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Production and accumulation of reef framework by calcifying corals and macroalgae on a remote Indian Ocean Cay.

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Abstract

Coral reefs face increasing pressures in response to unprecedented rates of environmental change at present. The coral reef physical framework is formed through the production of calcium carbonate ($CaCO_3$) and maintained by marine organisms, primarily hermatypic corals, crustose coralline algae (CCA), and other calcifying algae. The Kimberley bioregion, located in the northern part of Western Australia, has largely escaped land-based anthropogenic impacts and this study provides important metabolic data we are lacking on reef-building calcifying corals and macrophytes from an undisturbed set of marine habitats. Specimens of the dominant coral and algal taxa were collected from the reef platform of Browse Island located on the mid-shelf just inside the 200 m isobath off the Kimberley coast. During experimental light/dark incubations, all algae were net autotrophic producing 6–111 mmol O_2 m^{-2} day^{-1}. In contrast, most corals were net consumers of O_2 with average net fluxes ranging from −42 to 47 mmol O_2 m^{-2} day^{-1}. The net change in pH was generally negative for corals and calcifying algae (−0.01 to −0.08 h^{-1}). Corals, *Halimeda* (a calcifying green algae) and *Galaxaura* (a calcifying red algae) had positive calcification rates in light ranging from 4.2 to 18.4 g $CaCO_3$ m^{-2} d^{-1}. Resulting net calcification rates were all positive and ranged from 1.9 to 9.9 g $CaCO_3$ m^{-2} d^{-1} and were strongly correlated to net O_2 production. In intertidal habitats around Browse Island, estimated relative contributions of coral and *Halimeda* to the reef production of $CaCO_3$ were similar at around 600–840 g m^{-2} $year^{-1}$. The low reef platform had very low coral cover of $< 3\%$ which made a smaller contribution to calcification of ~240 g $CaCO_3$ m^{-2} $year^{-1}$. Calcification on the subtidal reef slope was predominantly from corals, producing ~1540 g $CaCO_3$ m^{-2} $year^{-1}$, twice that of *Halimeda*. The relative contributions of the main reef builders, in these undisturbed areas, to net community metabolism and $CaCO_3$ production and reef metabolism is important to understand exclusively climate-driven coral bleaching and mortality.

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1. Introduction

Oceans play a crucial role in slowing global climate change through the absorption and sequestration of approximately 25–30 % of the annual anthropogenic atmospheric carbon dioxide (CO_2) emissions (Le Quéré et al., 2013). When CO_2 enters the ocean, water chemistry changes occur that are collectively referred to as ocean acidification (OA; Doney et al., 2009). Coral reefs, as some of the world's most biologically complex ecosystems, support a diverse range of species and provide critically important resources for livelihoods, such as food, and coastal protection (Hoegh-Guldberg et al., 2007). With the unprecedented rate of environmental change at present, coral reefs face increasing pressures in response to rising atmospheric greenhouse gases, especially CO_2 (IPCC, 2014). Two of the most immediate impacts of rising CO_2 levels on coral reefs are increases in ocean temperatures, due to atmospheric heat absorption, and ocean acidification (Hoegh-Guldberg, 2007; Doney et al., 2009).

One of the most important determinants of overall reef function is the construction and maintenance of calcium carbonate (CaCO3) reef structure, which is vital to the myriad of ecosystem services that coral reefs provide (Hoegh-Guldberg et al., 2007; Andersson et al., 2013; Moberg and Folke, 1999). Coral reefs are known for their high photosynthetic production and calcification. Measurements of reef metabolism make it possible to characterize reef health in terms of these fundamental processes. Photosynthesis fixes CO_2 in organic materials, whereas the reverse reaction, respiration, releases it. Overall, the excess organic production in a coral reef community, i.e., the difference between gross primary production and respiration, acts as a CO_2 sink, while calcification acts as a source of CO_2 (Lewis, 1977; Kinsey, 1985).

The coral reef physical framework is formed through the production of calcium carbonate ($CaCO_3$) and maintained by marine organisms, primarily hermatypic corals, crustose coralline algae (CCA), and other calcifying algae. Scleractinian corals are primary reef builders in tropical environments producing $CaCO_3$ through skeletal deposition, adding to the three-dimensionality of the reef framework. For scleractinian corals, one of the most significant consequences of OA is the decrease in the concentration of carbonate ions (CO_2^{-3}). As coral's skeletons are made from the mineral phase of calcium carbonate, called aragonite, the saturation state of aragonite (Ω_{arg}) is often related to rates of calcification. Studies have demonstrated that, as CO_2 concentrations rise, the saturation state of aragonite (Ω_{arg}) decreases and, in turn, the rate at which corals calcify declines (Schneider and Erez, 2006; Langdon, 2005; Pandolfi et al., 2011; Venn et al., 2013). Projections suggest that future rates of coral reef community dissolution may exceed rates of $CaCO_3$ production (calcification), leading to net loss (Silverman et al., 2009; Hoegh-Guldberg et al., 2007). In scleractinian corals with zooxanthellae, the precipitation of $CaCO_3$ through calcification is tightly coupled to photosynthetic fixation of CO_2 and tends to be, on average, three times higher in daylight conditions than in darkness (Gattuso *et al.,* 1999). Calcification rates can increase further through feeding on phytoplankton and suspended particles (Houlbreque and Ferrier-Pages, 2009). Change in community structure is linked to the balance between community metabolism and calcification with the CO_2 flux of seawater (Kayanne et al., 2005). During bleaching events rates of primary production and respiration increase but community excess organic production decreases dramatically in reefs under thermal stress (Kayanne et al., 2005). Baseline reef metabolism in undisturbed areas like Browse Island are important to understand exclusively climate-driven coral bleaching and mortality.

Reef algae are an important component of many tropical marine ecosystems, including coral reefs, where their morphological diversity provides habitat and shelter for a number of invertebrate and fish species, with productivity sustaining higher trophic levels. Reef-building corals are generally considered to be the dominant components of healthy or pristine coral reefs, but inconspicuous turfs and encrusting coralline algae contribute substantially to reef primary production in these areas (Odum and Odum, 1955; Hatcher, 1997). The abundance of large frondose macroalgae is typically inversely related to coral abundance; macroalgae are common on reef flat, back reef, and inshore fringing reef areas, whereas corals are more common on reef slopes. In coastal environments, like corals, calcified macroalgae can also contribute significantly to the deposition of carbonates. Among the green calcifying algae (Chlorophyta), the genus *Halimeda* (order Bryopsidales) are widely distributed across tropical and subtropical environments and play important ecological roles in both habitat provisioning and biogenic sediment production. Production rates of *Halimeda* make it major contributor to $CaCO_3$ in reefs in the Caribbean, Tahiti and the Great Barrier Reef (Drew, 1983; Payri, 1988). In certain locations production can approach 1.4 kg $CaCO_3$ m^{-2} yr^{-1}, positioning *Halimeda* as a major contributor to carbonate budgets within shallow waters around the globe (Payri, 1988). This group further occupies a diverse range of environments (mangroves, seagrass beds, and coral reefs) and can produce structurally complex mounds which serve as critical habitat for a diversity of marine life (Rees et al., 2007).

