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.

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1. Introduction

Coral reefs in the Anthropocene era have been degraded for more than a century by overfishing and pollution, but now even remote reefs (where local pressures are low) face increasing stresses through anthropogenic climate change (Hughes et al., 2017b). With the currently unprecedented rate of environmental change, coral reefs face growing pressures in response to eutrophication (Hewitt et al., 2016), recurrent large scale weather events (marine heat waves, etc.), sedimentation (Hughes et al, 2017a), 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 et al., 2007; Doney et al., 2009; Perry et al., 2018). The pressures of global climate change 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).

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). Reefs support a diverse range of species that provide critically important resources, such as food, for coastal livelihoods (Hoegh-Guldberg et al., 2007). 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).

Community metabolism on a reef is a combination of the photosynthesis and dark respiration of the organisms that live there. Coral reefs are known for their high calcification and photosynthetic production, and measurements of reef metabolism make it possible to characterize reef health in terms of these fundamental processes. These functions are dependent on the maintenance of the framework structure of the reefs. Photosynthesis fixes CO_2 in organic materials, whereas the reverse reaction, dark respiration, releases it. 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). Despite the drawdown of CO_2 during the day via photosynthetic processes, most reef flats are sources of CO_2 to the atmosphere 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). Photosynthesis and calcification both consume inorganic carbon, but a proportion of CO_2 generated by calcification can be used for photosynthetic carbon fixation, so the combined processes can be viewed as reciprocally supportive (Gattuso et al., 1999).

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 (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.,

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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). Coral skeletons are made from the mineral phase of calcium carbonate (aragonite), and 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) with the majority of coral reefs unable to maintain positive net carbonate production globally by 2100 (Cornwall et al., 2021).

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). 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). In reefs under thermal stress, rates of primary production and dark respiration increase, but community excess organic production decreases dramatically (Kayanne et al., 2005).

Reef algae are also an often-overlooked important structural component of coral reef ecosystems. Their morphological diversity provides food (Overholtzer and Motta, 1999),

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habitat and shelter (Price et al., 2011) 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 turfing and encrusting coralline algae contribute substantially to reef benthic primary resources in these areas (Odum and Odum, 1955; Hatcher, 1997). The abundance of large frondose macroalgae is typically inversely related to coral abundance (Done, 1992; Hughes et al., 2017b); macroalgae are common on reef flat, back reef, and inshore fringing reef areas, whereas corals are more common on reef slopes (Purcell and Bellwood, 2001). Calcified macroalgae can also contribute significantly to the deposition of carbonates (Nelson, 2009). In particular, species of the genus *Halimeda* (order Bryopsidales), 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 algal (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 marine life (Rees et al., 2007).

The corals and algae dominating the benthos of these complex ecosystems have the potential to change the local chemistry of the water column (Duarte et al., 2013), superseding larger scale oceanographic and atmospheric influences (Kleypas et al., 2011). Metabolic processes can deplete or replenish oxygen, carbon, and nutrient concentrations either within

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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 reef contributions to changes in water column chemistry is difficult to predict because of the net effect of local oceanographic conditions, relative abundance of the different members of the reef community and their individual metabolic rates. 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 ion; e.g. Raven et al., 1995) during photosynthesis and release of CO_2 during dark 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). The effect on water column chemistry by hybrid organisms like calcifying primary producers, such as corals with zooxanthellae and calcifying algae, therefore becomes very challenging to measure in situ.

Coastal environments are frequently high-use areas by humans, impacted by multiple land- and sea-based human activities, and in such cases the potential for interaction between climate and other anthropogenic variables affecting biological responses exists (Harley et al., 2006; Schindler, 2006; Walther, 2010). Contrary to Southwestern Australia which has one of the fastest increasing rates of change from cumulative human impacts (Halpern et al., 2019), the Kimberley bioregion located in the northern part of Western Australia is unique, representing 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). It is host to extensive coastal reef systems, isolated offshore reefs and islands. Few process studies have been carried out in the

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213 region due to the remoteness of these reefs, some of which are located 100s of km from the

