSII efficiency in high light (Hennige et al., 2008; Harrison et al., 2015).

Light reduction did not significantly alter one of the most reliable indicators of photoacclimation, minimum saturation irradiance (E_k). *Symbiodinium* cells acclimated to low ambient PAR are usually characterised by low E_k (Chalker et al., 1983) and reductions in E_k reflect changes in the effective absorption cross section of PSII (Kolber and

Falkowski, 1993; Rodolfo-Metalpa et al., 2008), as has been demonstrated in shaded seagrass (Collier et al., 2009) and sponges (Biggerstaff et al., 2015). E_k is constantly changing in relation to irradiance, only occasionally matching instantaneous irradiance and is hence highly variable (Sakshaug et al., 1997; Ralph and Gademann, 2005). While this study found no significant difference between E_k in any of the treatments, E_k clearly declined in the shaded treatments, but variation was high and it is expected that more replication would have been needed to demonstrate this statistically.

Another strong indication of photoacclimation that can be derived from the RLCs is photosynthetic efficiency in the light-limited region (α). High α values are usually associated with photosynthetic organisms that are low-light acclimated, as they are more effective at rapidly utilising low irradiances (e.g. Hennige et al., 2008). In the 95% treatment group, α showed a marked decline over time but recovered rapidly to pre-shading levels after 14 days of recovery. In contrast, the 70% treatment showed no discernible difference over the course of the experiment. Neither reactions are typical for shade-adapted *Symbiodinium* and were unexpected. Estimates of α are strongly influenced by sampling frequency in the light-limited region of the RLC (Jassby and Platt, 1976; Ralph and Gademann, 2005). Therefore, it is possible that the RLC sampling methodology had insufficient resolution to adequately estimate α in the shaded treatment.

4.2. Implications for sponge bioerosion on turbid Southeast Asian reefs

Reefs in Southeast Asia are increasingly threatened by anthropogenic terrestrial processes, such as intensive deforestation and coastal urbanisation, which are leading to substantial loading of sediment in coastal waters (Spalding et al., 2001; Baum et al., 2015). Suspended sediment, particularly finer particles, decreases light availability for photosynthetic taxa, resulting in compressed depth distribution zones, and reduced growth and survival (Fabricius, 2005; Erfemeijer et al., 2012). In clonoid sponges, heightened light availability and *Symbiodinium* density have been associated with increases in bioerosion rates, growth and competitive ability (Hill, 1996; Schönberg, 2006). Evidence from *C. orientalis* and *C. varians* suggests that photosynthate is translocated from *Symbiodinium* cells to sponge host and that this supplements heterotrophic uptake (Weisz et al., 2010; Fang et al., 2016). Therefore, the capacity to photoacclimate to changing light conditions is vital for guaranteeing survival and possible proliferation of *Symbiodinium*-harbouring sponges on degraded, turbid reefs.

Our study found no tissue necrosis or significant reduction in sponge size after 25 days of extremely reduced light availability. This initially suggests that the photoacclimated intracellular *Symbiodinium* cells continued to meet the carbon demands of the host *C. aff. viridis*. However, work on other clonoids has shown that they are able to survive in total darkness for periods of up to 20 days (*C. orientalis*; Fang et al., 2017) or even months at a time with their *Symbiodinium* removed (*C. varians*; Riesgo et al., 2014). The persistence of these species in the absence of photosynthetically-derived carbon demonstrates other mechanisms, beyond photoacclimation, for survival in extreme light-limitation. These are likely to include increased heterotrophically-acquired carbon and reliance on existing lipid stores, which are thought to support survival and recovery in bleached corals (e.g. Grottoli et al., 2004; Grottoli et al., 2006). Evidence from *C. orientalis* suggests the latter mechanism may be more important in clonoids; Fang et al. (2017) found that heterotrophic uptake was unchanged in *C. orientalis* during 20 days in complete darkness. Conversely, Pineda et al. (2017a) found that the species has extensive lipid stores which declined considerably (but not significantly) during recovery from exposure to high suspended sediment loads, suggesting that these stores aid recovery. The absence of long term *in situ* shading experiments limits possible conclusions on the survivability of *Symbiodinium*-harbouring clonoids on persistently extremely turbid reefs. Nevertheless, the evidence from this study and others (e.g. Pineda et al., 2016; Fang et al., 2017)

suggests that they are capable of surviving and recovering from intermediate periods of exceptionally low levels of light availability (as might be associated with dredging events).