Community metabolism on a reef is a combination of the net photosynthesis and respiration of the organisms that live there. The corals and algae dominating the benthos of these complex ecosystems have the potential to change the chemistry of the water column (Duarte et al., 2013), despite global oceanographic and atmospheric influences (Kleypas et al., 2011). Metabolic processes can deplete or replenish oxygen, carbon, and nutrient concentrations either within hydrodynamic boundary layers over time (Shashar et al., 1993; Zeebe et al. 1999; Anthony et al., 2011; Shamberger et al., 2011) or in larger water masses as they move across a given reef (Barnes, 1983; Barnes and Lazar, 1993; Frankignoulle et al., 1996; Gattuso et al., 1996a; Niggel et al., 2010; Wild et al., 2010). The magnitude of the metabolic changes in water column chemistry depends on the relative abundance of the different members of the reef community, their individual metabolic rates and the local oceanographic conditions. In addition to producing and consuming O_2, photosynthetic organisms alter concentrations of dissolved inorganic carbon through uptake of dissolved inorganic carbon (CO_2 or bicarbonate; e.g. Raven et al., 1995) during photosynthesis and release of CO_2 during respiration thus altering the pH of the surrounding water column (Murru and Sandgren, 2004). Calcifying organisms also alter the biogeochemistry in the water column by releasing CO_2 and H^+ ions during the production of $CaCO_3$ and thus decreasing the pH (Jokiel, 2011). How calcifying primary producers such as corals with zooxanthellae and calcifying algae affect water column chemistry is therefore more difficult to predict.

Mesocosm experiments have shown that reef-building (hermatypic) corals tend to reduce pH and consume O_2 (e.g. (Gattuso et al., 2015; Smith et al., 2013)) whereas calcifying macroalgae increase pH and O_2 during daytime (Borowitzka and Larkum, 1987; Smith et al., 2013). Both corals and calcifying macroalgae reduce pH and O_2 concentrations due to respiration during nighttime, but the rates of change differ among species (Smith et al., 2013). There are limited numbers of studies examining the individual effects of key primary producers on water chemistry in the same study, and thus, we lack knowledge of the relative contributions of the main reef builders to net community metabolism and $CaCO_3$ production on most coral reefs.

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The Kimberley bioregion located in the northern part of Western Australia is host to extensive coastal reef systems, isolated offshore reefs and islands. It represents one of the few "very low impact" tropical coast and shelf areas globally – only 3.7% of the global oceans fall in this category (Halpern et al., 2008) – highlighting its significance as an undisturbed reef habitat. Few process studies have been carried out in the region due to the remoteness of these reefs, some of which are located 100s of km from the coastline, meaning that fieldwork and data acquisition can be difficult and costly. Here, we compare metabolic and calcification rates of the dominant intertidal taxa of macroalgae and coral at Browse Island, a small island in the Kimberley, something never previously examined in these systems. Rates of net metabolism and calcification were determined in on-ship incubations in October 2016, April 2017 and October 2017. These rates were upscaled for the dominant benthic community types using the proportional cover of the benthos.

2. Methods

2.1 Study site

Browse Island is located on the mid-shelf just inside the 200 m isobath off the Kimberley coast in northern Western Australia (14°6'S, 123°32'E; Fig. 1). The island is surrounded by a small (~ 4.5 km^2) planar platform reef consisting of a shallow lagoon, an extensive reef flat that is conspicuously absent to the northeast of the island, and a well-defined reef crest and slope. Tides are semidiurnal with a maximum range of < 5 m, exposing the reef crest and reef platform habitats during low tides. The intertidal habitats are characterised by low species richness and dominated by small turfing algae and calcified macroalgae of the genus *Halimeda* (15–22% and 6–9% cover respectively) (Olsen et al., 2017). Coral assemblages are well developed with cover of 5–8% in the intertidal habitats and 18% on the shallow reef slope (< 10 m) (Olsen et al., 2017).

2.2 Algae and coral collection

Specimens of the dominant coral and algal taxa were collected from the reef platform by hand during low tide, immediately brought back to the vessel and kept in a holding tank with circulating seawater. Macroalgae included the calcifying green alga *Halimeda opuntia*, which was the dominant species of *Halimeda* on the reef platform, the green alga *Caulerpa* sp., and the calcifying red alga *Galaxaura* sp. Pieces of turf algae (turf) as well as turf attached to a piece of rock (turf + substrate) were measured. In April 2016, drift algae of the genus *Sargassum* found floating on the water surface were also included although this taxa was not been found growing anywhere on the reef. Hermatypic corals included *Pocillopora* sp., *Goniastrea* sp., *Porites* sp., *Heliopora* sp., *Acropora* sp. and *Seriatopora* sp. Whole pieces of coral small enough to fit inside the incubation cores (inner diameter ~90 mm) were collected to minimise tissue damage. All coral samples were > 50 mm diameter and therefore operationally defined as adults and estimated to be at least 2 to 7 years old depending on the taxa (Trapon et al., 2013).

2.3 Light and dark incubations

Light and dark incubations were undertaken on the back deck of the research vessel. Four 60 L holding tanks were placed in a shade-free spot under natural light conditions, filled with seawater and connected to a flow-through seawater system, which ensured the setup remained at ambient temperature. Photosynthetically active radiation (PAR) was recorded with a HOBO Micro Station logger (H21-002, Onset) placed inside one of the tanks. Each holding tank contained six 1.56 L clear Perspex incubation cores fitted with stirring caps. A port in the cap of each core allowed for sample collection using a syringe. As the sample was removed, the same volume of liquid was automatically replaced from the flowthrough tank into the core so that the core volume remained constant through the experiment.

Individual specimens of algae and coral were placed in 6–12 replicate incubation cores per taxa except where not enough individuals could be found. Table 1 shows the taxa incubated during each sampling trip and the number of replicates. Water samples from the holding tanks were measured at each time point as controls and, in addition, in October 2017, a separate seawater control (six replicate incubation cores with seawater) was included. After a period of acclimation (1–2 h), incubations were run over a four-hour period. The light incubations were conducted while the sun was at its zenith providing full irradiance to the samples. After two hours, the tubs were covered with a black lid ensuring no light could enter and the samples incubated for two hours in the dark.