214 coastline, meaning that fieldwork and data acquisition can be difficult and costly. So that reefs

215 can continue to deliver ecosystem services into the future metabolic measurements of reef

216 organisms are necessary to characterize reef health in terms of fundamental processes such as

217 photosynthesis, respiration and calcification (Madin et al., 2016; Carlot et al., 2022). However,

218 there are limited numbers of studies examining the individual effects of key primary producers

219 on water chemistry in the same study, and thus, we lack knowledge of the relative contributions

220 of the main reef builders to net community metabolism and $CaCO_3$ production on most coral

221 reefs. Here, we compare metabolic and calcification rates of the dominant intertidal taxa of

222 macroalgae and coral at Browse Island, a small island in the Kimberley, something never

223 previously examined in these systems. Rates of metabolism and calcification were determined

224 in on-ship incubations in October 2016, April 2017 and October 2017. Using the proportional

225 cover of the dominant benthic community, these rates were upscaled to gain whole of

226 community metabolism estimates for the island habitats.

227

228 **2. Methods**

229 *2.1 Study site*

230 Browse Island is located on the mid-shelf just inside the 200 m isobath off the Kimberley coast

231 in northern Western Australia (14°6'S, 123°32'E; Fig. 1). The island is surrounded by a small

232 (~ 4.5 km^2) planar platform reef consisting of a shallow lagoon, an extensive reef flat that is

233 conspicuously absent to the northeast of the island, and a well-defined reef crest and slope.

234 Tides are semidiurnal with a maximum range of < 5 m, exposing the reef crest and reef platform

235 habitats during low tides. The intertidal habitats are characterised by low species richness and

236 dominated by small turfing algae and calcified macroalgae of the genus *Halimeda* (15–22%

237 and 6–9% cover respectively)) (Olsen et al., 2017). Coral assemblages are well developed with

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399 cover of 5–8% in the intertidal habitats and 18% on the shallow reef slope (< 10 m) (Olsen et

400 al., 2017).

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402 *2.2 Algae and coral collection*

403 Specimens of the dominant coral and algal taxa were collected from the reef platform by hand

404 during low tide, immediately brought back to the vessel and kept in a holding tank with

405 circulating seawater. Macroalgae included the calcifying green alga *Halimeda opuntia*, which

406 was the dominant species of *Halimeda* on the reef platform, the green alga *Caulerpa* sp., and

407 the calcifying red alga *Galaxaura* sp. Pieces of turf algae (turf) as well as turf attached to a

408 piece of rock (turf + substrate) were measured. In April 2016, drift algae of the genus

409 *Sargassum* found floating on the water surface were also included although this taxa was not

410 been found growing anywhere on the reef. Hermatypic corals included *Pocillopora* sp.,

411 *Goniastrea* sp., *Porites* sp., *Heliopora* sp., *Acropora* sp. and *Seriatopora* sp. Whole pieces of

412 coral small enough to fit inside the incubation cores (inner diameter ~90 mm) were collected

413 to minimise tissue damage. All coral samples were > 50 mm diameter and therefore

414 operationally defined as adults and estimated to be at least 2 to 7 years old depending on the

415 taxa (Trapon et al., 2013).

416

417 *2.3 Light and dark incubations*

418 Light and dark incubations were undertaken on the back deck of the research vessel. Four 60

419 L holding tanks were placed in a shade-free spot under natural light conditions, filled with

420 seawater and connected to a flow-through seawater system driven by an Ozito PSDW-350 watt

421 Dirty Water Submersible Water Pump with a maximum flow rate of 7,000 litres/hour, which

422 ensured the setup remained at ambient temperature (Fig. 2). The intensity of photosynthetically

423 active radiation (PAR) was recorded for each set of incubations with a HOBO Micro Station

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425 logger (H21-002, Onset) placed inside one of the tanks. Six 1.56 L clear Perspex incubation

426 cores (24 total per incubation) fitted with stirring caps, were placed in each holding tank and

427 spaced evenly apart to minimise shading (Fig. 2).

