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, and calcifying algae. The northern part of Western Australia, known as the Kimberley, has largely escaped land-based anthropogenic impacts and this study provides important metabolic data on reef-building organisms from an undisturbed set of marine habitats. From the reef platform of Browse Island, located on the mid-shelf just inside the 200 m isobath off the Kimberley coast, specimens of the dominant coral (6 species) and algal (5 species) taxa were collected and incubated ex-situ in light and dark shipboard experimental mesocosms for 4 hours to measure rates of calcification and production patterns of oxygen. During experimental light/dark incubations, all algae were net autotrophic producing 6 to 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}). Resulting net calcification rates (1.9 to 9.9 g $CaCO_3$ m^{-2} d^{-1}) for corals, and calcifying algae (*Halimeda* and *Galaxura*) were all positive 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 to 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*. These data provide the first measures of community metabolism from the offshore reef systems of the Kimberley. The relative contributions of the main reef builders, in these undisturbed areas, to net community metabolism and $CaCO_3$ production is important to understand exclusively climate-driven negative effects on tropical reefs.

1. Introduction

The functioning of healthy coral reefs, as some of the world's most biologically (Stuart-Smith et al., 2018) and structurally complex ecosystems (Hughes et al., 2017b), results in a number of ecosystem services. They provide coastal protection, with reef structures acting to dampen wind and wave driven surges (Perry et al., 2018) and support a diverse range of species that provide critically important resources (such as food) for coastal livelihoods (Hoegh-Guldberg et al., 2007). However, coastal coral reefs in the Anthropocene era have been degraded for more than a century by overfishing and pollution (Hughes et al., 2017b). With the current unprecedented rate of environmental change, coral reefs face growing pressures. These range from localised eutrophication (Hewitt et al., 2016) and sedimentation (Hughes et al, 2017a), to larger scale recurrent weather events (marine heat waves; Moore et al., 2012) and rising atmospheric greenhouse gases (especially carbon dioxide, CO_2; IPCC, 2014) that result in increasing ocean temperatures (due to atmospheric heat absorption) and ocean acidification (OA) (Hoegh-Guldberg, 2007; Doney et al., 2009; Perry et al., 2018). Once thought protected by the very nature of their isolation, remote reefs are also now showing impacts by increasing stressors brought about by anthropogenic climate change (Hughes et al., 2017b).

As one of the most important determinants of overall reef function, the construction and maintenance of the calcium carbonate ($CaCO_3$) reef structure (the accumulation of which requires the net production of calcium carbonate by resident taxa; Cornwall et al., 2021) 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). The coral reef physical framework is formed and maintained through the production of calcium carbonate ($CaCO_3$) by marine organisms, primarily hermatypic corals, crustose coralline algae (CCA), and other calcifying algae (Vecsei, 2004; Perry et al., 2008; Perry et al., 2012). Scleractinian corals are primary reef builders in tropical environments, producing $CaCO_3$ through skeletal deposition. This net calcium carbonate production is a balance between gross production minus the loss due to physical, chemical, and biological erosion (Cornwall et al., 2021). The net calcium carbonate production and related potential vertical accretion of reefs is increasingly threatened by anthropogenic climate change (Perry et al., 2018). For scleractinian corals, one of the most significant consequences of OA is the decrease in the concentration of carbonate ions (CO_2^{-3}) (Kleypas and Yates, 2009). Projections suggest that future rates of coral reef community dissolution may exceed rates of $CaCO_3$ production (calcification), with the majority of coral reefs unable to maintain positive net carbonate production globally by 2100 (i.e., net loss) (Cornwall et al., 2021; Silverman et al., 2009; Hoegh-Guldberg et al., 2007).

These global climate change pressures are causing shifts in the composition of coral reef species, and the urgent focus now is on identifying, quantifying and maintaining reef ecosystem function so that coral reefs can continue to persist and deliver ecosystem services into the future (Harborne et al., 2017). To do this it is necessary to characterize reef health in terms of metabolism which includes calcification but also fundamental processes such as photosynthesis and respiration (Madin et al., 2016; Carlot et al., 2022). Photosynthesis fixes CO_2 in organic materials, whereas the reverse reaction (dark respiration) releases it. In scleractinian corals with zooxanthellae, the precipitation of $CaCO_3$ through calcification is tightly coupled to photosynthetic fixation of CO_2 and on average tends to be 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). Overall, the excess organic production in a coral reef community (i.e., the difference between gross primary production and dark respiration) acts as a CO_2 sink, while calcification acts as a source of CO_2 (Lewis, 1977; Kinsey, 1985). Most reef flats are sources of CO_2 to the atmosphere despite the drawdown of CO_2 during the day via photosynthetic processes. This is due to their low net fixation of CO_2 and rather large release of CO_2 by precipitation of calcium carbonate (Ware et al, 1992; Gattuso et al, 1993; Gattuso et al, 1995; Smith, 1995; Frankignoulle et al, 1996; Gattuso et al, 1996b).