On moderately turbid reefs such as Sampela (Hennige et al., 2008), *C. aff. viridis* is capable of photoacclimating to compensate for reductions in light availability. Nevertheless, the species is absent from the reef despite plenty of available substrate, suggesting that other factors are contributing towards its absence. Light limitation is just one consequence of turbidity and the species may be affected by the other direct impacts (rather than indirect shading) of the high concentration of suspended sediment (Bell et al., 2015). Like many tropical sponges that rely on filter-feeding to provide nutritional intake, *C. aff. viridis* is potentially vulnerable to clogging by fine sediments (e.g. Bannister et al., 2012). With only minor selective control over filtering intake (Reiswig, 1971a), the clogging of a sponge's inhalant canals and aquiferous system can cause reductions in pumping and feeding efficiency (Reiswig, 1971b; Gerrodette and Flechsig, 1979). While clonoid sponge may be somewhat resilient to these stressors in isolation, the reality is that light limitation, sediment suspension and sediment settlement coincide on turbid reefs. It is the combination of these impacts that is potentially limiting the capacity of clonoid sponges such as *C. aff. viridis* to survive in these environments. Extensive experimental work by Pineda et al. (2016, 2017a, 2017b, 2017c) has shown that *C. orientalis* is relatively resilient (0% mortality) to the isolated impacts of light attenuation, suspended sediment and sediment smothering but incurred 20% mortality when these impacts occur in unison. This is reflected in the negative relationship between the abundance of *C. orientalis* and proportion of fine sediments at survey locations on the Great Barrier Reef (Ramsby et al., 2017). Although our current experiment has shown that *C. aff. viridis* can photoacclimate to compensate for reduced light availability, it remains to be seen how the sponge copes with the other impacts of suspended or settled sediment. Any conclusions about the persistence of *C. aff. viridis* and other *Symbiodinium*-harbouring sponges on turbid reefs are consequently limited.

5. Conclusions

Symbiodinium cells in *C. aff. viridis* are capable of substantially and rapidly altering their photophysiology in response to conditions of significantly reduced light availability and reversing these changes once light conditions are restored. If these results are cautiously extrapolated to other *Symbiodinium*-containing clonoids, these sponges are unlikely to be light-limited on turbid reefs but absences may be due to the other (or the combination of) potential impacts of high sediment loading. Finally, while *C. aff. viridis* is capable of photoacclimating and surviving moderate periods of extremely reduced light availability, this may not be sustainable over a prolonged timescale.

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References

Anthony, K.R., Fabricius, K.E., 2000. Shifting roles of heterotrophy and autotrophy in