428

429 Depending upon abundance, individual specimens of algae and coral were placed in 6 to 12

430 replicate incubation cores per taxa except where not enough individuals could be found. Table

431 1 shows the taxa incubated during each sampling trip and the number of replicates. Water

432 samples from the holding tanks were measured at each time point as controls and, in addition,

433 in October 2017, a separate seawater control (six replicate incubation cores with seawater) was

434 included. After a period of acclimation (1 to 2 h), incubations were run over a four-hour period.

435 The light incubations were conducted while the sun was at its zenith providing full irradiance

436 to the samples. After two hours, the tubs were covered with a black lid ensuring no light could

437 enter and the samples incubated for two hours in the dark.

438

439 To estimate oxygen production or consumption during the incubations, a 40 mL water sample

440 was extracted from each of the 24 cores and the four tubs at the start of the incubations and

441 hourly thereafter. A port in the cap of each core allowed for sample collection using a syringe.

442 As the sample was removed, the same volume of liquid was automatically replaced from the

443 flowthrough tank into the core so that the core volume remained constant through the

444 experiment. Samples were immediately analysed for temperature and dissolved oxygen (O_2)

445 with a YSI 5100 bench-top oxygen and temperature meter with YSI 5010 BOD stirring probe,

446 calibrated daily in air. Sample pH was determined using a TPS Aqua pH meter with an Ionode

447 probe, calibrated daily with pH 7.00 and 10.00 buffers. A second 35 mL water sample was

448 collected from each core and tub and split between one 10 mL glass vacutainer for alkalinity

449 and duplicate 10 mL sterile vials for nutrient analyses. Nutrient samples were immediately

460 frozen and alkalinity samples were stored cool and dark. At the end of the incubation, algal and

461 coral specimens were frozen. All samples were transported to Perth, Western Australia, to be

462 analysed.

463

464 *2.4 Surface areas of coral and algal specimens*

465 Metabolic measurements were standardised by surface area of the incubated specimens since

466 this represents the area available for photosynthesis and nutrient uptake. The surface area of

467 specimens of coral, *Halimeda* and turf + substrate were estimated using a single wax dipping

468 method (Veal et al., 2010). Specimens were dried, weighed and then dipped in paraffin wax at

469 65°C. The waxed samples were weighed again, and the weight of the wax calculated. The

470 surface area was estimated from the wax weights against a calibration curve constructed by

471 wax dipping geometric wooden objects of known size. The surface areas of the remaining taxa,

472 were estimated from photographs in ImageJ (Rueden et al., 2017). The 'footprint' of each

473 sample, i.e. the surface area of reef occupied by the organism, was also estimated by tracing

474 the outline of the specimen photographed from straight above in ImageJ.

475

476 *2.5 Chemical analyses*

477 Concentrations of nitrate + nitrite (hereafter referred to as nitrate), ammonium, phosphate and

478 dissolved silica in water samples were analysed in duplicate by flow injection analysis (Lachat

479 QuickChem 8000) with detection by absorbance at specific wavelengths for silica [QuikChem

480 Method 31-114-27-1-D], nitrate [Quikchem Method 31-107-04-1-A] and phosphate

481 [QuikChem Method 31-115-01-1-G]), and by fluorescence for ammonia according to Watson

482 et al. 2005. Detection limits were 0.02 μmol L^{-1} for all inorganic nutrient species, with a

483 standard error of $< 0.7\%$.

484

485 From SOP3b in Dickson et al. 2007, total alkalinity was determined for single replicates to the

486 nearest 5 μmol L^{-1} equivalent (hereafter referred to as μmol L^{-1}) using an open cell Metrohm

487 titrator (841 Titrando, Burette: 800 Dosino 10 mL) with a Metrohm micro-glass pH probe

488 calibrated with Certipur buffer solutions at pH 2.00, 4.01, 7.00, and 10.00 (at 25.0°C). Samples

489 were kept in a Jubalo F12 temperature control water bath prior to decanting a 10 mL aliquot of

490 sample into a vessel with a water jacket maintaining temperature at 25.0°C. Samples were

491 titrated with 0.012 N HCl, standardised against sodium carbonate (99.95 to 100.05 wt%) with

492 an initial volume of titrant added to reach pH 3.5. Titrations were run to an end-point of pH 3

493 with Gran plot (Excel macro) to determine the total alkalinity endpoint near pH 4.2. Carbonate

494 system parameters were calculated from pH (measured during the incubations) and total

495 alkalinity using the package 'seacarb' (Gattuso et al., 2018) in R (R Core Team, 2018).