One notable exception to this is in algal-dominated reef communities, which are sinks for atmospheric CO_2. They exhibit larger excess community production and/or a lower community calcification, (e.g., Kayanne et al, 1995; Gattuso et al, 1996a; Gattuso et al, 1997). The morphological diversity of reef algae provides food (Overholtzer and Motta, 1999), habitat and shelter (Price et al., 2011) for a number of invertebrate and fish species, with productivity sustaining higher trophic levels. Calcified macroalgae can also contribute significantly to the deposition of carbonates (Nelson, 2009). In particular, species of the genus *Halimeda* are widely distributed across tropical and subtropical environments, contribute significantly to reef calcification and productivity rates because of their fast growth and rapid turnover rates (Vroom et al., 2003, Smith et al., 2004, Nelson, 2009) compared to corals or coralline red algae (CRA). Calcification rates of *Halimeda* make it a major contributor to $CaCO_3$ in reefs in the Caribbean (Blair and Norris, 1988; Nelson, 2009), Tahiti and the Great Barrier Reef (Drew, 1983; Payri, 1988). In certain locations, precipitation of calcium carbonate can approach 2.9 kg $CaCO_3$ m^{-2} yr^{-1}, positioning *Halimeda* as a major contributor to carbonate budgets within shallow waters around the globe (Price et al., 2011). This group further occupies a diverse range of environments (mangroves, seagrass beds, and coral reefs) and can produce structurally complex mounds that serve as critical habitat for a diversity of important marine life (Rees et al., 2007).

Here, we compare metabolic and calcification rates of the dominant intertidal taxa of coral and macroalgae at Browse Island, a small island in the Kimberley bioregion located in the northern part of Western Australia. Unlike Southwestern Australia, which has one of the fastest increasing rates of change from cumulative human impacts (Halpern et al., 2019), the Kimberley 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). Few process studies have been carried out in the region due to the remoteness of these reef habitats, some of which are located 100s of km from the coastline, meaning that fieldwork and data acquisition can be difficult and costly. Rates of metabolism and calcification were determined in on-ship incubations in October 2016, April 2017 and October 2017. Using the proportional cover of the dominant benthic community, these rates were upscaled to gain whole of community metabolism estimates for the Browse Island habitats and provide new insights into reef ecosystem health and functioning in the absence of localised land- and sea-based anthropogenic variables (Harley et al., 2006; 157 Schindler, 2006; Walther, 2010).

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 driven by an Ozito PSDW-350 watt Dirty Water Submersible Water Pump with a maximum flow rate of 7,000 litres/hour, which ensured the setup remained at ambient temperature (Fig. 2). The intensity of photosynthetically active radiation (PAR) was recorded for each set of incubations with a HOBO Micro Station logger (H21-002, Onset) placed inside one of the tanks. Six 1.56 L clear Perspex incubation cores (24 total per incubation) fitted with stirring caps, were placed in each holding tank and spaced evenly apart to minimise shading (Fig. 2).

Depending upon abundance, individual specimens of algae and coral were placed in 6 to 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 to2 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. 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. 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%.

From SOP3b in Dickson et al. 2007, total alkalinity was determined for single replicates 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 to100.05 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 (mmol day^{-1} m^{-2}) 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 (mmol day^{-1} m^{-2}) 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

Nutrient concentrations were low and similar among sampling trips (Table 2), as is characteristic of tropical Eastern Indian Ocean offshore waters (McLaughlin et al., 2019). Concentrations of nitrate were 0.05 to 0.17 µmol L^{-1}, ammonium 0.12 to 0.13 µmol L^{-1}, phosphate 0.07to 0.1 µmol L^{-1}, and silicate 2.3 to 3 µmol L^{-1}. Oxygen was around 0.19 mmol L^{-1} to 0.22 mmol L^{-1} and salinity 34.2 to 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 to 1587 µE m^{-2} s^{-1} and slightly higher in October. Temperatures were 28.3 to 32.8°C and highest in April. Carbonate system parameters were not obtained for April 2016 due to instrument error, and some minor differences in pCO2, HCO_3^{-}, $CO3_2^{-}$, DIC and Ω Aragonite were noted between October 2016 and 2017 (Table 2). 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).

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 dark respiration was minimal. No corrections were therefore applied. In the light incubations O_2 productivity fluxes were positive for all taxa (Fig. 3, top panel). The highest light flux of O_2 of ~380 mmol m^{-2} day^{-1} was measured for *Galaxaura* in October 2017 (Fig. 3, top). Corals generally produced 100 to 260 mmol O_2 m^{-2} day^{-1} in the light, except *Heliopora*, which had a flux of 50 to 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 dark respiration, with mean fluxes of −15 to −190 mmol O_2 m^{-2} day^{-1} (Fig. 3, middle). All algae were net autotrophic and produced 6 to 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. 3, 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}.

In the light incubations, pH generally increased by 0.03 to 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. 4, top panel). In dark incubations, mean pH decreased for all taxa by 0.02 to 0.21 h^{-1} indicative of a net increase in CO_2 through dark respiration (Fig. 4, middle). Non-calcifying algae (*Sargassum*, *Caulerpa* and turf) raised net pH by 0.02 to 0.05 h^{-1} (assuming equal periods of light and darkness) (Fig. 4, 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. 5). 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. 6, top panel). In the dark, calcifying rates were smaller and just under half of the rates were negative suggesting dissolution of $CaCO_3$ (Fig. 6, middle panel). The resulting net calcification rates (based on equal periods of light and dark - monthly average sunrise and sunset at Browse Island of 0552 and 1739 for April, and 0519 and 1754 for October; WillyWeather, 2022) were all positive and ranged from 1.9 to 9.9 g $CaCO_3$ m^{-2} d^{-1} (Fig. 6, 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. 7).

