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REPORT

Complex and interactive effects of ocean acidification and temperature on epilithic and endolithic coral-reef turf algal assemblages

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Abstract Turf algal assemblages are ubiquitous primary producers on coral reefs, but little is known about the response of this diverse group to ocean acidification (OA) across different temperatures. We tested the hypothesis that CO_2 influences the functional response of epilithic and endolithic turf assemblages to increasing temperature. Replicate carbonate plugs covered by turf were collected from the reef and exposed to ambient and high pCO_2 (1000 µatm) conditions for 3 weeks. Each pCO_2 treatment was replicated across six temperatures (24.0–31.5 °C) that spanned the full seasonal temperature range on a fringing reef in Moorea, French Polynesia, and included one warming treatment (3 °C above daily average temperatures). Temperature and CO_2 enrichment had complex, and sometimes interactive, effects on turf metabolism and growth. Photosynthetic and respiration rates were enhanced by increasing temperature, with an interactive effect of CO_2 enrichment. Photosynthetic rates were amplified by high CO_2 in the warmest temperatures, while the increase in respiration rates with temperature were enhanced under ambient CO_2. Epilithic turf growth rates were not affected by temperature, but increased in response to CO_2 enrichment. We found that CO_2 and temperature interactively affected the endolithic assemblage, with the highest growth rates under CO_2 enrichment, but only at the warmest temperatures. These results demonstrate how OA may influence algal physiology and growth across a range of ecologically relevant temperatures, and indicate that the effects of CO_2 enrichment on coral-reef turf assemblages can be temperature dependent. The complex effects of CO_2 enrichment and temperature across a suite of algal responses illustrates the importance of incorporating multiple stressors into global change experiments.

Keywords Epilithic algal matrix · Global change · Photosynthesis · Primary production · Physiology

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Introduction

Global change is occurring at an unprecedented rate in the earth's history, with significant consequences for marine ecosystems (Doney et al. 2009; IPCC 2013). Increasing anthropogenic carbon dioxide (CO_2) emissions are causing a reduction in mean surface ocean pH through ocean acidification (OA) (Caldeira and Wickett 2003) and an increase in sea surface temperatures (IPCC 2013). We have advanced our understanding of the response of many marine organisms to decreasing ocean pH and warming

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temperatures, separately in most cases, through a plethora of single-stressor controlled laboratory experiments. Much of this work has focused on commercially valuable or ecologically important calcifying species (Fabry et al. 2008; Doney et al. 2009; Kroeker et al. 2010), because of the negative implications of OA, and its associated decreasing calcium carbonate ($CaCO_3$) saturation state (Ω), on biomineralization (Gattuso and Hansson 2011; Chan and Connolly 2013). Studies exploring the effects of OA combined with warming have primarily focused on thermally sensitive taxa, such as reef-building corals (Pörtner 2008) and have found that temperature can influence organismal responses to OA (Kroeker et al. 2013). However, many of these studies have used only a few temperature treatments. Testing biological responses to OA across a full suite of temperatures that organisms experience in situ is necessary to provide a more complete understanding of potential interactions between warming and OA now and into the future.

A key group of non-calcifying photoautotrophs that are markedly understudied with respect to global change are the turf algae. Turf assemblages (also referred to as algal turfs, epilithic algal matrix, EAM, or mat-forming algae) are diverse multi-species communities generally consisting of algae and cyanobacteria that range in height and density depending on location, season and herbivory regimes (Carpenter 1986; Steneck and Dethier 1988; Harris et al. 2015). Turfs are one of the most ubiquitous primary producers across temperate and tropical marine ecosystems, covering up to 70–80% of hard substrata and fulfilling a suite of important ecological functions (Borowitzka 1981; Copertino et al. 2005). For example, the high abundance and rapid turnover of turfs provide an important food source to grazers (Carpenter 1986) and can ameliorate negative effects of low pH on calcification of underlying crustose coralline algae (Short et al. 2014). However, turf assemblages can also negatively impact benthic communities by inhibiting algal recruitment (Worm and Chapman 1998) and by decreasing the abundance of juvenile and adult corals through direct and indirect competitive exclusion (Vermeij et al. 2010). The epilithic component of turf assemblages thus has an important influence on the trajectory of benthic community structure. While turf communities in temperate systems generally respond positively to OA (Russell et al. 2009; Connell and Russell 2010; Falkenberg et al. 2014), little is known about the response of tropical algal turf assemblages (see also Bender et al. 2014; Ober et al. 2016). Because turf assemblages differ in form and function across ecosystems, there is a significant gap in our ability to predict the effects of OA on tropical turf algal assemblages, particularly within the framework of natural thermal variability.

The endolithic (or euendolith) community is a frequently overlooked component of the turf algal assemblage, comprised of microboring cyanobacteria, algae, fungi and microorganisms concentrated beneath the substratum surface (Golubic et al. 1981) (Fig. 1). Endoliths are pervasive in hard bottom ecosystems, where they act as the principal bioeroding agents by penetrating and actively dissolving living and dead invertebrate skeletons (Golubic et al. 1981). They are particularly important on coral reefs where they contribute to carbonate dissolution (Tribollet et al. 2009) and primary production (Tribollet 2008). The role of endoliths as bioeroders and primary producers could become more significant in the near future if OA and warming increase endolithic production and growth, and thus the capacity for biologically mediated carbonate dissolution.

To date, most of the research on the response of marine primary producers to OA has focused on calcification and photosynthesis (Beer and Koch 1996; Koch et al. 2013).