To estimate oxygen production or consumption during the incubations, a 40 mL water sample was extracted from each of the 24 cores and the four tubs at the start of the incubations and hourly thereafter. Samples were immediately analysed for temperature and dissolved oxygen (O_2) with a YSI 5100 bench-top oxygen and temperature meter with YSI 5010 BOD stirring probe, calibrated daily in air. Sample pH was determined using a TPS Aqua pH meter with an Ionode probe, calibrated daily with pH 7.00 and 10.00 buffers. A second 35 mL water sample was collected from each core and tub and split between one 10 mL glass vacutainer for alkalinity and duplicate 10 mL sterile vials for nutrient analyses. Nutrient samples were immediately frozen and alkalinity samples were stored cool and dark. At the end of the incubation, algal and coral specimens were frozen. All samples were transported to Perth, Western Australia, to be analysed.

2.4 Surface areas of coral and algal specimens

Metabolic measurements were standardised by surface area of the incubated specimens since this represents the area available for photosynthesis and nutrient uptake. The surface area of specimens of coral, *Halimeda* and turf + substrate were estimated using a single wax dipping method (Veal et al., 2010). Specimens were dried, weighed and then dipped in paraffin wax at 65°C. The waxed samples were weighed again, and the weight of the wax calculated. The surface area was estimated from the wax weights against a calibration curve constructed by wax dipping geometric wooden objects of known size. The surface areas of the remaining taxa, were estimated from photographs in ImageJ (Rueden et al., 2017). The 'footprint' of each sample, i.e. the surface area of reef occupied by the organism, was also estimated by tracing the outline of the specimen photographed from straight above in ImageJ.

2.5 Chemical analyses

Concentrations of nitrate + nitrite (hereafter referred to as nitrate), ammonium, phosphate and dissolved silica in water samples were analysed in duplicate by flow injection analysis (Lachat QuickChem 8000) with detection by absorbance at specific wavelengths for silica [QuikChem Method 31-114-27-1-D], nitrate [Quikchem Method 31-107-04-1-A] and phosphate [QuikChem Method 31-115-01-1-G]), and by fluorescence for ammonia according to Watson et al. 2005. Detection limits were 0.02 µmol L^{-1} for all inorganic nutrient species, with a standard error of < 0.7%.

Total alkalinity was determined to the nearest 5 µmol L^{-1} equivalent (hereafter referred to as µmol L^{-1}) using an open cell Metrohm titrator (841 Titrando, Burette: 800 Dosino 10 mL) with a Metrohm micro-glass pH probe calibrated with Certipur buffer solutions at pH 2.00, 4.01, 7.00, and 10.00 (at 25.0°C). Samples were kept in a Jubalo F12 temperature control water bath prior to decanting a 10 mL aliquot of sample into a vessel with a water jacket maintaining temperature at 25.0°C. Samples were titrated with 0.012 N HCl, standardised against sodium carbonate (99.95–100.05 wt%) with an initial volume of titrant added to reach pH 3.5. Titrations were run to an end-point of pH 3 with Gran plot (Excel macro) to determine the total alkalinity endpoint near pH 4.2. Carbonate system parameters were calculated from pH (measured during the incubations) and total alkalinity using the package ‘seacarb’ (Gattuso et al., 2018) in R (R_Core_Team 2018). Alkalinity and carbonate parameters were not determined in April 2016.

2.6 Oxygen fluxes and calcification rate calculations

The changes in O_2 concentrations during light- and dark incubations were expressed as mmol per day assuming stable hourly production rates over 24 h. Any replicates where O_2 did not increase during both of the light intervals or did not decrease during both of the dark intervals were excluded from further analysis. Net fluxes of O_2 per day were calculated for each sample assuming a 12-h photoperiod. Calcification rates of corals and calcifying algae (*Halimeda opuntia*. and *Galaxaura* sp.) were estimated using the alkalinity anomaly method (Smith and Key, 1975) uncorrected for changes in nutrient concentration (Chisholm and Gattuso, 1991) where precipitation of one mole of $CaCO_3$ leads to the reduction of total alkalinity by two molar equivalents. Rates per surface area were obtained by dividing these values by the surface area of each specimen.

A census-based approach was used to estimate the amount of $CaCO_3$ and O_2 produced by a single taxon per unit area of reef surface per year (Shaw et al., 2016). The rates of calcification and net O_2 production per day were divided by the ‘footprint’ area of each specimen. To estimate the relative contributions from each taxon to community production per m^2 of reef, these rates were multiplied by the relative percent cover in each of the major habitats. Estimates of percent cover based on drop camera image analysis were obtained from Olsen et al. (2017). The productivity rates for individual coral species were combined into one value for coral.

2.7 Statistical analyses

The relationships between net changes in pH and O_2 and between net O_2 production and net calcification (in light and dark incubations) were examined by linear regression. Significance of regressions were calculated for algae, calcified algae and corals and the 95% confidence intervals for the slope of each line in R (R_Core_Team, 2018). Regressions were examined with ANOVA and deemed significant if $p < 0.05$.

3 Results

3.1 Experimental conditions

The ambient conditions during the incubations are shown in Table 2. Nutrient concentrations were low, as is characteristic of tropical Eastern Indian Ocean offshore waters (McLaughlin et al., 2019), and similar among sampling trips. Concentrations of nitrate were < 0.17 µmol L^{-1}, ammonium <0.13 µmol L^{-1}, phosphate < 0.1 µmol L^{-1}, and silicate < 3 µmol L^{-1}. Oxygen was around 6–7 mg L^{-1} and salinity 34.2–34.8 ppt. Light and temperature conditions in the incubations were representative of *in situ* conditions on the reef platform and were similar among trips. PAR levels were 1500–1587 µE m^{-2} s^{-1} and slightly higher in October, whereas temperatures were 28.3–32.8°C and highest in April. Carbonate system parameters were not obtained for April 2016, and some differences were noted between October 2016 and 2017. Alkalinity and pH were both higher in 2016, and there were associated minor differences in the concentrations of the carbonate species and the aragonite saturation state (Table 2).