3.4 Contributions to community production

In intertidal habitats (lagoon and high reef platform) around Browse Island, the estimated relative contributions of coral (8 % cover) and *Halimeda* (7 % cover) to the reef production of $CaCO_3$ were similar, around 600 to 840 g m^{-2} $year^{-1}$ (Fig. 8, top panel). The low reef platform had very low coral cover of < 3% (Fig. 8, middle), which therefore made a smaller contribution to calcification of ~240 g $CaCO_3$ m^{-2} $year^{-1}$ in this habitat (Fig. 8, top). In contrast, calcification on the subtidal reef slope was predominantly from corals (19 % cover), which produced ~1540 g $CaCO_3$ m^{-2} $year^{-1}$, around twice the amount compared to *Halimeda* (7 % cover). *Galaxaura*, which had high measured rates of productivity and calcification, was extremely rare (0.02 % total cover found only in October 2017; Olsen et al., 2017) and thus 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 to 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. 8, second panel from top).

4 Discussion

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). The organisms investigated in the present study 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 dark respiration, but the metabolic measurements showed clear differences among taxonomic groups. Algae had higher positive net O_2 fluxes with rates of 18 to 350 µmol 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. Although autotrophic, our data indicates that the majority of the corals we studied utilise heterotrophic supply through feeding to help sustain growth in addition to photosynthesis by zooxanthellae (Houlbreque and Ferrier-Pages, 2009). 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 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 dark 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. 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's observations where pH and O_2 relationship gradients 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.

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. Coral growth can be measured in several ways: linear extension rate, global skeletal growth and calcification rate (measured using the alkalinity technique or by ^{45}Ca incorporation) (Houlbreque and Ferrier-Pages, 2009). Methods to calculate calcification can vary in accuracy. 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; Houlbreque and Ferrier-Pages, 2009). The alkalinity 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, or use of radioisotopes was limited. Rates of net community calcification for reef flats worldwide range from 7.3 to 90 mol (730 to 9000 g) $CaCO_3$ m^{-2} $year^{-1}$ with an average of 47 mol (4700 g) $CaCO_3$ m^{-2} $year^{-1}$ (Atkinson, 2011). The patterns found in the present study — higher calcification rates in daylight compared to in darkness for all corals and calcifying algae — are typical. However, the coral $CaCO_3$ production rates per reef area (7 to 8% cover low reef platform, 19% reef slope) measured here (240 g m^{-2} $year^{-1}$ for low reef platform, 610 to 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. In 2016, the dark rates of calcification in corals were less than 50% of the rates in light with some (*Porites* and *Heliopora)* negative. Dark rates of calcification in 2017 were negative or near zero for all species except *Porites*, *Pocillopora* and *Seriatopora*. Houlbreque et al. (2004) showed that coral feeding enhances dark calcification rates in scleractinian corals, but incubations in our study were done in absence of supplemental feeding. The trend observed here may be due to some dissolution of $CaCO_3$ due to the reduced pH during dark incubations or could be an artefact of the experimental conditions. This result should therefore be taken with some caution, in particular for *Porites* in October 2016, which saw the largest decrease (Fig. 5, middle panel). However, 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 to 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 to 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 to 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 to 8.7% cover on Browse, which corresponds to ~150 to 250 g dw m^{-2}).

Nutrient capacity is one important driver of productivity in many reef ecosystems. The rate at which nutrients are recycled between the constituents of the system (the ambient nutrient availability, and the nutrients stored within plant and animal biomass) depends on input from a variety of sources (e.g., associated with seasonal rains or upwelling) (DeAngelis, 1992; Hatcher, 1990). Coral reefs, typically have low ambient nutrient availability and receive little sustained exogenous nutrient input (Hatcher, 1990; Szmant, 2002), thus the high rates of production found within these ecosystems are largely attributed to the nutrients stored and cycled by living biomass (Pomeroy, 1974; DeAngelis et al., 1989; Sorokin, 1995). Fishes typically make up a substantial component of living biomass on coral reefs and represent an important reservoir of nutrients in these ecosystems (Allgeier et al., 2014). Contrary to our expectations given its remote location in an area of apparently low anthropogenic impacts, the reef platform around Browse Island was depauperate with a conspicuous lack of diversity in key groups including macroalgae, macroinvertebrates and teleost browsers (Bessey et al., 2020). McLaughlin et al. (2019) found surface water standing stock nutrient concentrations low along Kimberley shelf. Conditions at Browse Island were similar with low water column nutrients for nitrate, ammonia and phosphate during all trips. Understanding how changes in animal populations alter nutrient dynamics on large ecological scales is a relatively recent endeavour (Doughty et al., 2015). Allgeier et al. (2016) showed that targeted fishing of higher trophic levels reduces the capacity of coral reef fish communities to store and recycle nutrients by nearly half. Fish-mediated nutrients enhance coral growth (Meyer et al., 1983) and primary production (Allgeier et al., 2013), and may regulate nutrient ratios at the ecosystem scale (Allgeier et al., 2014).