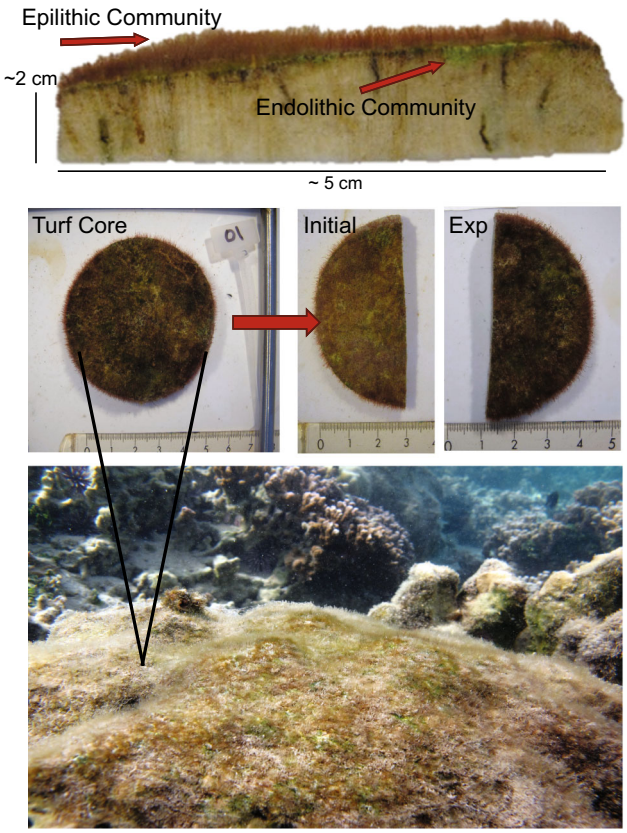

Fig. 1 Cores of turf-covered carbonate were collected from the fringing reef on the north shore of Moorea, French Polynesia. Whole cores were cut in half, with one half used for initial estimates of biomass (initial) and the second half used in experimental treatments (exp). The epilithic community was sampled by scraping the surface community, while the endolithic community was sampled by scraping into the core until no green pigmentation was visible

Because CO_2 is the primary substrate for the photosynthetic enzyme RubisCo, the increased availability of dissolved CO_2 in the near-future ocean may enhance photosynthesis and potentially fuel algal growth (Holbrook et al. 1988; Koch et al. 2013). A possible caveat to this expectation is variability in algal response depending on the presence and activity of carbon concentrating mechanisms (CCMs) (Giordano et al. 2005). Many species of algae have evolved CCMs to elevate CO_2 concentrations at the site of photosynthetic carbon fixation to compensate for lower concentrations of dissolved CO_2 relative to other carbon compounds in seawater (Giordano et al. 2005). A suite of marine algae have demonstrated positive growth responses to OA (Kroeker et al. 2010, 2013; Johnson et al. 2014b), with the exception of calcifying algae. The potential stimulatory effects of higher CO_2 concentrations on photosynthesis of calcifying algae could be outweighed by the negative consequences for calcification. Adding further complexity to our understanding of algal responses to global change is the neutral response of some calcifying and fleshy species of algae to OA (Comeau et al. 2013a; Campbell et al. 2014; Johnson et al. 2014b).

Warming ocean temperatures are another consequence of increasing CO_2 emissions that have important implications for marine algae. Temperature influences the speed of biochemical reactions and organismal metabolism (Gillooly et al. 2001), and warmer temperatures have the potential to increase metabolic rates (Beer and Koch 1996), within an optimal threshold. Algal photosynthesis, for example, typically increases with increasing temperature until an optimum rate is reached, after which rates quickly decline (Raven and Geider 1988; Davison 1991). Effects of temperature are inherently complex due to temporal variability within an ecosystem, particularly across seasons. Seasonal temperature increases correspond to higher rates of algal photosynthesis and growth (Yokohama 1973; Fong and Zedler 1993), and this photosynthesis–temperature relationship can subsequently influence the abundance and physiological performance of communities dominated by thermally sensitive macroalgae (Tait and Schiel 2013). However, enhanced algal metabolism in response to higher temperatures may not translate directly to long-term increases in algal growth due to thermal sensitivities (Schiel et al. 2004). Furthermore, seasonal variations in temperature can influence the response of algal physiology and growth to both OA and warming, with significant and synergistic effects at seasonal maximum temperatures (Martin and Gattuso 2009). To fully understand the response of benthic algae to global change, it will be informative to understand the functional relationship of algal physiology and growth across ecologically relevant temperatures and explore how this relationship is influenced by OA.

The results of single-stressor experiments (OA or warming) can be difficult to apply to natural systems because OA and warming are occurring concurrently. Multiple-stressor experiments may provide additional information for elucidating both the independent and combined effects of environmental variability on the metabolism and abundance of ecologically important algae. While multiple-stressor experiments may reveal potential interactive or synergistic effects, the results can be convoluted and the underlying mechanisms driving organismal responses can be difficult to disentangle. For example, warming frequently exacerbates the negative effects of OA on algal calcification (Martin and Gattuso 2009; Diaz-Pulido et al. 2012; Johnson and Carpenter 2012), but warming and OA do not always act synergistically (Campbell et al. 2016). Species-specific effects, potential complexities due to CCMs, and the paucity of multiple-stressor experiments preclude our ability to confidently understand the response of diverse algal assemblages to global change.