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3.2 Changes in oxygen and pH

Changes in dissolved O_2 differed among taxa and between light and dark incubations. In the seawater controls O_2 changed by < 0.01 mmol h^{-1} in both light and dark incubations, showing that the contribution of any organisms in the seawater itself to O_2 production and respiration was minimal. No corrections were therefore applied. In the light incubations, when any change in O_2 resulted from primary production minus respiration, mean O_2 concentrations increased for all taxa (Fig. 2, top panel). The highest light flux of O_2 of ~380 mmol m^{-2} day^{-1} was measured for *Galaxaura* in October 2017 (Fig. 2, top). Corals generally produced 100–260 mmol O_2 m^{-2} day^{-1} in the light, except *Heliopora,* which had a flux of 50–80 mmol O_2 m^{-2} day^{-1}. All taxa consumed O_2 during the dark incubations when changes in O_2 are due to respiration, with mean fluxes of −15 to −190 mmol O_2 m^{-2} day^{-1} (Fig. 2, middle). All algae were net autotrophic and produced 6–111 mmol O_2 m^{-2} day^{-1} with the highest net O_2 flux measured for *Galaxaura* and turf at 111 and 36 mmol O_2 m^{-2} day^{-1} respectively (Fig. 2, bottom). In contrast, around half of the corals were net consumers of O_2 and average net fluxes spanned a wide range from −42 to 47 mmol O_2 m^{-2} day^{-1}. It is important to note that coral specimens tested in the incubations were 50–90 mm (smallest diameter) and that the patterns observed may be specific to smaller coral colonies.

In the light incubations, pH generally increased by 0.03–0.25 h^{-1} for all taxa, except for *Halimeda* in April 2016 and October 2017, which showed no change or a very small increase (Fig. 3, top panel). In dark incubations, mean pH decreased for all taxa by 0.02–0.21 h^{-1} indicative of a net increase in CO_2 through respiration (Fig. 3, middle). Non-calcifying algae (*Sargassum*, *Caulerpa* and turf) raised net pH by 0.02–0.05 h^{-1} (assuming equal periods of light and darkness) (Fig. 3, bottom panel). The net change in pH was generally negative for corals and calcifying algae (−0.01 to −0.08 h^{-1}), except for the coral *Goniastrea* in April and October 2016 (0.01 h^{-1}) and the calcifying alga *Galaxaura* (0.03 h^{-1}; Fig. 3, bottom).

Net changes in pH are largely driven by metabolic uptake and release of CO_2. We found positive relationships between changes in pH and net production or consumption of O_2 except in seawater controls where changes in O_2 and pH were minor (Fig. 4). The relationships for algae, calcifying algae and coral were all significant, but had relatively low adjusted r^2 values of 0.59, 0.46 and 0.19 respectively, suggesting significant variability among species and individuals within each of these groups.

3.3 Calcification Rates

Corals, *Halimeda* and *Galaxaura* had positive calcification rates in light ranging from 4.2 to 18.4 g $CaCO_3$ m^{-2} d^{-1} (Fig. 5, top panel). In the dark, calcifying rates were smaller and just under half of the rates were negative suggesting dissolution of $CaCO_3$ (Fig. 5, middle panel). The resulting net calcification rates (assuming equal periods of light and darkness) were all positive and ranged from 1.9 to 9.9 g $CaCO_3$ m^{-2} d^{-1} (Fig. 5, bottom). Rates of calcification were strongly linearly correlated to net O_2 production and were significantly higher in light than in darkness for both corals and algae (Fig. 6).

3.4 Contributions to community production

In intertidal habitats around Browse Island, the estimated relative contributions of coral and *Halimeda* to the reef production of $CaCO_3$ were similar, around 600–840 g m^{-2} $year^{-1}$ (Fig. 7, top panel). The low reef platform had very low coral cover of < 3% (Fig. 7, middle), which therefore made a smaller contribution to calcification of ~240 g $CaCO_3$ m^{-2} $year^{-1}$ in this habitat (Fig. 7, top). In contrast, calcification on the subtidal reef slope was predominantly from corals, which produced ~1540 g $CaCO_3$ m^{-2} $year^{-1}$, around twice the amount compared to *Halimeda*. *Galaxaura*, which had high measured rates of productivity and calcification, was extremely rare and its contribution to community calcification and productivity were negligible. Turf was responsible for the majority of the O_2 production in all habitats and produced an estimated 8–13 mmol O_2 m^{-2} d^{-1} compared to < 2 for *Halimeda* mmol O_2 m^{-2} d^{-1} and −4 to −1 mmol O_2 m^{-2} d^{-1} for corals (Fig. 7, second panel from top).

4 Discussion

The Kimberley coastal region (located in remote north-western Australia) has a macrotidal regime where spring tidal ranges can reach up to 11 m in some locations (McLaughlin et al., 2020; Kowalik, 2004). The region contains thousands of islands with a total reef area estimated to be ~2000 km^2 (Kordi and O'Leary, 2016), inhabited by diverse coral reef and seagrass communities (Richards et al., 2015; Wells et al., 1995). Recent work has revealed the strongly tide-dominated circulation that can occur on Kimberley reef platforms (Lowe et al., 2015). Browse Island has the only emergent mid-shelf reef in the Kimberley bioregion and its benthic structure is very different from both inner and outer shelf reefs. The region-wide averages of coral cover and macroalgal cover are 23.8% and 7.1% (Richards et al., 2018) respectively, but at Browse Island the relationship is reversed with macroalgae more dominant at 28% total cover to that of 9% for coral. On the Browse Island reef platform the same pattern is observed where averages were 5-8% for coral and 32% for macroalgae, differing from those of the regional averages of 14.4% and 15.5% of coral and macroalgae respectively (Richards et al., 2018).

Observations from shallow benthic habitats, like those at Browse Island, have shown that seawater O_2 and carbonate chemistry vary over diel cycles related to patterns in photosynthesis and respiration (e.g. Duarte et al., 2013). Primary production and the uptake of CO_2 during daylight hours result in elevated pH and an elevated aragonite saturation state (Ω_{arag}) during the day when calcification rates peak. The process of calcification decreases pH in the surrounding water, but for calcifying autotrophs CO_2 uptake and fixation through photosynthesis can potentially offset changes to the carbonate chemistry caused by calcification (Smith et al., 2013). Methods to calculate calcification can vary in accuracy where overestimates of calcification rates can result from calculations based on changes in alkalinity, while those relying on $CaCO_3$ content and growth measurements, either through staining or tagging segments, may produce minimum estimates as loss of new tissue is not accounted for (Hart and Kench, 2007). The method employed in the present study was the best possible option when working in a remote location where actual growth rates cannot be easily assessed.

The organisms investigated here showed typical patterns of O_2 production in daylight and consumption in darkness to other similar island reef systems as a result of photosynthesis and respiration, but the metabolic measurements showed clear differences among taxa and functional groups. Algae had higher positive net O_2 fluxes with rates of 5.7–111.6 mg O_2 m^{-2} day^{-1}, of which the red calcifying alga *Galaxaura* sp. had the highest rate of net productivity by far. For corals, the relatively high O_2 increase measured in daylight was coupled with high rates of respiration in darkness, creating a negligible or negative net O_2 production for most species, except *Porites* sp. in April 2016 and *Seriatopora* sp. in October 2016 and 2017 which were net positive. This indicates that the majority of the corals are largely heterotrophic and rely on feeding in addition to photosynthesis by zooxanthellae to sustain growth. These patterns are generally in agreement with those reported elsewhere, for example, fleshy and calcifying algae showed net diel O_2 production, whereas corals generally

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consumed O_2 , i.e. were net heterotrophic, on islands in the South Pacific (*Porites* sp.) and the Caribbean (*Madracis* sp.) (Smith et al., 2013).

