

REPORT

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

Maggie D. Johnson^{1,2} · Steeve Comeau^{3,4} · Coulson A. Lantz^{4,5} · Jennifer E. Smith¹

Received: 1 November 2016 / Accepted: 29 May 2017 / Published online: 7 June 2017
© Springer-Verlag Berlin Heidelberg 2017

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 CO₂ 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 *p*CO₂ (1000 µatm) conditions for 3 weeks. Each *p*CO₂ 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 CO₂ 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 CO₂ enrichment. Photosynthetic rates were amplified by high CO₂ in the warmest temperatures, while the increase in respiration rates with temperature were enhanced under ambient CO₂. Epilithic turf growth rates were not affected by temperature, but increased in response to CO₂ enrichment. We found that CO₂ and temperature interactively affected the endolithic assemblage, with the highest growth rates under CO₂ 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 CO₂ enrichment on coral-reef turf assemblages can be temperature dependent. The complex effects of CO₂ enrichment and temperature across a suite of algal responses illustrates the importance of incorporating multiple stressors into global change experiments.

Communicated by Biology Editor Dr. Anastazia Banaszak

Electronic supplementary material The online version of this article (doi:10.1007/s00338-017-1597-2) contains supplementary material, which is available to authorized users.

✉ Maggie D. Johnson
johnsonmd4@si.edu

¹ Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University of California, 9500 Gilman Drive, La Jolla, San Diego, CA 92093-0202, USA

² Smithsonian Tropical Research Institute, Apartado Balboa, 0843-03092 Ancón, Republic of Panama

³ Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91330-8303, USA

⁴ School of Earth and Environment and ARC Centre in Coral Reef Studies, The University of Western Australia, Crawley, WA 6009, Australia

⁵ School of Environment Science and Engineering, Southern Cross University, Military Road, Lismore, NSW 2480, Australia

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

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 (CO₂) 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

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).

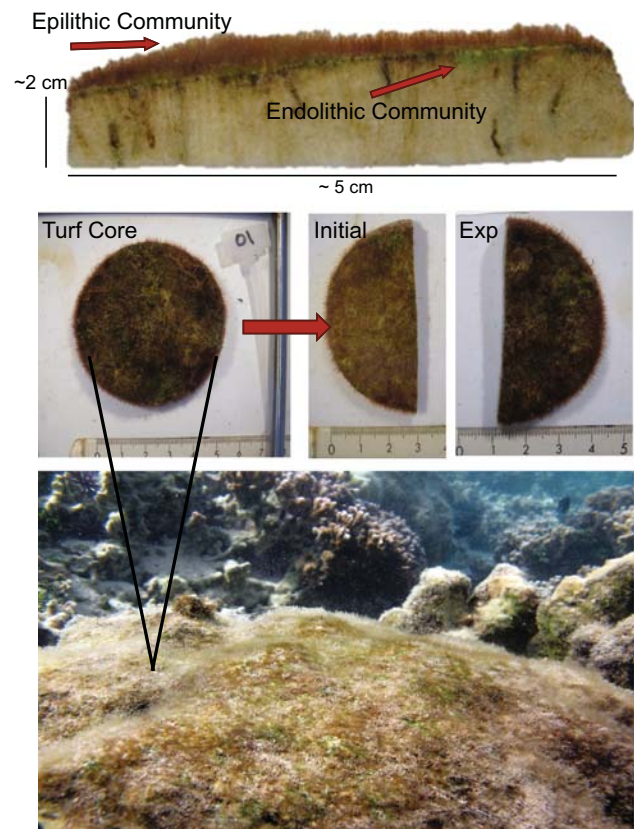


Fig. 1 Cores of turf-covered carbonate were collected from the fringing reef on the north shore of Moorea, French Polynesia. Whole cores were cut in half, with one half used for initial estimates of biomass (initial) and the second half used in experimental treatments (exp). The epilithic community was 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 $p\text{CO}_2$ conditions (OA) expected by the end of the century in pessimistic carbon emission scenarios ($\sim 1000 \mu\text{atm}$) (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 ($17^\circ 29' 02.07''\text{S}$, $149^\circ 50' 19.38''\text{W}$). Intact turf communities (Fig. 1) were collected as cores (~ 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 (\pm SD) surface area of each half-core was 15.5 ± 1.6 cm². 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 μ m) 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 CO₂ 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 CO₂ treatment (~ 400 μ atm) or a high CO₂ treatment (~ 1000 μ atm) that simulated OA and the pH conditions expected by the end of the century under increasing CO₂ 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 CO₂ on seawater, all tanks were continuously bubbled with ambient air. The pH of CO₂ 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 CO₂ was injected into CO₂ 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 $\pm 3 \mu\text{mol kg}^{-1}$ ($n = 12$).