The goal of this study was to determine how effects of OA on turf algae manifest across a range of ecologically relevant temperatures. We tested the hypothesis that CO_2 enrichment would change turf assemblage metabolic (photosynthesis and respiration) and growth responses to temperature. We conducted controlled laboratory experiments where we manipulated CO_2 concentrations to simulate present-day (ambient) and high pCO_2 conditions (OA) expected by the end of the century in pessimistic carbon emission scenarios ($\sim$1000 µatm) (IPCC 2013). We crossed CO_2 treatments with six temperatures that represent the full range of temperatures experienced by turf assemblages on a fringing reef in Moorea, French Polynesia, and included one warming treatment. By exploring turf assemblage responses to OA across a range of temperatures, we provide new information on how an ecologically important group of algae may respond to OA and warming within the context of natural variations in temperature.

Materials and methods

Sample collection

This study was conducted in the mesocosm facilities at the Richard B. Gump South Pacific research station in Moorea, French Polynesia in January–February 2015. Turf assemblages were collected from the fringing reef located west of Cook's Bay on the north shore of Moorea (17°29′02.07″S, 149°50′19.38″W). Intact turf communities (Fig. 1) were collected as cores ($\sim$6 cm diameter) from dead mounding *Porites* corals at a depth of 1–2 m, with one core per dead

coral. A pneumatic drill with a diamond tipped hole-saw was used to drill 4–5 cm into the carbonate. Only unshaded turf assemblages that were on a horizontal plane were selected. The carbonate cores covered with turf were then transported to the Gump station and maintained in flowing seawater for further processing.

Cores were cut to a height of ~2 cm with a diamond band saw (Gryphon C-40) and then sliced in half. The average (±SD) surface area of each half-core was 15.5 ± 1.6 cm^2. One half of the core was destructively sampled for an initial estimate of turf biomass, and the second half of the core was used in the experimental treatment (Fig. 1). Visible invertebrates were removed, and the exposed carbonate on the underside of each experimental core was coated with marine epoxy (Aquamend) and attached to a rigid plastic mesh (Vexar) base. Turf assemblages were allowed to recover from processing for 24 h. We collected field samples to characterize the dominant functional groups of the initial epilithic turf assemblage and conducted a coarse digital photographic analysis to quantify the common functional groups (see Electronic supplementary material, ESM, Supplementary methods).

Experimental design

After processing, turf assemblages were randomly assigned to one of 12 150-L tanks, with six cores per tank. Each tank received a constant flow of filtered seawater (pore size ~100 μm) at a rate of 0.3–0.4 L min^{-1}, yielding roughly 3–4 full water exchanges per day. Tanks were fitted with clear, UV-transparent plexiglass lids and temperature, pH and light were controlled in each tank independently.

Turfs were exposed to a combination of six temperature treatments and two CO_2 treatments, with one tank per treatment. Temperature treatments ranged from 24 to 31.5 °C at 1.5 °C increments (24.0, 25.5, 27.0, 28.5, 30.0 and 31.5 °C), spanning the full seasonal range of temperatures experienced by organisms on the fringing reef of Moorea (Leichter 2015). The 31.5 °C treatment was chosen to represent the 0.5–2 °C increase in seawater temperature commonly predicted by the end of the century (IPCC 2013), and was ~3 °C above the daily average temperature (Leichter 2015). Each temperature treatment was crossed with either an ambient CO_2 treatment (~400 μatm) or a high CO_2 treatment (~1000 μatm) that simulated OA and the pH conditions expected by the end of the century under increasing CO_2 emissions scenarios (RCP 8.5) (IPCC 2013). To reduce temperature shock to turfs, all tanks were initially set to the ambient temperature (~28.5 °C) and then temperature was incrementally changed by 0.5 °C over a period of 6 d, or until the treatment temperature was reached.

We were logistically constrained to 12 tanks and chose a regression design with six temperature treatments. This OA mesocosm facility has been widely used for similar experiments since 2010, with designs using up to three tank replicates per treatment. Across at least ten experiments, there have been no significant effects of tank on biological responses of corals and algae to OA and temperature (Edmunds 2011; Edmunds et al. 2012; Comeau et al. 2013a, b, 2014a, b; Johnson et al. 2014a; Evensen and Edmunds 2016; Edmunds and Yarid 2017; Lenz and Edmunds 2017). Because we were interested in how turf algae responded to OA across many temperatures, we opted to increase the number of temperature treatments and decrease tank replication. To account for potential issues of pseudoreplication by having multiple replicates within one tank, we calculated tank averages for each response variable and used these averages in statistical analyses. It is unlikely that replicate cores within one tank affected each other because we positioned turf assemblages at a minimum of 5 cm apart and maintained a high volume and flow rate of seawater into the tanks.

Treatment conditions

To simulate effects of increasing atmospheric CO_2 on seawater, all tanks were continuously bubbled with ambient air. The pH of CO_2 enrichment treatments was maintained with a pH-stat. Tank pH was continuously monitored by pH electrodes connected to a digital controller (Aquacontroller, Neptune Systems), and pure CO_2 was injected into CO_2 enrichment treatment tanks by computer-controlled solenoid valves to maintain the targeted pH (7.7 total scale pH, pH_T). Turfs were exposed to treatment conditions for 3 weeks, following the 6 d acclimation period to temperature treatments.

The carbonate chemistry of each tank was monitored by direct measurements of pH_T, total alkalinity (A_T), temperature and salinity. Tank pH conditions were monitored daily with a handheld pH meter (Orion 3-stars, Thermo Scientific) and combination pH probe (Orion Ross Ultra, Thermo Scientific). The pH probe was calibrated every other day with Tris/HCl buffer following standard protocols (Dickson et al. 2007). The Neptune pH-stat probe was calibrated weekly with NBS buffers, and cross-calibrated with the higher accuracy Ross Ultra probe. These pH values were corrected and adjusted daily to maintain pH within the targeted range. Accuracy of the Ross Ultra pH probe measurements was verified by comparisons to discrete samples measured with a temperature-controlled spectrophotometer (Perkin Elmer) and the pH indicator dye m-cresol, following Dickson et al. (2007). Spectrophotometric pH yielded values within 1% of values measured by the pH meter and probe. Potential temporal variation in

tank pH was assessed once during the experiment by discrete pH measurements at 0600 and 1800 hrs. There was little variability in pH between time points ($<\sim 0.05$ units). For consistency, we made discrete measurements of tank pH with the Ross Ultra probe at 0900 hrs.

