

1 **Production and accumulation of reef framework by calcifying corals and macroalgae on**
2 **a remote Indian Ocean cay.**

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12

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 $\text{mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$.
25 In contrast, most corals were net consumers of O_2 with average net fluxes ranging from -42 to
26 47 $\text{mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$. 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 $9.9 \text{ g CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$) 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 $\text{g m}^{-2} \text{ year}^{-1}$. The low reef platform had very low coral cover of $< 3\%$ which made
32 a smaller contribution to calcification of $\sim 240 \text{ g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$. Calcification on the subtidal
33 reef slope was predominantly from corals, producing $\sim 1540 \text{ g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$, 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.

38 **1. Introduction**

39 Coral reefs in the Anthropocene era have been degraded for more than a century by overfishing
40 and pollution, but now even remote reefs (where local pressures are low) face increasing
41 stresses through anthropogenic climate change (Hughes et al., 2017b). With the currently
42 unprecedented rate of environmental change, coral reefs face growing pressures in response to
43 eutrophication (Hewitt et al., 2016), recurrent large scale weather events (marine heat waves,
44 etc.), sedimentation (Hughes et al, 2017a), and rising atmospheric greenhouse gases (especially
45 carbon dioxide, CO₂; IPCC, 2014) that result in increasing ocean temperatures (due to
46 atmospheric heat absorption) and ocean acidification (OA) (Hoegh-Guldberg, 2007; Doney et
47 al., 2009; Perry et al., 2018). The pressures of global climate change are causing shifts in the
48 composition of coral reef species, and the urgent focus now is on identifying, quantifying and
49 maintaining reef ecosystem function so that coral reefs can continue to persist and deliver
50 ecosystem services into the future (Harborne et al., 2017).

51
52 The functioning of healthy coral reefs, as some of the world's most biologically (Stuart-Smith
53 et al., 2018) and structurally complex ecosystems (Hughes et al., 2017b), results in a number
54 of ecosystem services. They provide coastal protection, with reef structures acting to dampen
55 wind and wave driven surges (Perry et al., 2018). Reefs support a diverse range of species that
56 provide critically important resources, such as food, for coastal livelihoods (Hoegh-Guldberg
57 et al., 2007). As one of the most important determinants of overall reef function, the
58 construction and maintenance of the calcium carbonate (CaCO₃) reef structure (the
59 accumulation of which requires the net production of calcium carbonate by resident taxa;
60 Cornwall et al., 2021), is vital to the myriad of ecosystem services that coral reefs provide
61 (Hoegh-Guldberg et al., 2007; Andersson et al., 2013; Moberg and Folke, 1999).

62

63 Community metabolism on a reef is a combination of the photosynthesis and dark respiration
64 of the organisms that live there. Coral reefs are known for their high calcification and
65 photosynthetic production, and measurements of reef metabolism make it possible to
66 characterize reef health in terms of these fundamental processes. These functions are dependent
67 on the maintenance of the framework structure of the reefs. Photosynthesis fixes CO₂ in organic
68 materials, whereas the reverse reaction, dark respiration, releases it. Overall, the excess organic
69 production in a coral reef community (i.e., the difference between gross primary production
70 and dark respiration) acts as a CO₂ sink, while calcification acts as a source of CO₂ (Lewis,
71 1977; Kinsey, 1985). Despite the drawdown of CO₂ during the day via photosynthetic
72 processes, most reef flats are sources of CO₂ to the atmosphere due to their low net fixation of
73 CO₂ and rather large release of CO₂ by precipitation of calcium carbonate (Ware et al, 1992;
74 Gattuso et al, 1993; Gattuso et al, 1995; Smith, 1995; Frankignoulle et al, 1996; Gattuso et al,
75 1996b). One notable exception to this is in algal-dominated reef communities, which are sinks
76 for atmospheric CO₂. They exhibit larger excess community production and/or a lower
77 community calcification, (e.g., Kayanne et al, 1995; Gattuso et al, 1996a; Gattuso et al, 1997).
78 Photosynthesis and calcification both consume inorganic carbon, but a proportion of CO₂
79 generated by calcification can be used for photosynthetic carbon fixation, so the combined
80 processes can be viewed as reciprocally supportive (Gattuso et al., 1999).

81

82 The coral reef physical framework is formed through the production of calcium carbonate
83 (CaCO₃) and maintained by marine organisms, primarily hermatypic corals, crustose coralline
84 algae (CCA), and other calcifying algae (Vecsei, 2004; Perry et al., 2008; Perry et al., 2012).
85 Scleractinian corals are primary reef builders in tropical environments, producing CaCO₃
86 through skeletal deposition. This net calcium carbonate production is a balance between gross
87 production minus the loss due to physical, chemical, and biological erosion (Cornwall et al.,

88 2021). The net calcium carbonate production and related potential vertical accretion of reefs is
89 increasingly threatened by anthropogenic climate change (Perry et al., 2018). For scleractinian
90 corals, one of the most significant consequences of OA is the decrease in the concentration of
91 carbonate ions (CO_2^{-3}) (Kleypas and Yates, 2009). Coral skeletons are made from the mineral
92 phase of calcium carbonate (aragonite), and the saturation state of aragonite (Ω_{arg}) is often
93 related to rates of calcification. Studies have demonstrated that, as CO_2 concentrations rise, the
94 saturation state of aragonite (Ω_{arg}) decreases and, in turn, the rate at which corals calcify
95 declines (Schneider and Erez, 2006; Langdon, 2005; Pandolfi et al., 2011; Venn et al., 2013).
96 Projections suggest that future rates of coral reef community dissolution may exceed rates of
97 CaCO_3 production (calcification), leading to net loss (Silverman et al., 2009; Hoegh-Guldberg
98 et al., 2007) with the majority of coral reefs unable to maintain positive net carbonate
99 production globally by 2100 (Cornwall et al., 2021).

100

101 In scleractinian corals with zooxanthellae, the precipitation of CaCO_3 through calcification is
102 tightly coupled to photosynthetic fixation of CO_2 and on average tends to be three times
103 higher in daylight conditions than in darkness (Gattuso et al., 1999). Calcification rates can
104 increase further through feeding on phytoplankton and suspended particles (Houlbreque and
105 Ferrier-Pages, 2009). Change in community structure is linked to the balance between
106 community metabolism and calcification with the CO_2 flux of seawater (Kayanne et al.,
107 2005). In reefs under thermal stress, rates of primary production and dark respiration
108 increase, but community excess organic production decreases dramatically (Kayanne et al.,
109 2005).

110

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

113 habitat and shelter (Price et al., 2011) for a number of invertebrate and fish species, with
114 productivity sustaining higher trophic levels. Reef-building corals are generally considered to
115 be the dominant components of healthy or pristine coral reefs, but inconspicuous turfing and
116 encrusting coralline algae contribute substantially to reef benthic primary resources in these
117 areas (Odum and Odum, 1955; Hatcher, 1997). The abundance of large frondose macroalgae
118 is typically inversely related to coral abundance (Done, 1992; Hughes et al., 2017b);
119 macroalgae are common on reef flat, back reef, and inshore fringing reef areas, whereas corals
120 are more common on reef slopes (Purcell and Bellwood, 2001). Calcified macroalgae can also
121 contribute significantly to the deposition of carbonates (Nelson, 2009). In particular, species of
122 the genus *Halimeda* (order Bryopsidales), widely distributed across tropical and subtropical
123 environments, contribute significantly to reef calcification and productivity rates because of
124 their fast growth and rapid turnover rates (Vroom et al., 2003, Smith et al., 2004, Nelson, 2009)
125 compared to corals or coralline red algal (CRA). Calcification rates of *Halimeda* make it a
126 major contributor to CaCO₃ in reefs in the Caribbean (Blair and Norris, 1988; Nelson, 2009),
127 Tahiti and the Great Barrier Reef (Drew, 1983; Payri, 1988). In certain locations, precipitation
128 of calcium carbonate can approach 2.9 kg CaCO₃ m⁻² yr⁻¹, positioning *Halimeda* as a major
129 contributor to carbonate budgets within shallow waters around the globe (Price et al., 2011).
130 This group further occupies a diverse range of environments (mangroves, seagrass beds, and
131 coral reefs) and can produce structurally complex mounds that serve as critical habitat for a
132 diversity of marine life (Rees et al., 2007).

133

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

138 hydrodynamic boundary layers over time (Shashar et al., 1993; Zeebe et al. 1999; Anthony et
139 al., 2011; Shamberger et al., 2011) or in larger water masses as they move across a given reef
140 (Barnes, 1983; Barnes and Lazar, 1993; Frankignoulle et al., 1996; Gattuso et al., 1996a;
141 Niggel et al., 2010; Wild et al., 2010). The magnitude of reef contributions to changes in water
142 column chemistry is difficult to predict because of the net effect of local oceanographic
143 conditions, relative abundance of the different members of the reef community and their
144 individual metabolic rates. In addition to producing and consuming O₂, photosynthetic
145 organisms alter concentrations of dissolved inorganic carbon through uptake of dissolved
146 inorganic carbon (CO₂ or bicarbonate ion; e.g. Raven et al., 1995) during photosynthesis and
147 release of CO₂ during dark respiration, thus altering the pH of the surrounding water column
148 (Murru and Sandgren, 2004). Calcifying organisms also alter the biogeochemistry in the water
149 column by releasing CO₂ and H⁺ ions during the production of CaCO₃ and thus decreasing the
150 pH (Jokiel, 2011). The effect on water column chemistry by hybrid organisms like calcifying
151 primary producers, such as corals with zooxanthellae and calcifying algae, therefore becomes
152 very challenging to measure in situ.

