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Dissolved inorganic nutrient enrichment does not affect sponge growth or condition

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ABSTRACT: Changing land use and an increasing human population have led to increased terrestrial runoff, which delivers nutrients, pesticides, and heavy metals into aquatic ecosystems. Elevated nutrient levels can adversely affect nearshore corals by reducing the amount of light reaching the benthos, exacerbating coral disease and bleaching, as well as stimulating algal growth, but the effects on other reef taxa are poorly understood. We investigated the effects of dissolved inorganic nutrient enrichment and changes in irradiance on the growth and condition of 5 common Great Barrier Reef sponges: 4 sponges with photosynthetic symbionts and 1 lacking photosynthetic symbionts. Concentrations of up to 7 µM total dissolved inorganic nitrogen (DIN) did not significantly affect the growth, condition, or chl *a* content of any sponge species after 10 wk exposure. However, 2 species lost >20% volume across all nutrient treatments, suggesting that aquarium conditions may have been suboptimal for these species. Irradiance (80 vs. 160 µmol quanta m^{-2} s^{-1}) did not affect 4 of the 5 sponge species; however, higher irradiance resulted in higher organic content and chl *a* levels in the bioeroding sponge *Cliona orientalis*, the only studied species that associates with the photosynthetic dinoflagellate *Symbiodinium*, suggesting that sponge–*Symbiodinium* associations may be more sensitive to irradiance levels than sponge–*Cyanobacteria* associations. While elevated nutrient levels are exacerbating the decline of reef-building corals, exposure to the average DIN levels within flood plumes that reach inshore reefs appears to have negligible effects on reef sponges.

KEY WORDS: Nitrogen · Phosphorus · Light · Pollution

1. INTRODUCTION

Intensified agricultural land use and modification of coastal landscapes has increased terrestrial runoff, carrying nutrients, sediments, and pollutants into the marine environment (Brodie et al. 2011, 2012, Waterhouse et al. 2012). For example, rivers now carry over 5 times more nutrients into the Great Barrier Reef (GBR) lagoon than before European settlement (Kroon et al. 2012). Seasonal floods cause acute runoff-related stresses (Schaffelke et al. 2012, Fabricius et al. 2016), but chronic nutrient enrichment (dissolved inorganic nitrogen and phosphorus) can also occur in nearshore locations with limited exposure to oligotrophic water (Smith et al. 1981, Goreau 1992). While rivers and streams represent point sources of

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nutrient pollution, plumes of sediments and nutrients can cover hundreds of km^2 and increase turbidity for prolonged periods (Bainbridge et al. 2012, Fabricius et al. 2016). Increased levels of nutrients and sediments are not just problematic for GBR reefs, but for coral reefs globally (Haas et al. 2016, Pawlik et al. 2016).

Terrestrial runoff contains dissolved (≤0.4 µm) and particulate (≥0.4 µm) nutrients that may be inorganic or organic. Each nutrient type has different lifetimes and impacts on coral reef ecosystems (Fabricius 2005). In particular, dissolved inorganic nitrogen (DIN; ammonium, nitrite, and nitrate) forms a large component of the nitrogen pollution in the GBR lagoon (Brodie et al. 2012). However, DIN is rapidly taken up by phytoplankton, leading to phytoplankton blooms (Furnas et al. 2005, Bainbridge et al. 2012) and reducing irradiance reaching the benthos. While coral reefs do occur in nutrient-rich habitats (Perry et al. 2012), the benthic community differs from that found in oligotrophic locations, including higher macroalgal cover and richness of heterotrophic taxa (De'ath & Fabricius 2010). Overall, DIN enrichment contributes to poor coral health (Wiedenmann et al. 2013), but the effects of DIN on other reef taxa are less well known.

Sponges are highly efficient filter feeders and may benefit from DIN enrichment via increased dissolved or particulate carbon food sources (Bainbridge et al. 2012) or from enhanced nitrification activity by sponge-associated microbes (Southwell et al. 2008, Fiore et al. 2010, 2013). During wet seasons and floods, DIN levels on the inshore GBR can increase by an order of magnitude (e.g. from ~0.2 to >2 µM; Devlin et al. 2011). High nutrient loads would increase the availability of food for sponges, which is thought to be a primary driver of sponge distributions, including the high abundance of heterotrophic sponges on coastal reefs (Wilkinson & Cheshire 1989) and the greater abundance of heterotrophic sponges in the Caribbean relative to the Pacific (Pawlik et al. 2016). In particular, the abundance of bioeroding sponges is strongly related to nutrient gradients (Rose & Risk 1985, Holmes 2000, Ward-Paige et al. 2005, Chaves-Fonnegra & Zea 2007, Nava et al. 2014). The connection between sponges and high nutrient levels may be driven by accelerated growth or increased energy reserves resulting from nutrient-enhanced heterotrophy or microbial metabolism if microbial metabolites are translocated to the sponge host. Despite this hypothetical link between nutrient enrichment and sponge growth, studies to date suggest that nutrient enrichment does not directly benefit sponge growth (Roberts et al. 2006, Gochfeld et al. 2012, Easson et al. 2014), sponge protein content (Gochfeld et al. 2012, but see Easson et al. 2014), or alter sponge microbial community composition (Simister et al. 2012, Luter et al. 2014).