Concurrent with changes in O_2 were changes in seawater pH, where pH increased in daylight (except for *Halimeda* in April 2016 where no change was measured) and decreased in darkness. The effects of metabolic activity on bulk pH (uptake and release of CO_2 through photosynthesis and respiration) cannot be directly separated from that of calcification, which is associated with the release of H+ ions thereby decreasing pH (Jokiel, 2011). However, differences were observed in the net pH change in incubations between calcifiers and non-calcifiers. The net effect of non-calcifiers on seawater pH was positive while the majority of calcifiers caused net pH to decline. The process of calcification decreases pH in the surrounding water, but for calcifying autotrophs CO_2 uptake and fixation through photosynthesis can potentially offset changes to the carbonate chemistry caused by calcification (Smith et al., 2013). In the present study, *Halimeda* (April 2016) and *Goniastrea* (April and October 2016) caused relatively minor increases in pH, whereas the calcifying alga *Galaxaura* elevated pH by, on average, 0.03 units, comparable to the net effect of non-calcifiers. This is not surprising given the high rate of O_2 production measured for *Galaxaura*, which is associated with sufficient levels of CO_2 fixation to compensate for the reduction in pH associated with calcification in this species. A strong link was observed between metabolism and pH in all taxa, demonstrated as linear relationships between changes in pH and O_2 during the incubations. Previous research by Smith et al. (2013) identified two broad patterns; metabolic changes in O_2 in non-calcifiers (fleshy and turf algae) linked to large changes in pH (steep slopes), and metabolic changes in O_2 in calcifying organisms (*Porites* sp. *Madracis* sp. and *Halimeda* sp.) producing little or no change in pH (shallow slopes). This is contrary to the present study observations where slopes of relationships between pH and O_2 were similar for calcifiers and non-calcifiers. Non-calcifying organisms were found to consistently have a net positive effect on both pH and O_2. Change in pH for the same net change in O_2 was elevated for non-calcifiers compared to calcifiers. This difference can be attributed to the process of calcification, which reduces the 'baseline pH' in these relationships.

Production and accumulation of reef framework carbonate is controlled by the relative rates of, and the interactions between, a range of ecologically, physically and chemically driven production and erosion processes (Perry et al., 2008; Montaggioni and Braithwaite, 2009), with the relative importance of different taxa for $CaCO_3$ production differing among reefs and among habitats within reefs. Rates of net community calcification for reef flats worldwide range from 7.3 to 90 mol (730–9000 g) $CaCO_3$ m^{-2} $year^{-1}$ with an average of 47 mol (4700 g) $CaCO_3$ m^{-2} $year^{-1}$ (Atkinson, 2011). Patterns found in the present study — higher calcification rates in daylight compared to in darkness for all corals and calcifying algae — are therefore typical. However, the coral $CaCO_3$ production rates per reef area (7–8% cover low reef platform, 19% reef slope) measured here (240 g m^{-2} $year^{-1}$ for low reef platform, 610–756 g m^{-2} $year^{-1}$ in the other intertidal habitats, and 1536 g m^{-2} $year^{-1}$ on the reef slope) were somewhat lower than values reported elsewhere. Several of the taxa showed negligible production or even dissolution of $CaCO_3$ in darkness. The resulting strong relationship between net carbonate production and net carbonate consumption is consistent with previous studies both *in situ* and in mesocosms (Albright et al., 2013).

Corals are typically the primary framework-producing components on a tropical reef and dominate carbonate production per unit area (Vecsei, 2004), however additional $CaCO_3$ is produced by calcareous crustose coralline algae (CCA) and calcareous algae of the genus

Halimeda, (e.g. Payri, 1988). Sprawling lithophytic species of *Halimeda*, like the majority of the *Halimeda* around Browse Island, tend to be fast growing and have high calcification rates (Hart and Kench, 2007). Rates of calcification per area of 100% Halimeda cover have been estimated to 400–1667 g $CaCO_3$ m^{-2} $year^{-1}$ (in Hart and Kench, 2007 Suppl info). In other locations, *Halimeda* has been estimated to contribute around 1100–2400 g $CaCO_3$ m^{-2} $year^{-1}$ to benthic carbonate production (Drew, 1983; Freile et al., 1995; Hudson, 1985; Kangwe et al., 2012; Payri, 1988; Rees et al., 2007), which is higher than the 600–840 g $CaCO_3$ m^{-2} $year^{-1}$ estimated for *Halimeda opuntia* in the intertidal habitats in the present study. These rates depend both on the intrinsic calcification rates and on the abundance or cover of algae (6.1–8.7% cover on Browse, which corresponds to ~150–250 g dw m^{-2}).

While the estimates provided here approximate the relative contributions of *Halimeda* and coral to $CaCO_3$ production, they do not add up to a whole system budget. There are other organisms likely to contribute significantly. For example, the present study did not measure metabolic or calcification rates of encrusting coralline algae, which, although making up a modest 1.0–3.0% of the benthic cover in the lagoon and reef platform habitats at Browse Island, become more prominent at 11.8–14.1% on the reef crest and slope (Olsen, unpublished data). To calculate the true $CaCO_3$ production per area of reef, the calcification rate would need to be multiplied by the benthic cover of coralline algae and the square of the benthic rugosity (Eakin, 1996). Using typical values for rugosity from Eakin (1996) of 1–1.4 for the lagoon and reef platform and 1.7–2 for the reef crest and slope, and assuming a typical calcification rate of 1500–2500 g m^{-2} $year^{-1}$ (for 100% flat-surface cover) (Hart and Kench, 2007), the contribution of encrusting coralline algae to calcification in the lagoon and reef platform would be minor at 70–134 g $CaCO_3$ m^{-2} $year^{-1}$. However, they could produce a significant amount of 980–1360 g $CaCO_3$ m^{-2} $year^{-1}$ on the reef crest and slope, which is

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somewhere in between the production rates estimated for *Halimeda* and corals. Encrusting coralline algae may therefore contribute significantly to the $CaCO_3$ budget at Browse Island, at least in deeper habitats. These values are similar to those measured elsewhere, for example 870–3770 g $CaCO_3$ m^{-2} $year^{-1}$ at Uva reef in the eastern Pacific (Eakin, 1996).