153

154 Coastal environments are frequently high-use areas by humans, impacted by multiple land- and
155 sea-based human activities, and in such cases the potential for interaction between climate and
156 other anthropogenic variables affecting biological responses exists (Harley et al., 2006;
157 Schindler, 2006; Walther, 2010). Contrary to Southwestern Australia which has one of the
158 fastest increasing rates of change from cumulative human impacts (Halpern et al., 2019), the
159 Kimberley bioregion located in the northern part of Western Australia is unique, representing
160 one of the few “very low impact” tropical coast and shelf areas globally – only 3.7% of the
161 global oceans fall in this category (Halpern et al., 2008). It is host to extensive coastal reef
162 systems, isolated offshore reefs and islands. Few process studies have been carried out in the

163 region due to the remoteness of these reefs, some of which are located 100s of km from the
164 coastline, meaning that fieldwork and data acquisition can be difficult and costly. So that reefs
165 can continue to deliver ecosystem services into the future metabolic measurements of reef
166 organisms are necessary to characterize reef health in terms of fundamental processes such as
167 photosynthesis, respiration and calcification (Madin et al., 2016; Carlot et al., 2022). However,
168 there are limited numbers of studies examining the individual effects of key primary producers
169 on water chemistry in the same study, and thus, we lack knowledge of the relative contributions
170 of the main reef builders to net community metabolism and CaCO₃ production on most coral
171 reefs. Here, we compare metabolic and calcification rates of the dominant intertidal taxa of
172 macroalgae and coral at Browse Island, a small island in the Kimberley, something never
173 previously examined in these systems. Rates of metabolism and calcification were determined
174 in on-ship incubations in October 2016, April 2017 and October 2017. Using the proportional
175 cover of the dominant benthic community, these rates were upscaled to gain whole of
176 community metabolism estimates for the island habitats.

177

178 **2. Methods**

179 *2.1 Study site*

180 Browse Island is located on the mid-shelf just inside the 200 m isobath off the Kimberley coast
181 in northern Western Australia (14°6'S, 123°32'E; Fig. 1). The island is surrounded by a small
182 (~ 4.5 km²) planar platform reef consisting of a shallow lagoon, an extensive reef flat that is
183 conspicuously absent to the northeast of the island, and a well-defined reef crest and slope.
184 Tides are semidiurnal with a maximum range of < 5 m, exposing the reef crest and reef platform
185 habitats during low tides. The intertidal habitats are characterised by low species richness and
186 dominated by small turfing algae and calcified macroalgae of the genus *Halimeda* (15–22%
187 and 6–9% cover respectively) (Olsen et al., 2017). Coral assemblages are well developed with

188 cover of 5–8% in the intertidal habitats and 18% on the shallow reef slope (< 10 m) (Olsen et
189 al., 2017).

190

191 *2.2 Algae and coral collection*

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

205

206 *2.3 Light and dark incubations*

207 Light and dark incubations were undertaken on the back deck of the research vessel. Four 60
208 L holding tanks were placed in a shade-free spot under natural light conditions, filled with
209 seawater and connected to a flow-through seawater system driven by an Ozito PSDW-350 watt
210 Dirty Water Submersible Water Pump with a maximum flow rate of 7,000 litres/hour, which
211 ensured the setup remained at ambient temperature (Fig. 2). The intensity of photosynthetically
212 active radiation (PAR) was recorded for each set of incubations with a HOBO Micro Station

213 logger (H21-002, Onset) placed inside one of the tanks. Six 1.56 L clear Perspex incubation
214 cores (24 total per incubation) fitted with stirring caps, were placed in each holding tank and
215 spaced evenly apart to minimise shading (Fig. 2).

216

217 Depending upon abundance, individual specimens of algae and coral were placed in 6 to 12
218 replicate incubation cores per taxa except where not enough individuals could be found. Table
219 1 shows the taxa incubated during each sampling trip and the number of replicates. Water
220 samples from the holding tanks were measured at each time point as controls and, in addition,
221 in October 2017, a separate seawater control (six replicate incubation cores with seawater) was
222 included. After a period of acclimation (1 to 2 h), incubations were run over a four-hour period.
223 The light incubations were conducted while the sun was at its zenith providing full irradiance
224 to the samples. After two hours, the tubs were covered with a black lid ensuring no light could
225 enter and the samples incubated for two hours in the dark.

226

227 To estimate oxygen production or consumption during the incubations, a 40 mL water sample
228 was extracted from each of the 24 cores and the four tubs at the start of the incubations and
229 hourly thereafter. A port in the cap of each core allowed for sample collection using a syringe.
230 As the sample was removed, the same volume of liquid was automatically replaced from the
231 flowthrough tank into the core so that the core volume remained constant through the
232 experiment. Samples were immediately analysed for temperature and dissolved oxygen (O₂)
233 with a YSI 5100 bench-top oxygen and temperature meter with YSI 5010 BOD stirring probe,
234 calibrated daily in air. Sample pH was determined using a TPS Aqua pH meter with an Ionode
235 probe, calibrated daily with pH 7.00 and 10.00 buffers. A second 35 mL water sample was
236 collected from each core and tub and split between one 10 mL glass vacutainer for alkalinity
237 and duplicate 10 mL sterile vials for nutrient analyses. Nutrient samples were immediately

238 frozen and alkalinity samples were stored cool and dark. At the end of the incubation, algal and
239 coral specimens were frozen. All samples were transported to Perth, Western Australia, to be
240 analysed.

241

242 *2.4 Surface areas of coral and algal specimens*

243 Metabolic measurements were standardised by surface area of the incubated specimens since
244 this represents the area available for photosynthesis and nutrient uptake. The surface area of
245 specimens of coral, *Halimeda* and turf + substrate were estimated using a single wax dipping
246 method (Veal et al., 2010). Specimens were dried, weighed and then dipped in paraffin wax at
247 65°C. The waxed samples were weighed again, and the weight of the wax calculated. The
248 surface area was estimated from the wax weights against a calibration curve constructed by
249 wax dipping geometric wooden objects of known size. The surface areas of the remaining taxa,
250 were estimated from photographs in ImageJ (Rueden et al., 2017). The ‘footprint’ of each
251 sample, i.e. the surface area of reef occupied by the organism, was also estimated by tracing
252 the outline of the specimen photographed from straight above in ImageJ.

253

254 *2.5 Chemical analyses*

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

262

263 From SOP3b in Dickson et al. 2007, total alkalinity was determined for single replicates to the
264 nearest 5 $\mu\text{mol L}^{-1}$ equivalent (hereafter referred to as $\mu\text{mol L}^{-1}$) using an open cell Metrohm
265 titrator (841 Titrand, Burette: 800 Dosino 10 mL) with a Metrohm micro-glass pH probe
266 calibrated with Certipur buffer solutions at pH 2.00, 4.01, 7.00, and 10.00 (at 25.0°C). Samples
267 were kept in a Jubalo F12 temperature control water bath prior to decanting a 10 mL aliquot of
268 sample into a vessel with a water jacket maintaining temperature at 25.0°C. Samples were
269 titrated with 0.012 N HCl, standardised against sodium carbonate (99.95 to 100.05 wt%) with
270 an initial volume of titrant added to reach pH 3.5. Titrations were run to an end-point of pH 3
271 with Gran plot (Excel macro) to determine the total alkalinity endpoint near pH 4.2. Carbonate
272 system parameters were calculated from pH (measured during the incubations) and total
273 alkalinity using the package 'seacarb' (Gattuso et al., 2018) in R (R Core Team, 2018).
274 Alkalinity and carbonate parameters were not determined in April 2016.

275

276 *2.6 Oxygen fluxes and calcification rate calculations*

277 The changes in O_2 concentrations during light- and dark incubations were expressed as mmol
278 per day assuming stable hourly production rates over 24 h. Any replicates where O_2 did not
279 increase during both of the light intervals or did not decrease during both of the dark intervals
280 were excluded from further analysis. Net fluxes of O_2 per day ($\text{mmol day}^{-1} \text{m}^{-2}$) were calculated
281 for each sample assuming a 12 h photoperiod. Calcification rates of corals and calcifying algae
282 (*Halimeda opuntia*. and *Galaxaura* sp.) were estimated using the alkalinity anomaly method
283 (Smith and Key, 1975) uncorrected for changes in nutrient concentration (Chisholm and
284 Gattuso, 1991) where precipitation of one mole of CaCO_3 leads to the reduction of total
285 alkalinity by two molar equivalents. Rates per surface area ($\text{mmol day}^{-1} \text{m}^{-2}$) were obtained by
286 dividing these values by the surface area of each specimen.

287

288 A census-based approach was used to estimate the amount of CaCO₃ and O₂ produced by a
289 single taxon per unit area of reef surface per year (Shaw et al., 2016). The rates of calcification
290 and net O₂ production per day were divided by the ‘footprint’ area of each specimen. To
291 estimate the relative contributions from each taxon to community production per m² of reef,
292 these rates were multiplied by the relative percent cover in each of the major habitats. Estimates
293 of percent cover based on drop camera image analysis were obtained from Olsen et al. (2017).
294 The productivity rates for individual coral species were combined into one value for coral.

295

296 *2.7 Statistical analyses*

297 The relationships between net changes in pH and O₂ and between net O₂ production and net
298 calcification (in light and dark incubations) were examined by linear regression. Significance
299 of regressions were calculated for algae, calcified algae and corals and the 95% confidence
300 intervals for the slope of each line in R (R Core Team, 2018). Regressions were examined with
301 ANOVA and deemed significant if $p < 0.05$.