On the other hand, nutrient enrichment may hinder the symbiosis between sponges and their microbial symbionts. In resource exchange mutualisms, nutrient enrichment can remove nutrient limitation (e.g. nitrogen or phosphorus) of the phototroph to the detriment of the heterotroph (Kiers et al. 2010, Shantz & Burkepile 2014, Shantz et al. 2016). Therefore, DIN enrichment may have adverse consequences for sponges with photosynthetic symbionts if the symbiosis is destabilised by increasing symbiont density. For instance, one study suggested that DIN enrichment disrupted the symbiosis between *Cyanobacteria* and the sponge *Aplysina cauliformis*, as chlorophyll levels were found to increase, suggesting an increased density of *Cyanobacteria*, while sponge protein levels decreased, indicating reduced sponge condition (Easson et al. 2014). However, other studies reported that chlorophyll levels in photosymbiotic sponges were unaffected by DIN enrichment (Roberts et al. 2006, Gochfeld et al. 2012). Thus, whether DIN enrichment destabilises the symbiosis between sponges and *Cyanobacteria* is unclear, and the effects of elevated DIN on sponges hosting *Symbiodinium* have not previously been investigated.

Terrestrial runoff also contains sediments and particulate matter in addition to dissolved nutrients (Fabricius et al. 2016). Large particles remain suspended in the water column, thereby limiting the light reaching the benthos (Bainbridge et al. 2012). However, large particles settle out near the river mouth while flocs of small particles and nutrients travel further, triggering phytoplankton blooms, and limiting irradiance on reefs farther from shore (Bainbridge et al. 2012). For sponges with photosynthetic symbionts, reductions in irradiance can slow their growth (Thacker 2005, Roberts et al. 2006, Erwin & Thacker 2008, Freeman & Thacker 2011) and can also reduce chlorophyll levels in some species (Pineda et al. 2016). The growth of bioeroding sponges, in particular, appears to be negatively affected by decreased irradiance (Hill 1996, Cebrian & Uriz 2006, Schönberg 2006, Pineda et al. 2016), likely due to their association with *Symbiodinium* (Weisz et al. 2010, Hill et al. 2011). Since reduced irradiance can co-occur with nutrient enrichment, it is difficult to discern the independent effects of irradiance and nutrients during flood events. Moreover, the effects of light and nutrients may vary between sponge spe-

cies due to their relative dependence on autotrophic production and heterotrophic feeding or their ability to switch between nutritional modes (Anthony & Fabricius 2000, Grottoli et al. 2006, Freeman et al. 2015). To investigate the effects of DIN enrichment and irradiance on sponges, we exposed sponges with and without photosynthetic symbionts to concentrations of dissolved nutrients simulating flood plume conditions under 2 light levels and measured effects on sponge growth and energy reserves.

2. MATERIALS AND METHODS

2.1. Sponge collection and acclimation

In April 2017, whole sponges (*Carteriospongia foliascens*, *Cliona orientalis*, *Cymbastella coralliophila*, *Ircinia ramosa*, and *Stylissa flabelliformis*) were collected using SCUBA between 1 and 9 m depth (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m634p077_supp.pdf). All species are known to associate with diverse populations of microbial symbionts, with *C. foliascens, C. coralliophila*, and *I. ramosa* hosting *Cyanobacteria*; *C. orientalis* hosting *Symbiodinium*; and *S. flabelliformis* lacking photosymbionts but hosting a diverse community of heterotrophic microorganisms (Wilkinson 1982, Pineda et al. 2016). All sponges were transported to the Australian Institute of Marine Science (Townsville, Queensland) and acclimated in outdoor aquaria at 27°C. After 10 d, each sponge was cut into smaller explants (n = 4–11, dependent on the size of the donor sponge; ~15 cm^2) to provide sufficient experimental replication for each sponge genotype. To measure growth of the encrusting *C. orientalis*, the sponge and its underlying calcium carbonate substratum was cut into rectangular explants and laid on its side whereby the sponge was now on the side of the explant (~6 cm^2) and the top surface was clean substratum.

All explants were labelled according to the donor sponge, allowed to heal for 6 wk, and then allocated into 36 experimental aquaria (50 l). Explants from the same sponge were allocated into different treatments; most sponges were represented by 1 explant per treatment, but some sponges were represented by multiple explants per treatment, and a few sponges had insufficient explants for all treatments. As a result, each aquarium contained explants from 1–3 sponges of each species and 8–11 total explants (Table S2). Tank temperature was maintained at 26.9 ± 0.1°C (mean ± SD) using a computer-controlled system. Sponges were fed daily with a 1.5×10^6 cells l^{-1} final concentration of cultured microalgae (*Isochryisis galbana*, *Nanochloropsis oceanica*, *Pavlova lutheri, Dunaliella* sp.) and a diatom (*Chaetocerous muelleri*) ranging from 2 to 10 µm in diameter.

2.2. Nutrient and light treatments

Nutrient treatments were designed to enrich seawater DIN to concentrations relevant to inshore reefs during flood events; from 1 to 10 µmol l^{-1} (Devlin et al. 2011). Two dissolved nutrient treatments were established, representing medium and high levels of nutrient enrichment, while a third treatment contained no nutrient amendment (control). Additions of 14.9 or 29.8 g of soluble fertilizer (Yates Thrive, NPK 25:5:8.8) were added to 60 l reservoirs of 0.04 µm filtered seawater to achieve the medium and high treatment levels, respectively. Doses were pumped from the reservoirs at 0.01 l min^{-1} into 0.04 µm filtered seawater entering the experimental aquaria at 0.8 l min^{-1}. Nutrient reservoirs were depleted every 3–4 d and were replaced twice weekly. The aquaria were part of an open, flow-through system, and the flow rate was sufficient to replace the water in each aquarium every 62 min.

As nutrient enrichment co-occurs with reduced irradiance during flood events, the 3 nutrient treatments were fully crossed with 2 light conditions (80 and 160 µmol quanta m^{-2} s^{-1}), resulting in 6 treatments that were each replicated in 6 aquaria. Light was provided by Aquaillumination Sol LED lamps (C2 Development). Sponges were exposed to treatment conditions for 10 wk.