- coral energetics under varying turbidity. *J. Exp. Mar. Biol. Ecol.* 252, 221–253.
- Ateweberhan, M., Peary, D.A., Keshavmurthy, S., Chen, A., Schleyer, M.H., Sheppard, C.R.C., 2013. Climate change impacts on coral reefs: synergies with local effects, possibilities for acclimation, and management implications. *Mar. Pollut. Bull.* 74, 526–539.
- Ban, S.S., Graham, N.A., Connolly, S.R., 2014. Evidence for multiple stressor interactions and effects on coral reefs. *Glob. Chang. Biol.* 20, 681–697.
- Bannister, R., Battershill, C., De Nys, R., 2012. Suspended sediment grain size and mineralogy across the continental shelf of the Great Barrier Reef: impacts on the physiology of a coral reef sponge. *Cont. Shelf Res.* 32, 86–95.
- Bartley, R., Bainbridge, Z.T., Lewis, S.E., Kroon, P.J., Wilkinson, S.N., Brodie, J.E., Silburn, D.M., 2014. Relating sediment impacts on coral reefs to watershed sources, processes and management: a review. *Sci. Total Environ.* 468, 1138–1153.
- Baum, G., Januar, H.I., Perse, S.C., Kunzmann, A., 2015. Local and regional impacts of pollution on coral reefs along the Thousand Islands north of the megacity Jakarta, Indonesia. *PLoS One* 10, e0138271.
- Beer, S., Ilan, M., 1998. In situ measurements of photosynthetic irradiance responses of two Red Sea sponges growing under dim light conditions. *Mar. Biol.* 131, 613–617.
- Beer, S., Ilan, M., Eshel, A., Weil, A., Brickner, I., 1998. Use of pulse amplitude modulated (PAM) fluorometry for in situ measurements of photosynthesis in two Red Sea faviid corals. *Mar. Biol.* 131, 607–612.
- Bell, J.J., Davy, S.K., Jones, T., Taylor, M.W., Webster, N.S., 2013. Could some coral reefs become sponge reefs as our climate changes? *Glob. Chang. Biol.* 19, 2613–2624.
- Bell, J.J., McGrath, E., Biggerstaff, A., Bates, T., Bennett, H., Marlow, J., Shaffer, M., 2015. Sediment impacts on marine sponges. *Mar. Pollut. Bull.* 94, 5–13.
- Biggerstaff, A., Smith, D.J., Jompa, J., Bell, J.J., 2015. Photoacclimation supports environmental tolerance of a sponge to turbid low-light conditions. *Coral Reefs* 34, 1049–1061.
- Biggerstaff, A., Smith, D.J., Jompa, J., Bell, J.J., 2017. Metabolic responses of a phototrophic sponge to sedimentation supports transitions to sponge-dominated reefs. *Sci. Rep.* 7, 2725.
- Carballo, J.L., Bautista, E., Nava, H., Cruz-Barraza, J.A., Chávez, J.A., 2013. Boring sponges, an increasing threat for coral reefs affected by bleaching events. *Ecol. Evol.* 3, 872–886.
- Chalker, B., Dunlap, W., Oliver, J., 1983. Bathymetric adaptations of reef-building corals at Davies Reef, Great Barrier Reef, Australia. II. Light saturation curves for photosynthesis and respiration. *J. Exp. Mar. Biol. Ecol.* 73, 37–56.
- Collier, C.J., Lavery, P.S., Ralph, P.J., Masini, R.J., 2009. Shade-induced response and recovery of the seagrass *Posidonia sinuosa*. *J. Exp. Mar. Biol. Ecol.* 370, 89–103.
- Crabbe, J.M., Smith, D.J., 2005. Sediment impacts on growth rates of *Acropora* and *Porites* corals from fringing reefs of Sulawesi, Indonesia. *Coral Reefs* 24, 437–441.