Temperature was independently maintained by dual-stage temperature controllers (Aqualogic) in each tank set to chill or heat water to within $\pm 1^\circ\text{C}$ 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 $\sim 650 \mu\text{mol photon m}^{-2} \text{s}^{-1}$, 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 $110 \text{ mol photon m}^{-2} \text{d}^{-1}$. 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 ($689 \mu\text{mol photon m}^{-2} \text{s}^{-1}$) 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 $\sim 950 \mu\text{mol photon m}^{-2} \text{s}^{-1}$. 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 , $\text{mg O}_2 \text{L}^{-1}$) 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 $\pm 0.1 \text{ mg L}^{-1}$. 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, $\pm 0.01^\circ\text{C}$). 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 $\text{mg O}_2 \text{cm}^{-2} \text{h}^{-1}$.

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 CO₂ on metabolic rates, epilithic growth and endolithic growth were analyzed with an analysis of covariance (ANCOVA) with CO₂ 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 CO₂ (OA)

treatments (Table 1). The daily average (\pm 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 μ mol kg⁻¹. The remaining carbonate parameters were calculated at a measured salinity of 35.7, yielding a daily average *p*CO₂ of 387 ± 21 and 969 ± 7 μ atm for the ambient and OA treatments, respectively (Table 1). Ambient *p*CO₂ in this experiment was consistent with ambient values reported in previous studies using the same experimental setup, which have ranged ~ 385 – 417 μ atm (Comeau et al. 2013a, b, 2014a, b; Johnson et al. 2014a).

The daily maximum irradiance for tank conditions was ~ 650 μ mol 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 (\pm SD) of the epilithic turf assemblage by coarse functional group was: $42 \pm 10\%$ filamentous red algae, $34 \pm 7\%$ filamentous brown/green algae, $22 \pm 7\%$ 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 CO₂ on turf metabolism, which includes light-saturated photosynthesis (net and gross) and respiration (Fig. 2; Table 2). Net photosynthesis (CO₂ \times temperature: $F_{1,1} = 10.53$, $p = 0.012$) and gross photosynthesis (CO₂ \times temperature: $F_{1,1} = 5.23$, $p = 0.050$) were highest under CO₂ 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 CO₂ treatments: ambient or high CO₂

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 (pCO₂ and aragonite saturation state (Ω_{Ar}))

increasing temperature, but more under ambient CO₂ (CO₂ × temperature: $F_{1,1} = 9.35$, $p = 0.016$) (Table 2; Fig. 2b). The significance of the interaction between temperature and CO₂ enrichment precludes interpretation of the main effects, but indicates that temperature is important for contextualizing the effects of CO₂ on turf metabolism.

Epilithic growth

The epilithic algal community grew significantly more with CO₂ 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 CO₂ 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 CO₂ 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 CO₂ 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 CO₂ match what we expected based on known temperature effects on metabolic rates and potential CO₂ limitation of photosynthesis under present-day conditions. The significant effect of CO₂ enrichment on photosynthesis at warmer temperatures was likely the result of both higher metabolic rates and increased availability of CO₂ 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).

