1   **Production and accumulation of reef framework by calcifying corals and macroalgae on**

2   **a remote Indian Ocean cay.**

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13   **Abstract**

14   Coral reefs face increasing pressures in response to unprecedented rates of environmental

15   change at present. The coral reef physical framework is formed through the production of

16   calcium carbonate ($CaCO_3$) and maintained by marine organisms, primarily hermatypic corals,

17   and calcifying algae. The northern part of Western Australia, known as the Kimberley, has

18   largely escaped land-based anthropogenic impacts and this study provides important metabolic

19   data on reef-building organisms from an undisturbed set of marine habitats. From the reef

20   platform of Browse Island, located on the mid-shelf just inside the 200 m isobath off the

21   Kimberley coast, specimens of the dominant coral (6 species) and algal (5 species) taxa were

22   collected and incubated ex-situ in light and dark shipboard experimental mesocosms for 4 hours

23   to measure rates of calcification and production patterns of oxygen. During experimental

24   light/dark incubations, all algae were net autotrophic producing 6 to 111 mmol O_2 m^{-2} day^{-1}.

25   In contrast, most corals were net consumers of O_2 with average net fluxes ranging from −42 to

26   47 mmol O_2 m^{-2} day^{-1}. The net change in pH was generally negative for corals and calcifying

27   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

28   corals, and calcifying algae (*Halimeda* and *Galaxura*) were all positive and were strongly

29   correlated to net O_2 production. In intertidal habitats around Browse Island, estimated relative

30   contributions of coral and *Halimeda* to the reef production of $CaCO_3$ were similar at around

31   600 to 840 g m^{-2} year^{-1}. The low reef platform had very low coral cover of < 3% which made

32   a smaller contribution to calcification of ~240 g $CaCO_3$ m^{-2} year^{-1}. Calcification on the subtidal

33   reef slope was predominantly from corals, producing ~1540 g $CaCO_3$ m^{-2} year^{-1}, twice that of

34   *Halimeda*. These data provide the first measures of community metabolism from the offshore

35   reef systems of the Kimberley. The relative contributions of the main reef builders, in these

36   undisturbed areas, to net community metabolism and $CaCO_3$ production is important to

37   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

63   builders in tropical environments, producing $CaCO_3$ through skeletal deposition. This net

64   calcium carbonate production is a balance between gross production minus the loss due to

65   physical, chemical, and biological erosion (Cornwall et al., 2021). The net calcium carbonate

66   production and related potential vertical accretion of reefs is increasingly threatened by

67   anthropogenic climate change (Perry et al., 2018). For scleractinian corals, one of the most

68   significant consequences of OA is the decrease in the concentration of carbonate ions (CO_2^{-3})

69   (Kleypas and Yates, 2009). Projections suggest that future rates of coral reef community

70   dissolution may exceed rates of $CaCO_3$ production (calcification), with the majority of coral

71   reefs unable to maintain positive net carbonate production globally by 2100 (i.e., net loss)

72   (Cornwall et al., 2021; Silverman et al., 2009; Hoegh-Guldberg et al., 2007).

73

74   These global climate change pressures are causing shifts in the composition of coral reef

75   species, and the urgent focus now is on identifying, quantifying and maintaining reef ecosystem

76   function so that coral reefs can continue to persist and deliver ecosystem services into the future

77   (Harborne et al., 2017). To do this it is necessary to characterize reef health in terms of

78   metabolism which includes calcification but also fundamental processes such as photosynthesis

79   and respiration (Madin et al., 2016; Carlot et al., 2022). Photosynthesis fixes CO_2 in organic

80   materials, whereas the reverse reaction (dark respiration) releases it. In scleractinian corals with

81   zooxanthellae, the precipitation of $CaCO_3$ through calcification is tightly coupled to

82   photosynthetic fixation of CO_2 and on average tends to be three times higher in daylight

83   conditions than in darkness (Gattuso et al., 1999). Calcification rates can increase further

84   through feeding on phytoplankton and suspended particles (Houlbreque and Ferrier-Pages,

85   2009). Overall, the excess organic production in a coral reef community (i.e., the difference

86   between gross primary production and dark respiration) acts as a CO_2 sink, while calcification

87   acts as a source of CO_2 (Lewis, 1977; Kinsey, 1985). Most reef flats are sources of CO_2 to the

88   atmosphere despite the drawdown of CO_2 during the day via photosynthetic processes. This is

89   due to their low net fixation of CO_2 and rather large release of CO_2 by precipitation of calcium

90   carbonate (Ware et al, 1992; Gattuso et al, 1993; Gattuso et al, 1995; Smith, 1995;

91   Frankignoulle et al, 1996; Gattuso et al, 1996b).

92

93   One notable exception to this is in algal-dominated reef communities, which are sinks for

94   atmospheric CO_2. They exhibit larger excess community production and/or a lower community

95   calcification, (e.g., Kayanne et al, 1995; Gattuso et al, 1996a; Gattuso et al, 1997). The

96   morphological diversity of reef algae provides food (Overholtzer and Motta, 1999), habitat and

97   shelter (Price et al., 2011) for a number of invertebrate and fish species, with productivity

98   sustaining higher trophic levels. Calcified macroalgae can also contribute significantly to the

99   deposition of carbonates (Nelson, 2009). In particular, species of the genus *Halimeda* are

100   widely distributed across tropical and subtropical environments and contribute significantly to

101   reef calcification and productivity rates because of their fast growth and rapid turnover rates

102   (Vroom et al., 2003, Smith et al., 2004, Nelson, 2009) compared to corals or coralline red algae

103   (CRA). Calcification rates of *Halimeda* make it a major contributor to $CaCO_3$ in reefs in the

104   Caribbean (Blair and Norris, 1988; Nelson, 2009), Tahiti and the Great Barrier Reef (Drew,

105   1983; Payri, 1988). In certain locations, precipitation of calcium carbonate can approach 2.9

106   kg $CaCO_3$ m^{-2} yr^{-1}, positioning *Halimeda* as a major contributor to carbonate budgets within

107   shallow waters around the globe (Price et al., 2011). This group further occupies a diverse

108   range of environments (mangroves, seagrass beds, and coral reefs) and can produce structurally

109   complex mounds that serve as critical habitat for a diversity of important marine life (Rees et

110   al., 2007).