- De'ath, G., Fabricius, K., 2010. Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. *Ecol. Appl.* 20, 840–850.
- Einbinder, S., Mass, T., Brokovich, E., Dubinsky, Z., Erez, J., Tchernov, D., 2009. Changes in morphology and diet of the coral *Stylophora pistillata* along a depth gradient. *Mar. Ecol. Prog. Ser.* 381, 167–174.
- Ertemeijer, P.L., Riegl, B., Hoeksema, B.W., Todd, P.A., 2012. Environmental impacts of dredging and other sediment disturbances on corals: a review. *Mar. Pollut. Bull.* 64, 1737–1765.
- Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Pollut. Bull.* 50, 125–146.
- Falkowski, P.G., 1980. Light-shade adaptation in marine phytoplankton. In: Falkowski, P.G. (Ed.), *Primary Productivity in the Sea*. Plenum Publishing, New York, NY, pp. 99–117.
- Falkowski, P.G., Dubinsky, Z., 1981. Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. *Nature* 289, 172–174.
- Falkowski, P.G., Raven, J.A., 2013. *Aquatic Photosynthesis*. Princeton University Press, NJ.
- Fang, J.K., Schönberg, C.H., Hoegh-Guldberg, O., Dove, S., 2016. Day-night ecophysiology of the photosymbiotic bioeroding sponge *Cliona orientalis* Thiele, 1900. *Mar. Biol.* 163, 1–12.
- Fang, J.K., Schönberg, C.H., Hoegh-Guldberg, O., Dove, S., 2017. Symbiotic plasticity of *Symbiodinium* in a common excavating sponge. *Mar. Biol.* 164, 104.
- Fine, M., Steindler, L., Loya, Y., 2004. Endolithic algae photoacclimate to increased irradiance during coral bleaching. *Mar. Freshw. Res.* 55, 115–121.
- Frieler, K., Meinshausen, M., Golly, A., Mengel, M., Lebek, K., Donner, S.D., Hoegh-Guldberg, O., 2013. Limiting global warming to 2 °C is unlikely to save most coral reefs. *Nat. Clim. Chang.* 3, 165–170.
- Gerrodette, T., Flechsig, A., 1979. Sediment-induced reduction in the pumping rate of the tropical sponge *Verongia lacunosa*. *Mar. Biol.* 55, 103–110.
- Golbuu, Y., van Woesik, R., Richmond, R.H., Harrison, P., Fabricius, K.E., 2011. River discharge reduces reef coral diversity in Palau. *Mar. Pollut. Bull.* 62, 824–831.
- Grottoli, A.G., Rodrigues, L.J., Juarez, C., 2004. Lipids and stable carbon isotopes in two species of Hawaiian corals, *Porites compressa* and *Montipora verrucosa*, following a bleaching event. *Mar. Biol.* 145, 621–631.
- Grottoli, A.G., Rodrigues, L.J., Palardy, J.E., 2006. Heterotrophic plasticity and resilience in bleached corals. *Nature* 440, 1186–1189.
- Harrison, J.W., Silsbe, G.M., Smith, R.E., 2015. Photophysiology and its response to visible and ultraviolet radiation in freshwater phytoplankton from contrasting light regimes. *J. Plankton Res.* 37, 472–488.
- Hennige, S.J., Smith, D.J., Perkins, R., Consalvey, M., Paterson, D.M., Suggett, D.J., 2008. Photoacclimation, growth and distribution of massive coral species in clear and turbid waters. *Mar. Ecol. Prog. Ser.* 369, 77–88.
- Hennige, S.J., Smith, D.J., Walsh, S., McGinley, M.P., Warner, M.E., Suggett, D.J., 2010. Acclimation and adaptation of scleractinian coral communities along environmental gradients within an Indonesian reef system. *J. Exp. Mar. Biol. Ecol.* 391, 143–152.