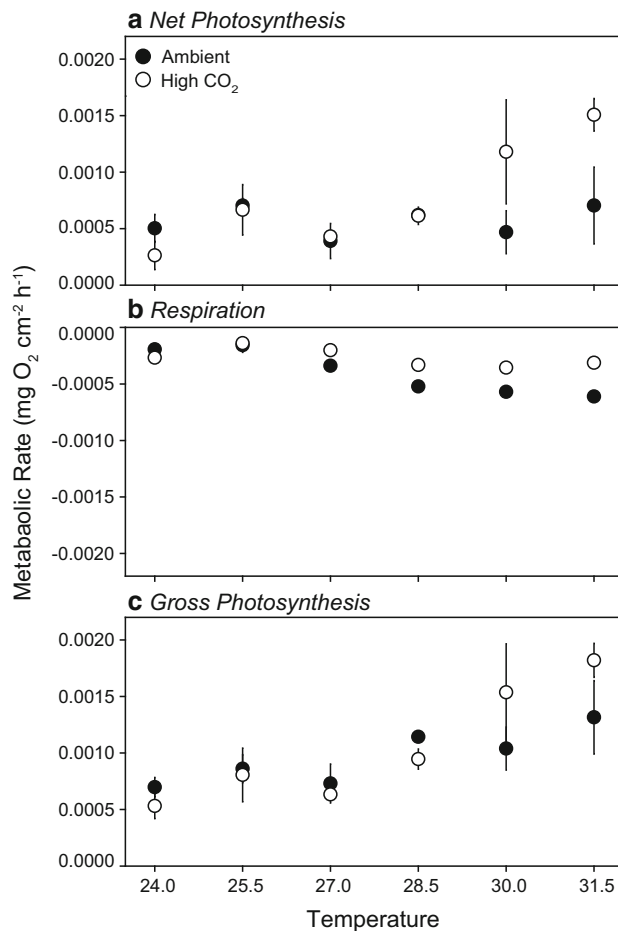


Fig. 2 Mean (\pm SE) **a** light-saturated net photosynthesis **b** respiration and **c** gross photosynthesis of epilithic turf algae under six temperature treatments and two $p\text{CO}_2$ levels ($n = 3$). Present-day conditions (ambient CO_2) are represented by closed circles, and simulated OA conditions (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 \times CO_2	1	10.53	0.012
Respiration	Temperature	1	30.36	0.001
	CO_2	1	10.73	0.011
	Temperature \times CO_2	1	9.35	0.016
Gross photosynthesis	Temperature	1	36.62	<0.001
	CO_2	1	0.60	0.461
	Temperature \times CO_2	1	5.23	0.050
Epilithic growth	Temperature	1	1.48	0.260
	CO_2	1	7.86	0.023
	Temperature \times CO_2	1	1.27	0.293
Endolithic growth	Temperature	1	0.28	0.616
	CO_2	1	8.00	0.022
	Temperature \times 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

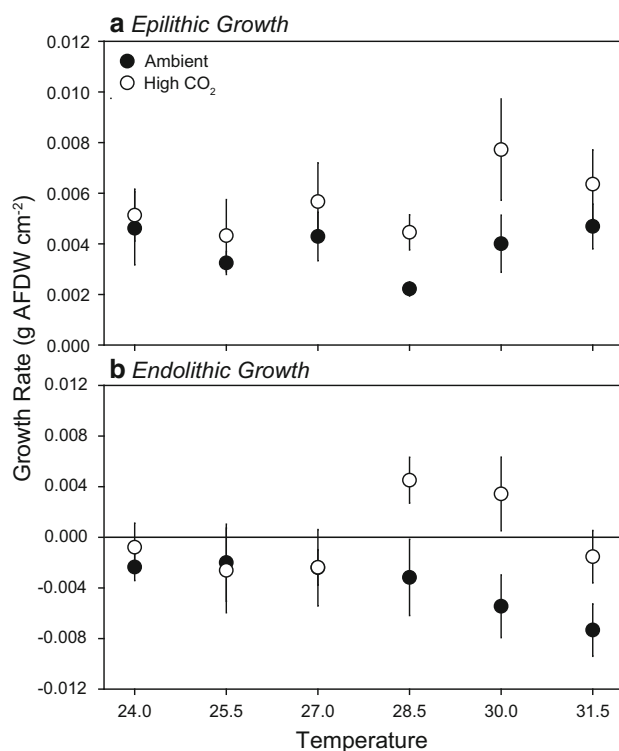


Fig. 3 Mean (\pm SE) growth rates of the **a** epilithic turf community and **b** the endolithic assemblage in response to simulated ocean acidification (OA) and warming ($n = 6$). Present-day conditions (ambient CO₂) are represented by closed circles and simulated OA conditions (high CO₂) are represented by open circles

increased CO₂ 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 CO₂ 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 CO₂ in the surrounding seawater increases the diffusion of CO₂ 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 CO₂ 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 CO₂ (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 CO₂ had a stimulatory effect on endolithic growth, particularly at the warmest temperatures, which indicates that increasing availability of CO₂ may relieve potential carbon limitation, and more so at warmer temperatures. Endolithic bioerosion has already been shown to increase with higher CO₂ (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-calculifying 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 CO₂ 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 CO₂ 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.