496 Alkalinity and carbonate parameters were not determined in April 2016.

497

498 *2.6 Oxygen fluxes and calcification rate calculations*

499 The changes in O_2 concentrations during light- and dark incubations were expressed as mmol

500 per day assuming stable hourly production rates over 24 h. Any replicates where O_2 did not

501 increase during both of the light intervals or did not decrease during both of the dark intervals

502 were excluded from further analysis. Net fluxes of O_2 per day (mmol day^{-1} m^{-2}) were calculated

503 for each sample assuming a 12 h photoperiod. Calcification rates of corals and calcifying algae

504 (*Halimeda opuntia*. and *Galaxaura* sp.) were estimated using the alkalinity anomaly method

505 (Smith and Key, 1975) uncorrected for changes in nutrient concentration (Chisholm and

506 Gattuso, 1991) where precipitation of one mole of $CaCO_3$ leads to the reduction of total

507 alkalinity by two molar equivalents. Rates per surface area (mmol day^{-1} m^{-2}) were obtained by

508 dividing these values by the surface area of each specimen.

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

522

523 *2.7 Statistical analyses*

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

529

530 **3   Results**

531 *3.1 Experimental conditions*

532 Nutrient concentrations were low and similar among sampling trips (Table 2), as is
533 characteristic of tropical Eastern Indian Ocean offshore waters (McLaughlin et al., 2019).
534 Concentrations of nitrate were 0.05 to 0.17 µmol L^{-1}, ammonium 0.12 to 0.13 µmol L^{-1},
535 phosphate 0.07 to 0.1 µmol L^{-1}, and silicate 2.3 to 3 µmol L^{-1}. Oxygen was around 0.19 mmol
536 L^{-1} to 0.22 mmol L^{-1} and salinity 34.2 to 34.8 ppt. Light and temperature conditions in the
537 incubations were representative of *in situ* conditions on the reef platform and were similar
538 among trips. PAR levels were 1500 to 1587 µE m^{-2} s^{-1} and slightly higher in October.
539 Temperatures were 28.3 to 32.8°C and highest in April. Carbonate system parameters were

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not obtained for April 2016 due to instrument error, and some minor differences in pCO2, HCO3$^-$, 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

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595 algae (*Sargassum*, *Caulerpa* and turf) raised net pH by 0.02 to 0.05 h^{-1} (assuming equal

596 periods of light and darkness) (Fig. 4, bottom panel). The net change in pH was generally

597 negative for corals and calcifying algae (-0.01 to -0.08 h^{-1}), except for the coral *Goniastrea*

598 in April and October 2016 (0.01 h^{-1}) and the calcifying alga *Galaxaura* (0.03 h^{-1}; Fig. 3,

599 bottom).

600

601 Net changes in pH are largely driven by metabolic uptake and release of CO_2. We found

602 positive relationships between changes in pH and net production or consumption of O_2 except

603 in seawater controls where changes in O_2 and pH were minor (Fig. 5). The relationships for

604 algae, calcifying algae and coral were all significant, but had relatively low adjusted r^2 values

605 of 0.59, 0.46 and 0.19 respectively, suggesting significant variability among species and

606 individuals within each of these groups.

607

608 *3.3 Calcification Rates*

609 Corals, *Halimeda* and *Galaxaura* had positive calcification rates in light ranging from 4.2 to

610 18.4 g $CaCO_3$ m^{-2} d^{-1} (Fig. 6, top panel). In the dark, calcifying rates were smaller and just

611 under half of the rates were negative suggesting dissolution of $CaCO_3$ (Fig. 6, middle panel).