- Hill, M., 1996. Symbiotic zooxanthellae enhance boring and growth rates of the tropical sponge *Anthosigmella varians* forma *variens*. *Mar. Biol.* 125, 649–654.
- Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. *Science* 328, 1523–1528.
- Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R., Dubi, A., Hatzitolos, E., 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318, 1737–1742.
- Jassby, A.D., Platt, T., 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnol. Oceanogr.* 21, 540–547.
- Kolber, Z., Falkowski, P.G., 1993. Use of active fluorescence to estimate phytoplankton photosynthesis in situ. *Limnol. Oceanogr.* 38, 1646–1665.
- López-Victoria, M., Zea, S., 2005. Current trends of space occupation by encrusting excavating sponges on Colombian coral reefs. *Mar. Ecol.* 26, 33–41.
- MacIntyre, H.L., Kana, T.M., Anning, T., Geider, R.J., 2002. Photoacclimation of photosynthesis irradiance response curves and photosynthetic pigments in microalgae and cyanobacteria. *J. Phycol.* 38, 17–38.
- Maina, J., De Moel, H., Zinke, J., Madin, J., McClanahan, T., Vermaat, J.F., 2013. Human deforestation outweighs future climate change impacts of sedimentation on coral reefs. *Nat. Commun.* 4, 1986.
- Marlow, J., Schönberg, C.H.L., Davy, S.K., Haris, A., Jompa, J., Bell, J.J., 2018. Bioeroding sponge assemblages: the importance of substrate availability and sediment. *J. Mar. Biol. Assoc. UK* 1–16. <https://doi.org/10.1017/S0025315418000164>.
- Maxwell, K., Johnson, G.N., 2000. Chlorophyll fluorescence - a practical guide. *J. Exp. Bot.* 51, 659–668.
- McClanahan, T.R., Graham, N.A., Darling, E.S., 2014. Coral reefs in a crystal ball: predicting the future from the vulnerability of corals and reef fishes to multiple stressors. *Curr. Opin. Environ. Sustain.* 7, 59–64.
- McManus, J.W., Polsenberg, J.F., 2004. Coral-algal phase shifts on coral reefs: ecological and environmental aspects. *Prog. Oceanogr.* 60, 263–279.
- Morgan, K.M., Perry, C.T., Smithers, S.G., Johnson, J.A., Daniell, J.J., 2016. Evidence of extensive reef development and high coral cover in nearshore environments: implications for understanding coral adaptation in turbid settings. *Sci. Rep.* 6, 29616.
- Munday, P.L., 2004. Habitat loss, resource specialization, and extinction on coral reefs. *Glob. Chang. Biol.* 10, 1642–1647.
- Normile, D., 2016. El Niño's warmth devastating reefs worldwide. *Science* 352, 15–16.
- Norström, A.V., Nyström, M., Lokrantz, J., Folke, C., 2009. Alternative states on coral reefs: beyond coral-macroalgal phase shifts. *Mar. Ecol. Prog. Ser.* 376, 295–306.
- Pineda, M.C., Strehlow, B., Duckworth, A., Doyle, J., Jones, R., Webster, N.S., 2016. Effects of light attenuation on the sponge holobiont-implications for dredging management. *Sci. Rep.* 6, 39038.
- Pineda, M.C., Strehlow, B., Stempel, M., Duckworth, A., Jones, R., Webster, N.S., 2017a. Effects of suspended sediments on the sponge holobiont with implications for dredging management. *Sci. Rep.* 7, 4925.
- Pineda, M.C., Strehlow, B., Kamp, J., Duckworth, A., Jones, R., Webster, N.S., 2017b. Effects of combined dredging-related stressors on sponges: a laboratory approach using realistic scenarios. *Sci. Rep.* 7, 5155.
- Pineda, M.C., Strehlow, B., Stempel, M., Duckworth, A., den Haan, J., Jones, R., Webster, N.S., 2017c. Effects of sediment smothering on the sponge holobiont with implications for dredging management. *Sci. Rep.* 7, 5156.
- Pollock, F.J., Lamb, J.B., Field, S.N., Heron, S.F., Schaffelke, B., Shedrawi, G., Bourne, D.G., Willis, B.L., 2014. Sediment and turbidity associated with offshore dredging increase coral disease prevalence on nearby reefs. *PLoS One* 9, e102498.
- Ralph, P.J., Gademann, R., 2005. Rapid light curves: a powerful tool to assess photosynthetic activity. *Aquat. Bot.* 82, 222–237.
- Ramsby, B.D., Hoogenboom, M.O., Whalan, S., Webster, N.S., Thompson, A., 2017. A decadal analysis of bioeroding sponge cover on the inshore Great Barrier Reef. *Sci. Rep.* 7, 2706.
- Ramus, J.A., 1990. Form-function analysis of photon capture for seaweeds. *Hydrobiologia* 204, 65–71.
- Reiswig, H.M., 1971a. Particle feeding in natural populations of three marine demosponges. *Biol. Bull.* 141, 568–591.
- Reiswig, H.M., 1971b. In situ pumping activities of tropical Demospongiae. *Mar. Biol.* 9, 38–50.
- Richardson, K., Beardall, J., Raven, J.A., 1983. Adaptation of unicellular algae to irradiance: an analysis of strategies. *New Phytol.* 93, 157–191.
- Riesgo, A., Peterson, K., Richardson, C., Heist, T., Strehlow, B., McCauley, M., Cotman, C., Hill, M., Hill, A., 2014. Transcriptomic analysis of differential host gene expression upon uptake of symbionts: a case study with *Symbiodinium* and the major bioeroding sponge *Cliona varians*. *BMC Genomics* 15, 376.