A_T was measured every 3 d on discrete water samples collected at 0900 hrs. Open-cell potentiometric titrations were conducted following the protocols of Dickson et al. (2007) with an automated titrator (T50, Mettler-Toledo) fit with a DG115-SC pH probe (Mettler-Toledo). Titrations were conducted on certified reference material (Reference Material for Oceanic CO_2 Measurements, Batch 140, A. Dickson, Scripps Institution of Oceanography) before every set of titrations. The average accuracy of reference material A_T titrations was ± 3 µmol kg^{-1} ($n = 12$).

Temperature was independently maintained by dual-stage temperature controllers (Aqualogic) in each tank set to chill or heat water to within ± 1 °C of the targeted temperature. Temperature was measured with a high precision (0.001 °C) traceable digital thermometer (Fisher-Scientific) at 0900 hrs to coincide with pH and A_T measurements. Salinity of each tank was measured every week with a benchtop conductivity meter (YSI 3100, YSI). The remaining parameters of the carbonate system were calculated using R (R Core Development Team 2014) with the package seacarb (Lavigne et al. 2014).

Each tank was illuminated with an LED modular light (Aquaillumination Sol) set to ~ 650 µmol photon m^{-2} s^{-1}, simulating the average daily irradiance on the Moorea back reef at a depth of 2 m. Lights were programmed for a 12:12 h photoperiod. To simulate natural diel light cycles, the light intensity was gradually increased from darkness to maximum intensity over a period of 4 h. Maximum irradiance was maintained for 4 h, and then light intensity was gradually decreased to darkness over the subsequent 4 h, yielding a daily integrated photosynthetically active radiation (PAR) value of approximately 110 mol photon m^{-2} d^{-1}. Light levels in each tank were measured during periods of maximum irradiance with a submerged 4π quantum sensor (LI-193) attached to a LiCor LI-1400 m. To reduce potential lighting and flow effects within tanks, turf assemblages were haphazardly repositioned every other day during the experiment.

Turf assemblage metabolism

At the end of the experiment, and prior to final biomass sampling, three turf assemblages were randomly selected from each tank for physiological measurements of dark respiration and light-saturated photosynthesis (hereafter referred to as photosynthesis). Preliminary incubations were conducted on a subset of three turf assemblages from the ambient treatment (ambient, 28.5 °C) to construct net photosynthesis versus irradiance curves (P-E curves) and determine saturating irradiance (ESM Fig. S1). To ensure that light was not limiting during photosynthesis incubations, we selected a PAR value for incubations that exceeded saturating irradiance (689 µmol photon m^{-2} s^{-1}) but preceded photoinhibition (no photoinhibition was detected at the highest irradiance).

Incubation chambers were illuminated by one seven-color LED module (AquaIllumination, Hydra) set to ~ 950 µmol photon m^{-2} s^{-1}. Incubations in darkness and under saturating irradiance were conducted with the same turf core to estimate net photosynthesis and dark respiration, respectively, by monitoring changes in dissolved oxygen (DO, mg O_2 L^{-1}) over time. Dark incubations were conducted first, after which the water was changed and incubations were then conducted in the light. Gross photosynthesis was calculated by adding respiration rates to net photosynthesis rates, based on the common assumption that dark and light respiration are approximately equivalent.

Metabolic incubation chambers consisted of 2-L translucent plastic storage containers with a gasket-sealed lid. The lid had one hole drilled in the top to hold an optical DO probe (Hach IntelliCal LDO101). The oxygen probe was calibrated daily using water-saturated air (100%) following factory calibration protocols. The probe was wrapped in parafilm to ensure a tight seal and connected to a portable meter (Hach HQ40d), accurate to ± 0.1 mg L^{-1}. Temperature and DO were measured every minute for 15–20 min for each light and dark incubation. Water flow was maintained in each incubation chamber by a submersible mini aquarium pump (302 L h^{-1}, Aquatop), and temperature (for each respective temperature treatment) was maintained by a temperature-controlled water bath (LAUDA ECO, ± 0.01 °C). Two incubations were conducted simultaneously for one temperature treatment, and additional blank incubations were conducted to calculate and subtract background changes in DO (e.g., microbial activity) in the incubated water. Rates were calculated as the linear slope of DO concentration over the duration of the incubation. Benthic surface area is a frequently assessed metric in both field surveys (e.g., percent cover of different benthic functional groups), and areal primary production is an important metric that has implications for ecosystem processes (Hatcher 1988), thus scaling metabolic rates to surface area is both meaningful and practical. Metabolic rates were standardized to core surface area and are expressed as mg O_2 cm^{-2} h^{-1}.