302

303 **3 Results**

304 *3.1 Experimental conditions*

305 Nutrient concentrations were low and similar among sampling trips (Table 2), as is
306 characteristic of tropical Eastern Indian Ocean offshore waters (McLaughlin et al., 2019).,
307 Concentrations of nitrate were 0.05 to 0.17 $\mu\text{mol L}^{-1}$, ammonium 0.12 to 0.13 $\mu\text{mol L}^{-1}$,
308 phosphate 0.07 to 0.1 $\mu\text{mol L}^{-1}$, and silicate 2.3 to 3 $\mu\text{mol L}^{-1}$. Oxygen was around 0.19 mmol
309 L^{-1} to 0.22 mmol L^{-1} and salinity 34.2 to 34.8 ppt. Light and temperature conditions in the
310 incubations were representative of *in situ* conditions on the reef platform and were similar
311 among trips. PAR levels were 1500 to 1587 $\mu\text{E m}^{-2} \text{s}^{-1}$ and slightly higher in October.
312 Temperatures were 28.3 to 32.8°C and highest in April. Carbonate system parameters were

313 not obtained for April 2016 due to instrument error, and some minor differences in pCO₂,
314 HCO₃⁻, CO₃²⁻, DIC and Ω Aragonite were noted between October 2016 and 2017 (Table 2).
315 Alkalinity and pH were both higher in 2016, and there were associated minor differences in
316 the concentrations of the carbonate species and the aragonite saturation state (Table 2).

317

318 3.2 Changes in oxygen and pH

319 Changes in dissolved O₂ differed among taxa, and between light and dark incubations. In the
320 seawater controls O₂ changed by < 0.01 mmol h⁻¹ in both light and dark incubations, showing
321 that the contribution of any organisms in the seawater itself to O₂ production and dark
322 respiration was minimal. No corrections were therefore applied. In the light incubations O₂
323 productivity fluxes were positive for all taxa (Fig. 3, top panel). The highest light flux of O₂
324 of ~380 mmol m⁻² day⁻¹ was measured for *Galaxaura* in October 2017 (Fig. 3, top). Corals
325 generally produced 100 to 260 mmol O₂ m⁻² day⁻¹ in the light, except *Heliopora*, which had
326 a flux of 50 to 80 mmol O₂ m⁻² day⁻¹. All taxa consumed O₂ during the dark incubations
327 when changes in O₂ are due to dark respiration, with mean fluxes of -15 to -190 mmol O₂
328 m⁻² day⁻¹ (Fig. 3, middle). All algae were net autotrophic and produced 6 to 111 mmol O₂
329 m⁻² day⁻¹ with the highest net O₂ flux measured for *Galaxaura* and turf at 111 and 36 mmol
330 O₂ m⁻² day⁻¹ respectively (Fig. 3, bottom). In contrast, around half of the corals were net
331 consumers of O₂ and average net fluxes spanned a wide range from -42 to 47 mmol O₂ m⁻²
332 day⁻¹.

333

334 In the light incubations, pH generally increased by 0.03 to 0.25 h⁻¹ for all taxa, except for
335 *Halimeda* in April 2016 and October 2017, which showed no change or a very small increase
336 (Fig. 4, top panel). In dark incubations, mean pH decreased for all taxa by 0.02 to 0.21 h⁻¹
337 indicative of a net increase in CO₂ through dark respiration (Fig. 4, middle). Non-calcifying

338 algae (*Sargassum*, *Caulerpa* and turf) raised net pH by 0.02 to 0.05 h⁻¹ (assuming equal
339 periods of light and darkness) (Fig. 4, bottom panel). The net change in pH was generally
340 negative for corals and calcifying algae (-0.01 to -0.08 h⁻¹), except for the coral *Goniastrea*
341 in April and October 2016 (0.01 h⁻¹) and the calcifying alga *Galaxaura* (0.03 h⁻¹; Fig. 3,
342 bottom).

343

344 Net changes in pH are largely driven by metabolic uptake and release of CO₂. We found
345 positive relationships between changes in pH and net production or consumption of O₂ except
346 in seawater controls where changes in O₂ and pH were minor (Fig. 5). The relationships for
347 algae, calcifying algae and coral were all significant, but had relatively low adjusted *r*² values
348 of 0.59, 0.46 and 0.19 respectively, suggesting significant variability among species and
349 individuals within each of these groups.

350

351 3.3 Calcification Rates

352 Corals, *Halimeda* and *Galaxaura* had positive calcification rates in light ranging from 4.2 to
353 18.4 g CaCO₃ m⁻² d⁻¹ (Fig. 6, top panel). In the dark, calcifying rates were smaller and just
354 under half of the rates were negative suggesting dissolution of CaCO₃ (Fig. 6, middle panel).

355 The resulting net calcification rates (based on equal periods of light and dark_ - monthly
356 average sunrise and sunset at Browse Island of 0552 and 1739 for April, and 0519 and 1754
357 for October; WillyWeather, 2022) were all positive and ranged from 1.9 to 9.9 g CaCO₃ m⁻²
358 d⁻¹ (Fig. 6, bottom). Rates of calcification were strongly linearly correlated to net O₂
359 production and were significantly higher in light than in darkness for both corals and algae
360 (Fig. 7).

361

362 3.4 Contributions to community production

363 In intertidal habitats (lagoon and high reef platform) around Browse Island, the estimated
364 relative contributions of coral (8 % cover) and *Halimeda* (7 % cover) to the reef production
365 of CaCO₃ were similar, around 600 to 840 g m⁻² year⁻¹ (Fig. 8, top panel). The low reef
366 platform had very low coral cover of < 3% (Fig. 8, middle), which therefore made a smaller
367 contribution to calcification of ~240 g CaCO₃ m⁻² year⁻¹ in this habitat (Fig. 8, top). In
368 contrast, calcification on the subtidal reef slope was predominantly from corals (19 % cover),
369 which produced ~1540 g CaCO₃ m⁻² year⁻¹, around twice the amount compared to *Halimeda*
370 (7 % cover). *Galaxaura*, which had high measured rates of productivity and calcification, was
371 extremely rare (0.02 % total cover found only in October 2017; Olsen et al., 2017) and thus
372 its contribution to community calcification and productivity were negligible. Turf was
373 responsible for the majority of the O₂ production in all habitats and produced an estimated 8
374 to 13 mmol O₂ m⁻² d⁻¹ compared to < 2 for *Halimeda* mmol O₂ m⁻² d⁻¹ and -4 to -1 mmol O₂
375 m⁻² d⁻¹ for corals (Fig. 8, second panel from top).

376

377 4 Discussion

378 This study investigated the metabolism of coral and algae on the reef of remote Browse Island,
379 found on the mid-shelf region of the Kimberley in Western Australia. Due to its remoteness,
380 Browse Island presented a unique opportunity to observe these organisms in a pristine habitat
381 where direct anthropogenic pressures are minimal. The Island has semidiurnal tides reaching
382 a maximum range of 5 m (Olsen et al., 2017), half the magnitude of tides experienced by reefs
383 closer to the coast (McLaughlin et al., 2019), and its benthic structure is very different from
384 both Kimberley inner and outer shelf reefs. Lowe et al. (2015) have revealed that strongly tide-
385 dominated circulation can occur on Kimberley reef platforms and the trapping of water on a
386 reef, such as that found at Browse Island, can provide benefits for reef organisms in terms of
387 avoiding aerial exposure. However, it can dramatically increase the residence (or flushing)

388 times of reefs, which can lead to extreme diel variations in water quality (Lowe et al., 2015).
389 Seawater O₂ and carbonate chemistry can vary over diel tidal cycles, like those found at Browse
390 Island, and are related to patterns in autotrophic photosynthesis and dark respiration (e.g.,
391 Duarte et al., 2013). Primary production and the uptake of CO₂ by coral and algae during
392 daylight hours results in elevated pH and an elevated aragonite saturation state (Ω_{arag}) during
393 the day when calcification rates peak. The process of calcification decreases pH in the
394 surrounding water, but for calcifying autotrophs CO₂ uptake and fixation through
395 photosynthesis can potentially offset changes to the carbonate chemistry caused by
396 calcification (Anthony et al., 2011; Smith et al., 2013).

397

398 Mesocosm experiments have shown that reef-building (hermatypic) corals tend to reduce pH
399 and consume O₂ (e.g. (Gattuso *et al.* 2015; Smith *et al.* 2013)), whereas calcifying macroalgae
400 increase pH and O₂ during daytime (Borowitzka and Larkum 1987; Smith *et al.* 2013). Both
401 corals and calcifying macroalgae reduce pH and O₂ concentrations due to respiration during
402 nighttime, but the rates of change differ among species (Smith *et al.* 2013). The organisms
403 investigated in the present study showed typical patterns of O₂ production in daylight and
404 consumption in darkness to other similar island reef systems as a result of photosynthesis and
405 dark respiration, but the metabolic measurements showed clear differences among taxonomic
406 groups. Algae had higher positive net O₂ fluxes with rates of 18 to 350 $\mu\text{mol O}_2 \text{ m}^{-2} \text{ day}^{-1}$, of
407 which the red calcifying alga *Galaxaura* sp. had the highest rate of net productivity by far. For
408 corals, the relatively high O₂ increase measured in daylight was coupled with high rates of
409 respiration in darkness, creating a negligible or negative net O₂ production for most species,
410 except *Porites* sp. in April 2016 and *Seriatopora* sp. in October 2016 and 2017 which were net
411 positive. Although autotrophic, our data indicates that the majority of the corals we studied
412 utilise heterotrophic supply through feeding to help sustain growth in addition to

413 photosynthesis by zooxanthellae (Houlbreque and Ferrier-Pages, 2009). These patterns are
414 generally in agreement with those reported elsewhere, for example, fleshy and calcifying algae
415 showed net diel O₂ production, whereas corals generally consumed O₂, i.e. were net
416 heterotrophic, on islands in the South Pacific (*Porites* sp.) and the Caribbean (*Madracis* sp.)
417 (Smith et al., 2013).