612 The resulting net calcification rates (based on equal periods of light and dark - monthly

613 average sunrise and sunset at Browse Island of 0552 and 1739 for April, and 0519 and 1754

614 for October; WillyWeather, 2022) were all positive and ranged from 1.9 to 9.9 g $CaCO_3$ m^{-2}

615 d^{-1} (Fig. 6, bottom). Rates of calcification were strongly linearly correlated to net O_2

616 production and were significantly higher in light than in darkness for both corals and algae

617 (Fig. 7).

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619 *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

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. The Island has 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), and its benthic structure is very different from both Kimberley inner and outer shelf reefs. Lowe et al. (2015) have revealed that strongly tide-dominated circulation can occur on Kimberley reef platforms and the trapping of water on a reef, such as that found at Browse Island, can provide benefits for reef organisms in terms of avoiding aerial exposure. However, it can dramatically increase the residence (or flushing)

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661 times of reefs, which can lead to extreme diel variations in water quality (Lowe et al., 2015).

662 Seawater O_2 and carbonate chemistry can vary over diel tidal cycles, like those found at Browse

663 Island, and are related to patterns in autotrophic photosynthesis and dark respiration (e.g.,

664 Duarte et al., 2013). Primary production and the uptake of CO_2 by coral and algae during

665 daylight hours results in elevated pH and an elevated aragonite saturation state (Ω_{arag}) during

666 the day when calcification rates peak. The process of calcification decreases pH in the

667 surrounding water, but for calcifying autotrophs CO_2 uptake and fixation through

668 photosynthesis can potentially offset changes to the carbonate chemistry caused by

669 calcification (Anthony et al., 2011; Smith et al., 2013).

670

671 Mesocosm experiments have shown that reef-building (hermatypic) corals tend to reduce pH

672 and consume O_2 (e.g. (Gattuso *et al.* 2015; Smith *et al.* 2013)), whereas calcifying macroalgae

673 increase pH and O_2 during daytime (Borowitzka and Larkum 1987; Smith *et al.* 2013). Both

674 corals and calcifying macroalgae reduce pH and O_2 concentrations due to respiration during

675 nighttime, but the rates of change differ among species (Smith *et al.* 2013). The organisms

676 investigated in the present study showed typical patterns of O_2 production in daylight and

677 consumption in darkness to other similar island reef systems as a result of photosynthesis and

678 dark respiration, but the metabolic measurements showed clear differences among taxonomic

679 groups. Algae had higher positive net O_2 fluxes with rates of 18 to 350 µmol O_2 m^{-2} day^{-1}, of

680 which the red calcifying alga *Galaxaura* sp. had the highest rate of net productivity by far. For

681 corals, the relatively high O_2 increase measured in daylight was coupled with high rates of

682 respiration in darkness, creating a negligible or negative net O_2 production for most species,

683 except *Porites* sp. in April 2016 and *Seriatopora* sp. in October 2016 and 2017 which were net

684 positive. Although autotrophic, our data indicates that the majority of the corals we studied

685 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 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; (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 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

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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

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 (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.

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1003   The higher cover of *Halimeda* and the low coral cover at Browse Island compared to other

1004   reefs in the region mean that corals and *Halimeda* contribute equally to productivity rates of

1005   CaCO$_3$ on the Browse Island reef flat, however, their relative contributions to the reef

1006   framework and sedimentary budget of the reef is unknown. To gain an understanding of the

1007   relationships between carbonate production and sinks on the reef, further study into the types

1008   and amounts of CaCO$_3$ material found in each reef sink is necessary. The Kimberley coastal

1009   shelf, which is characterised by coral reef environments with clear, low nutrient waters and

1010   low productivity, has largely escaped land-based anthropogenic impacts, but has been

1011   negatively affected by climate-driven coral bleaching and mortality, for example from heat

1012   waves at Scott Reef in 1998 and 2016 (Smith et al., 2008, Gilmour et al., 2013 and Hughes et

1013   al., 2017) and Ashmore Reef in 2003 and 2010 (Ceccarelli et al., 2011 and Heyward, 2011).