The Kimberley region-wide averages of coral cover and macroalgal cover are 23.8% and 7.1% (Richards et al., 2015) respectively. However, this relationship at Browse Island is reversed, with macroalgae more dominant at 28% total cover to that of coral at 9% total cover. On the Browse Island reef platform, the same pattern is observed where averages were 5 to 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., 2015). 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 to 3.0% of the benthic cover in the lagoon and reef platform habitats at Browse Island, become more prominent at 11.8 to 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 to 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 to 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 to 134 g $CaCO_3$ m^{-2} $year^{-1}$. However, they could produce a significant amount of 980 to 1360 g $CaCO_3$ m^{-2} $year^{-1}$ on the reef crest and slope, which is 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 to 3770 g $CaCO_3$ m^{-2} $year^{-1}$ at Uva reef in the eastern Pacific (Eakin, 1996).

Metabolic rates of primary producers are clearly influenced by a multitude of factors including hydrodynamics, irradiance, and nutrient availability (Smith et al., 2013). We were able to detect considerable diurnal changes in water chemistry due to metabolic rates, since our experiments were conducted in small enclosed mesocosms. The effect of metabolism on water chemistry is expected to dissipate downstream in a more turbulent or dynamic environment (Anthony et al. 2011). However, coral and algae metabolic rates and resultant flux from diffusive boundary layer also increases with flow rates (Carpenter et al. 1991; Lesser et al. 1994; Bruno and Edmunds 1998; Mass et al. 2010). Because our experiments were conducted in near no-flow chambers (mesocosm water was replenished with fresh seawater in small amounts during sample extraction), our measurements are conservative values and likely represent the lower range of potential effects that these reef organisms have on surrounding water chemistry, however where residence times can be extended, particularly when trapping of water on the reef at low tides occurs, our results are likely reflective of how these benthic organisms affect water chemistry in the lagoonal habitats of Browse Island.

5 Conclusions

This study investigated the metabolism of coral and algae on the reef of remote Browse Island, found on the mid-shelf region of the Kimberley in Western Australia. Due to its remoteness, Browse Island presented a unique opportunity to observe these organisms in a pristine habitat where direct anthropogenic pressures are minimal. Browse Island is the only emergent mid-shelf reef in the Kimberley bioregion having semidiurnal tides reaching a maximum range of 5 m (Olsen et al., 2017), half the magnitude of tides experienced by reefs closer to the coast (McLaughlin et al., 2019). Its benthic structure is very different from both Kimberley inner (e.g. Montgomery Reef, Adele and Cassini Islands) and outer (e.g. Ashmore Reef and Rowley Shoals) shelf reefs. The relative contributions of algae and corals to reef productivity are likely to differ across the Kimberley 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 (differences in height from place to place on the reef surface) 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).

There is lack of sufficient observations of pCO2, nutrients and research on the upper ocean carbon cycle from the Indian Ocean (Sreeush et al., 2020), and which are critical to modelling of ocean acidification in the region (Panchang and Ambokar, 2021). The uptake of carbon dioxide by the ocean alters the composition of seawater chemistry with elevated partial pressures of carbon dioxide (pCO2) causing seawater pH and the $CaCO_3$ saturation state to decrease (Feely et al, 2004). Ocean acidification directly threatens crucial trophic levels of the marine ecosystem. Baseline reef measurements in undisturbed areas like Browse Island are important to understand exclusively climate-driven stressors in lieu of local anthropogenic pressures normally associated with coastal tropical reefs. 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

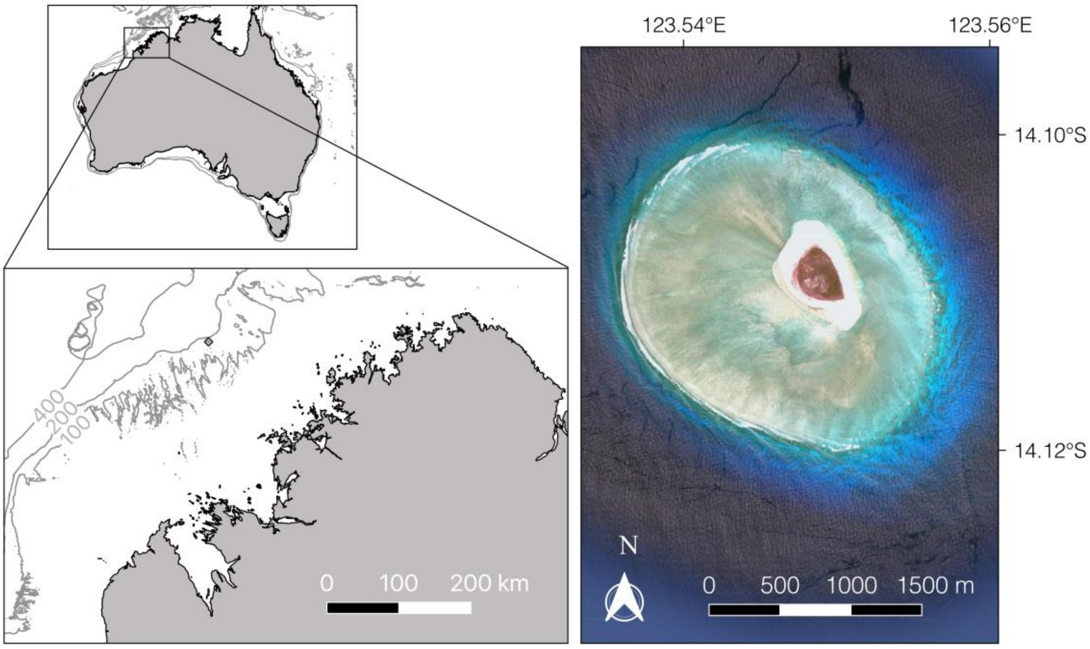

Figure 1. The study site, Browse Island (diamond, bottom left map), is located just inside the 200-m isobath on the continental shelf. The small map (top left) shows the location of the island relative to the Australian coastline with the 100, 200 and 400 m isobaths marked in gray. The satellite image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

Figure 2. Experimental setup of respirometry incubations for Browse Island coral and macroalgae.