418

419 Concurrent with changes in O₂ were changes in seawater pH, where pH increased in daylight
420 (except for *Halimeda* in April 2016 where no change was measured) and decreased in darkness.
421 The effects of metabolic activity on bulk pH (uptake and release of CO₂ through photosynthesis
422 and dark respiration) cannot be directly separated from that of calcification, which is associated
423 with the release of H⁺ ions thereby decreasing pH (Jokiel, 2011). However, differences were
424 observed in the net pH change in incubations between calcifiers and non-calcifiers. The net
425 effect of non-calcifiers on seawater pH was positive while the majority of calcifiers caused net
426 pH to decline. In the present study, *Halimeda* (April 2016) and *Goniastrea* (April and October
427 2016) caused relatively minor increases in pH, whereas the calcifying alga *Galaxaura* elevated
428 pH by, on average, 0.03 units, comparable to the net effect of non-calcifiers. This is not
429 surprising given the high rate of O₂ production measured for *Galaxaura*, which is associated
430 with sufficient levels of CO₂ fixation to compensate for the reduction in pH associated with
431 calcification in this species. A strong link was observed between metabolism and pH in all taxa,
432 demonstrated as linear relationships between changes in pH and O₂ during the incubations.
433 Previous research by Smith et al. (2013) identified two broad patterns: metabolic changes in
434 O₂ in non-calcifiers (fleshy and turf algae) linked to large changes in pH (steep slopes), and
435 metabolic changes in O₂ in calcifying organisms (*Porites* sp. *Madracis* sp. and *Halimeda* sp.)
436 producing little or no change in pH (shallow slopes). This is contrary to the present study's
437 observations where pH and O₂ relationship gradients were similar for calcifiers and non-

438 calcifiers. Non-calcifying organisms were found to consistently have a net positive effect on
439 both pH and O₂. Change in pH for the same net change in O₂ was elevated for non-calcifiers
440 compared to calcifiers.

441

442 Production and accumulation of reef framework carbonate is controlled by the relative rates of,
443 and the interactions between, a range of ecologically, physically and chemically driven
444 production and erosion processes (Perry et al., 2008; Montaggioni and Braithwaite, 2009), with
445 the relative importance of different taxa for CaCO₃ production differing among reefs and
446 among habitats within reefs. Coral growth can be measured in several ways: linear extension
447 rate, global skeletal growth and calcification rate (measured using the alkalinity technique or
448 by ⁴⁵Ca incorporation) (Houlbreque and Ferrier-Pages, 2009). Methods to calculate
449 calcification can vary in accuracy where overestimates of calcification rates can result from
450 calculations based on changes in alkalinity, while those relying on CaCO₃ content and growth
451 measurements, either through staining or tagging segments, may produce minimum estimates
452 as loss of new tissue is not accounted for (Hart and Kench, 2007; Houlbreque and Ferrier-
453 Pages, 2009). The alkalinity method employed in the present study was the best possible option
454 when working in a remote location where actual growth rates cannot be easily assessed, or use
455 of radioisotopes limited. Rates of net community calcification for reef flats worldwide range
456 from 7.3 to 90 mol (730 to 9000 g) CaCO₃ m⁻² year⁻¹ with an average of 47 mol (4700 g)
457 CaCO₃ m⁻² year⁻¹ (Atkinson, 2011). The patterns found in the present study — higher
458 calcification rates in daylight compared to in darkness for all corals and calcifying algae — are
459 typical. However, the coral CaCO₃ production rates per reef area (7 to 8% cover low reef
460 platform, 19% reef slope) measured here (240 g m⁻² year⁻¹ for low reef platform, 610 to 756 g
461 m⁻² year⁻¹ in the other intertidal habitats, and 1536 g m⁻² year⁻¹ on the reef slope) were
462 somewhat lower than values reported elsewhere. In 2016, the dark rates of calcification in

463 corals were less than 50% of the rates in light with some (*Porites* and *Heliopora*) negative.
464 Dark rates of calcification in 2017 were negative or near zero for all species except *Porites*,
465 *Pocillopora* and *Seriatopora*. Houlbreque et al. (2004) showed that coral feeding enhances dark
466 calcification rates in scleractinian corals, but incubations in our study were done in absence of
467 supplemental feeding. The trend observed here may be due to some dissolution of CaCO₃ due
468 to the reduced pH during dark incubations or could be an artefact of the experimental
469 conditions. This result should therefore be taken with some caution, in particular for *Porites* in
470 October 2016, which saw the largest decrease (Fig. 5, middle panel). However, the resulting
471 strong relationship between net carbonate production and net carbonate consumption is
472 consistent with previous studies both *in situ* and in mesocosms (Albright et al., 2013).

473

474 Corals are typically the primary framework-producing components on a tropical reef and
475 dominate carbonate production per unit area (Vecsei, 2004), however additional CaCO₃ is
476 produced by calcareous crustose coralline algae (CCA) and calcareous algae of the genus
477 *Halimeda*, (e.g. Payri, 1988). Sprawling lithophytic species of *Halimeda*, like the majority of
478 the *Halimeda* around Browse Island, tend to be fast growing and have high calcification rates
479 (Hart and Kench, 2007). Rates of calcification per area of 100% *Halimeda* cover have been
480 estimated to 400 to 1667 g CaCO₃ m⁻² year⁻¹ (in Hart and Kench, 2007 Suppl info). In other
481 locations, *Halimeda* has been estimated to contribute around 1100 to 2400 g CaCO₃ m⁻² year⁻¹
482 to benthic carbonate production (Drew, 1983; Freile et al., 1995; Hudson, 1985; Kangwe et al.,
483 2012; Payri, 1988; Rees et al., 2007), which is higher than the 600 to 840 g CaCO₃ m⁻² year⁻¹
484 estimated for *Halimeda opuntia* in the intertidal habitats in the present study. These rates
485 depend both on the intrinsic calcification rates and on the abundance or cover of algae (6.1 to
486 8.7% cover on Browse, which corresponds to ~150 to 250 g dw m⁻²).

487

488 Nutrient capacity is one important driver of productivity in many reef ecosystems. The rate at
489 which nutrients are recycled between the constituents of the system (the ambient nutrient
490 availability, and the nutrients stored within plant and animal biomass) depends on input from
491 a variety of sources (e.g., associated with seasonal rains or upwelling) (DeAngelis, 1992;
492 Hatcher, 1990). Coral reefs, typically have low ambient nutrient availability and receive little
493 sustained exogenous nutrient input (Hatcher, 1990; Szmant, 2002), thus the high rates of
494 production found within these ecosystems are largely attributed to the nutrients stored and
495 cycled by living biomass (Pomeroy, 1974; DeAngelis et al., 1989; Sorokin, 1995). Fishes
496 typically make up a substantial component of living biomass on coral reefs and represent an
497 important reservoir of nutrients in these ecosystems (Allgeier et al., 2014). Contrary to our
498 expectations given its remote location in an area of apparently low anthropogenic impacts, the
499 reef platform around Browse Island was depauperate with a conspicuous lack of diversity in
500 key groups including macroalgae, macroinvertebrates and teleost browsers (Bessey et al.,
501 2020). McLaughlin et al. (2019) found surface water standing stock nutrient concentrations
502 low along Kimberley shelf. Conditions at Browse Island were similar with low water column
503 nutrients for nitrate, ammonia and phosphate during all trips. Understanding how changes in
504 animal populations alter nutrient dynamics on large ecological scales is a relatively recent
505 endeavour (Doughty et al., 2015). Allgeier et al. (2016) showed that targeted fishing of higher
506 trophic levels reduces the capacity of coral reef fish communities to store and recycle nutrients
507 by nearly half. Fish-mediated nutrients enhance coral growth (Meyer et al., 1983) and primary
508 production (Allgeier et al., 2013), and may regulate nutrient ratios at the ecosystem scale
509 (Allgeier et al., 2014).

510

511 The Kimberley region-wide averages of coral cover and macroalgal cover are 23.8% and 7.1%
512 (Richards et al., 2015) respectively. However, this relationship at Browse Island is reversed,

513 with macroalgae more dominant at 28% total cover to that of coral at 9% total cover. On the
514 Browse Island reef platform, the same pattern is observed where averages were 5 to 8% for
515 coral and 32% for macroalgae, differing from those of the regional averages of 14.4% and
516 15.5% of coral and macroalgae respectively (Richards et al., 2015). While the estimates
517 provided here approximate the relative contributions of *Halimeda* and coral to CaCO₃
518 production, they do not add up to a whole system budget. There are other organisms likely to
519 contribute significantly. For example, the present study did not measure metabolic or
520 calcification rates of encrusting coralline algae, which, although making up a modest 1.0 to
521 3.0% of the benthic cover in the lagoon and reef platform habitats at Browse Island, become
522 more prominent at 11.8 to 14.1% on the reef crest and slope (Olsen, unpublished data). To
523 calculate the true CaCO₃ production per area of reef, the calcification rate would need to be
524 multiplied by the benthic cover of coralline algae and the square of the benthic rugosity (Eakin,
525 1996). Using typical values for rugosity from Eakin (1996) of 1 to 1.4 for the lagoon and reef
526 platform and 1.7–2 for the reef crest and slope, and assuming a typical calcification rate of
527 1500 to 2500 g m⁻² year⁻¹ (for 100% flat-surface cover) (Hart and Kench, 2007), the
528 contribution of encrusting coralline algae to calcification in the lagoon and reef platform would
529 be minor at 70 to 134 g CaCO₃ m⁻² year⁻¹. However, they could produce a significant amount
530 of 980 to 1360 g CaCO₃ m⁻² year⁻¹ on the reef crest and slope, which is somewhere in between
531 the production rates estimated for *Halimeda* and corals. Encrusting coralline algae may
532 therefore contribute significantly to the CaCO₃ budget at Browse Island, at least in deeper
533 habitats. These values are similar to those measured elsewhere, for example 870 to 3770 g
534 CaCO₃ m⁻² year⁻¹ at Uva reef in the eastern Pacific (Eakin, 1996).