2.3. Nutrient sampling

Dissolved and particulate nutrients were sampled weekly in both the dosing reservoirs and in the aquaria. Due to pump failure, dosing reservoirs were occasionally empty on the day of water sampling, and the water samples from these time points have thus been omitted from the analysis, leaving 9 measurements for the control and medium treatments and 5 measurements for the high treatment. Samples for particulate organic carbon (POC) and particulate nitrogen (PN) were filtered onto pre-combusted Whatman glass fibre filters (250 ml), acidified using hydrochloric acid, and analysed on a Shimadzu TOC-V analyser with a total nitrogen unit and solid sample module. Particulate values were compared to marine sediment standards. For dissolved nutrients,

seawater samples (10 ml) were taken from each dosing reservoir and aquarium and filtered using 0.45 µm Sartorius Minisart Cellulose Acetate filters. Samples for dissolved organic carbon (DOC) and dissolved nitrogen (DN) were acidified with hydrochloric acid and measured on a Shimadzu TOC-L analyser. Duplicate samples for DIN (NH_4^+, NO_{2+3}, NO_2^-) and phosphate (PO_4^{3-}) were measured on a Seal AA3 segmented flow analyser and referenced against OSIL standards and in-house reference samples. Samples for POC, PN, DIN, and PO_4^{3-} were kept frozen at −20°C until measurement, while samples for DOC and DN were kept at 4°C. Dissolved organic nitrogen (DON) was calculated as the difference between DN and DIN. Nitrate (NO_3^-) was calculated as the difference between NO_{2+3} and NO_2^-.

2.4. Sponge growth

To determine the effect of nutrients on growth, sponge volume (to the nearest ±0.5 ml) and surface area (to the nearest ±0.1 mm^2) were measured at the beginning and end of the experiment (10 wk interval). Sponge volume was assessed using a standard water displacement technique (Wilkinson & Vacelet 1979) for all species except the bioeroding *C. orientalis*. Sponge growth was estimated as the difference in sponge volume over the course of the experiment as a percentage of the initial volume. Sponges were briefly exposed to air during volume measurement. Due to its encrusting morphology, growth of *C. orientalis* was measured using change in surface area over the course of the experiment. Area was calculated from photographs of the top surface in ImageJ software (Abramoff et al. 2014). The growth of *C. orientalis* was calculated as the change in surface area relative to the initial area. For all species, sample sizes were ≥9 in each treatment (Table S3).

2.5. Sponge organic matter and chlorophyll *a* (chl *a*)

Sponge organic matter was used as a proxy for sponge condition. Organic matter was measured at the end of the experiment by freeze-drying the sponge tissue, weighing the dried tissue (~0.130 g), burning it at 450°C for 3 h, and weighing the remaining ash. Organic matter was calculated as the difference between the dry weight and ash weight as a proportion of the dry weight. For all species, sample sizes were ≥9 in each treatment (Table S3).

Chl *a* was used as a proxy for determining whether treatment affected photosymbiosis. At the end of the experiment, chlorophyll was extracted from frozen sponge tissue (~170 mg) following homogenization in a bead beater with 1 ml of 95% ethanol. Pigments were extracted twice from each sample, both extracts were pooled, and absorbance was recorded at 630, 645, 660, and 750 nm using a Powerwave microplate reader (BIO-TEK Instruments). For all species, sample sizes were ≥10 in each treatment (Table S3).

2.6. Statistical analyses

Nutrient levels within dosing reservoirs were analysed using a linear mixed model with nutrient dose and time as predictors. Nutrient levels within sponge aquaria were analysed using linear mixed models with nutrient dose, light treatment, time, as well as nutrient:time and nutrient:light interactions as predictors and aquarium as a random effect to account for autocorrelations between measurements taken in the same tank. Where significant differences were detected among nutrient treatments or nutrient:light combinations, all pairs of treatments were compared using linear contrasts, and p-values were corrected using a single-step correction.

Sponge responses were analysed using linear mixed models with nutrient treatment, light treatment, and a nutrient:light interaction as predictors. Tank and sponge were included as random effects to account for correlations within aquaria and among measurements on explants from the same donor genotype. Where significant differences were detected among nutrient treatments or nutrient:light combinations, all pairs of treatment levels were compared using linear contrasts, and p-values were corrected using single-step correction. All models were verified to meet the assumptions of normality of residuals and heteroscedasticity using histograms of the residuals and plots of fitted versus residual values. Values are presented as means ± SD unless otherwise noted.

3. RESULTS

3.1. Nutrient and light conditions

The medium and high dosing reservoirs contained higher DOC, total DN, DON, and inorganic nutrients (total DIN, NH_4^+, NO_2^- NO_3^-, PO_4^{3-}) compared to the control reservoir (Tables S4 & S5). However, only the

medium nutrient reservoir had an altered ratio of DIN:PO_4^{3-}, with reduced DIN:PO_4^{3-} compared to the control reservoir (Table S5). Concentrations of particulate C and N were consistent across all dosing reservoirs (Tables S4 & S5).

In the nutrient-enriched aquaria, DN, DON, DIN, and PO_4^{3-} increased relative to control aquaria, but DOC, particulate C, and PN did not differ (Figs. 1 & 2, Tables 1 & 2). Total DIN in the sponge aquaria was 1.4 ± 0.2, 3.4 ± 0.9, and 5.8 ± 1.5 µmol l^{-1} for the control, medium, and high treatments, respectively (Table S6). Elevated DIN in the enriched aquaria was associated with higher concentrations of NO_2^-, NO_3^-, and NH_4^+ (Fig. 3, Table 2) and a decreased ratio of DIN:PO_4^{3-} (Fig. 2B). Importantly, the concentration of all nutrients varied over time and differences between treatments varied over the course of the experiment, particularly for DIN compounds (Fig. 3, Table 1).