111

112 Here, we compare metabolic and calcification rates of the dominant intertidal taxa of coral and

113 macroalgae at Browse Island, a small island in the Kimberley bioregion located in the northern

114 part of Western Australia. Unlike Southwestern Australia, which has one of the fastest

115 increasing rates of change from cumulative human impacts (Halpern et al., 2019), the

116 Kimberley represents one of the few "very low impact" tropical coast and shelf areas globally

117 – only 3.7% of the global oceans fall in this category (Halpern et al., 2008). Few process studies

118 have been carried out in the region due to the remoteness of these reef habitats, some of which

119 are located 100s of km from the coastline, meaning that fieldwork and data acquisition can be

120 difficult and costly. Rates of metabolism and calcification were determined in on-ship

121 incubations in October 2016, April 2017 and October 2017. Using the proportional cover of

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

123 metabolism estimates for the Browse Island habitats and provide new insights into reef

124 ecosystem health and functioning in the absence of localised land- and sea-based anthropogenic

125 variables (Harley et al., 2006; 157 Schindler, 2006; Walther, 2010).

126

127 **2. Methods**

128 *2.1 Study site*

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

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

131 (~ 4.5 km^2) planar platform reef consisting of a shallow lagoon, an extensive reef flat that is

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

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

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

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

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

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

138   al., 2017).

139

140   *2.2 Algae and coral collection*

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

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

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

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

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

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

147   *Sargassum* found floating on the water surface were also included although this taxon was not

148   found growing anywhere on the reef during sampling trips. Hermatypic corals included

149   *Pocillopora* sp., *Goniastrea* sp., *Porites* sp., *Heliopora* sp., *Acropora* sp. and *Seriatopora* sp.

150   Whole pieces of coral small enough to fit inside the incubation cores (inner diameter ~90 mm)

151   were collected to minimise tissue damage. All coral samples were > 50 mm diameter and

152   therefore operationally defined as adults and estimated to be at least 2 to 7 years old depending

153   on the taxa (Trapon et al., 2013).

154

155   *2.3 Light and dark incubations*

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

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

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

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

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

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

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

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

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

165

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

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

168 1 shows the taxa incubated during each sampling trip and the number of replicates. Water

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

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

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

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

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

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

175

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

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

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

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

180 flowthrough tank into the core so that the core volume remained constant throughout the

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

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

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

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

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

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

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

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

189 analysed.

190

191 *2.4 Surface areas of coral and algal specimens*

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

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

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

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

196 65°C. The waxed samples were weighed again, and the weight of the wax calculated. The

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

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

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

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

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

202

203 *2.5 Chemical analyses*

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

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

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

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

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

209 et al. 2005. Detection limits were 0.02 $\mu mol\ L^{-1}$ for all inorganic nutrient species, with a

210 standard error of < 0.7%.

211

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

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

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

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

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

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

218 titrated with 0.012 N HCl, standardised against sodium carbonate (99.95 to100.05 wt%) with

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

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

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

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

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

224

225 *2.6 Oxygen fluxes and calcification rate calculations*

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

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

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

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

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

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

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

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

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

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

236

237   A census-based approach was used to estimate the amount of $CaCO_3$ and O_2 produced by a

238   single taxon per unit area of reef surface per year (Shaw et al., 2016). The rates of calcification

239   and net O_2 production per day were divided by the 'footprint' area of each specimen. To

240   estimate the relative contributions from each taxon to community production per m^2 of reef,

241   these rates were multiplied by the relative percent cover in each of the major habitats. Estimates

242   of percent cover based on drop camera image analysis were obtained from Olsen et al. (2017).

243   The productivity rates for individual coral species were combined into one value for coral.

244

245   *2.7 Statistical analyses*

246   The relationships between net changes in pH and O_2 and between net O_2 production and net

247   calcification (in light and dark incubations) were examined by linear regression. Significance

248   of regressions were calculated for algae, calcified algae and corals and the 95% confidence

249   intervals for the slope of each line in R (R Core Team, 2018). Regressions were examined with

250   ANOVA and deemed significant if $p < 0.05$.

251

252   **3   Results**

253   *3.1 Experimental conditions*

254   Nutrient concentrations were low and similar among sampling trips (Table 2), as is

255   characteristic of tropical Eastern Indian Ocean offshore waters (McLaughlin et al., 2019).

256   Concentrations of nitrate were 0.05 to 0.17 µmol L^{-1}, ammonium 0.12 to 0.13 µmol L^{-1},

257   phosphate 0.07 to 0.1 µmol L^{-1}, and silicate 2.3 to 3 µmol L^{-1}. Oxygen was 0.19 mmol L^{-1} to

258   0.22 mmol L^{-1} and salinity 34.2 to 34.8 ppt. Light and temperature conditions in the

259   incubations were representative of *in situ* conditions on the reef platform and were similar

260   among trips. PAR levels were 1500 µE m^{-2} s^{-1} in April and slightly higher to 1587 µE m^{-2} s^{-1}

261   in October. Temperatures were 28.3 to 32.8°C and highest in April. Carbonate system

262   parameters were not obtained for April 2016 due to instrument error, and some minor

263   differences in pCO2, HCO_3^-, $CO_3{_2}^-$, DIC and Ω Aragonite were noted between October 2016

264   and 2017 (Table 2). Alkalinity and pH were both higher in 2016, and there were associated

265   minor differences in the concentrations of the carbonate species and the aragonite saturation

266   state (Table 2).

267

268   *3.2 Changes in oxygen and pH*

269   Changes in dissolved O_2 differed among taxa, and between light and dark incubations. In the

270   seawater controls O_2 changed by < 0.01 mmol h^{-1} in both light and dark incubations, showing

271   that the contribution of any organisms in the seawater itself to O_2 production and dark

272   respiration was minimal. No corrections were therefore applied. In the light incubations O_2

273   productivity fluxes were positive for all taxa (Fig. 3, top panel). The highest light flux of O_2

274   of ~380 mmol m^{-2} day^{-1} was measured for *Galaxaura* in October 2017 (Fig. 3, top). Corals

275   generally produced 100 to 260 mmol O_2 m^{-2} day^{-1} in the light, except *Heliopora,* which had

276   a flux of 50 to 80 mmol O_2 m^{-2} day^{-1}. All taxa consumed O_2 during the dark incubations

277   when changes in O_2 are due to dark respiration, with mean fluxes of -15 to -190 mmol O_2

278   m^{-2} day^{-1} (Fig. 3, middle). All algae were net autotrophic and produced 6 to 111 mmol O_2

279   m^{-2} day^{-1} with the highest net O_2 flux measured for *Galaxaura* and turf at 111 and 36 mmol

280   O_2 m^{-2} day^{-1} respectively (Fig. 3, bottom). In contrast, around half of the corals were net

281   consumers of O_2 and average net fluxes spanned a wide range from -42 to 47 mmol O_2 m^{-2}

282   day^{-1}.