535

536 Metabolic rates of primary producers are clearly influenced by a multitude of factors including
537 hydrodynamics, irradiance, and nutrient availability (Smith et al., 2013). We were able to detect

538 considerable diurnal changes in water chemistry due to metabolic rates, since our experiments
539 were conducted in small enclosed mesocosms. The effect of metabolism on water chemistry is
540 expected to dissipate downstream in a more turbulent or dynamic environment (Anthony et al.
541 2011). However, coral and algae metabolic rates and resultant flux from diffusive boundary
542 layer also increases with flow rates (Carpenter et al. 1991; Lesser et al. 1994; Bruno and
543 Edmunds 1998; Mass et al. 2010). Because our experiments were conducted in near no-flow
544 chambers (mesocosm water was replenished with fresh seawater in small amounts during
545 sample extraction), our measurements are conservative values and likely represent the lower
546 range of potential effects that these reef organisms have on surrounding water chemistry,
547 however where residence times can be extended, particularly when trapping of water on the
548 reef at low tides occurs, our results are likely reflective of how these benthic organisms affect
549 water chemistry in the lagoonal habitats of Browse Island.

550

551 **5 Conclusions**

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

563

564 The higher cover of *Halimeda* and the low coral cover at Browse Island compared to other
565 reefs in the region mean that corals and *Halimeda* contribute equally to productivity rates of
566 CaCO₃ on the Browse Island reef flat, however, their relative contributions to the reef
567 framework and sedimentary budget of the reef is unknown. To gain an understanding of the
568 relationships between carbonate production and sinks on the reef, further study into the types
569 and amounts of CaCO₃ material found in each reef sink is necessary. The Kimberley coastal
570 shelf, which is characterised by coral reef environments with clear, low nutrient waters and
571 low productivity, has largely escaped land-based anthropogenic impacts, but has been
572 negatively affected by climate-driven coral bleaching and mortality, for example from heat
573 waves at Scott Reef in 1998 and 2016 (Smith et al., 2008, Gilmour et al., 2013 and Hughes et
574 al., 2017) and Ashmore Reef in 2003 and 2010 (Ceccarelli et al., 2011 and Heyward, 2011).

575

576 There is lack of sufficient observations of pCO₂, nutrients and research on the upper ocean
577 carbon cycle from the Indian Ocean (Sreeush et al., 2020), and which are critical to modelling
578 of ocean acidification in the region (Panchang and Ambokar, 2021). The uptake of carbon
579 dioxide by the ocean alters the composition of seawater chemistry with elevated partial
580 pressures of carbon dioxide (pCO₂) causing seawater pH and the CaCO₃ saturation state to
581 decrease (Feely et al, 2004). Ocean acidification directly threatens crucial trophic levels of
582 the marine ecosystem. Baseline reef measurements in undisturbed areas like Browse Island
583 are important to understand exclusively climate-driven stressors in lieu of local
584 anthropogenic pressures normally associated with coastal tropical reefs. The effects of
585 temperature stressors on reef communities and their productivity remain to be investigated in
586 this region. The effects of temperature stressors on reef communities and their productivity
587 remain to be investigated in this region. Different components of the reef around Browse

588 Island are likely to have different vulnerabilities to warming and heat waves. Future
589 environmental stressors leading to changes in benthic community composition, structure and
590 subsequent changes in reef productivity and in rates of production of CaCO₃, could have
591 major implications for Browse Island.

592

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594 investigation, resources, methodology, visualisation, and writing (original draft preparation);
595 Cindy Bessey - Investigation, resources, project administration, and writing (review and
596 editing); Gary A. Kendrick - Conceptualization, funding acquisition, project administration,
597 supervision, and writing (review and editing); John Keesing - Conceptualization, funding
598 acquisition, investigation, resources, supervision, and writing (review and editing); Ylva S.
599 Olsen - Conceptualization, formal analysis, investigation, project administration, resources,
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601

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605

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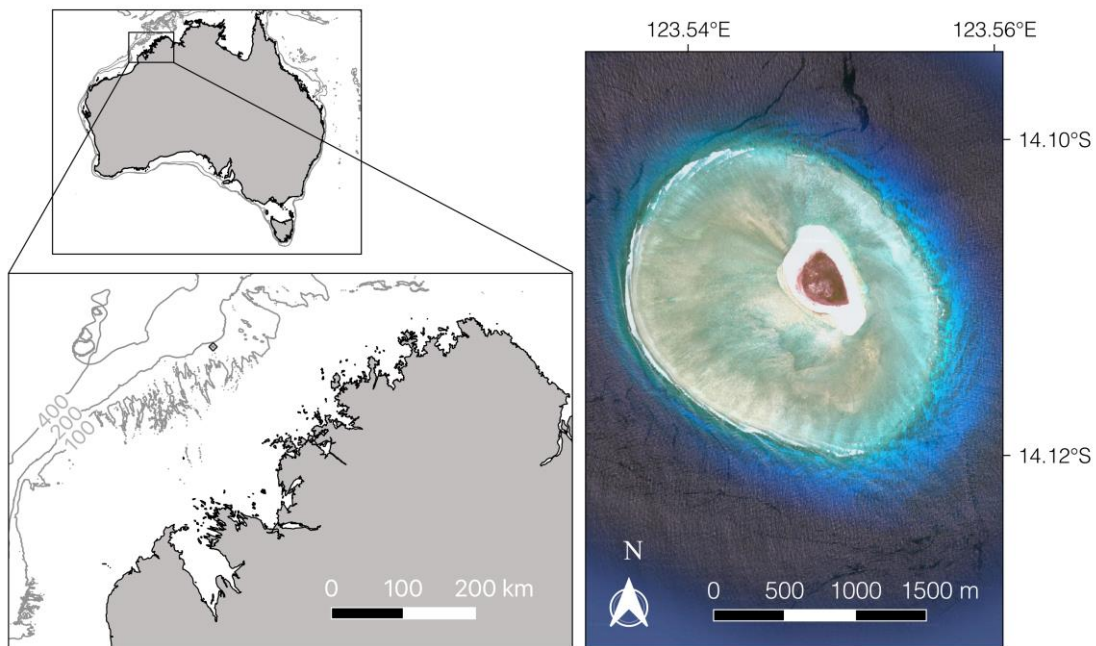
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613 **Figures**



614

615 **Figure 1.** The study site, Browse Island (diamond, bottom left map), is located just inside the
616 200-m isobath on the continental shelf. The small map (top left) shows the location of the island
617 relative to the Australian coastline with the 100, 200 and 400 m isobaths marked in gray. The
618 satellite image (right; © Google Earth 2018) shows the extent of the reef.

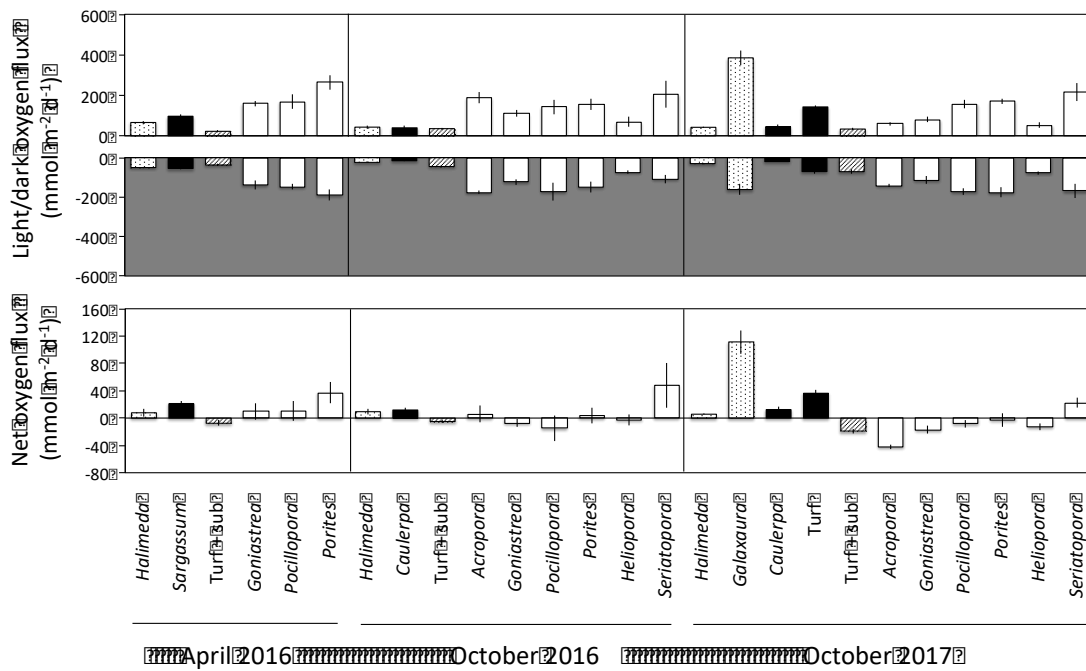
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Figure 2. Experimental setup of respirometry incubations for Browse Island coral and macroalgae.