Acknowledgements This project was funded in part by the US National Science Foundation (OCE 14-15268 to RC Carpenter and PJ Edmunds) and by Grants awarded to NA Price and JE Smith. MDJ thanks RC Carpenter, PJ Edmunds and NA Price for the encouragement, funding and support to implement this experiment. The authors also thank the Scripps family foundation and the Bohn family for their generosity and support; VW Moriarty, E Dohnam, JL Harris, MD Fox, A Emanuel and E Jacobs for field and lab assistance. We thank two anonymous reviewers for constructive and insightful feedback.

References

- Alsterberg C, Eklöf JS, Gamfeldt L, Havenhand JN, Sundbäck K (2013) Consumers mediate the effects of experimental ocean acidification and warming on primary producers. *Proc Natl Acad Sci USA* 110:8603–8608
- Beer S, Koch E (1996) Photosynthesis of marine macroalgae and seagrasses in globally changing CO₂ environments. *Mar Ecol Prog Ser* 141:199–204
- Bender D, Diaz-Pulido G, Dove S (2014) Warming and acidification promote cyanobacterial dominance in turf algal assemblages. *Mar Ecol Prog Ser* 517:271–284
- Borowitzka MA (1981) Algae and grazing in coral reef ecosystems. *Endeavour* 5:99–106
- Caldeira K, Wickett ME (2003) Anthropogenic carbon sand ocean pH. *Nature* 425:365
- Campbell JE, Fisch J, Langdon C, Paul VJ (2016) Increased temperature mitigates the effects of ocean acidification in calcified green algae (*Halimeda* spp.). *Coral Reefs* 35:357–368
- Campbell JE, Craft JD, Muehllehner N, Langdon C, Paul VJ (2014) Responses of calcifying algae (*Halimeda* spp.) to ocean acidification: implications for herbivores. *Mar Ecol Prog Ser* 514:43–56
- Carpenter RC (1985) Relationships between primary production and irradiance in coral-reef algal communities. *Limnol Oceanogr* 30:784–793
- Carpenter RC (1986) Partitioning herbivory and its effects on coral-reef algal communities. *Ecol Monogr* 56:345–363
- Carpenter RC (1990) Competition among marine macroalgae—a physiological perspective. *J Phycol* 26:6–12
- Chan NCS, Connolly SR (2013) Sensitivity of coral calcification to ocean acidification: a meta-analysis. *Glob Chang Biol* 19:282–290
- Comeau S, Carpenter RC, Edmunds PJ (2013a) Effects of feeding and light intensity on the response of the coral *Porites rus* to ocean acidification. *Mar Biol* 160:1127–1134
- Comeau S, Edmunds PJ, Spindel NB, Carpenter RC (2013b) The responses of eight coral-reef calcifiers to increasing partial pressure of CO₂ do not exhibit a tipping point. *Limnol Oceanogr* 58:388–398
- Comeau S, Carpenter RC, Edmunds PJ (2014a) Effects of irradiance on the response of the coral *Acropora pulchra* and the calcifying alga *Hydrolithon reinboldii* to temperature elevation and ocean acidification. *J Exp Mar Bio Ecol* 453:28–35
- Comeau S, Edmunds PJ, Spindel NB, Carpenter RC (2014b) Diel pCO₂ oscillations modulate the response of the coral *Acropora hyacinthus* to ocean acidification. *Mar Ecol Prog Ser* 501:99–111
- Connell SD, Russell BD (2010) The direct effects of increasing CO₂ and temperature on non-calcifying organisms: increasing the potential for phase shifts in kelp forests. *Proc R Soc Lond B Biol Sci* 277:1409–1415
- Copertino M, Connell SD, Cheshire A (2005) The prevalence and production of turf-forming algae on a temperate subtidal coast. *Phycologia* 44:241–248
- Davison IR (1991) Environmental effects on algal photosynthesis: temperature. *J Phycol* 27:2–8
- Diaz-Pulido G, Gouezo M, Tilbrook B, Dove S, Anthony KRN (2011) High CO₂ enhances the competitive strength of seaweeds over corals. *Ecol Lett* 14:156–162
- Diaz-Pulido G, Anthony KRN, Kline DI, Dove S, Hoegh-Guldberg O (2012) Interactions between ocean acidification and warming on the mortality and dissolution of coralline algae. *J Phycol* 48:32–39