5 Conclusions

Browse Island is the only emergent mid-shelf reef in the Kimberley bioregion and is host to a different benthic community composition compared to the closest reefs both inshore (e.g. Montgomery Reef, Adele and Cassini Islands) and offshore (e.g. Ashmore Reef and Rowley Shoals). The relative contributions of algae and corals to reef productivity are likely to differ across the shelf, with corals becoming more important in offshore waters and algal calcifiers being important on the mid-shelf. Estimated aerial production rates did not take into account the relief of the substrate. The reef platform surrounding Browse Island has relatively low surface relief, whereas the reef slope and crest have high rugosity, which means production rates in the latter environments may be underestimated. Despite these limitations, the rates estimated in this study are similar to those measured elsewhere.

The higher cover of *Halimeda* and the low coral cover at Browse Island compared to other reefs in the region mean that corals and *Halimeda* contribute equally to productivity rates of $CaCO_3$ on the Browse Island reef flat, however, their relative contributions to the reef framework and sedimentary budget of the reef is unknown. To gain an understanding of the relationships between carbonate production and sinks on the reef, further study into the types and amounts of $CaCO_3$ material found in each reef sink is necessary. The Kimberley coastal shelf, which is characterised by coral reef environments with clear, low nutrient waters and low productivity, has largely escaped land-based anthropogenic impacts, but has been negatively affected by climate-driven coral bleaching and mortality, for example from heat waves at Scott Reef in 1998 and 2016 (Smith et al., 2008, Gilmour et al., 2013 and Hughes et al., 2017) and Ashmore Reef in 2003 and 2010 (Ceccarelli et al., 2011 and Heyward, 2011). The effects of temperature stressors on reef communities and their productivity remain to be investigated in this region. Different components of the reef around Browse Island are likely to have different vulnerabilities to warming and heat waves. Future environmental stressors leading to changes in benthic community composition, structure and subsequent changes in reef productivity and in rates of production of $CaCO_3$, could have major implications for Browse Island.

Author contribution: M. James McLaughlin – Conceptualization, formal analysis, investigation, resources, methodology, visualisation, and writing (original draft preparation); Cindy Bessey - Investigation, resources, project administration, and writing (review and editing); Gary A. Kendrick - Conceptualization, funding acquisition, project administration, supervision, and writing (review and editing); John Keesing - Conceptualization, funding acquisition, investigation, resources, supervision, and writing (review and editing); Ylva S. Olsen - Conceptualization, formal analysis, investigation, project administration, resources, methodology, visualisation, and writing (original draft preparation)

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Figures

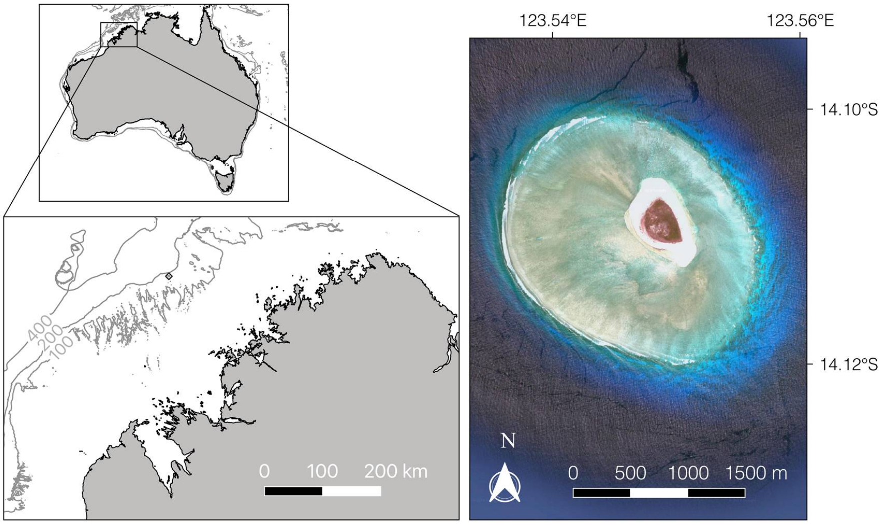


Figure 1. The study site, Browse Island (diamond, bottom left map), is located just inside the 200-m isobath on the continental shelf. The small map (top left) shows the location of the island relative to the Australian coastline with the 100, 200 and 400 m isobaths marked in gray. The satellite image (right; © Google Earth 2018) shows the extent of the reef.

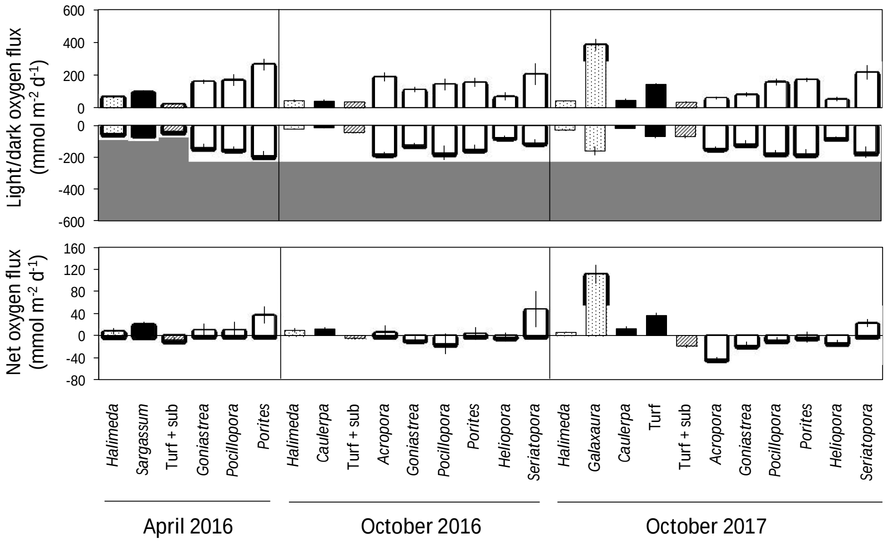


Figure 2. Net changes in oxygen (means ± se) in light (top) and dark (middle) incubations of calcifying algae (stippled), macroalgae and turf (black), turf + substrate (diagonal stripes) and coral (white) standardised by specimen surface area. The bottom panel shows the net daily production of oxygen (means ± se) assuming a 12-h photoperiod and stable rates of photosynthesis and respiration over a 24-h period.