283

284   In the light incubations, pH generally increased by 0.03 to 0.25 h^{-1} for all taxa, except for

285   *Halimeda* in April 2016 and October 2017, which showed no change or a very small increase

286   (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).

312   *3.4 Contributions to community production*

313   In intertidal habitats (lagoon and high reef platform) around Browse Island, the estimated

314   relative contributions of coral (8 % cover) and *Halimeda* (7 % cover) to the reef production

315   of $CaCO_3$ were similar, around 600 to 840 g m^{-2} $year^{-1}$ (Fig. 8, top panel). The low reef

316   platform had very low coral cover of < 3% (Fig. 8, middle), which therefore made a smaller

317   contribution to calcification of ~240 g $CaCO_3$ m^{-2} $year^{-1}$ in this habitat (Fig. 8, top). In

318   contrast, calcification on the subtidal reef slope was predominantly from corals (19 % cover),

319   which produced ~1540 g $CaCO_3$ m^{-2} $year^{-1}$, around twice the amount compared to *Halimeda*

320   (7 % cover). *Galaxaura*, which had high measured rates of productivity and calcification, was

321   extremely rare (0.02 % total cover found only in October 2017; Olsen et al., 2017) and thus

322   its contribution to community calcification and productivity were negligible. Turf was

323   responsible for the majority of the O_2 production in all habitats and produced an estimated 8

324   to 13 mmol O_2 m^{-2} d^{-1} compared to < 2 mmol O_2 m^{-2} d^{-1} for *Halimeda* and −4 to −1 mmol O_2

325   m^{-2} d^{-1} for corals (Fig. 8, second panel from top).

326

327   **4   Discussion**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

342 utilise heterotrophic supply through feeding to help sustain growth in addition to

343 photosynthesis by zooxanthellae (Houlbreque and Ferrier-Pages, 2009). These patterns are

344 generally in agreement with those reported elsewhere. For example, fleshy and calcifying algae

345 showed net diel O_2 production, whereas corals generally consumed O_2, i.e. were net

346 heterotrophic, on islands in the South Pacific (*Porites* sp.) and the Caribbean (*Madracis* sp.)

347 (Smith et al., 2013).

348

349 Concurrent with changes in O_2 were changes in seawater pH, where pH increased in daylight

350 (except for *Halimeda* in April 2016 where no change was measured) and decreased in darkness.

351 The effects of metabolic activity on bulk pH (uptake and release of CO_2 through photosynthesis

352 and dark respiration) cannot be directly separated from that of calcification, which is associated

353 with the release of H^+ ions thereby decreasing pH (Jokiel, 2011). However, differences were

354 observed in the net pH change in incubations between calcifiers and non-calcifiers. The net

355 effect of non-calcifiers on seawater pH was positive while the majority of calcifiers caused net

356 pH to decline. In the present study, *Halimeda* (April 2016) and *Goniastrea* (April and October

357 2016) caused relatively minor increases in pH, whereas the calcifying alga *Galaxaura* elevated

358 pH by, on average, 0.03 units, comparable to the net effect of non-calcifiers. This is not

359 surprising given the high rate of O_2 production measured for *Galaxaura*, which is associated

360 with sufficient levels of CO_2 fixation to compensate for the reduction in pH associated with

361 calcification in this species. A strong link was observed between metabolism and pH in all taxa,

362 demonstrated as linear relationships between changes in pH and O_2 during the incubations.

363 Previous research by Smith et al. (2013) identified two broad patterns: metabolic changes in

364 O_2 in non-calcifiers (fleshy and turf algae) linked to large changes in pH (steep slopes), and

365 metabolic changes in O_2 in calcifying organisms (*Porites* sp. *Madracis* sp. and *Halimeda* sp.)

366 producing little or no change in pH (shallow slopes). This is contrary to the present study's

367 observations where pH and O_2 relationship gradients were similar for calcifiers and non-

368 calcifiers. Non-calcifying organisms were found to consistently have a net positive effect on

369 both pH and O_2. Change in pH for the same net change in O_2 was elevated for non-calcifiers

370 compared to calcifiers.

371

372 Production and accumulation of reef framework carbonate is controlled by the relative rates of,

373 and the interactions between, a range of ecologically, physically and chemically driven

374 production and erosion processes (Perry et al., 2008; Montaggioni and Braithwaite, 2009), with

375 the relative importance of different taxa for $CaCO_3$ production differing among reefs and

376 among habitats within reefs. Coral growth can be measured in several ways: linear extension

377 rate, global skeletal growth and calcification rate (measured using the alkalinity technique or

378 by ^{45}Ca incorporation) (Houlbreque and Ferrier-Pages, 2009). Methods to calculate

379 calcification can vary in accuracy. Overestimates of calcification rates can result from

380 calculations based on changes in alkalinity, while those relying on $CaCO_3$ content and growth

381 measurements (either through staining or tagging segments), may produce minimum estimates

382 as loss of new tissue is not accounted for (Hart and Kench, 2007; Houlbreque and Ferrier-

383 Pages, 2009). The alkalinity method employed in the present study was the best possible option

384 when working in a remote location where actual growth rates cannot be easily assessed, or use

385 of radioisotopes was limited. Rates of net community calcification for reef flats worldwide

386 range from 7.3 to 90 mol (730 to 9000 g) $CaCO_3$ m^{-2} $year^{-1}$ with an average of 47 mol (4700

387   g) $CaCO_3$ m^{-2} year^{-1} (Atkinson, 2011). The patterns found in the present study — higher

388   calcification rates in daylight compared to in darkness for all corals and calcifying algae — are

389   typical. However, the coral $CaCO_3$ production rates per reef area (7 to 8% cover low reef

390   platform, 19% reef slope) measured here (240 g m^{-2} year^{-1} for low reef platform, 610 to 756 g

391   m^{-2} year^{-1} in the other intertidal habitats, and 1536 g m^{-2} year^{-1} on the reef slope) were

392   somewhat lower than values reported elsewhere. In 2016, the dark rates of calcification by

393   corals were less than 50% of the rates in light with some (*Porites* and *Heliopora)* negative.