Epilithic and endolithic growth

Growth of the epilithic turf community on the surface of the core and the endolithic community within the carbonate matrix of the core were determined by quantifying the

absolute change in organic biomass using ash-free dry weight (AFDW). One half of the whole turf core was destructively sampled for initial estimates of epilithic turf biomass and endolithic biomass (initial), and the second half was exposed to experimental treatments (exp) (Fig. 1). To determine initial epilithic biomass, half of the initial core was scraped with a straight-edge razor blade, without removing the underlying carbonate. The scraped turf was dried at 60 °C for 24 h, weighed, and then combusted at 500 °C for 4 h in a muffle furnace. The combusted sample was reweighed, and the difference between the dried and combusted sample is the AFDW, or the organic biomass of the epilithic turf community. The turf core was photographed with a ruler for scale, and planar surface area was determined using image analysis software (ImageJ). Biomass was normalized to the surface area of the scraped core. The same area on the initial core was then scraped a second time with a sharpened screwdriver to quantify the endolithic community within the carbonate matrix. The core was scraped until green pigmentation was no longer visible (~0.5–0.75 cm into the core), and the endolithic sample was similarly processed for AFDW.

Following metabolic incubations, the final experimental core was processed for biomass using the same procedure as above. The difference in the AFDW of the initial core and the final experimental core represents the change in organic biomass over the duration of the experiment, or absolute growth. Epilithic and endolithic growth is presented quantitatively as absolute growth and is expressed as g AFDW cm^{-2}.

Statistical analyses

We averaged metabolism and growth responses from replicates within a tank to calculate a tank mean for each response variable, and used this mean in subsequent analyses. All response variables met assumptions of normality, based on the Shapiro–Wilks test for normality. The effects of CO_2 on metabolic rates, epilithic growth and endolithic growth were analyzed with an analysis of covariance (ANCOVA) with CO_2 treatment as a fixed factor with two levels (ambient and high) and temperature as the covariate. Due to the apparent loss of endolithic biomass in the three lowest temperature treatments, we tested for a tank effect with a paired *t* test of initial and final endolithic biomass for the ambient treatment only. Statistical analyses were conducted in JMP v.10.

Results

Treatment conditions

Experimental manipulations successfully maintained target temperatures crossed with ambient and high CO_2 (OA) treatments (Table 1). The daily average (±SE) total scale pH (pH_T) was 8.05 ± 0.02 and 7.71 ± 0.00 for the ambient and OA treatments, respectively. Due to the high rate of fresh inflowing seawater (0.3–0.4 L min^{-1}), variability in total alkalinity (A_T) among all treatment tanks was minimal for the duration of the experiment, with a daily tank average of 2283 ± 1 μmol kg^{-1}. The remaining carbonate parameters were calculated at a measured salinity of 35.7, yielding a daily average pCO_2 of 387 ± 21 and 969 ± 7 μatm for the ambient and OA treatments, respectively (Table 1). Ambient pCO_2 in this experiment was consistent with ambient values reported in previous studies using the same experimental setup, which have ranged ~385–417 μatm (Comeau et al. 2013a, b, 2014a, b; Johnson et al. 2014a).

The daily maximum irradiance for tank conditions was ~650 μmol photon m^{-2} s^{-1}, and over a 12:12 h photoperiod that included a ramp cycle to simulate sunrise and sunset, the daily integrated PAR was ~112 mol photon m^{-2} d^{-1}.

Initial epilithic turf assemblage

The initial epilithic turf assemblage was dominated by filamentous red, brown and green algae and cyanobacteria. Brown and green filamentous algae were difficult to differentiate in photographic analyses and were categorized into one group. The average percent cover (±SD) of the epilithic turf assemblage by coarse functional group was: 42 ± 10% filamentous red algae, 34 ± 7% filamentous brown/green algae, 22 ± 7% cyanobacteria and 2% exposed carbonate (ESM Fig S2). The most common genera within the category of filamentous brown/green algae were *Sphacelaria*, *Ectocarpus*, *Feldmannia*, *Hinksia*, *Ostreobium* and *Cladophora*. The most common genera in the filamentous red algae were *Polysiphonia*, *Gelidiella* and *Gelidiopsis*. Two common cyanobacteria genera in the epilithic community were *Oscillatoria* and *Calothrix*. All genera identified are non-calcifying; thus, the epilithic turf community was comprised of fleshy filamentous algae and cyanobacteria.

Turf assemblage metabolism

There was a significant interactive effect of temperature and CO_2 on turf metabolism, which includes light-saturated photosynthesis (net and gross) and respiration (Fig. 2; Table 2). Net photosynthesis (CO_2 × temperature: $F_{1,1} = 10.53$, $p = 0.012$) and gross photosynthesis (CO_2 × temperature: $F_{1,1} = 5.23$, $p = 0.050$) were highest under CO_2 enrichment, but only at the warmest temperatures, 30 and 31.5 °C (Table 2; Fig. 2 a, c). Turf community respiration rates similarly increased with

Table 1 Turf assemblages were exposed to six temperatures crossed with two CO_2 treatments: ambient or high CO_2