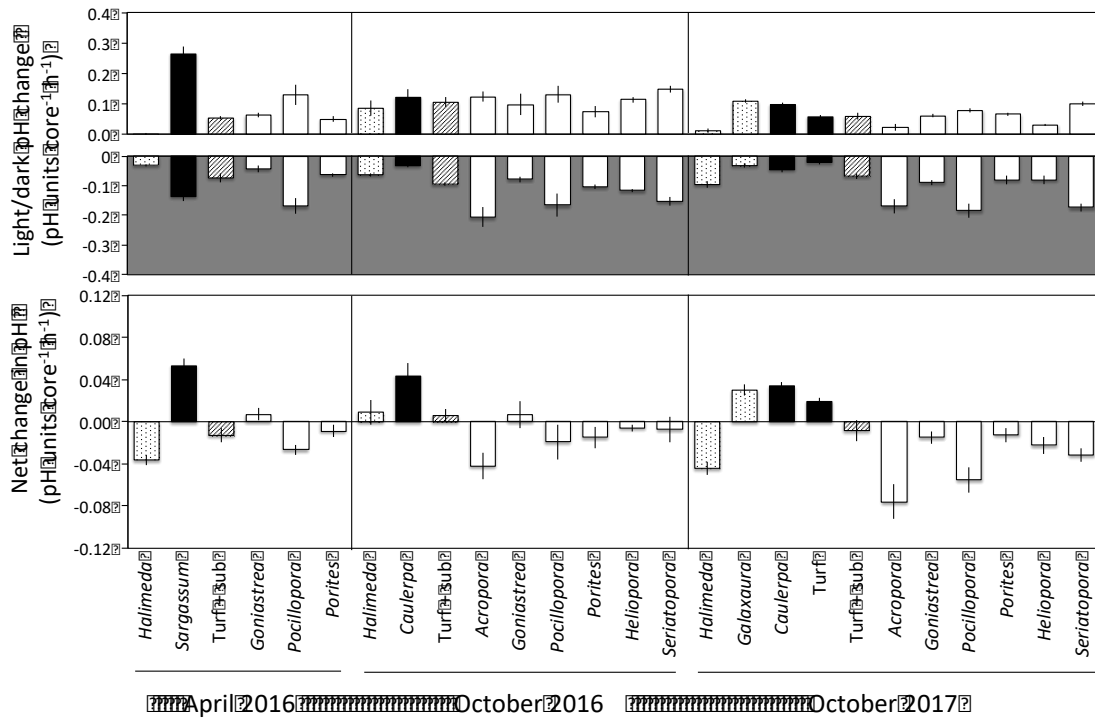
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622

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

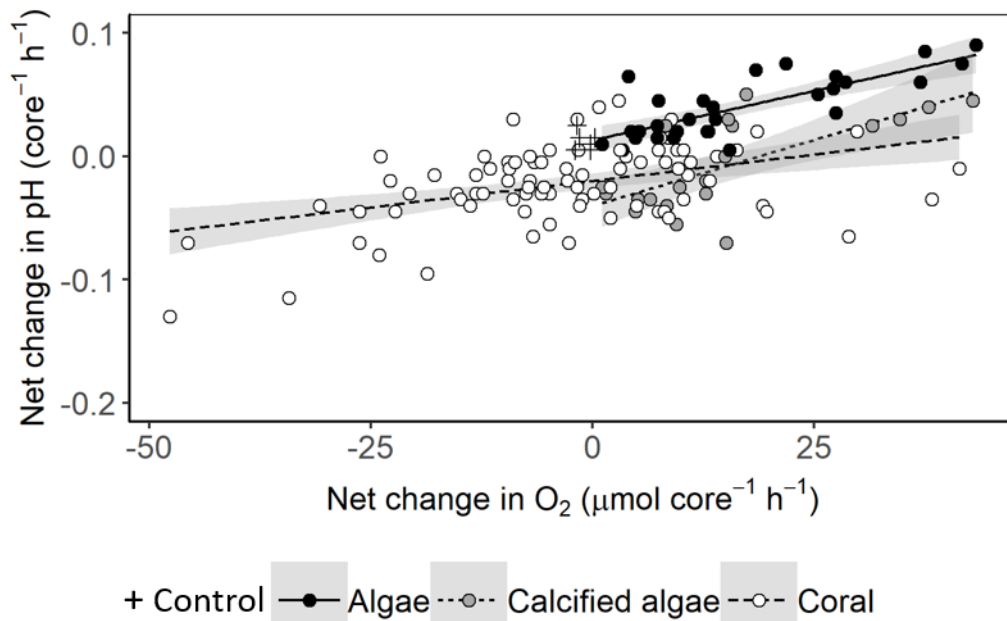
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630 **Figure 4.** Net changes in pH per hour for each 1.56-L incubation core (means \pm se) in light
 631 (top) and dark (middle) incubations calcifying algae (stippled), macroalgae and turf (black),
 632 turf + substrate (diagonal stripes) and coral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

634

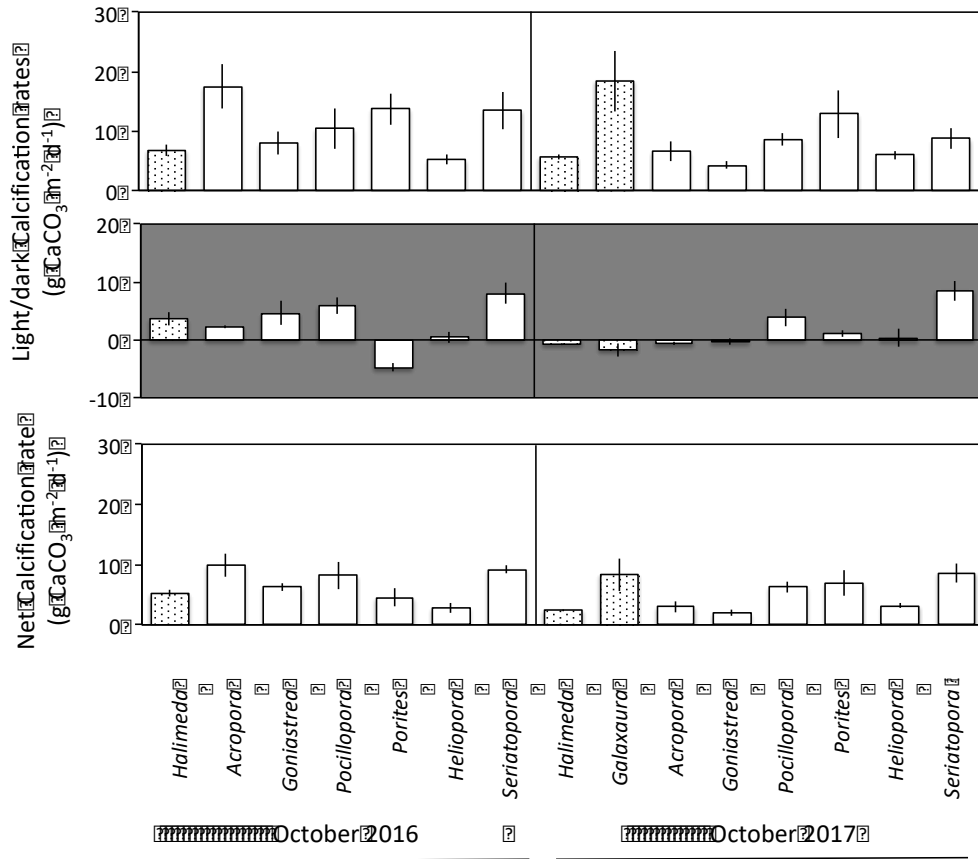


635

636 **Figure 5.** Net change in pH versus O₂ per 1.56-L incubation core assuming equal periods of
 637 light and darkness. Linear relationships are fitted with 95% confidence intervals shown in gray.

638 For algae; net change in pH = 0.13 + 0.0016 × net change in O₂ (ANOVA: F_{1,27} = 41.15, p
 639 <0.001). For calcified algae; net change in pH = -0.04 + 0.0021 × net change in O₂ (ANOVA:
 640 F_{1,19} = 17.86, p <0.001). For corals; net change in pH = -0.02 + 0.00086 × net change in O₂
 641 (ANOVA: F_{1,82} = 18.88, p <0.001).

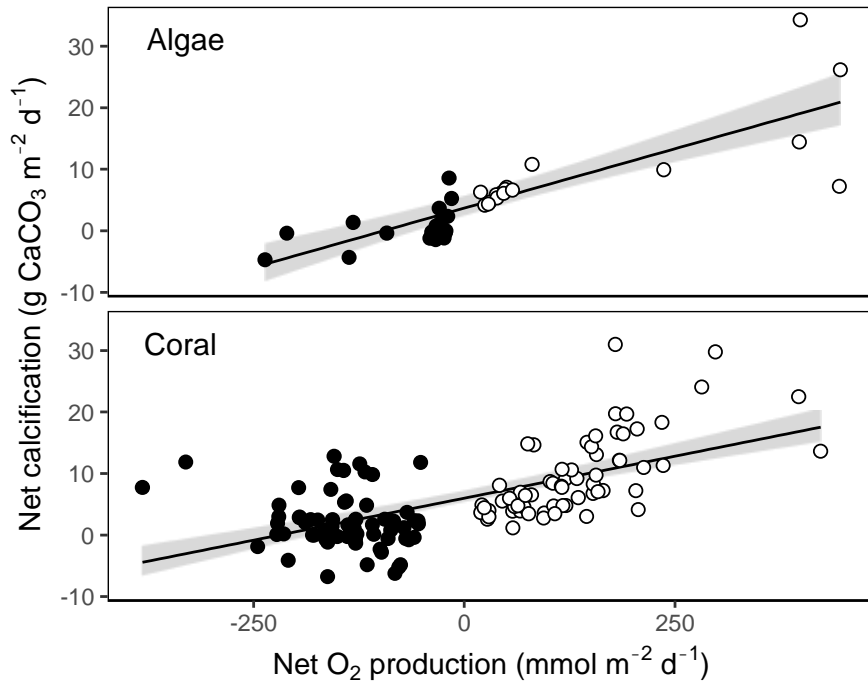
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643