394   Dark rates of calcification in 2017 were negative or near zero for all species except *Porites,*

395   *Pocillopora* and *Seriatopora*. Houlbreque et al. (2004) showed that coral feeding enhances dark

396   calcification rates in scleractinian corals, but incubations in our study were done in absence of

397   supplemental feeding. The trend observed here may be due to some dissolution of $CaCO_3$ due

398   to the reduced pH during dark incubations or could be an artefact of the experimental

399   conditions. This result should therefore be taken with some caution, in particular for *Porites* in

400   October 2016, which saw the largest decrease (Fig. 5, middle panel). However, the resulting

401   strong relationship between net carbonate production and net carbonate consumption is

402   consistent with previous studies both *in situ* and in mesocosms (Albright et al., 2013).

403

404   Corals are typically the primary framework-producing components on a tropical reef and

405   dominate carbonate production per unit area (Vecsei, 2004), however additional $CaCO_3$ is

406   produced by calcareous crustose coralline algae (CCA) and calcareous algae of the genus

407   *Halimeda*, (e.g. Payri, 1988). Sprawling lithophytic species of *Halimeda*, like the majority of

408   the *Halimeda* around Browse Island, tend to be fast growing and have high calcification rates

409   (Hart and Kench, 2007). Rates of calcification per area of 100% *Halimeda* cover have been

410   estimated to 400 to 1667 g $CaCO_3$ m^{-2} year^{-1} (in Hart and Kench, 2007 Suppl info). In other

411   locations, *Halimeda* has been estimated to contribute around 1100 to 2400 g $CaCO_3$ m^{-2} year^{-1}

412   to benthic carbonate production (Drew, 1983; Freile et al., 1995; Hudson, 1985; Kangwe et al.,

413   2012; Payri, 1988; Rees et al., 2007), which is higher than the 600 to 840 g $CaCO_3$ m^{-2} $year^{-1}$

414   estimated for *Halimeda opuntia* in the intertidal habitats in the present study. These rates

415   depend both on the intrinsic calcification rates and on the abundance or cover of algae (6.1 to

416   8.7% cover on Browse, which corresponds to ~150 to 250 g dw m^{-2}).

417

418   Nutrient capacity is one important driver of productivity in many reef ecosystems. The rate at

419   which nutrients are recycled between the constituents of the system (the ambient nutrient

420   availability, and the nutrients stored within plant and animal biomass) depends on input from

421   a variety of sources (e.g., associated with seasonal rains or upwelling) (DeAngelis, 1992;

422   Hatcher, 1990). Coral reefs, typically have low ambient nutrient availability and receive little

423   sustained exogenous nutrient input (Hatcher, 1990; Szmant, 2002), thus the high rates of

424   production found within these ecosystems are largely attributed to the nutrients stored and

425   cycled by living biomass (Pomeroy, 1974; DeAngelis et al., 1989; Sorokin, 1995). Fishes

426   typically make up a substantial component of living biomass on coral reefs and represent an

427   important reservoir of nutrients in these ecosystems (Allgeier et al., 2014). Contrary to our

428   expectations given its remote location in an area of apparently low anthropogenic impacts, the

429   reef platform around Browse Island was depauperate with a conspicuous lack of diversity in

430   key groups including macroalgae, macroinvertebrates and teleost browsers (Bessey et al.,

431   2020). McLaughlin et al. (2019) found surface water standing stock nutrient concentrations

432   low along Kimberley shelf. Conditions at Browse Island were similar with low water column

433   nutrients for nitrate, ammonia and phosphate during all trips. Understanding how changes in

434   animal populations alter nutrient dynamics on large ecological scales is a relatively recent

435   endeavour (Doughty et al., 2015). Allgeier et al. (2016) showed that targeted fishing of higher

436   trophic levels reduces the capacity of coral reef fish communities to store and recycle nutrients

437   by nearly half. Fish-mediated nutrients enhance coral growth (Meyer et al., 1983) and primary

438   production (Allgeier et al., 2013), and may regulate nutrient ratios at the ecosystem scale

439   (Allgeier et al., 2014).

440

441   The Kimberley region-wide averages of coral cover and macroalgal cover are 23.8% and 7.1%

442   (Richards et al., 2015) respectively. However, this relationship at Browse Island is reversed,

443   with macroalgae more dominant at 28% total cover to that of coral at 9% total cover. On the

444   Browse Island reef platform, the same pattern is observed where averages were 5 to 8% for

445   coral and 32% for macroalgae, differing from those of the regional averages of 14.4% and

446   15.5% of coral and macroalgae respectively (Richards et al., 2015). While the estimates

447   provided here approximate the relative contributions of *Halimeda* and coral to $CaCO_3$

448   production, they do not add up to a whole system budget. There are other organisms likely to

449   contribute significantly. For example, the present study did not measure metabolic or

450   calcification rates of encrusting coralline algae, which, although making up a modest 1.0 to

451   3.0% of the benthic cover in the lagoon and reef platform habitats at Browse Island, become

452   more prominent at 11.8 to 14.1% on the reef crest and slope (Olsen, unpublished data). To

453   calculate the true $CaCO_3$ production per area of reef, the calcification rate would need to be

454   multiplied by the benthic cover of coralline algae and the square of the benthic rugosity (Eakin,

455   1996). Using typical values for rugosity from Eakin (1996) of 1 to 1.4 for the lagoon and reef

456   platform and 1.7 to 2 for the reef crest and slope, and assuming a typical calcification rate of

457   1500 to 2500 g m^{-2} year^{-1} (for 100% flat-surface cover) (Hart and Kench, 2007), the

458   contribution of encrusting coralline algae to calcification in the lagoon and reef platform would

459   be minor at 70 to 134 g $CaCO_3$ m^{-2} year^{-1}. However, they could produce a significant amount

460   of 980 to 1360 g $CaCO_3$ m^{-2} year^{-1} on the reef crest and slope, which is somewhere in between

461   the production rates estimated for *Halimeda* and corals. Encrusting coralline algae may

462 therefore contribute significantly to the $CaCO_3$ budget at Browse Island, at least in deeper

463 habitats. These values are similar to those measured elsewhere, for example 870 to 3770 g

464 $CaCO_3$ m^{-2} year^{-1} at Uva reef in the eastern Pacific (Eakin, 1996).

465

466 Metabolic rates of primary producers are clearly influenced by a multitude of factors including

467 hydrodynamics, irradiance, and nutrient availability (Smith et al., 2013). We were able to detect

468 considerable diurnal changes in water chemistry due to metabolic rates, since our experiments

469 were conducted in small enclosed mesocosms. The effect of metabolism on water chemistry is

470 expected to dissipate downstream in a more turbulent or dynamic environment (Anthony et al.