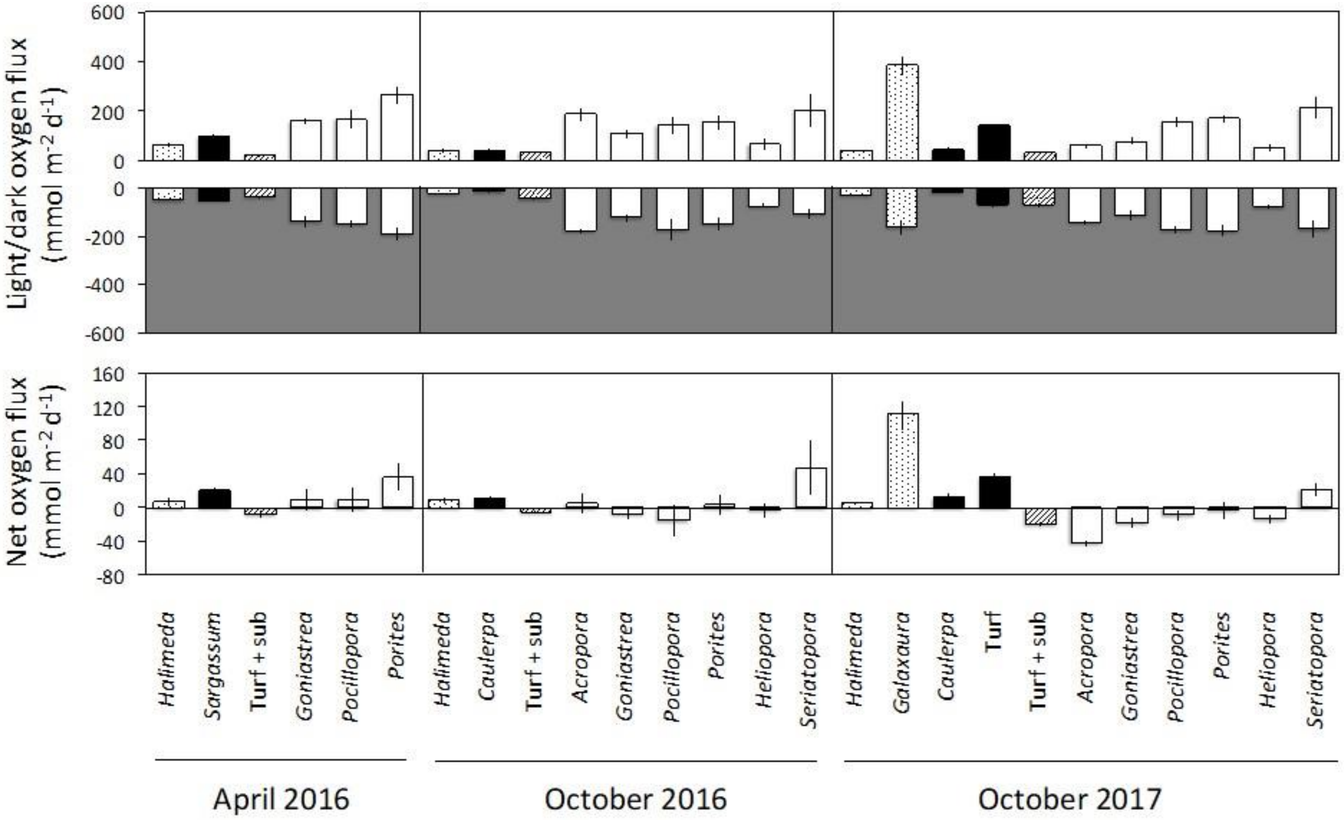

Figure 3. Net changes in oxygen (means ± se) in light (top) and dark (middle) incubations of calcifying algae (stippled), macroalgae and turf (black), turf + substrate (diagonal stripes) and coral (white) standardised by specimen surface area. The bottom panel shows the net daily production of oxygen (means ± se) assuming a 12-h photoperiod and stable rates of photosynthesis and dark respiration over a 24-h period.