- Dickson AG, Sabine CL, Christian JR (2007) Guide to best practices for ocean CO₂ measurements. PISCES Special Publication 3. North Pacific Marine Science Organization, Sidney, BC, p 176
- Doney SC, Balch WM, Fabry VJ, Feely RA (2009) Ocean acidification: a critical emerging problem for the ocean sciences. *Oceanography* 22:16–25
- Edmunds PJ (2011) Zooplanktivory ameliorates the effects of ocean acidification on the reef coral *Porites* spp. *Limnol Oceanogr* 56:2402–2410
- Edmunds PJ, Yarid A (2017) The effects of ocean acidification on wound repair in the coral *Porites* spp. *J Exp Mar Bio Ecol* 486:98–104
- Edmunds PJ, Brown D, Moriarty V (2012) Interactive effects of ocean acidification and temperature on two scleractinian corals from Moorea, French Polynesia. *Glob Chang Biol* 18:2173–2183
- Edmunds PJ, Comeau S, Lantz C, Andersson A, Briggs C, Cohen A, Gattuso JP, Grady JM, Gross K, Johnson M, Muller EB (2016) Integrating the effects of ocean acidification across functional scales on tropical coral reefs. *BioScience* 2016:biw023
- Evensen NR, Edmunds PJ (2016) Interactive effects of ocean acidification and neighboring corals on the growth of *Pocillopora*. *Mar Biol* 163:1–11
- Fabry VJ, Seibel BA, Feely RA, Orr JC (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J Mar Sci* 65:414–432
- Falkenberg LJ, Russell BD, Connell SD (2013) Contrasting resource limitations of marine primary producers: implications for competitive interactions under enriched CO₂ and nutrient regimes. *Oecologia* 172:575–583
- Falkenberg LJ, Connell SD, Russell BD (2014) Herbivory mediates the expansion of an algal habitat under nutrient and CO₂ enrichment. *Mar Ecol Prog Ser* 497:87–92
- Fong P, Zedler JB (1993) Temperature and light effects on the seasonal succession of algal communities in shallow coastal lagoons. *J Exp Mar Bio Ecol* 171:259–272
- Gattuso JP, Hansson L (2011) Ocean acidification: background and history. In: Gattuso JP, Hansson L (eds) *Ocean acidification*. Oxford University Press, Oxford, UK, pp 1–20
- Ghedini G, Russell BD, Connell SD (2015) Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances. *Ecol Lett* 18:182–187
- Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science* 293:2248–2251
- Giordano M, Beardall J, Raven JA (2005) CO₂ concentrating mechanisms in algae: mechanisms, environmental modulation, and evolution. *Annu Rev Plant Biol* 56:99–131
- Golubic S, Friedmann I, Schneider J (1981) The lithobiontic ecological niche, with special reference to microorganisms. *J Sediment Petrol* 51:475–478
- Harris JL, Lewis LS, Smith JE (2015) Quantifying scales of spatial variability in algal turf assemblages on coral reefs. *Mar Ecol Prog Ser* 532:41–57
- Hatcher BG (1988) Coral reef primary productivity: a beggar's banquet. *Trends Ecol Evol* 3:106–111
- Holbrook GP, Beer S, Spencer WE, Reiskind JB, Davis JS, Bowes G (1988) Photosynthesis in marine macroalgae: evidence for carbon limitation. *Can J Bot* 66:577–582
- IPCC (2013) *Climate change: the physical science basis. Contribution of working group one to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge
- Johnson MD, Carpenter RC (2012) Ocean acidification and warming decrease calcification in the crustose coralline alga *Hydrolithon onkodes* and increase susceptibility to grazing. *J Exp Mar Bio Ecol* 434:94–101
- Johnson MD, Moriarty VW, Carpenter RC (2014a) Acclimatization of the crustose coralline alga *Porolithon onkodes* to variable pCO₂. *PLoS ONE* 9:e87678
- Johnson MD, Price NN, Smith JE (2014b) Contrasting effects of ocean acidification on tropical fleshy and calcareous algae. *PeerJ* 2:e411
- Koch M, Bowes G, Ross C, Zhang X-H (2013) Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Glob Chang Biol* 19:103–132
- Kroeker KJ, Kordas RL, Crim RN, Singh GG (2010) Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol Lett* 13:1419–1434