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

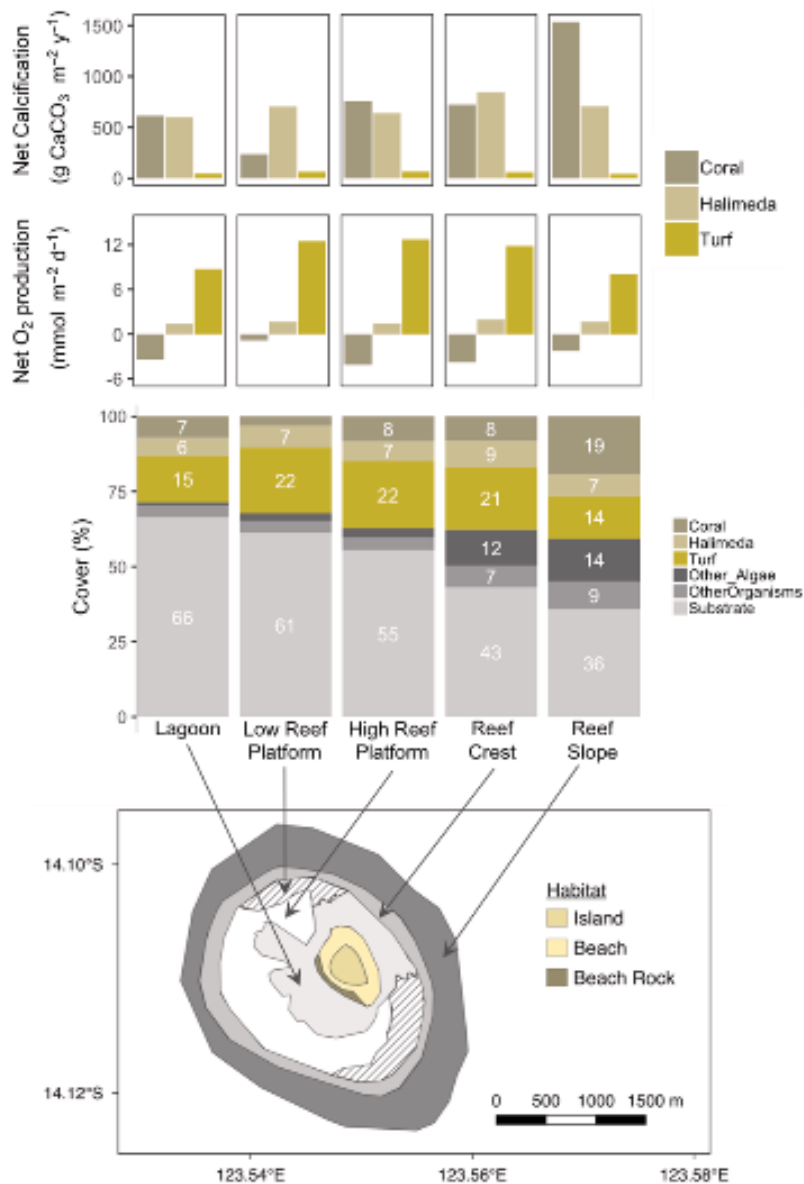
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649 **Figure 7.** Relationship between net calcification rate and net productivity for calcifying algae
 650 (top) and corals (bottom). Open circles indicate rates measured in light and closed circles rates
 651 measured in dark. Linear fits are shown with 95% confidence intervals in gray. For calcified
 652 algae; net calcification = $3.6 + 0.039 \times \text{net O}_2 \text{ production}$ (ANOVA: $F_{1,32} = 67.0$, $p < 0.001$).
 653 For corals; net calcification = $5.99 + 0.027 \times \text{net O}_2 \text{ production}$ (ANOVA: $F_{1,126} = 82.2$, p
 654 < 0.001).

655



656

657 **Figure 8.** Map of the reef around Browse Island showing the major habitat types (bottom
 658 panel). Reef surface percent cover of coral, *Halimeda*, turf and other categories in each habitat
 659 (middle panel) based on drop-camera image analysis data from (Olsen *et al.* 2017). Net
 660 calcification and net oxygen production by coral, *Halimeda* and turf per m⁻² of reef (top two
 661 panels) scaled up by multiplying rates obtained from incubations of each taxon by the percent
 662 cover in each habitat.

663 **Tables**

664 **Table 1.** Taxa measured in on-ship incubation experiments including the number of replicate
 665 specimens measured (one specimen per incubation core). Some of the specimens were not
 666 included in the final analysis due to sampling errors or due to O₂ not increasing during both of
 667 the light intervals or not decreasing during both of the dark intervals; the resulting number of
 668 specimens used are shown in brackets.

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

669

670

671 **Table 2.** Ambient concentrations of parameters measured during incubations (means \pm se);
672 nutrients ($\text{NO}_3^- + \text{NO}_2^-$ = nitrate + nitrite, NH_4^+ = ammonium, PO_4^{3-} = orthophosphate, Si =
673 silica) and oxygen (O_2), total alkalinity (TAlk), Photosynthetically Active Radiation (PAR),
674 temperature (T) and salinity. Calculated carbonate system parameters (means \pm se); CO_2
675 partial pressure ($p\text{CO}_2$), concentrations of HCO_3^- , CO_3^{2-} and dissolved inorganic carbon
676 (DIC), and the saturation state of aragonite (Ω Aragonite). In April 2016, two replicate PAR
677 measurements were taken at 11:00, 12:00 and 13:00 h. In October 2016 and 2017, PAR was
678 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
$\text{NO}_3^- + \text{NO}_2^-$ ($\mu\text{mol L}^{-1}$)	0.15 ± 0.04	0.05 ± 0.01	0.17 ± 0.01
NH_4^+ ($\mu\text{mol L}^{-1}$)	0.12 ± 0.02	0.13 ± 0.01	0.13 ± 0.01
PO_4^{3-} ($\mu\text{mol L}^{-1}$)	0.08 ± 0.01	0.07 ± 0.00	0.09 ± 0.00
Si ($\mu\text{mol L}^{-1}$)	2.74 ± 0.04	2.93 ± 0.04	2.30 ± 0.02
O_2 ($\mu\text{mol L}^{-1}$)	19.3 ± 0.19	20.8 ± 0.16	23.4 ± 0.29
PAR 11–13 h ($\mu\text{E m}^{-2} \text{s}^{-1}$)	1499.6	1587.1	1587.0
T ($^\circ\text{C}$)	32.8 ± 0.1	31.2 ± 0.1	28.3 ± 0.1
Salinity (ppt)	34.8	34.5	34.2
TAlk ($\mu\text{mol L}^{-1}$)	NA	2408 ± 5	2390 ± 2
pH	8.17 ± 0.02	8.14 ± 0.02	8.11 ± 0.01
<u>Calculated carbonate system parameters</u>			
$p\text{CO}_2$ (uatm)	NA	295 ± 14	335 ± 17
HCO_3^- (mmol kg^{-1})	NA	1.61 ± 0.03	1.69 ± 0.02
CO_3^{2-} (mmol kg^{-1})	NA	0.30 ± 0.006	0.26 ± 0.006
DIC (mmol kg^{-1})	NA	1.93 ± 0.02	1.97 ± 0.02
Ω Aragonite	NA	5.02 ± 0.11	4.27 ± 0.10