Irradiance levels in the low and high light treatments were 79.5 ± 5.4 and 157.8 ± 13.2 µmol quanta m^{-2} s^{-1}, respectively. The irradiance treatment had small, but significant, effects on nutrient levels within the sponge aquaria (Figs. 1–3, Table 1). DN concentration was slightly higher in the higher irradiance treatment (Fig. 1), whereas most DIN compounds were slightly lower (Fig. 3, Table S6). Small but significant decreases were observed in NO_3^-, total DIN, and the DIN:PO_4^{3-} ratio in the higher irradiance treatment (Figs. 2 & 3, Table 1). The concentration of NH_4^+ depended on both the irradiance and nutrient treatments (Fig. 3A): in aquaria from the control and medium treatments, NH_4^+ was similar between irradiance treatments (Table 1; control: $z = -0.8$, $p = 0.97$; medium: $z = -0.6$, $p = 0.99$), whereas in aquaria from the high treatment, NH_4^+ was 33% higher at 80 versus 160 µmol quanta m^{-2} s^{-1} ($z = -6.0$, $p \leq 0.01$).

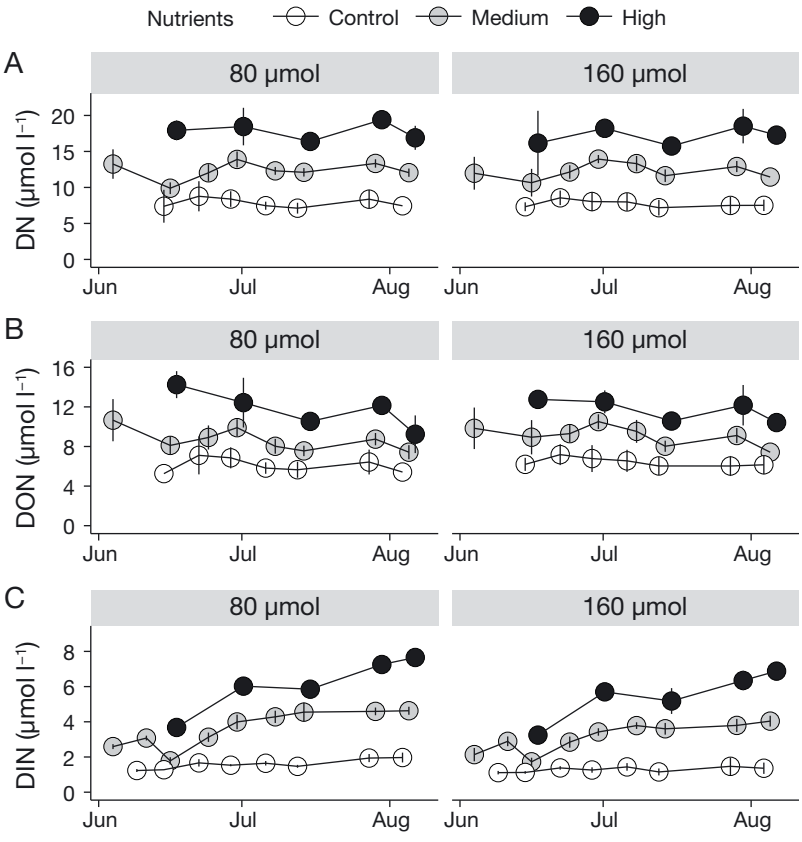

Fig. 1. Dissolved nitrogen concentrations in experimental aquaria for (A) total dissolved nitrogen (DN), (B) dissolved organic nitrogen (DON), (C) total dissolved inorganic nitrogen (DIN; NH_4^++NO_3^-+NO_2^-). Circles represent control, medium dose, and high dose aquaria. Left and right panels separate irradiance at 80 and 160 µmol quanta m^{-2} s^{-1}, respectively. Error bars show SD

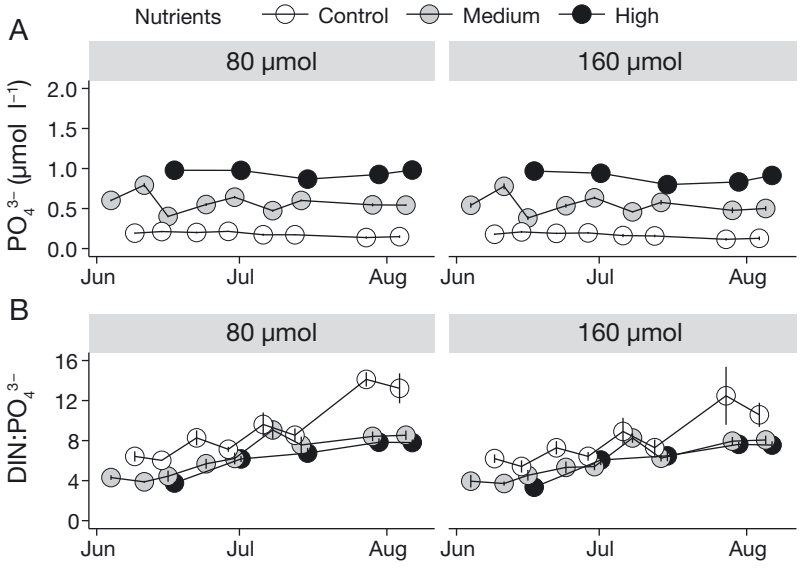

Fig. 2. Phosphate concentrations in experimental aquaria for (A) phosphate (PO_4^{3-}), (B) DIN:PO_4^{3-} ratio. Other details as in Fig. 1