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1015   There is lack of sufficient observations of pCO2, nutrients and research on the upper ocean

1016   carbon cycle from the Indian Ocean (Sreeush et al., 2020), and which are critical to modelling

1017   of ocean acidification in the region (Panchang and Ambokar, 2021). The uptake of carbon

1018   dioxide by the ocean alters the composition of seawater chemistry with elevated partial

1019   pressures of carbon dioxide (pCO2) causing seawater pH and the CaCO$_3$ saturation state to

1020   decrease (Feely et al, 2004). Ocean acidification directly threatens crucial trophic levels of

1021   the marine ecosystem. Baseline reef measurements in undisturbed areas like Browse Island

1022   are important to understand exclusively climate-driven stressors in lieu of local

1023   anthropogenic pressures normally associated with coastal tropical reefs. The effects of

1024   temperature stressors on reef communities and their productivity remain to be investigated in

1025   this region. The effects of temperature stressors on reef communities and their productivity

1026   remain to be investigated in this region. Different components of the reef around Browse

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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.

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1054 **Figures**
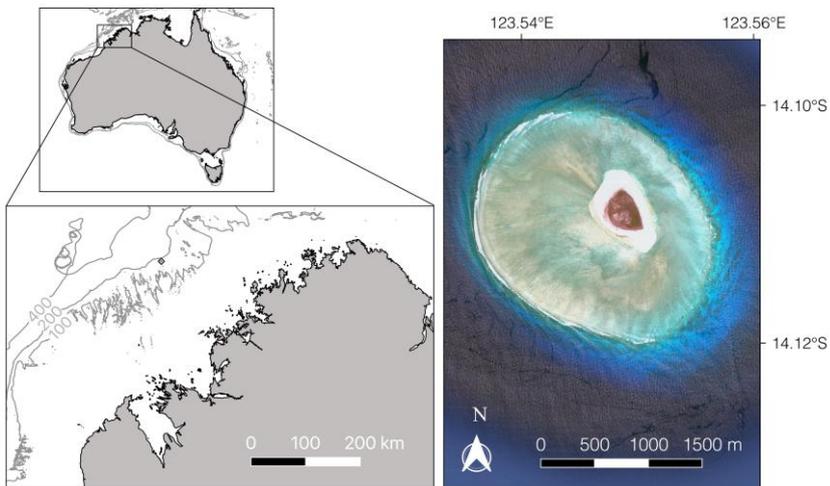
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1056 **Figure 1.** The study site, Browse Island (diamond, bottom left map), is located just inside the

1057 200-m isobath on the continental shelf. The small map (top left) shows the location of the island

1058 relative to the Australian coastline with the 100, 200 and 400 m isobaths marked in gray. The

1059 satellite image (right; © Google Earth 2018) shows the extent of the reef.

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

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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.

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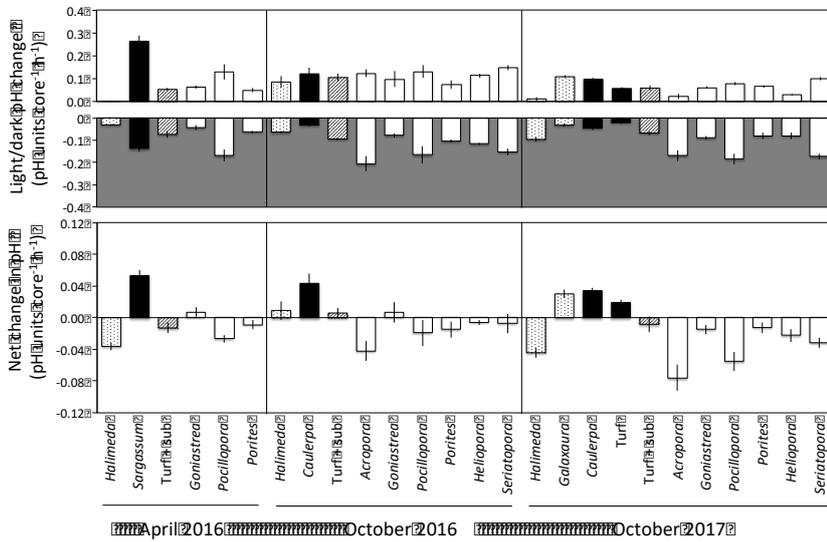
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Figure 4. Net changes in pH per hour for each 1.56-L incubation core (means ± se) in light
(top) and dark (middle) incubations calcifying algae (stippled), macroalgae and turf (black),
turf + substrate (diagonal stripes) and coral (white). The bottom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