471 2011). However, coral and algae metabolic rates and resultant flux from the diffusive boundary

472 layer also increases with flow rates (Carpenter et al. 1991; Lesser et al. 1994; Bruno and

473 Edmunds 1998; Mass et al. 2010). Because our experiments were conducted in near no-flow

474 chambers (mesocosm water was replenished with fresh seawater in small amounts during

475 sample extraction), our measurements are conservative values and likely represent the lower

476 range of potential effects that these reef organisms have on surrounding water chemistry,

477 however where residence times can be extended, particularly when trapping of water on the

478 reef at low tides occurs, our results are likely reflective of how these benthic organisms affect

479 water chemistry in the lagoonal habitats of Browse Island.

480

481 **5 Conclusions**

482 This study investigated the metabolism of coral and algae on the reef of remote Browse

483 Island, found on the mid-shelf region of the Kimberley in Western Australia. Due to its

484 remoteness, Browse Island presented a unique opportunity to observe these organisms in a

485 pristine habitat where direct anthropogenic pressures are minimal. Browse Island is the only

486 emergent mid-shelf reef in the Kimberley bioregion having semidiurnal tides reaching a

487   maximum range of 5 m (Olsen et al., 2017), half the magnitude of tides experienced by reefs

488   closer to the coast (McLaughlin et al., 2019). Its benthic structure is very different from both

489   Kimberley inner (e.g., Montgomery Reef, Adele and Cassini Islands) and outer (e.g.,

490   Ashmore Reef and Rowley Shoals) shelf reefs. The relative contributions of algae and corals

491   to reef productivity are likely to differ across the Kimberley shelf, with corals becoming more

492   important in offshore waters and algal calcifiers being important on the mid-shelf. Estimated

493   areal production rates did not take into account the relief (differences in height from place to

494   place on the reef surface) of the substrate. The reef platform surrounding Browse Island has

495   relatively low surface relief, whereas the reef slope and crest have high rugosity, which

496   means production rates in the latter environments may be underestimated. Despite these

497   limitations, the rates estimated in this study are similar to those measured elsewhere.

498

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

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

501    $CaCO_3$ on the Browse Island reef flat, however, their relative contributions to the reef

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

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

504   and amounts of $CaCO_3$ material found in each reef sink is necessary. The Kimberley coastal

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

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

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

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

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

510

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

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

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

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

515 pressures of carbon dioxide (pCO2) causing seawater pH and the $CaCO_3$ saturation state to

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

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

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

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

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

521 this region. Different components of the reef around Browse Island are likely to have

522 different vulnerabilities to warming and heat waves. Future environmental stressors leading

523 to changes in benthic community composition, structure and subsequent changes in reef

524 productivity and in rates of production of $CaCO_3$, could have major implications for Browse

525 Island.

526

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528 investigation, resources, methodology, visualisation, and writing (original draft preparation);

529 Cindy Bessey - Investigation, resources, project administration, and writing (review and

530 editing); Gary A. Kendrick - Conceptualization, funding acquisition, project administration,

531 supervision, and writing (review and editing); John Keesing - Conceptualization, funding

532 acquisition, investigation, resources, supervision, and writing (review and editing); Ylva S.

533 Olsen - Conceptualization, formal analysis, investigation, project administration, resources,

534 methodology, visualisation, and writing (original draft preparation)

535

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539

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541

542

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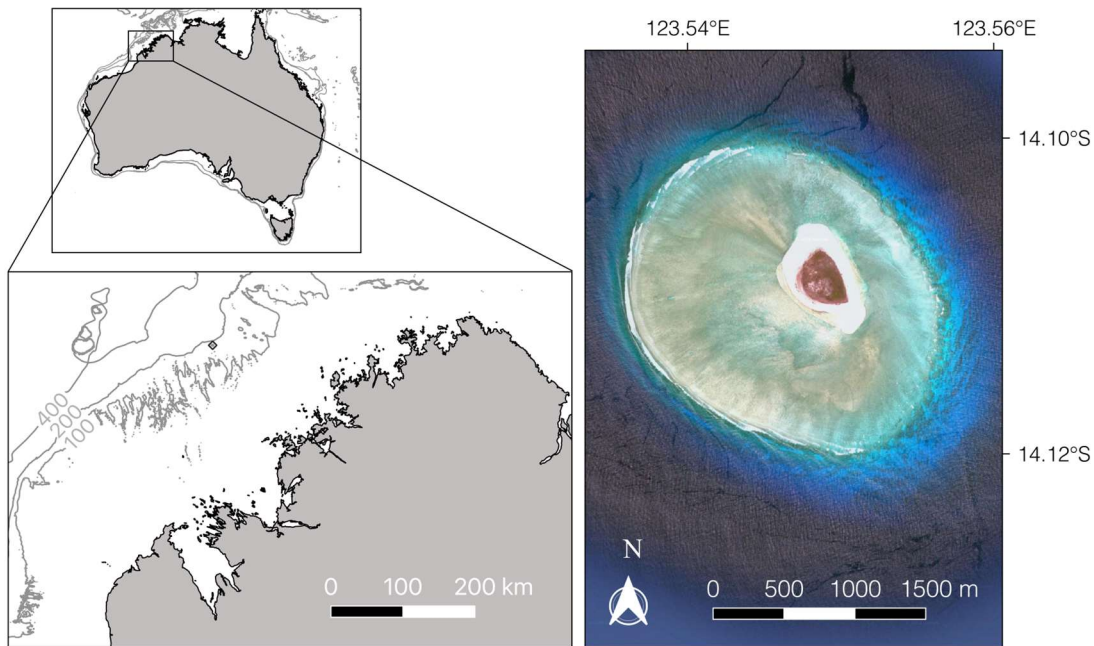
547

548 **Figures**

549

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

551 200-m isobath on the continental shelf. The small map (top left) shows the location of the island