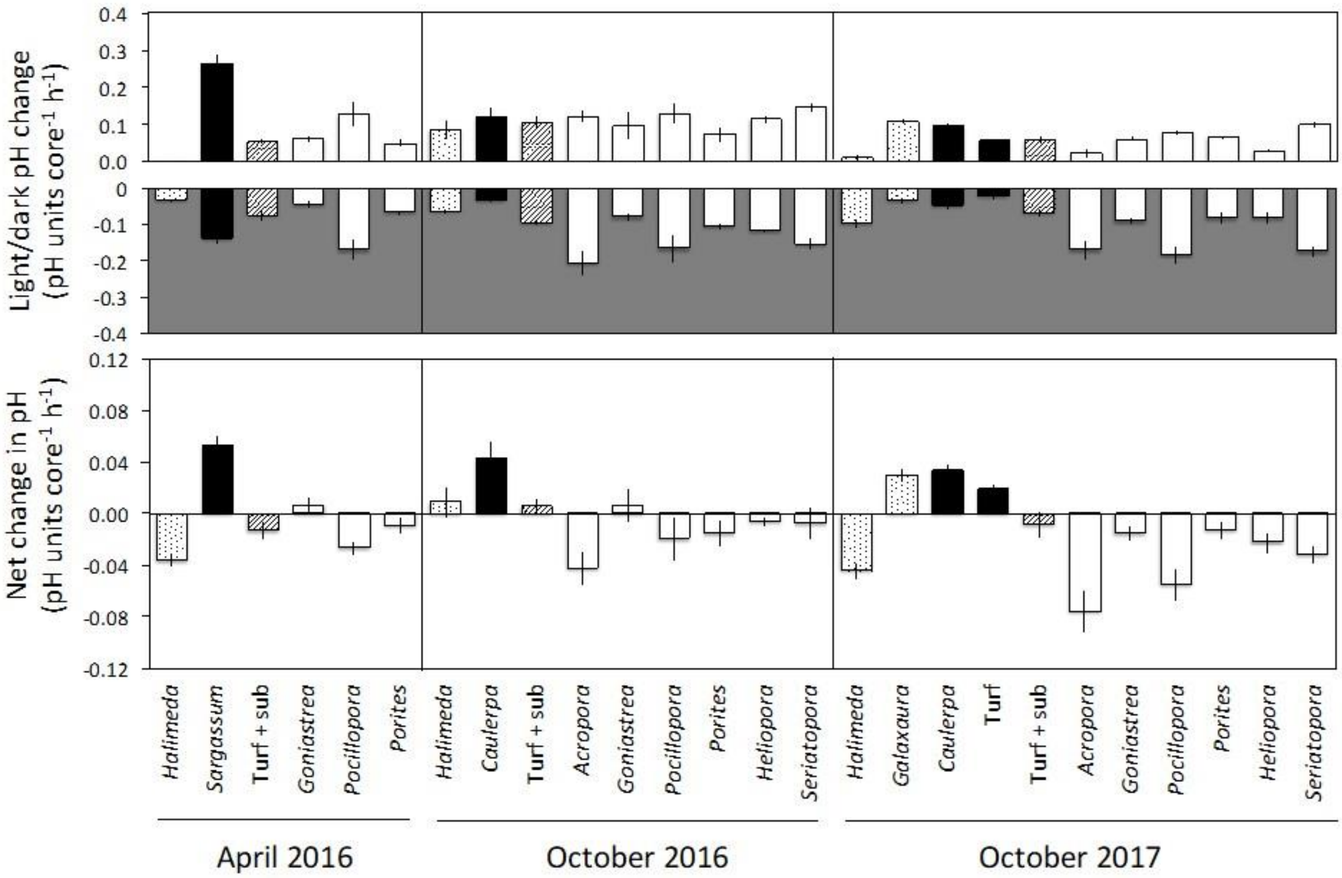

Figure 4. Net changes in pH per hour for each 1.56-L incubation core (means ± se) in light (top) and dark (middle) incubations calcifying algae (stippled), macroalgae and turf (black), turf + substrate (diagonal stripes) and coral (white). The bottom panel shows the net change in pH per hour (means ± se) assuming equal periods of light and darkness.

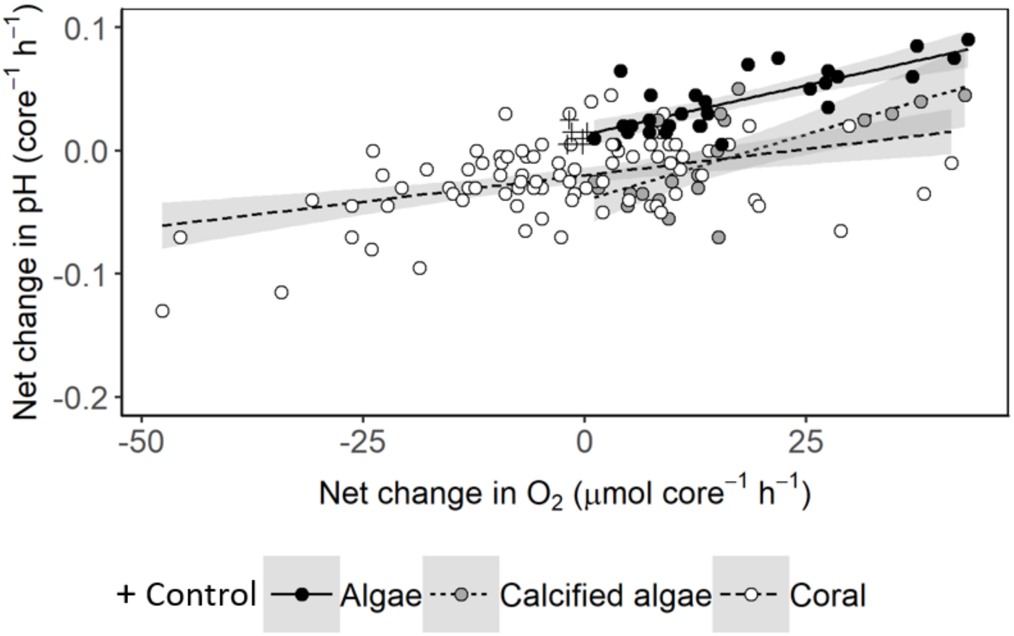

Figure 5. Net change in pH versus O$_2$ per 1.56-L incubation core assuming equal periods of light and darkness. Linear relationships are fitted with 95% confidence intervals shown in gray. For algae; net change in pH = 0.13 + 0.0016 × net change in O$_2$ (ANOVA: $F_{1,27} = 41.15$, p <0.001). For calcified 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).