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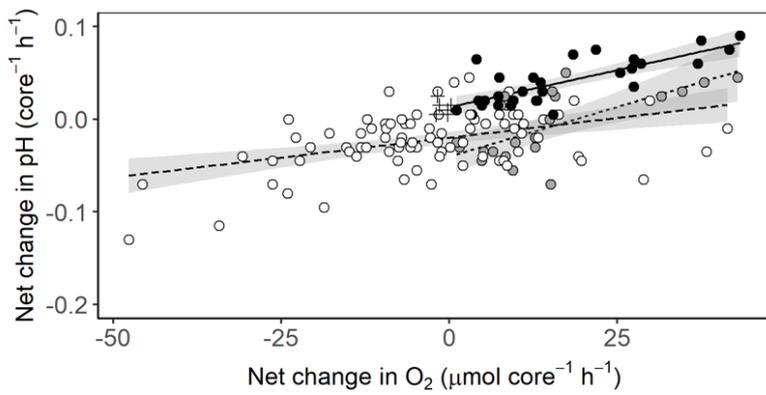
Figure 5. Net change in pH versus O_2 per 1.56-L incubation core assuming equal periods of

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).

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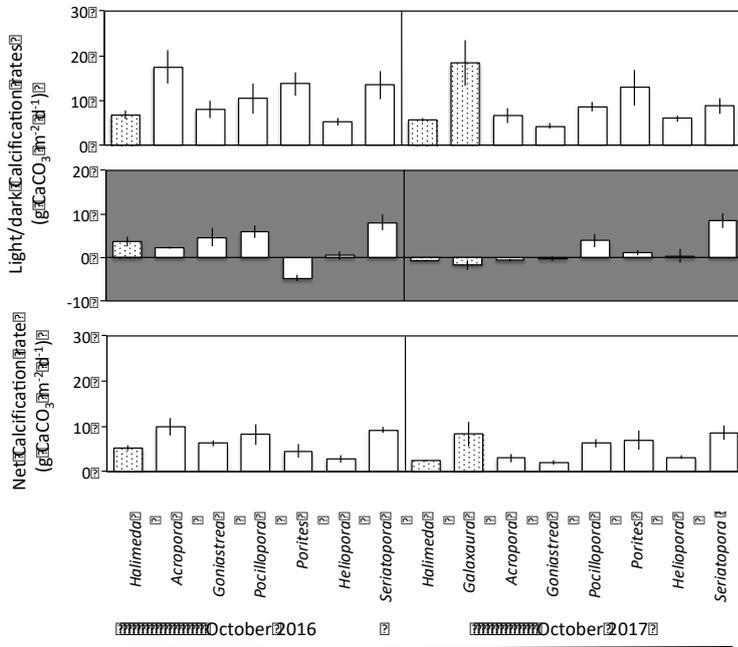
Figure 6. Calcification rates for corals (white) and calcifying algae (stippled) (means ± se) in

light (top) and dark (middle). The bottom panel shows the daily net calcification rate (means ±

se) assuming a 12-h photoperiod.