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

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

554

555

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

556

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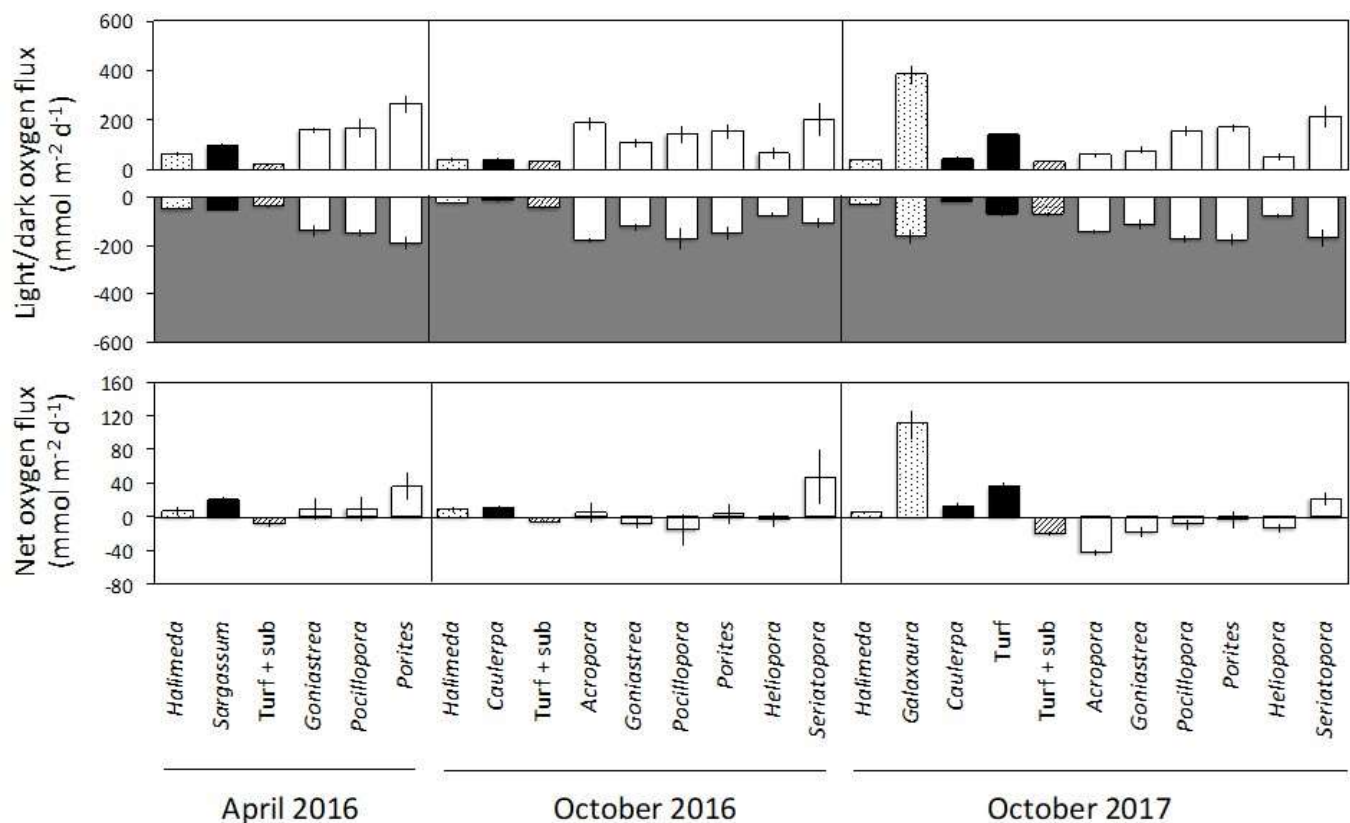
Figure 3. Net changes in oxygen (means ± se) in light (top) and dark (middle) incubations of calcifying algae (stippled), macroalgae and turf (black), turf + substrate (diagonal stripes) and coral (white) standardised by specimen surface area. The bottom panel shows the net daily production of oxygen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