Treatment	Temperature (°C)	pH_T	A_T (μmol kg^{-1})	pCO_2 (μatm)	Ω_{Ar}
24.0–ambient CO_2	23.99 ± 0.06	8.11 ± 0.01	2281 ± 3	326 ± 7	3.67 ± 0.04
24.0–high CO_2	24.00 ± 0.08	7.70 ± 0.01	2284 ± 3	990 ± 19	1.70 ± 0.02
25.5–ambient CO_2	25.41 ± 0.04	8.07 ± 0.01	2283 ± 2	348 ± 7	3.69 ± 0.04
25.5–high CO_2	25.46 ± 0.07	7.71 ± 0.01	2287 ± 2	974 ± 18	1.82 ± 0.03
27.0–ambient CO_2	26.97 ± 0.06	8.06 ± 0.01	2282 ± 2	374 ± 8	3.71 ± 0.04
27.0–high CO_2	27.01 ± 0.06	7.72 ± 0.01	2281 ± 2	941 ± 12	1.97 ± 0.02
28.5–ambient CO_2	28.42 ± 0.07	8.05 ± 0.01	2284 ± 2	388 ± 6	3.79 ± 0.03
28.5–high CO_2	28.55 ± 0.06	7.71 ± 0.00	2281 ± 3	963 ± 12	2.05 ± 0.02
30.0–ambient CO_2	29.87 ± 0.09	8.02 ± 0.01	2280 ± 3	420 ± 7	3.77 ± 0.04
30.0–high CO_2	29.88 ± 0.04	7.72 ± 0.00	2283 ± 4	960 ± 8	2.16 ± 0.01
31.5–ambient CO_2	31.33 ± 0.06	7.98 ± 0.01	2284 ± 3	466 ± 10	3.72 ± 0.05
31.5–high CO_2	31.25 ± 0.05	7.71 ± 0.01	2289 ± 2	984 ± 13	2.24 ± 0.02

Values are the daily mean (±SE) physical parameters measured for each tank over the course of the 3-week experiment ($n = 21$). Measured pH_T (total scale), temperature and total alkalinity (A_T) were used to derive the remaining carbonate parameters (pCO_2 and aragonite saturation state (Ω_{Ar})

increasing temperature, but more under ambient CO_2 ($CO_2 \times$ temperature: $F_{1,1} = 9.35$, $p = 0.016$) (Table 2; Fig. 2b). The significance of the interaction between temperature and CO_2 enrichment precludes interpretation of the main effects, but indicates that temperature is important for contextualizing the effects of CO_2 on turf metabolism.

Epilithic growth

The epilithic algal community grew significantly more with CO_2 enrichment, independent of temperature ($F_{1,1} = 7.863$, $p = 0.023$) (Table 2; Fig. 3a). While there was a trend for increasing growth with temperature, it was not significant ($F_{1,1} = 1.476$, $p = 0.260$), and there was no evidence of an interaction between temperature and OA on epilithic turf growth ($F_{1,1} = 1.268$, $p = 0.293$). The effects of CO_2 enrichment on epilithic turf growth were most pronounced at ambient temperature, 28.5 °C, and at the most common seasonal thermal maximum experienced by organisms on the reef, 30 °C. At these temperatures, OA increased epilithic growth by 90–100% (Fig. 3a).

Endolithic growth

There were no significant differences between the initial and final endolithic biomass in the ambient treatment ($t_5 = -1.05$, $p = 0.341$), which indicates that there was no significant tank effect in the ambient treatment, and that significant growth responses were a result of temperature or CO_2 treatments. Simulated OA significantly increased growth of the endolithic community ($F_{1,1} = 8.002, p = 0.022$), with an insignificant interactive effect of temperature and OA ($F_{1,1} = 4.128$, $p = 0.077$) and no effect of temperature ($F_{1,1} = 0.272$, $p = 0.616$) (Fig. 3b; Table 2). Endoliths demonstrated the strongest growth response to CO_2 enrichment in the three warmest temperature treatments which were at or above ambient temperature (28.5, 30 and 31.5 °C). At the warmest temperatures, OA increased endolithic growth 80–245% relative to ambient treatments (Fig. 3b).

Discussion

Turf assemblage metabolism

We found synergistic effects of simulated OA and temperature on turf assemblage metabolic rates. Simulated OA generally increased light-saturated photosynthesis and decreased respiration, and this response was exacerbated at the warmest temperatures of 30 and 31.5 °C. The positive effects of both increasing temperature and CO_2 match what we expected based on known temperature effects on metabolic rates and potential CO_2 limitation of photosynthesis under present-day conditions. The significant effect of CO_2 enrichment on photosynthesis at warmer temperatures was likely the result of both higher metabolic rates and increased availability of CO_2 for photosynthesis.

Across six temperatures, with two treatments that were above the daily average, we found no thermal threshold effect on turf metabolism. The thermal variability of this habitat, particularly in the shallows where samples were collected (1–2 m depth), may have acclimatized turf assemblages to warmer temperatures. Further, the magnitude of our warming treatment (~3 °C above daily average, but <1 °C above the seasonal maximum) was not enough to induce the hyperbolic response of algal metabolism to increasing temperature that has been documented in previous studies (Tait and Schiel 2013).