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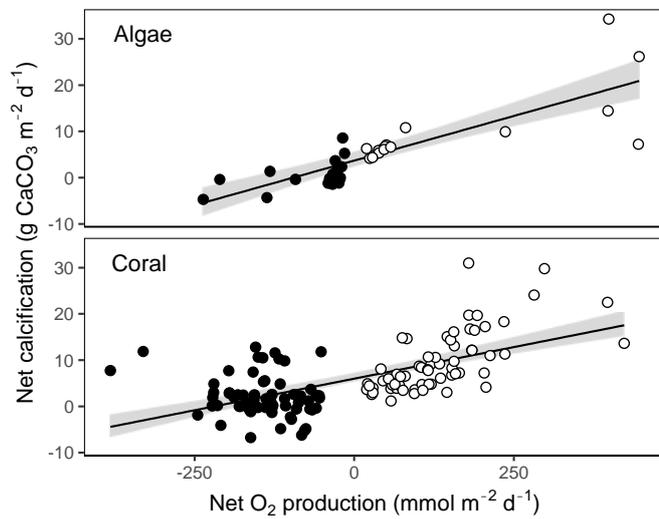
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Figure 7. Relationship between net calcification rate and net productivity for calcifying algae

(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).

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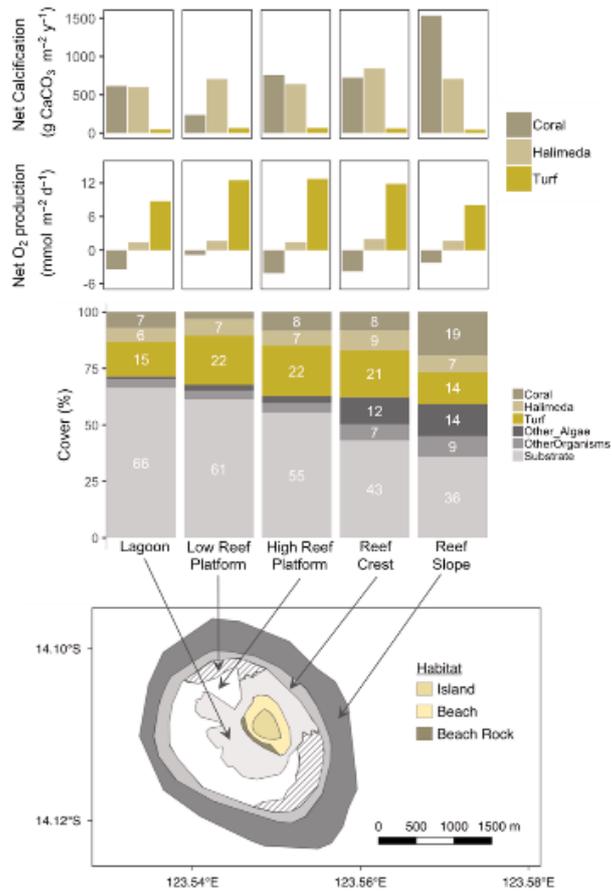
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Figure 8. Map of the reef around Browse Island showing the major habitat types (bottom

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.

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1111 **Tables**

1112 **Table 1.** Taxa measured in on-ship incubation experiments including the number of replicate

1113 specimens measured (one specimen per incubation core). Some of the specimens were not

1114 included in the final analysis due to sampling errors or due to O_2 not increasing during both of

1115 the light intervals or not decreasing during both of the dark intervals; the resulting number of

1116 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

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1119 **Table 2.** Ambient concentrations of parameters measured during incubations (means ± se);

1120 nutrients ($NO_3^- + NO_2^-$ = nitrate + nitrite, NH_4^+ = ammonium, PO_4^{3-} = orthophosphate, Si =

1121 silica) and oxygen (O_2), total alkalinity (TAlk), Photosynthetically Active Radiation (PAR),

1122 temperature (T) and salinity. Calculated carbonate system parameters (means ± se); CO_2

1123 partial pressure (pCO_2), concentrations of HCO_3^-, CO_3^{2-} and dissolved inorganic carbon

1124 (DIC), and the saturation state of aragonite (Ω Aragonite). In April 2016, two replicate PAR

1125 measurements were taken at 11:00, 12:00 and 13:00 h. In October 2016 and 2017, PAR was

1126 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			
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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