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564

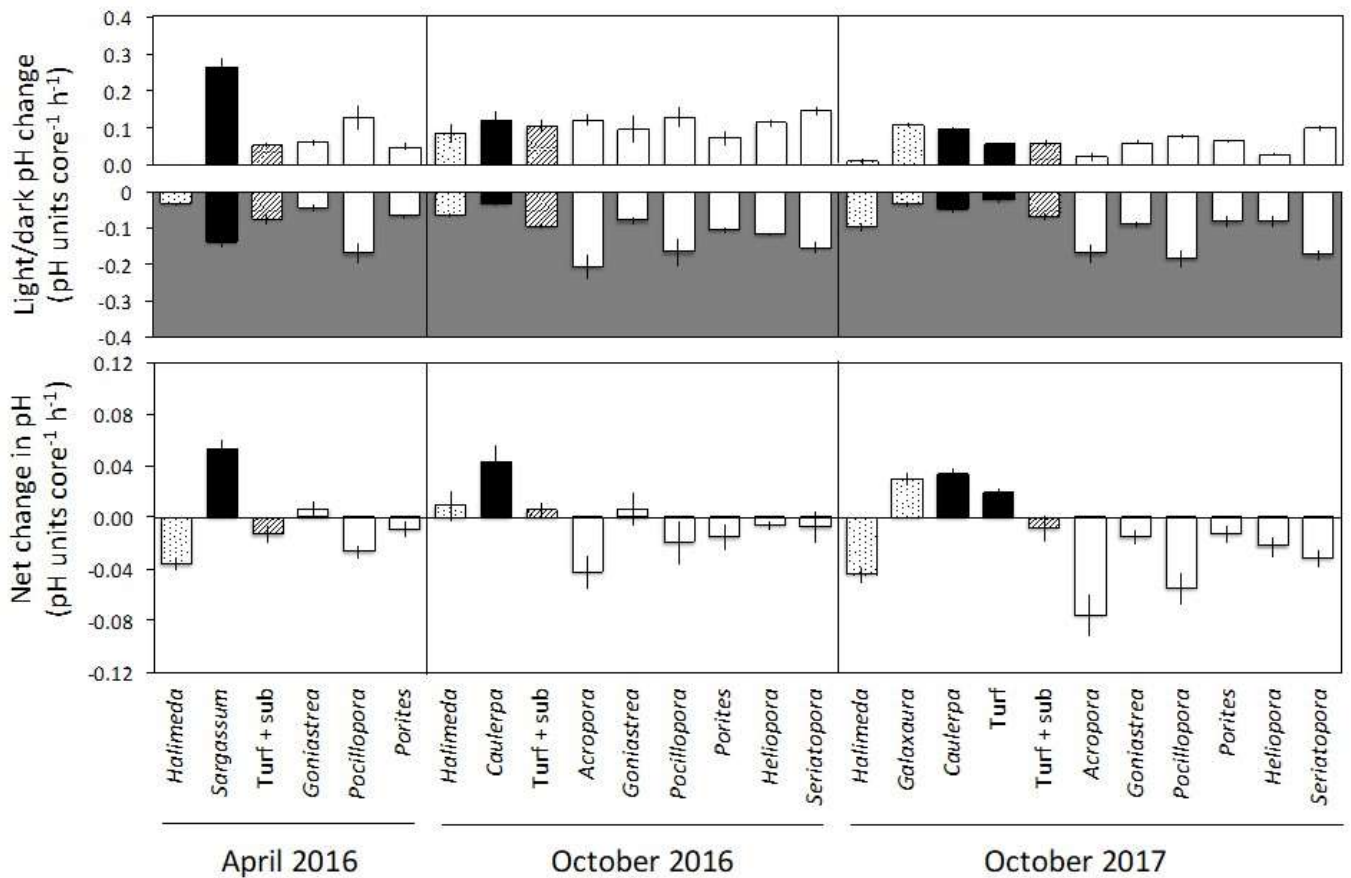



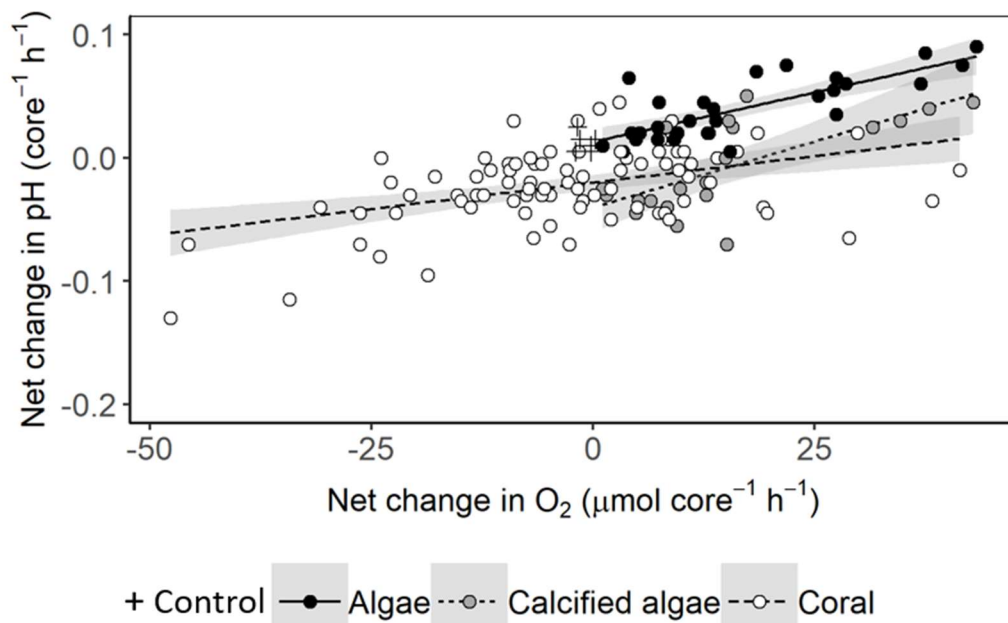
Figure 4. Net changes in pH per hour for each 1.56-L incubation core (means ± se) in light

(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.

569

570

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

572 light and darkness. Linear relationships are fitted with 95% confidence intervals shown in gray.

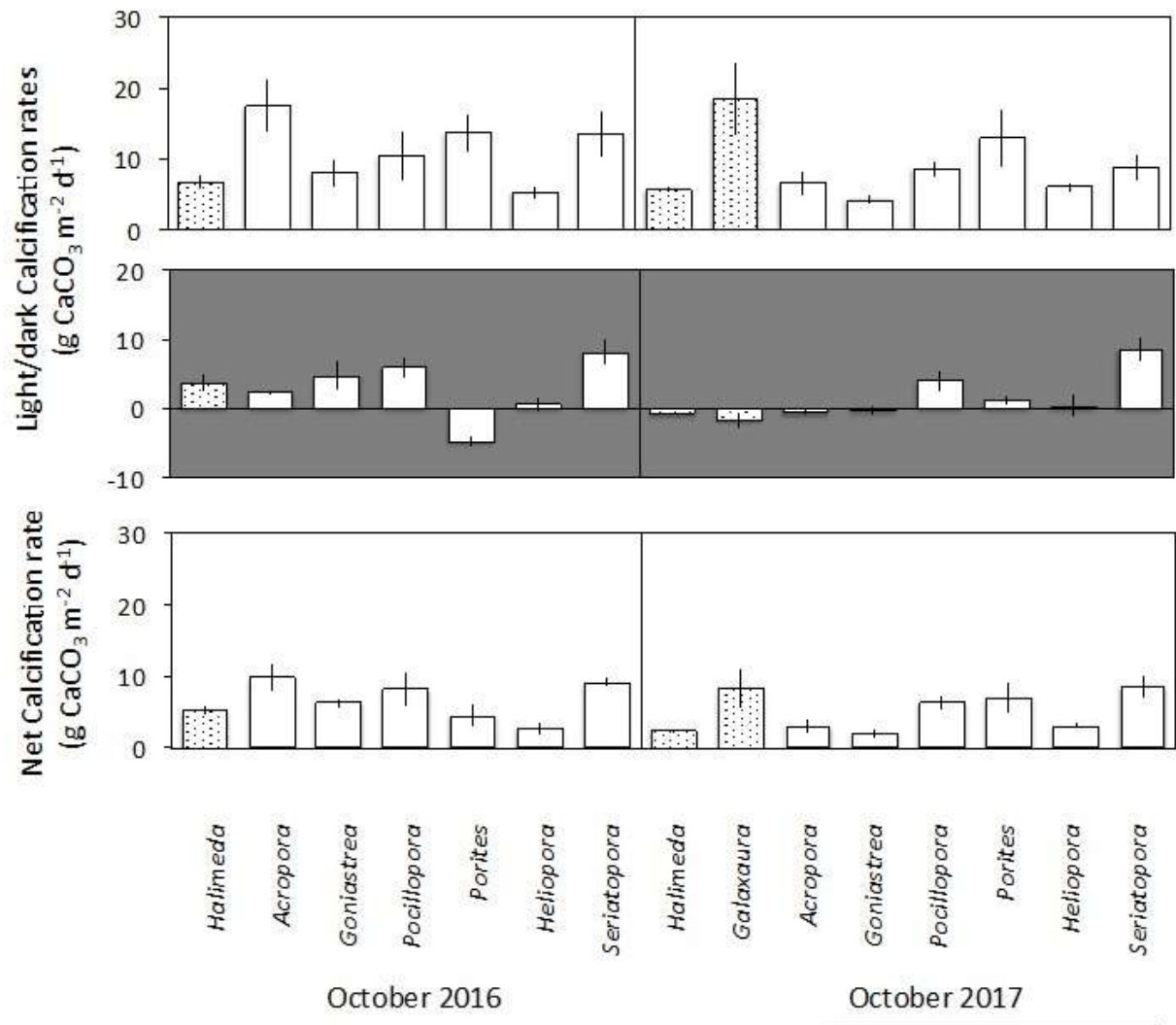
573 For algae; net change in pH = 0.13 + 0.0016 × net change in O_2 (ANOVA: $F_{1,27}$ = 41.15, p

574 <0.001). For calcified algae; net change in pH = −0.04 + 0.0021 × net change in O_2 (ANOVA:

575 $F_{1,19}$ = 17.86, p <0.001). For corals; net change in pH = −0.02 + 0.00086 × net change in O_2

576 (ANOVA: $F_{1,82}$ = 18.88, p <0.001).