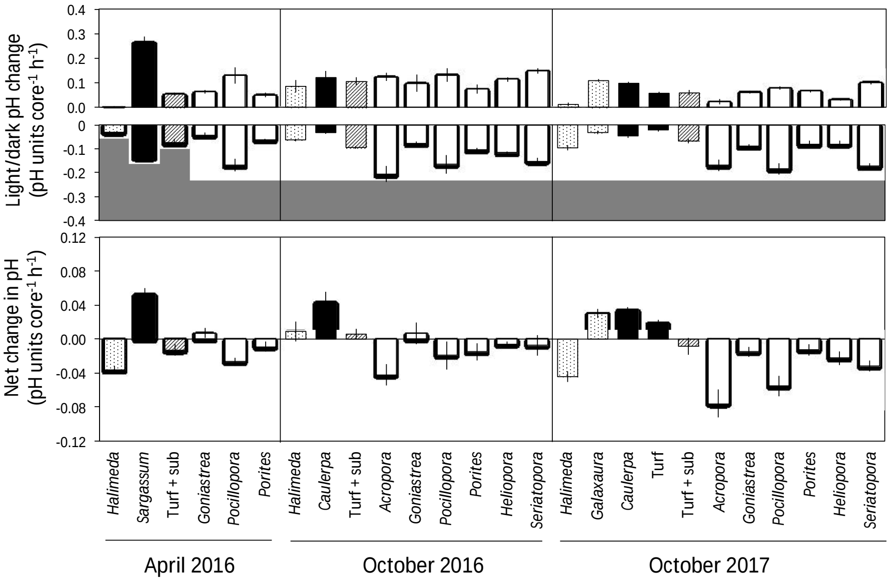


Figure 3. Net changes in pH per hour for each 1.56-L incubation core (means ± se) in light (top) and dark (middle) incubations calcifying algae (stippled), macroalgae and turf (black), turf + substrate (diagonal stripes) and coral (white). The bottom panel shows the net change in pH per hour (means ± se) assuming equal periods of light and darkness.

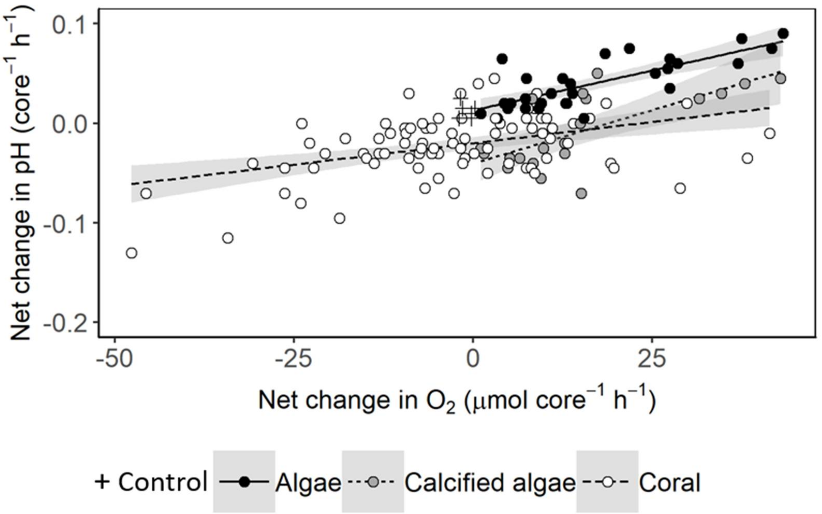
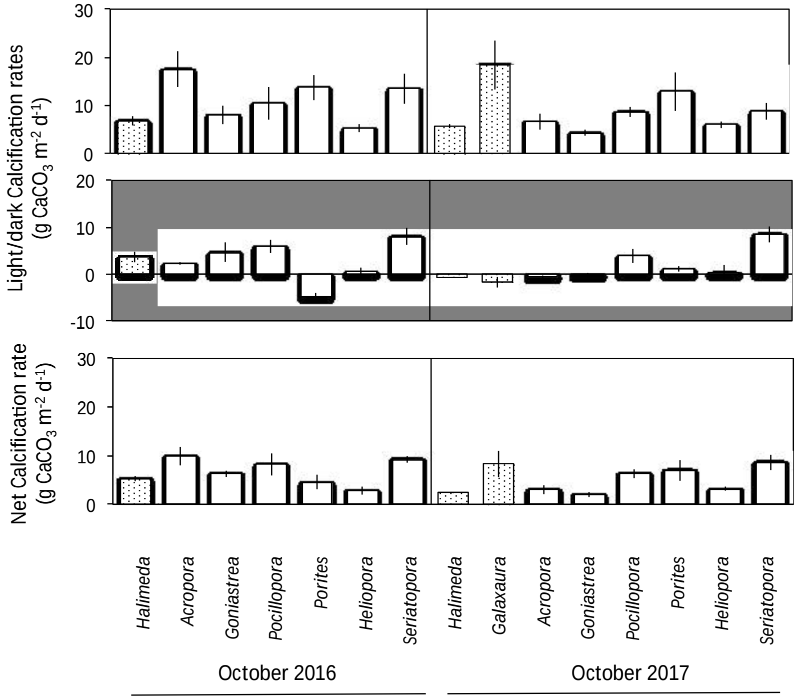


Figure 4. Net change in pH versus O_2 per 1.56-L incubation core assuming equal periods of light and darkness. Linear relationships are fitted with 95% confidence intervals shown in gray. For algae; net change in pH = 0.13 + 0.0016 × net change in O_2 (ANOVA: $F_{1,27} = 41.15$, p <0.001). For calcified algae; net change in pH = −0.04 + 0.0021 × net change in O_2 (ANOVA: $F_{1,19} = 17.86$, p <0.001). For corals; net change in pH = −0.02 + 0.00086 × net change in O_2 (ANOVA: $F_{1,82} = 18.88$, p <0.001).



543

544 **Figure 5.** Calcification rates for corals (white) and calcifying algae (stippled) (means ± se) in
545 light (top) and dark (middle). The bottom panel shows the daily net calcification rate (means ±
546 se) assuming a 12-h photoperiod.

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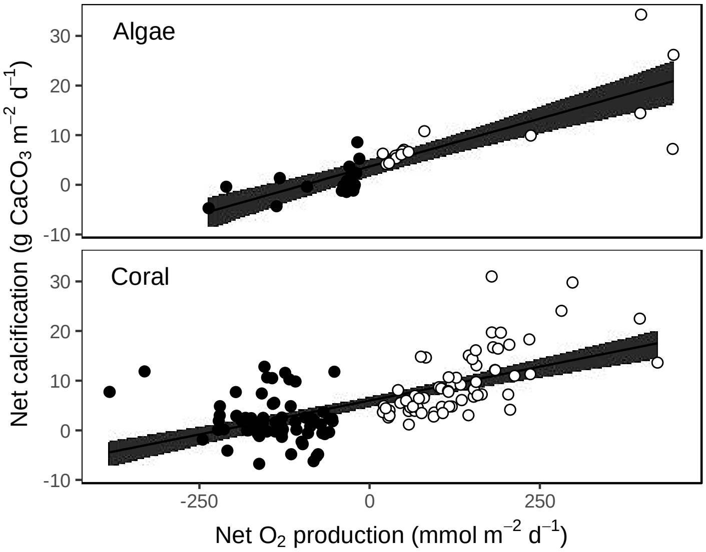

Figure 6. Relationship between net calcification rate and net productivity for calcifying algae (top) and corals (bottom). Open circles indicate rates measured in light and closed circles rates measured in dark. Linear fits are shown with 95% confidence intervals in gray. For calcified algae; net calcification = 3.6 + 0.039 × net O_2 production (ANOVA: $F_{1,32} = 67.0$, $p < 0.001$). For corals; net calcification = 5.99 + 0.027 × net O_2 production (ANOVA: $F_{1,126} = 82.2$, $p < 0.001$).