Table 1. Results of linear mixed models analysing nutrient levels within the experimental aquaria. The model included nutrient treatments, light treatments, time, a nutrient × light interaction term, nutrient × time interaction term, and a random intercept for each tank. Degrees of freedom (numerator, denominator), *F* statistic, and p-values are reported for each measured nutrient; p-values ≤0.05 are indicated in **bold**

	Nutrients			Light			Time			Nut. × Light			Nut. × Time		
	df	*F*	p	df	*F*	p	df	*F*	p	df	*F*	p	df	*F*	p
Particulate															
Organic C	2,12	1.0	0.39	1,12	<0.1	0.84	3,45	2.6	0.06	2,12	0.2	0.81	6,45	0.3	0.94
N	2,12	2.1	0.17	1,12	1.7	0.21	2,30	1.8	0.19	2,12	0.1	0.88	4,30	0.3	0.86
Dissolved															
Organic C	2,30	0.5	0.64	1,30	0.4	0.53	8,259	66.3	**<0.01**	2,30	0.3	0.77	16,259	0.6	0.91
N	2,30	77.2	**<0.01**	1,30	0.5	0.48	1,233	0.2	0.62	2,30	0.5	0.60	2,233	5.2	**0.01**
Organic N	2,30	11.0	**<0.01**	1,30	0.4	0.52	1,205	3.9	**0.05**	2,30	0.2	0.80	2,205	10.9	**<0.01**
Dissolved inorganic															
Total DIN	2,30	18.8	**<0.01**	1,30	10.5	**<0.01**	1,235	7.7	**0.01**	2,30	1.5	0.24	2,235	122.1	**<0.01**
NH_4^+	2,30	71.8	**<0.01**	1,30	1.3	0.27	1,235	6.5	**0.01**	2,30	17.2	**<0.01**	2,235	2.0	0.14
NO_2^-	2,30	43.7	**<0.01**	1,30	2.5	**0.13**	1,237	9.1	**<0.01**	2,30	0.5	0.63	2,237	44.0	**<0.01**
NO_3^-	2,30	31.2	**<0.01**	1,30	12.5	**<0.01**	1,237	31.8	**<0.01**	2,30	0.4	0.69	2,237	132.2	**<0.01**
PO_4^{3-}	2,30	297.8	**<0.01**	1,30	1.4	0.24	1,237	12.0	**<0.01**	2,30	1.3	0.28	2,237	0.2	0.79
Total DIN: PO_4^{3-}	2,30	14.3	**<0.01**	1,30	22.0	**<0.01**	1,235	288.5	**<0.01**	2,30	2.9	0.07	2,235	3.2	**0.04**

Table 2. Post hoc results from linear contrasts of nutrient doses within experimental aquaria. P-values were corrected using single-step correction; p-values ≤0.05 are indicated in **bold**. (–) indicates variables that were not significantly different between nutrient treatments (see Table 1). NH_4^+ significantly differed between nutrient treatments, but the difference depended on the irradiance level (see Section 3)

	Control vs. Med.		Med. vs. High		Control vs. High	
	Z	p	*Z*	p	*Z*	p
Particulate						
Organic C	–	–	–	–	–	–
N	–	–	–	–	–	–
Dissolved						
Organic C	–	–	–	–	–	–
N	6.9	**<0.01**	–6.3	**<0.01**	12.3	**<0.01**
Organic N	290.3	**0.22**	718.5	**<0.01**	1008.8	**<0.01**
Dissolved inorganic						
Total N	5.2	**<0.01**	1.3	0.37	4.9	**<0.01**
NH_4^+	–	–	–	–	–	–
NO_2	495.0	**<0.01**	203.6	**0.01**	291.5	**<0.01**
NO_3^-	298.2	**<0.01**	407.6	**<0.01**	705.8	**<0.01**
PO_4^{3-}	16.7	**<0.01**	11.1	**<0.01**	22.4	**<0.01**

3.2. Sponge growth

None of the sponge species exhibited significantly different growth rates in response to the nutrient treatments, light treatments, or any combination of nutrients and light (Fig. 4A, Table 3). Over the course of the 10 wk experiment, *Cymbastella coralliophila* increased in volume (11.5 ± 6.1%, corresponding to a growth rate of 4.9% volume mo^{-1}), while *Ircinia ramosa* (–6.4 ± 7.2%), *Carteriospongia foliascens* (–25.9 ± 10.9%), and *Stylissa flabelliformis* (–45.0 ± 10.7%) decreased in volume. Surface area growth of the encrusting sponge *Cliona orientalis* was similar amongst all treatments (Table 3), with an increase of 11.1 ± 6.7% in area for the 10 wk period, or 4.7% area mo^{-1}.

3.3. Sponge organic matter and chl *a*

No sponge species exhibited significantly different organic content (i.e. condition) in response to the nutrient treatments or combinations of nutrients and light (Fig. 4B, Table 3). However, organic content in *C. orientalis* was significantly affected by irradiance, with 7% more organic content at 160 versus 80 µmol m^{-2} s^{-1} (Table 3). *I. ramosa* had the highest organic content (73.8 ± 7.8%), followed by *S. flabelliformis* (56.5 ± 5.5%), *C. coralliophila* (41.2 ± 7.9%), *C. foliascens* (39.4 ± 4.9%), and *C. orientalis* (5.1 ± 0.1%).

Sponge chl *a* content did not differ between nutrient treatments or combinations of nutrient and light for any sponge species (Fig. 5, Table 3). However, chlorophyll levels in *C. orientalis* were significantly different between light treatments, with 35% more chl *a* at 160 versus 80 µmol quanta m^{-2} s^{-1} (Fig. 5). *I. ramosa* had the highest chl *a* µg g^{-1} wet weight (99.0 ± 34.3), followed by *C. coralliophila* (82.1 ± 23.2), *C. foliascens* (68.8 ± 20.7), and *C. orientalis* (57.2 ± 10.7; Fig. 5).