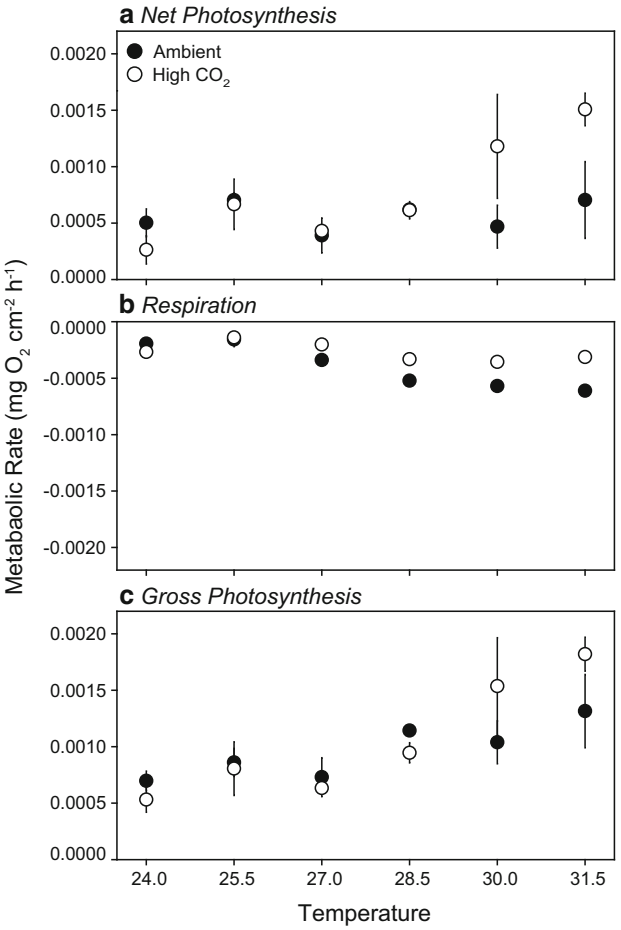

Fig. 2 Mean (±SE) **a** light-saturated net photosynthesis **b** respiration and **c** gross photosynthesis of epilithic turf algae under six temperature treatments and two pCO_2 levels ($n = 3$). Present-day conditions (ambient CO_2) are represented by *closed circles*, and simulated OA conditions (high CO_2) are represented by *open circles*. *Error bars* for respiration measurements were small and are obscured by the *circle symbol*

Epilithic and endolithic growth

We found that CO_2 enrichment significantly increased growth rates of both the epilithic and endolithic components of a turf algal assemblage dominated by filamentous algae, and that there were no combined effects of temperature. Our findings agree with studies in ecosystems outside the tropics, which have shown positive growth responses of algal turfs to CO_2 enrichment. For example, simulated OA increased biomass and percent cover of temperate turfs twofold–fourfold (Connell and Russell 2010; Short et al. 2014), and this response was exacerbated by nutrient enrichment (Russell et al. 2009; Falkenberg et al. 2013). These trends are further supported by studies of in situ benthic communities that have found that turf algae are among the few benthic functional groups to thrive in naturally low pH conditions (Porzio et al. 2013).

Table 2 Results of analysis of covariance (ANCOVA) for each response variable

Response variable	Factor	DF	*F*	*P*
Net photosynthesis	Temperature	1	13.78	**0.006**
	CO_2	1	3.62	0.094
	Temperature × CO_2	1	10.53	**0.012**
Respiration	Temperature	1	30.36	**0.001**
	CO_2	1	10.73	**0.011**
	Temperature × CO_2	1	9.35	**0.016**
Gross photosynthesis	Temperature	1	36.62	**<0.001**
	CO_2	1	0.60	0.461
	Temperature × CO_2	1	5.23	**0.050**
Epilithic growth	Temperature	1	1.48	0.260
	CO_2	1	7.86	**0.023**
	Temperature × CO_2	1	1.27	0.293
Endolithic growth	Temperature	1	0.28	0.616
	CO_2	1	8.00	**0.022**
	Temperature × CO_2	1	4.13	0.077

Temperature was treated as a continuous covariate in exploring effects of CO_2 on turf assemblage metabolism and growth. Due to significant interactive effects of temperature and CO_2 on metabolism, the non-significant interactive term was left in all ANCOVA models for consistency

Significant values are noted in bold

While turf assemblages have received limited attention in the global change literature, even less effort has been dedicated to understanding the impacts of global change on the endolithic component of turf assemblages. Similar to the response of the epilithic community, we found that CO_2 enrichment significantly increased growth rates of the endolithic community relative to the ambient treatment. Our findings corroborate the few previous studies showing that OA significantly increased biomass of the endolithic communities associated with coral and coralline algae substrata (Tribollet et al. 2009; Reyes-Nivia et al. 2013). The community composition and function of endolithic communities vary by substrata and differ between living and dead coral (Le Campion-Alsumard et al. 1995). Our findings thus build on these previous studies, which were conducted on dead carbonate blocks (Tribollet et al. 2009), recently dead coral carbonate skeleton (Reyes-Nivia et al. 2013) or with living coralline algae (Diaz-Pulido et al. 2012), by quantifying the response of endolithic communities associated with living turf algae assemblages to warming and high CO_2.

The significant increase in epilithic and endolithic biomass in response to CO_2 enrichment may have been driven by the increased availability of dissolved CO_2 for photosynthesis. The direction and magnitude of algal response to

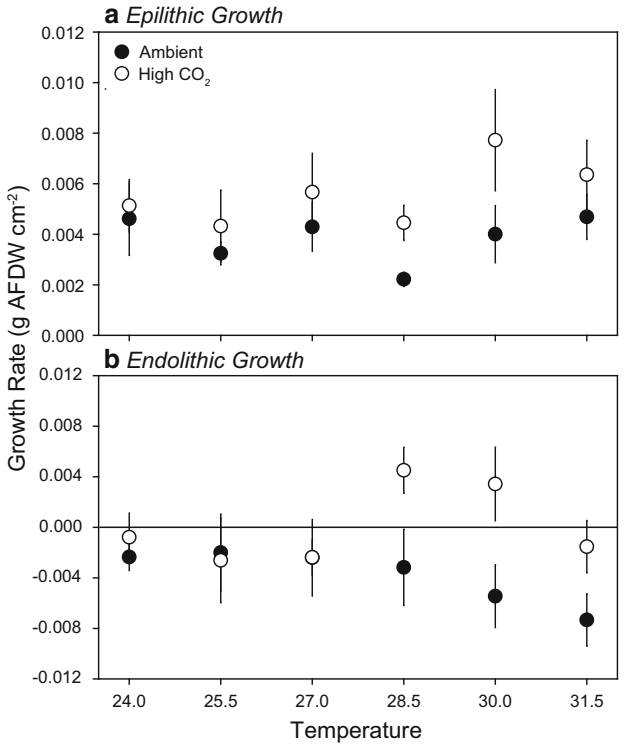

Fig. 3 Mean (±SE) growth rates of the **a** epilithic turf community and **b** the endolithic assemblage in response to simulated ocean acidification (OA) and warming ($n = 6$). Present-day conditions (ambient CO_2) are represented by *closed circles* and simulated OA conditions (high CO_2) are represented by *open circles*