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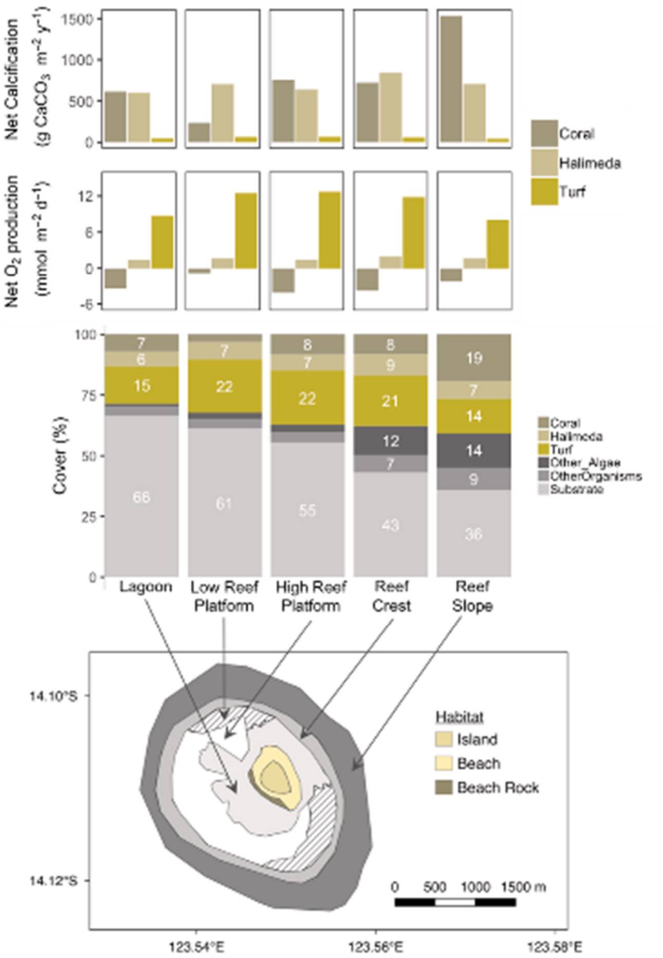

Figure 7. Map of the reef around Browse Island showing the major habitat types (bottom panel). Reef surface percent cover of coral, *Halimeda*, turf and other categories in each habitat (middle panel) based on drop-camera image analysis data from (Olsen *et al.* 2017). Net calcification and net oxygen production by coral, *Halimeda* and turf per m^{-2} of reef (top two panels) scaled up by multiplying rates obtained from incubations of each taxon by the percent cover in each habitat.

Tables

Table 1. Taxa measured in on-ship incubation experiments including the number of replicate specimens measured (one specimen per incubation core). Some of the specimens were not included in the final analysis due to sampling errors or due to O_2 not increasing during both of the light intervals or not decreasing during both of the dark intervals; the resulting number of specimens used are shown in brackets.

	Taxa	**Apr 2016**	**Oct 2016**	**Oct 2017**
Algae	*Halimeda opuntia*	6 (5)	6	6
	Turf algae + substrate	6 (5)	6	6
	Turf algae	-	-	6
	Sargassum sp.	12	-	-
	Caulerpa sp.	-	6	6
	Galaxaura sp.	-	-	6 (5)
Coral	*Pocillopora* sp.	6	6	6
	Goniastrea sp.	6 (5)	6	6
	Porites sp.	5	6	6
	Heliopora sp.	-	6 (5)	6
	Acropora sp.	-	5	6
	Seriatopora sp.	-	4	6
	Seawater control	-	-	6

Table 2. Ambient concentrations of parameters measured during incubations (means ± se); nutrients ($NO_3^- + NO_2^-$ = nitrate + nitrite, NH_4^+ = ammonium, PO_4^{3-} = orthophosphate, Si = silica) and oxygen (O_2), total alkalinity (TAlk), Photosynthetically Active Radiation (PAR), temperature (T) and salinity. Calculated carbonate system parameters (means ± se); CO_2 partial pressure (pCO_2), concentrations of HCO_3^-, CO_3^{2-} and dissolved inorganic carbon (DIC), and the saturation state of aragonite (Ω Aragonite). In April 2016, two replicate PAR measurements were taken at 11:00, 12:00 and 13:00 h. In October 2016 and 2017, PAR was measured every minute and values between 11:00 and 13:00 h averaged.

	Apr 2016	**Oct 2016**	**Oct 2017**
Number of replicates (n)	8	10	12
$NO_3^- + NO_2^-$ (µmol L^{-1})	0.15 ± 0.04	0.05 ± 0.01	0.17 ± 0.01
NH_4^+ (µmol L^{-1})	0.12 ± 0.02	0.13 ± 0.01	0.13 ± 0.01
PO_4^{3-} (µmol L^{-1})	0.08 ± 0.01	0.07 ± 0.00	0.09 ± 0.00
Si (µmol L^{-1})	2.74 ± 0.04	2.93 ± 0.04	2.30 ± 0.02
O_2 (mg L^{-1})	6.18 ± 0.06	6.66 ± 0.05	7.48 ± 0.09
PAR 11–13 h (µE m^{-2} s^{-1})	1499.6	1587.1	1587.0
T (°C)	32.8 ± 0.1	31.2 ± 0.1	28.3 ± 0.1
Salinity (ppt)	34.8	34.5	34.2
TAlk (µmol L^{-1})	NA	2408 ± 5	2390 ± 2
pH	8.17 ± 0.02	8.14 ± 0.02	8.11 ± 0.01
Calculated carbonate system parameters			
pCO_2 (uatm)	NA	295 ± 14	335 ± 17
HCO_3^- (mmol kg^{-1})	NA	1.61 ± 0.03	1.69 ± 0.02
CO_3^{2-} (mmol kg^{-1})	NA	0.30 ± 0.006	0.26 ± 0.006
DIC (mmol kg^{-1})	NA	1.93 ± 0.02	1.97 ± 0.02
Ω Aragonite	NA	5.02 ± 0.11	4.27 ± 0.10

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