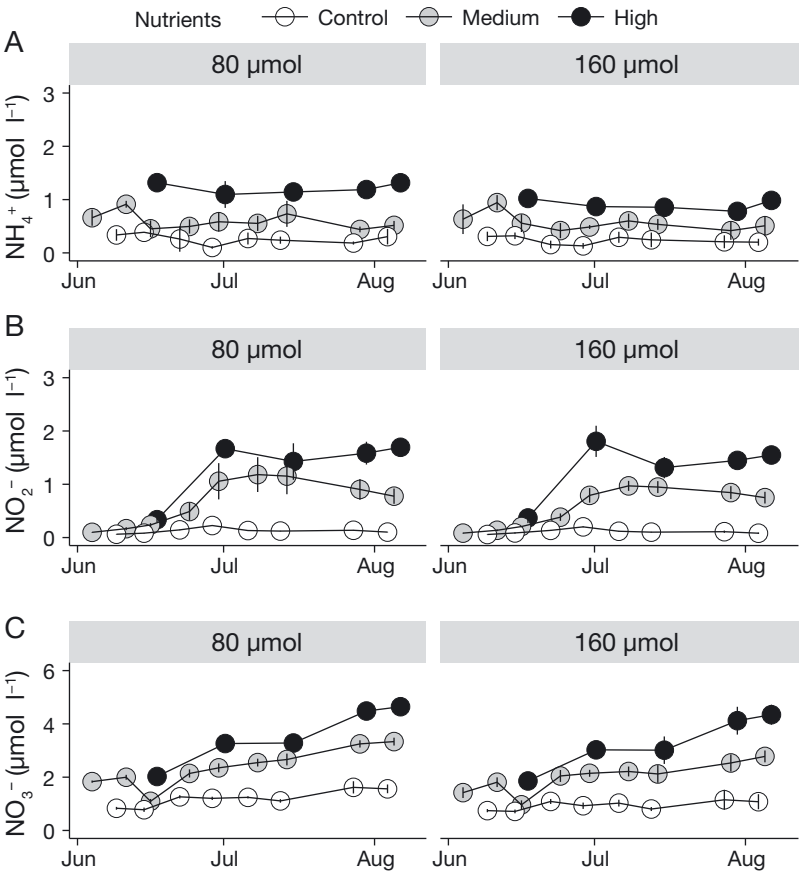

Fig. 3. Dissolved inorganic nitrogen concentrations in experimental aquaria for (A) ammonium (NH_4^+), (B) nitrite (NO_2^-), and (C) nitrate (NO_3^-). Other details as in Fig. 1

4. DISCUSSION

Nutrient enrichment is generally thought to benefit filter feeders and bioeroders (Birkeland 1988, Glynn 1997), with some species showing increased abundance, or exhibiting higher rates of bioerosion, in habitats with elevated nutrient levels (Rose & Risk 1985, Sammarco & Risk 1990, Risk et al. 1995, Ward-Paige et al. 2005, Fabricius & De'ath 2008). Importantly however, direct experimental evidence for the putative advantages provided by nutrient enrichment is lacking. DIN is an important component of runoff from agricultural or urban areas (Brodie et al. 2012), and previous research has shown that sponges exhibit either no response (Roberts et al. 2006, Gochfeld et al. 2012) or decreased growth/condition following DIN enrichment (Koopmans & Wijffels 2008, Easson et al. 2014). In our study, addition of DIN at levels experienced on the inshore GBR during flood plume events (Devlin & Schaffelke 2009, Devlin et al. 2011) caused no adverse effects on the health of 5 sponge species but also did not accelerate growth or improve sponge condition. These findings were consistent across sponges with and without photosynthetic symbionts. While the DIN exposure in this study was similar in magnitude to previous studies (Simister et al. 2012, Gochfeld et al. 2012), the sponges were exposed for more than twice as long in this study, further supporting our conclusion that DIN enrichment does not affect sponge growth or condition. However, the observed volume loss across several species suggests that aquarium conditions may have been suboptimal for sponge growth.

Sponges are fundamental to nutrient cycling on coral reefs due to their efficient filtration of seawater, including the consumption of DOM and POM and potentially the production of POM (Richter et al. 2001, de Goeij et al. 2013, McMurray et al. 2018, Rix et al. 2018). Additional inorganic nutrients can increase the DOC or POC pool in seawater, thereby increasing the potential food available for sponges (Maldonado et al. 2012). Numerous studies have demonstrated that sponges consume DOC and/or POC (reviewed by Maldonado et al. 2012, de Goeij et al. 2017), and POC levels positively correlate with sponge growth in the laboratory and in the field (Duckworth & Pomponi 2005, Koopmans & Wijffels 2008). However, in our study, nutrient amendment did not result in increased sponge growth or improved condition, and neither did DOC addition, although DOC was only significantly enriched in the nutrient reservoirs and not in the experimental aquaria. This distinction suggests that DOC was rapidly consumed by sponges or by microbial activity, although either scenario could have provided increased scope for sponge growth.