- Rodolfo-Metalpa, R., Huot, Y., Ferrier-Pages, C., 2008. Photosynthetic response of the Mediterranean zooxanthellate coral *Cladocora caespitosa* to the natural range of light and temperature. *J. Exp. Biol.* 211, 1579–1586.
- Rützler, K., 1990. Associations between Caribbean sponges and photosynthetic organisms. In: Rützler, K. (Ed.), *New Perspectives in Sponge Biology*. Smithsonian Institution Press, Washington DC, pp. 455–466.
- Rützler, K., 2002. Impact of crustose clionid sponges on Caribbean reef corals. *Acta Geol. Hisp.* 37, 61–72.
- Ryan, K.G., Cowie, R.O., Liggins, E., McNaughtan, D., Martin, A., Davy, S.K., 2009. The short-term effect of irradiance on the photosynthetic properties of Antarctic fast-ice microalgal communities. *J. Phycol.* 45, 1290–1298.
- Sakshaug, E., Bricaud, A., Dandonneau, Y., Falkowski, P.G., Kiefer, D.A., Legendre, L., Morel, A., Parslow, J., Takahashi, M., 1997. Parameters of photosynthesis: definitions, theory and interpretation of results. *J. Plankton Res.* 19, 1637–1670.
- Salinas-de-Leon, P., Dryden, C., Smith, D.J., Bell, J.J., 2013. Temporal and spatial variability in coral recruitment on two Indonesian coral reefs: consistently lower recruitment to a degraded reef. *Mar. Biol.* 160, 97–105.
- Schönberg, C.H.L., 2006. Growth and erosion of the zooxanthellate Australian bioeroding sponge *Cliona orientalis* are enhanced in light. In: *Proc 10th Int Coral Reef Symp* 1, pp. 168–174.
- Schönberg, C.H.L., Ortiz, J., 2009. Is sponge bioerosion increasing. In: *Proc 11th Int Coral Reef Symp* 1, pp. 527–530.
- Schönberg, C.H.L., Suwa, R., 2007. Why bioeroding sponges may be better hosts for symbiotic dinoflagellates than many corals. In: Custódio, M.R., Lôbo-Hajdu, G., Hajdu, E., Muricy, G. (Eds.), *Ser Livros Mus Nacional Rio de Janeiro* 28. *Porifera Research. Biodiversity, Innovation and Sustainability*. Publ. Museu Nac, Rio De Janeiro, pp. 569–580.
- Schönberg, C.H.L., Wilkinson, C., 2001. Induced colonization of corals by a clionid bioeroding sponge. *Coral Reefs* 20, 69–76.
- Schreiber, U., 2004. Pulse-Amplitude (PAM) fluorometry and saturation pulse method. In: Papageorgiou, G., Govindjee (Eds.), *Chlorophyll Fluorescence: A Signature of Photosynthesis*. Kluwer Academic Publishers, Dordrecht, pp. 279–319.
- Schreiber, U., Bilger, W., Neubauer, C., 1994. Chlorophyll fluorescence as a noninvasive indicator for rapid assessment of in vivo photosynthesis. In: Caldwell, M. (Ed.), *Schulze ED. Ecophysiology of Photosynthesis*. Springer, Berlin, pp. 49–70.
- Spalding, M., Ravilious, C., Green, E.P., 2001. *World Atlas of Coral Reefs*. Univ of California Press, Berkeley.
- Steindler, L., Beer, S., Peretzman-Shemer, A., Nyberg, C., Ilan, M., 2001. Photoadaptation of zooxanthellae in the sponge *Cliona vastifica* from the Red Sea, as measured in situ. *Mar. Biol.* 138, 511–515.
- Stender, Y., Jokiel, P.L., Rodgers, K.S., 2014. Thirty years of coral reef change in relation to coastal construction and increased sedimentation at Pelekane Bay, Hawaii. *PeerJ* 2, e300.
- Titlyanov, E.A., Shaposhnikova, M.G., Zvalinskii, V.I., 1980. Photosynthesis and adaptation of corals to irradiance. 1. Contents and native state of photosynthetic pigments in symbiotic microalga. *Photosynthetica* 14, 413–421.
- Vicente, V.P., 1978. An ecological evaluation of the west Indian demosponge *Anthosigmella varians* (Hadromerida: Spirastrellidae). *Bull. Mar. Sci.* 28, 771–779.
- Ward-Paige, C.A., Risk, M.J., Sherwood, O.A., Jaap, W.C., 2005. Clionid sponge surveys on the Florida reef tract suggest land-based nutrient inputs. *Mar. Pollut. Bull.* 51, 570–579.
- Weisz, J.B., Massaro, A.J., Ramsby, B.D., Hill, M.S., 2010. Zooxanthellar symbionts shape host sponge trophic status through translocation of carbon. *Biol. Bull.* 219, 189–197.
- Wisshak, M., Schönberg, C.H., Form, A., Freiwald, A., 2012. Ocean acidification accelerates reef bioerosion. *PLoS One* 7, e45124.
- Wisshak, M., Schönberg, C., Form, A.U., Freiwald, A., 2013. Effects of ocean acidification and global warming on reef bioerosion—lessons from a clionid sponge. *Aquat. Biol.* 19, 111–127.
- Wolanski, E., Martinec, J.A., Richmond, R.H., 2009. Quantifying the impact of watershed urbanization on a coral reef. Maunaloa Bay, Hawaii. *Estuar. Coast. Shelf Sci.* 84, 259–268.
- Ziegler, M., Roder, C., Büchel, C., Voolstra, C.R., 2015. Niche acclimatization in Red Sea corals is dependent on flexibility of host-symbiont association. *Mar. Ecol. Prog. Ser.* 533, 149–161.