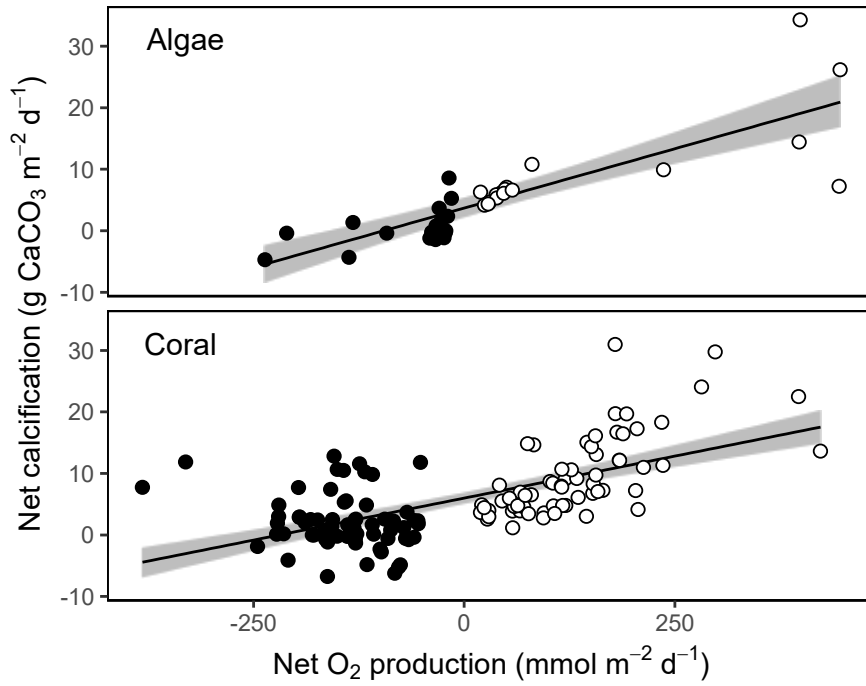
577

578

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

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

581   se) assuming a 12-h photoperiod.

582

583

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

585   (top) and corals (bottom). Open circles indicate rates measured in light and closed circles rates

586   measured in dark. Linear fits are shown with 95% confidence intervals in gray. For calcified

587   algae; net calcification = 3.6 + 0.039 × net O_2 production (ANOVA: $F_{1,32}$ = 67.0, p <0.001).

588   For corals; net calcification = 5.99 + 0.027 × net O_2 production (ANOVA: $F_{1,126}$ = 82.2, p

589   <0.001).

590

591

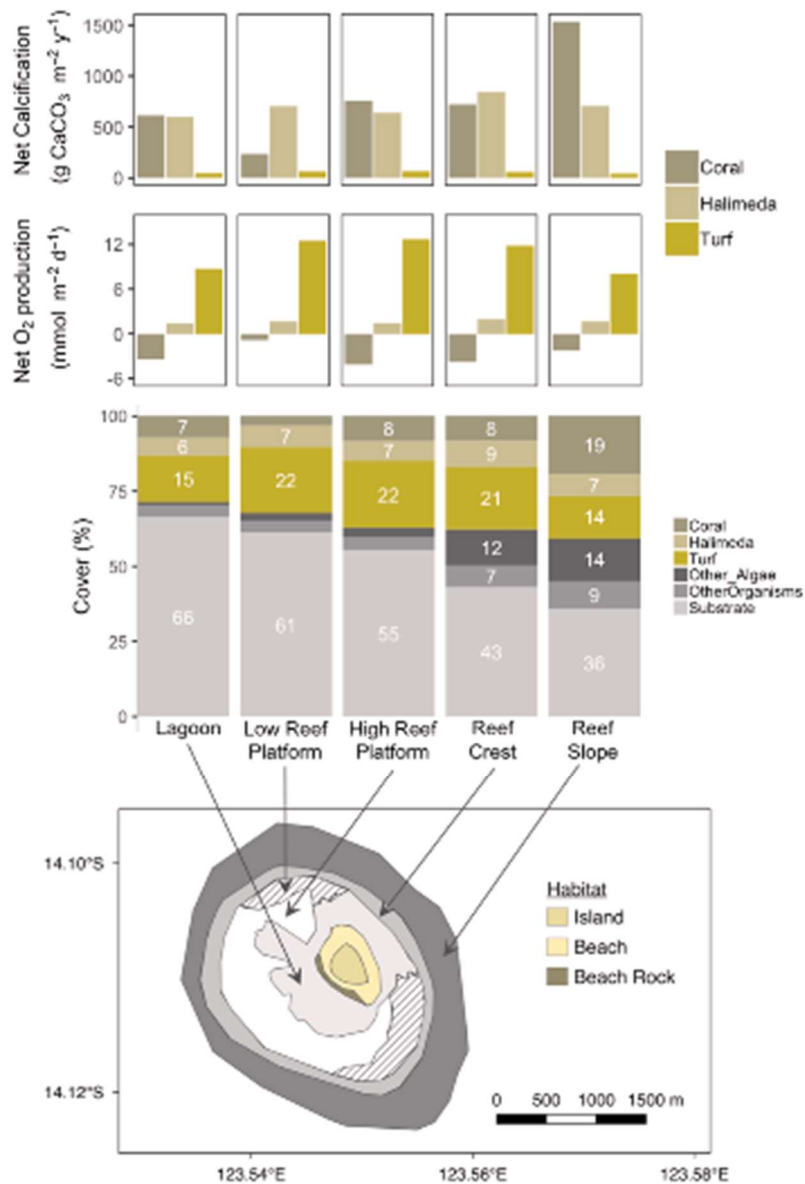



Figure 8. Map of the reef around Browse Island showing the major habitat types (bottom panel). Reef surface percent cover of coral, *Halimeda*, turf and other categories in each habitat (middle panel) based on drop-camera image analysis data from Olsen *et al.* 2017. Net calcification and net oxygen 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

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

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

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

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

603   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

604

605

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

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

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

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

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

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

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

613   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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