Nutrient treatments did not affect sponge growth rates, but the lack of growth or shrinkage of some species may have constrained the sponge responses. The lack of growth suggests that aquarium conditions may not have been optimal for all species; however, zero growth or shrinkage also occurs under natural conditions (Barthel 1986, Hoppe 1988, Abdo et al. 2006). Sponge growth rates vary seasonally and are thought to be correlated to temperature and

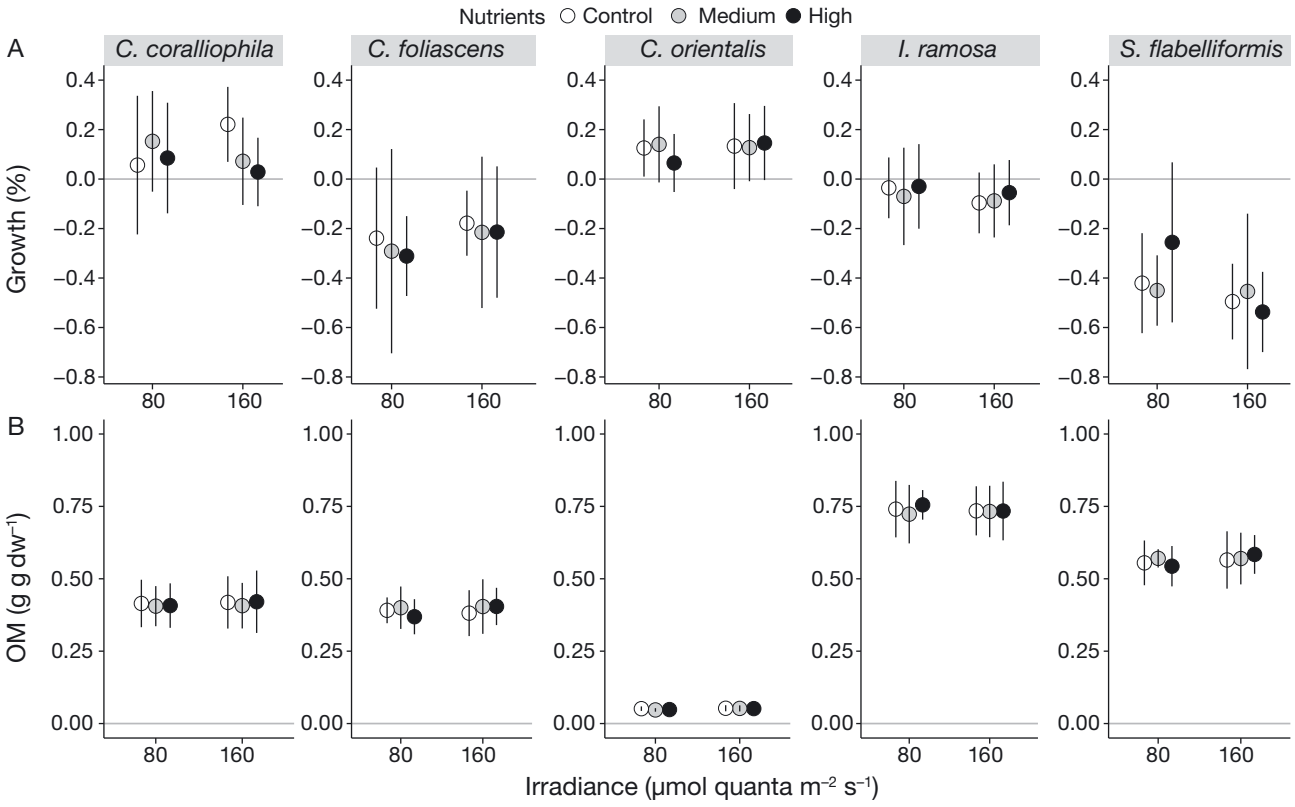

Fig. 4. (A) Sponge growth and (B) organic matter (OM; % dry weight, dw) under nutrient and light treatments. Circles represent sponges in control, medium, and high nutrient treatments. Error bars show SD. Growth of *C. orientalis* is calculated via change in surface area while the growth of all other species is calculated via change in volume. Sponge genera are listed in Table 3

Table 3. Results of linear mixed models for sponge growth, organic matter, and chlorophyll *a* content for each sponge species. The model included nutrient treatments, light treatments, time, a nutrients × light interaction term, and a random intercept for each sponge. Degrees of freedom (numerator, denominator), *F* statistic, and p-values are reported for each measured nutrient; p-values <0.05 are indicated in **bold**

	Nutrients			Light			Nutrients × Light		
	df	*F*	p	df	*F*	p	df	*F*	p
Growth rate									
Cymbastella coralliophila	2, 61.0	2.3	0.11	1, 61.0	<0.1	0.77	2, 61.0	1.6	0.21
Carteriospongia foliascens	2, 30.3	0.8	0.47	1, 30.3	3.2	0.08	2, 30.3	0.4	0.70
Cliona orientalis	2, 59.9	0.3	0.73	1, 61.0	<0.1	0.92	2, 59.4	1.0	0.37
Ircinia ramosa	2, 28.0	0.3	0.74	1, 28.0	0.8	0.37	2, 28.0	0.1	0.89
Stylissa flabelliformis	2, 28.0	0.3	0.74	1, 28.0	0.8	0.37	2, 28.0	0.1	0.89
Organic matter									
C. coralliophila	2, 23.8	0.4	0.66	1, 26.8	1.9	0.18	2, 26.3	0.3	0.73
C. foliascens	2, 21.7	0.6	0.56	1, 21.7	0.7	0.40	2, 22.0	0.7	0.48
C. orientalis	2, 63.1	2.0	0.14	1, 63.1	5.0	**0.03**	2, 63.1	0.3	0.76
I. ramosa	2, 22.4	0.8	0.48	2, 22.5	0.3	0.59	2, 22.4	0.4	0.68
S. flabelliformis	2, 9.8	0.2	0.81	1, 9.9	0.9	0.36	2, 9.9	0.6	0.55
Chlorophyll *a*									
C. coralliophila	2, 25.9	1.2	0.31	1, 27.2	2.8	0.10	2, 28.9	0.1	0.91
C. foliascens	2, 24.6	0.6	0.57	1, 24.4	0.1	0.75	2, 24.5	0.5	0.62
C. orientalis	2, 28.2	0.4	0.65	1, 28.2	4.8	**0.04**	2, 28.2	<0.1	0.99
I. ramosa	2, 53.3	0.1	0.94	1, 53.3	0.1	0.73	2, 53.2	<0.1	0.95