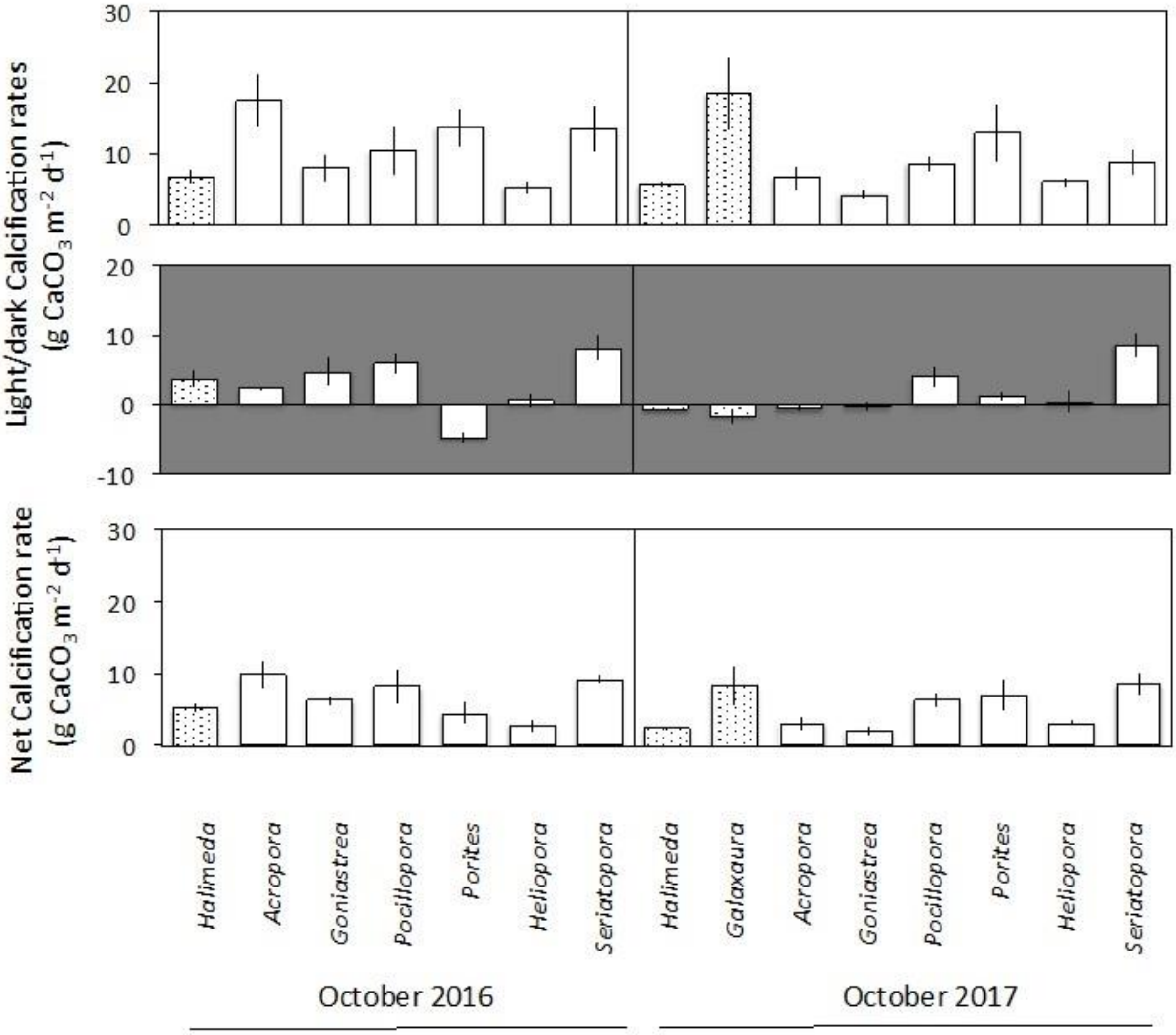

Figure 6. Calcification rates for corals (white) and calcifying algae (stippled) (means ± se) in light (top) and dark (middle). The bottom panel shows the daily net calcification rate (means ± se) assuming a 12-h photoperiod.