increased CO_2 may be linked to the presence and activity of CCMs. Even if CCMs are present in some species, turf assemblages may be functionally carbon limited due to the high density of autotrophs competing for CO_2 within the diffusive boundary layer, although the extent of limitation may be dependent on rates of water flow (Carpenter 1990; Larkum et al. 2003). Increasing the concentration of CO_2 in the surrounding seawater increases the diffusion of CO_2 across the diffusive boundary layer, and potentially relieves carbon limitation (Carpenter 1990). The increased biomass of epilithic turf algae in response to simulated OA supports the idea that CO_2 may be limiting for turf assemblages under present-day conditions, although the mechanisms underlying carbon limitation should be explored further.

The endolithic community is embedded within the carbonate matrix of the reef and is potentially more carbon limited than the epilithic community because it has less access to resources in the surrounding seawater. In addition to being carbon limited by habit, the common boring green alga *Ostreobium* sp. likely lacks CCMs and instead may rely on passive uptake of dissolved CO_2 (Tribollet et al. 2009). The response of the endolithic community to environmental change is tied to the associated epilithic substrata (Golubic et al. 1981). The epilithic community directly or indirectly influences the underlying endolithic community (Le Campion-Alsumard et al. 1995) by mediating the availability of key limiting resources such as light. High CO_2 had a stimulatory effect on endolithic growth, particularly at the warmest temperatures, which indicates that increasing availability of CO_2 may relieve potential carbon limitation, and more so at warmer temperatures. Endolithic bioerosion has already been shown to increase with higher CO_2 (Tribollet et al. 2009), and increases in endolithic biomass with OA may have additional negative implications for the persistence of the coral-reef carbonate matrix by further increasing the capacity for bioerosion.

The decoupling of simulated OA and warming on physiology and growth is interesting and likely complex. We might expect that, because photosynthesis provides the energy for growth, turf assemblage photosynthesis and growth would respond similarly to environmental pressures. However, we found different physiological and growth responses. A possible explanation may be limitation by external factors such as light. A discrepancy between metabolic incubations and tank conditions, from which growth was measured, was maximum irradiance. We maintained tank and incubations at or above saturating irradiance (Carpenter 1985), which reduces the likelihood that the amount of light provided was a limiting factor for turf assemblage growth and photosynthesis. However, decreased light availability within the turf canopy with increasing epilithic biomass may have caused light limitation within the canopy via self-shading and subsequently influenced growth rates.

Differences in physiological and growth responses could also be a result of changes in community structure. A detailed analysis of community composition was beyond the scope of this study. Based on a coarse analysis of percentage cover, the initial epilithic turf assemblage was a mixed-species assemblage comprised entirely of non-calcifying filamentous brown, red and green algae and cyanobacteria (ESM Fig. S2). The response of algae to warming and OA are often species specific (Comeau et al. 2013a; Campbell et al. 2014; Johnson et al. 2014b) and may depend on physiological mechanisms such as carbon acquisition strategies (e.g., CCMs) that can vary by species. Thus, it is possible that CO_2 enrichment may have fueled growth and photosynthesis in some species (Bender et al. 2014), but had neutral effects on others. The role of OA and warming in influencing community structure of turf assemblages is an important remaining question that should be explored in greater detail because of the implications for ecological interactions in a warmer and more acidic ocean.

Turf algae are important in their role as competitors with reef-building corals and other benthic organisms, where

they are frequently the dominant competitor (McCook et al. 2001), and the endolithic community is a key contributor to reef bioerosion. Higher growth rates by turf assemblages under warmer and more acidic conditions could increase the frequency of coral–turf interactions and occur alongside decreased rates of coral (Chan and Connolly 2013) and coralline algal calcification (Johnson and Carpenter 2012; Johnson et al. 2014a). The facilitation of turf and fleshy macroalgae by OA (Johnson et al. 2014b) could provide these fleshy species with a competitive advantage over corals and crustose coralline algae (Diaz-Pulido et al. 2011). OA and warming could, therefore, promote a shift from calcifier-dominated to fleshy algae-dominated systems. Ecosystem-scale changes also will likely be influenced by the strength of ecological interactions such as top-down control by herbivores which may mediate positive effects of OA and warming on algal production (Alsterberg et al. 2013; Ghedini et al. 2015). The combined effects of OA and warming on ecological interactions on coral reefs are highly complex, and more research is necessary to unravel the implications of global change at the ecosystem scale (Edmunds et al. 2016).

In summary, we demonstrate that the epilithic and endolithic components of a coral-reef turf algal assemblage had higher photosynthetic rates under warmer, more acidic conditions and that the turf assemblage grew significantly more with CO_2 enrichment. We contribute new information on the potential effects of global change on coral-reef turf algal assemblages across a wide range of temperatures and demonstrate complex physiological and growth responses to multiple simultaneous stressors. Both single- and multiple-stressor experiments can have limited applicability to natural systems by oversimplifying or complicating the effects of environmental change on organismal responses, respectively. Synthesizing the results of both types of experiments may be the most parsimonious approach to understanding the response of natural systems to the suite of ongoing changes in the environment. We suggest that future experiments incorporate multiple stressors and a full range of environmental conditions to more accurately contextualize biological responses to global environmental change.

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