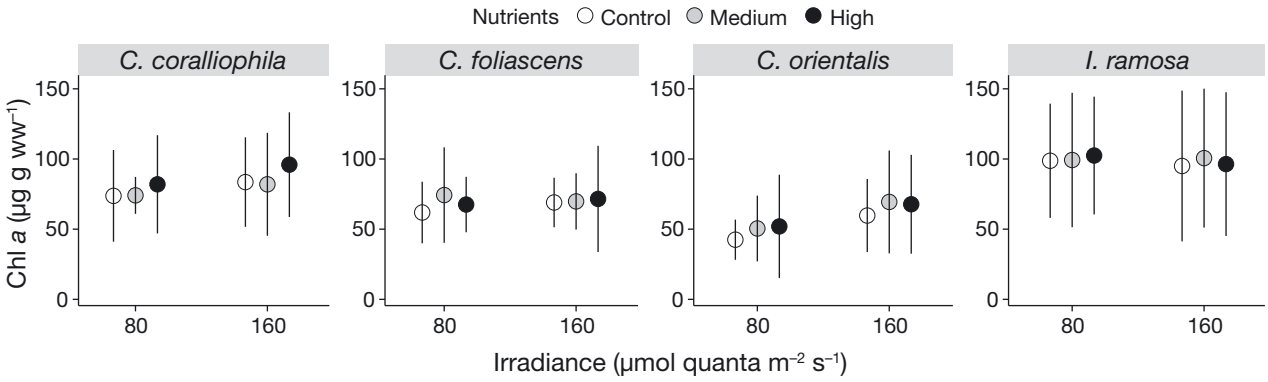

Fig. 5. Sponge chlorophyll *a* content (ww: wet weight). Details as in Fig. 4

reproductive cycles (Wilkinson & Vacelet 1979, Barthel 1986) and food availability (Wulff 2017). *Cliona orientalis* sponges consistently increased in area (4.7% mo^{-1}), which is an order of magnitude faster than growth in the field (0.4% mo^{-1}; calculated from Schönberg 2003), perhaps due to the availability of clean substrata or the absence of competition for space in the aquaria.

In resource exchange mutualisms, nutrient amendment can upset the nutritional exchange between heterotrophs and autotrophs (Shantz & Burkepile 2014, Shantz et al. 2016). More specifically, nutrient enrichment can remove the resource limitation of the phototrophic partner, which no longer requires the heterotroph to supply nutrients (Shantz et al. 2016). In this way, DIN enrichment can lead to increased *Symbiodinium* density in corals, which reduces the thermal tolerance of the symbiosis (Wooldridge 2014). DIN enrichment can also potentially disrupt the symbiotic partnership between sponges and *Cyanobacteria*, as nutrient enrichment increased chlorophyll and decreased protein in *Aplysina cauliformis* (Easson et al. 2014). However, in our study and in 2 previous experiments, inorganic nutrient enrichment did not affect the density of chl *a*, a proxy for photosymbiont density (Roberts et al. 2006, Gochfeld et al. 2012). Moreover, in studies where the density of *Cyanobacteria* was measured directly, no effect of DIN enrichment was observed (Gochfeld et al. 2012, Easson et al. 2014), suggesting that sponge symbioses are stable under nutrient enrichment.

As nitrogen enrichment can accelerate microbial growth rates, nutrient ratios can be as important to photosymbioses with microbes as total nutrient concentrations (Wiedenmann et al. 2013, Morris et al. 2019). In corals, high DIN:P ratios can have detrimental effects, with phosphorus limitation increasing the thermal sensitivity of the symbiotic partnership (Ezzat et al. 2016). In the current study, DIN:P was reduced, which may have mitigated any negative effects on the sponge symbioses. However, it is notable that no change in symbiont density (in terms of chl *a*) occurred at elevated DIN, suggesting that the sponge photosymbiont densities are unaffected by nutrient amendment.

During a flood event, DIN enrichment may coincide with reduced irradiance due to particulate material, suspended fine particles, or nutrient-induced phytoplankton blooms that reduce the light reaching the benthos (Bainbridge et al. 2012, Schaffelke et al. 2012). For all 5 sponge species, irradiance did not significantly affect sponge growth, although higher irradiance increased organic content and chl *a* levels in *C. orientalis*, suggesting that the condition of this species is tightly coupled to the performance of its photosymbiont, *Symbiodinium* (Hill 1996, Schönberg 2006, Fang et al. 2014, Achlatis et al. 2017). This finding supports field experiments where bioeroding sponges grew and eroded faster under higher irradiance (Hill 1996, Schönberg 2006), likely fuelled by increased carbon translocation from the *Symbiodinium* (Weisz et al. 2010). Irradiance appears to play a role in the success of *C. orientalis* on the inshore GBR, as *C. orientalis* cover has increased at locations with relatively low turbidity (low chl *a*) and intermediate DIN levels (Ramsby et al. 2017). Whilst many studies indicate that increased irradiance accelerates the growth of phototrophic sponges (Hill 1996, Thacker 2005, Roberts et al. 2006, Schönberg 2006, Freeman & Thacker 2011), some species are not affected (Erwin & Thacker 2008, this study), suggesting that sponge photosymbioses have species-specific responses to irradiance.

Despite the potential for inorganic and organic nutrients to increase the scope for sponge growth, nutrient (DIN+P) and organic (DOC) enrichment had no measured effect on GBR sponges and their photosymbionts. Thus, if sponges are to benefit from

coastal eutrophication, it is likely to be via particulate material rather than dissolved nutrient enrichment.

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