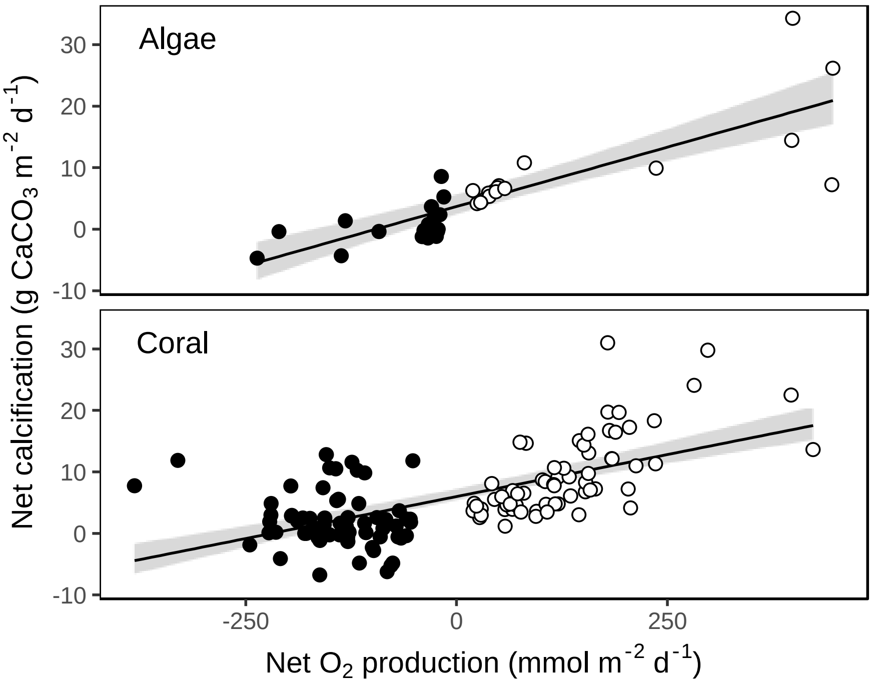

Figure 7. Relationship between net calcification rate and net productivity for calcifying algae (top) and corals (bottom). Open circles indicate rates measured in light and closed circles rates measured in dark. Linear fits are shown with 95% confidence intervals in gray. For calcified algae; net calcification = 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: $F_{1,126} = 82.2$, $p < 0.001$).

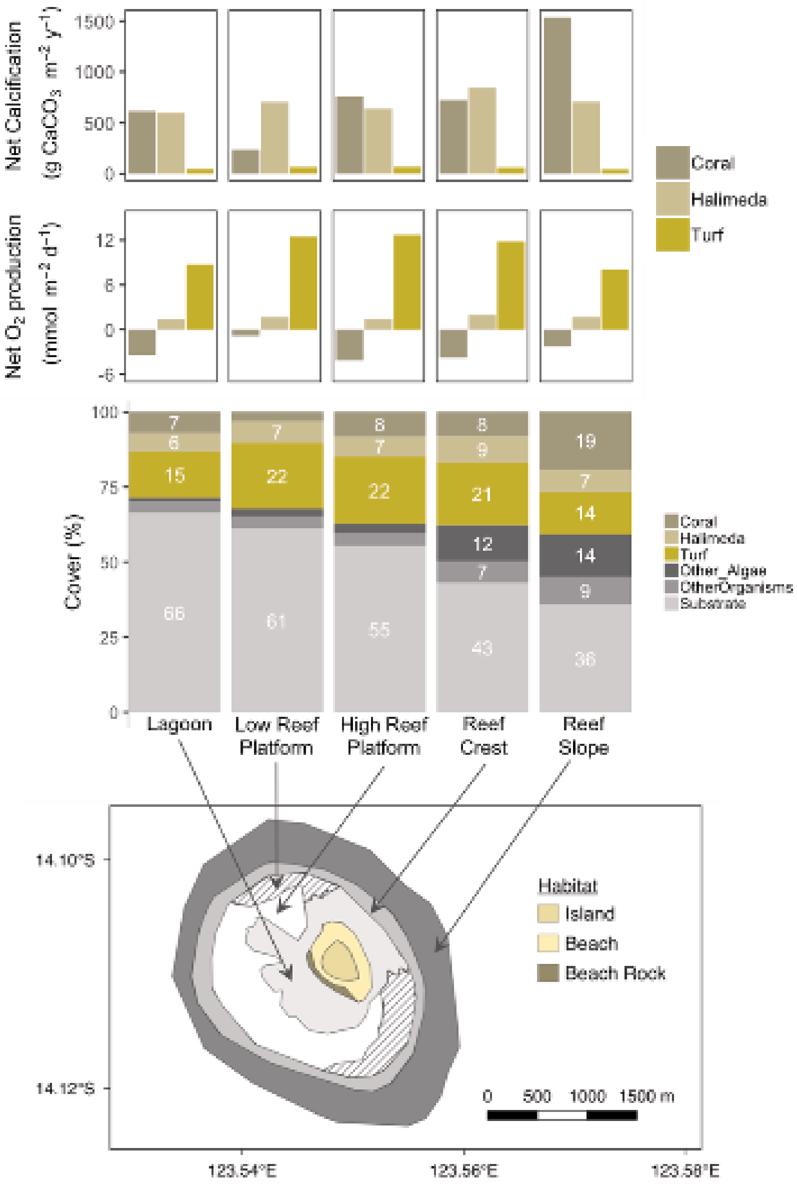

Figure 8. Map of the reef around Browse Island showing the major habitat types (bottom panel). Reef surface percent cover of coral, *Halimeda*, turf and other categories in each habitat (middle panel) based on drop-camera image analysis data from (Olsen *et al.* 2017). Net calcification and net oxygen 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 ($p$$CO_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 (µmol L^{-1})	19.3 ± 0.19	20.8 ± 0.16	23.4 ± 0.29
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			
$p$$CO_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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