- Kroeker KJ, Kordas RL, Crim R, Hendriks IE, Ramajo L, Singh GS, Duarte CM, Gattuso JP (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Glob Chang Biol* 19:1884–1896
- Larkum AWD, Koch EMW, Kuhl M (2003) Diffusive boundary layers and photosynthesis of the epilithic algal community of coral reefs. *Mar Biol* 142:1073–1082
- Lavigne H, Epitalon JM, Gattuso JP (2014) seacarb: seawater carbonate chemistry with R. R package version 3.0. R Foundation for Statistical Computing, Vienna
- Le Campion-Alsumard T, Golubic S, Hutchings P (1995) Microbial endoliths in skeletons of live and dead corals: *Porites lobata* (Moorea, French Polynesia). *Mar Ecol Prog Ser* 117:149–157
- Leichter J (2015) MCR LTER: coral reef: benthic water temperature, ongoing since 2005. Dataset knb-lter.ncr.1035.9, Moorea Coral Reef Long-term. Ecological Research. doi:10.6073/pasta/64651327973d5dfba8ef75f886f7d106
- Lenz EA, Edmunds PJ (2017) Branches and plates of the morphologically plastic coral *Porites rus* are insensitive to ocean acidification and warming. *J Exp Mar Bio Ecol* 486:188–194
- Martin S, Gattuso JP (2009) Response of Mediterranean coralline algae to ocean acidification and elevated temperature. *Glob Chang Biol* 15:2089–2100
- McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400–417
- Ober GT, Diaz-Pulido G, Thornber C (2016) Ocean acidification influences the biomass and diversity of reef-associated turf algal communities. *Mar Biol* 163:204
- Pörtner HO (2008) Ecosystem effects of ocean acidification in times of ocean warming: a physiologist's view. *Mar Ecol Prog Ser* 373:203–217
- Porzio L, Garrard SL, Buia MC (2013) The effect of ocean acidification on early algal colonization stages at natural CO₂ vents. *Mar Biol* 160:2247–2259
- Raven JA, Geider RJ (1988) Temperature and algal growth. *New Phytol* 110:441–461
- Reyes-Nivia C, Diaz-Pulido G, Kline D, Guldborg OH, Dove S (2013) Ocean acidification and warming scenarios increase microbioerosion of coral skeletons. *Glob Chang Biol* 19:1919–1929
- R Core Development Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Russell BD, Thompson J-AI, Falkenberg LJ, Connell SD (2009) Synergistic effects of climate change and local stressors: CO₂ and nutrient-driven change in subtidal rocky habitats. *Glob Chang Biol* 15:2153–2162
- Schiel DR, Steinbeck JR, Foster MS (2004) Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology* 85:1833–1839
- Short J, Kendrick GA, Falter J, McCulloch MT (2014) Interactions between filamentous turf algae and coralline algae are modified under ocean acidification. *J Exp Mar Bio Ecol* 456:70–77

- Steneck R, Dethier M (1988) A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476–498
- Tait LW, Schiel DR (2013) Impacts of temperature on primary productivity and respiration in naturally structured macroalgal assemblages. *PLoS ONE* 8:e74413
- Tribollet A (2008) The boring microflora in modern coral reef ecosystems: a review of its roles. In: Wisshak M, Tampanila L (eds) Current developments in bioerosion. Springer, Berlin, pp 67–94
- Tribollet A, Godinot C, Atkinson M, Langdon C (2009) Effects of elevated $p\text{CO}_2$ on dissolution of coral carbonates by microbial euendoliths. *Global Biogeochem Cycles* 23:3008
- Vermeij MJA, van Moorselaar I, Engelhard S, Hornlein C, Vonk SM, Visser PM (2010) The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. *PLoS ONE* 5:e14312
- Worm B, Chapman ARO (1998) Relative effects of elevated grazing pressure and competition from a red algal turf on two post-settlement stages of *Fucus evanescens* C. Ag. *J Exp Mar Bio Ecol* 220:247–268
- Yokohama Y (1973) A comparative study on photosynthesis temperature relationships and their seasonal changes in marine benthic algae. *Int Rev Hydrobiol* 58:463–472