679

680

681 **References**

- 682 Albright, R., Langdon, C., and Anthony, K.R.N.: (2013) Dynamics of seawater carbonate chemistry,
683 production, and calcification of a coral reef flat, central Great Barrier Reef, *Biogeosciences*, 10, 6747-
684 6758, <https://doi.org/10.5194/bg-10-6747-2013>, 2013.
- 685 Allgeier, J.E., Yeager, L.A. and Layman, C.A.: Consumers regulate nutrient limitation regimes and
686 primary production in seagrass ecosystems, *Ecology* 94, 521–529, [doi.org/ 10.1890/12-1122.1](https://doi.org/10.1890/12-1122.1), 2013.
- 687 Allgeier, J.E., Layman, C.A., Mumby, P.J. and Rosemond, A.D.: Consistent nutrient storage and
688 supply mediated by diverse fish communities in coral reef ecosystems, *Global Change Biology*, 20,
689 2459–2472, [doi.org/ 10.1111/gcb.12566](https://doi.org/10.1111/gcb.12566), 2014.
- 690 Allgeier, J.E., Valdivia, A., Cox, C., and Layman, C.A.: Fishing down nutrients on coral reefs, *Nature*
691 *Communications*, 7, 1-5, doi.org/10.1038/ncomms12461, 2016.
- 692 Andersson A.J., and Gledhill D.: Ocean acidification and coral reefs: Effects on breakdown,
693 dissolution, and net ecosystem calcification, *Annual Review of Marine Science*, 5, 321–48,
694 <https://doi.org/10.1146/annurev-marine-121211-172241>, 2013.
- 695 Anthony, K.R.N., Kleypas, J.A., and Gattuso, J.P.: Coral reefs modify their seawater carbon
696 chemistry—implications for impacts of ocean acidification, *Global Change Biology* , 17, 3655–3666,
697 [doi: 10.1111/j.1365-2486.2011.02510.x](https://doi.org/10.1111/j.1365-2486.2011.02510.x), 2011.
- 698 Atkinson, M.J.: Biogeochemistry of nutrients. In *Coral Reefs: An ecosystem in transition*, edited by:
699 Dubinsky, Z., and Stambler, N., Springer: London, 2011.
- 700 Barnes, D.J.: Profiling coral reef productivity and calcification using pH and oxygen electrodes,
701 *Journal of Experimental Marine Biology and Ecology*, 66, 149–161, [doi:10.1016/0022-](https://doi.org/10.1016/0022-0981(83)90036-9)
702 [0981\(83\)90036-9](https://doi.org/10.1016/0022-0981(83)90036-9), 1983.
- 703 Barnes, D.J., and Lazar, B.: Metabolic performance of a shallow reef patch near Eilat on the Red sea,
704 *Journal of Experimental Marine Biology and Ecology*, 174, 1–13, [doi:10.1016/0022-0981\(93\)90248-](https://doi.org/10.1016/0022-0981(93)90248-M)
705 [M](https://doi.org/10.1016/0022-0981(93)90248-M), 1993.
- 706 Bessey, C., Keesing, J.k., Mclaughlin, M.J., Rees, M., Tonks, M., Kendrick, G.A., and Olsen, Y.S.:
707 Teleost community composition and the role of herbivory on the intertidal reef of a small isolated
708 island in north-west Australia, *Marine and Freshwater Research*, 76, 684–696,
709 doi.org/10.1071/MF19066, 2020.
- 710 Blair, S.M., and Norris, J.N.: The deep-water species of *Halimeda* Lamouroux (Halimediaceae,
711 Chlorophyta) from San Salvador Island, Bahamas: species composition, distribution and depth
712 records, *Coral Reefs*, 6, 227–236, doi.org/10.1007/BF00302019, 1988.
- 713 Borowitzka, M.A., and Larkum, A.W.D.: Calcification in algae: Mechanisms and the role of
714 metabolism, *Critical Reviews in Plant Sciences*, 6, 1–45, doi.org/10.1080/07352688709382246, 1987.
- 715 Bruno, J.F. and Edmunds, P.J.: Metabolic consequences of phenotypic plasticity in the coral *Madracis*
716 *mirabilis*: the effect of morphology and water flow on aggregate respiration. *Journal of Experimental*
717 *Marine Biology and Ecology*, 229, 187–195, [doi.org/10.1016/s0022-0981\(98\)00050-1](https://doi.org/10.1016/s0022-0981(98)00050-1), 1998.
- 718 Carlot, J., Rouzé, H., Barneche, D.R., Mercière, A., Espiau, B., Cardini, U., Brandl, S.J., Casey, J.M.,
719 Pérez-Rosales, G., Adjeroud, M., Hédouin, L., and Parravicini, V.: Scaling up calcification,
720 respiration, and photosynthesis rates of six prominent coral taxa, *Ecology and Evolution*, 12, e8613,
721 doi.org/10.1002/ece3.8613, 2022.

- 722 Carpenter, R.C., Hackney, J.M., and Adey, W.H.: Measurements of primary productivity and
723 nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow, *Limnology and*
724 *Oceanography*, 36, 40–49, doi.org/ 10.4319/lo.1991.36.1.0040, 1991.
- 725 Ceccarelli, D.M., Jones, G.P., and McCook, L.J.: Interactions between herbivorous fish guilds and
726 their influence on algal succession on a coastal coral reef, *Journal of Experimental Marine Biology*
727 *and Ecology*, 399, 60–67, doi.org/10.1016/j.jembe.2011.01.019, 2011.
- 728 Chisholm, J.R.M., and Gattuso, J.-P.: Validation of the alkalinity anomaly technique for investigating
729 calcification of photosynthesis in coral reef communities, *Limnology and Oceanography*, 36, 1232–
730 1239, doi.org/10.4319/lo.1991.36.6.1232, 1991.
- 731 Cornwall, C.E., Comeau, S., Komder, N.A., Perry, C.T., van Hooidonk, R., DeCarlo, T.M., Pratchett,
732 M.S., Anderson, K.D., Browne, N., Carpenter, R., Diaz-Pulido, G., D'Olivo, J.P., Doo, S.S.,
733 Figueiredo, J., Fortunata, S.V.A., Kennedy, E., Lantz, C.A., McCulloch, M.T., Gonzalez-Rivero, M.,
734 Schoepf, V., Smithers, S.G., and Lowe, R.J.: Global declines in coral reef calcium carbonate
735 production under ocean acidification and warming, *Proceedings of the National Academy of Sciences*,
736 118, e2015265118, doi.org/10.1073/pnas.2015265118, 2021.
- 737 DeAngelis, D.L.: *Dynamics of Nutrient Cycling and Food Webs*: Chapman and Hall, London, 1992.
- 738 DeAngelis, D.L., Mulholland, P.J., Palumbo, A.V., Steinman, A.D., Huston, M.A. and Elwood, J.W.:
739 Nutrient dynamics and food-web stability, *Annual Review of Ecology and Systematics*, 20, 71–95,
740 www.jstor.org/stable/2097085, 1989.
- 741 Dickson, A., Gilmore, C.L., Christian, S., Christian, J.R. Guide to best practices for ocean CO₂
742 measurements. North Pacific Marine Science Organization, 2007.
- 743 Done, T.: Phase shifts in coral reef communities and their ecological significance. *Hydrobiologica*,
744 247, 121–132, doi.org/10.1007/BF0000821, 1992.
- 745 Doney, S.C., Fabry, V.J., Feely, R.A., and Kleypas, J.A.: Ocean acidification: the other CO₂ problem,
746 *Annual Review of Marine Science*, 1, 169–192, doi.org/ 10.1146/annurev.marine.010908.163834,
747 2009.
- 748 Doughty, C.E. Roman, J., Faurbyd, S., Wolfe, A., Haqea, A., Bakkerf, E.S., Malhia, Y., Dunning
749 Jr.g, J.B., and Svenninget, J.-C.: Global nutrient transport in a world of giants. *Proceedings of the*
750 *National Academy of Sciences USA*, 113, 868–873, doi.org/ 10.1073/pnas.1502549112, 2015.
- 751 Drew, E.A.: Halimeda biomass, growth rates and sediment generation on reefs in the central great
752 barrier reef province, *Coral Reefs*, 2, 101–110, doi.org/10.1007/BF02395280, 1983.
- 753 Duarte, C.M., Hendriks, I.E., Moore, T.S., Olsen, Y.S., Steckbauer, A., Ramajo, L., Carstensen, J.,
754 Trotter, J.A., and McCulloch, M.: Is Ocean Acidification an Open-Ocean Syndrome? Understanding
755 Anthropogenic Impacts on Seawater pH, *Estuaries and Coasts*, 36, 221–236, doi.org/ 10.1007/s12237-
756 013-9594-3, 2013.
- 757 Eakin, C.M.: Where have all the carbonates gone? A model comparison of calcium carbonate budgets
758 before and after the 1982–1983 El Nino at Uva Island in the eastern Pacific, *Coral Reefs*, 15, 109–119,
759 doi.org/10.1007/BF01771900, 1996.
- 760 Frankignoulle, M., Gattuso, J.P., Biondo, R., Bourge, I., CopinMontegut, G., and Pichon, M.: Carbon
761 fluxes in coral reefs II: eulerian study of inorganic carbon dynamics and measurement of air-sea CO₂
762 exchanges, *Marine Ecology Progress Series*, 145, 123–132, doi:10.3354/meps145123, 1996.
- 763 Freile, D., Milliman, J.D., and Hillis, L.: Leeward bank margin Halimeda meadows and draperies and
764 their sedimentary importance on the western Great Bahama Bank slope, *Coral Reefs*, 14, 27–33,
765 doi.org/10.1007/BF00304068, 1995.

- 766 Gattuso, J.-P., Pichon, M., Delesalle, B., and Frankignoulle, M.: Community metabolism and airsea
767 CO₂ fluxes in a coral reef ecosystem (Moorea, French Polynesia). *Marine Ecology Progress Series*,
768 96, 259-267, <http://www.jstor.org/stable/24833554>, 1993.
- 769 Gattuso, J.-P., Pichon, M., and Frankignoulle, M.: Biological control of air-sea CO₂ fluxes: Effect of
770 photosynthetic and calcifying marine organisms and ecosystems. *Marine Ecology Progress Series*,
771 129, 307- 312, doi.org/10.3354/meps129307, 1995.
- 772 Gattuso, J.-P., Frankignoulle, M., Smith, S.V., Ware, J.R., and Wollast, R.: Coral reefs and carbon
773 dioxide. *Science*, 271, 1298, doi.org/10.1126/science.271.5253.1298-a, 1996a.
- 774 Gattuso, J.-P., Pichon, M., Delesalle, B., Canon, C., and Frankignoulle, M.: Carbon fluxes in coral
775 reefs I: lagrangian measurement of community metabolism and resulting air-sea CO₂ disequilibrium,
776 *Marine Ecology Progress Series*, 145, 109–121, [doi:10.3354/meps145109](https://doi.org/10.3354/meps145109), 1996b.
- 777 Gattuso, J.-P., Payri, C.E., Pichon, M., Delesalle, B., and Frankignoulle, M.: Primary production,
778 calcification, and air-sea CO₂ fluxes of a macroalgal dominated coral reef community (Moorea,
779 French Polynesia), *Journal of Phycology*, 33, 729-738, [doi.org/ 10.1111/j.0022-3646.1997.00729.x](https://doi.org/10.1111/j.0022-3646.1997.00729.x),
780 1997.
- 781 Gattuso, J.-P., Allemand, D., and Frankignoulle, M.: Photosynthesis and calcification at cellular,
782 organismal and community levels in coral reefs: A review on interactions and control by carbonate
783 chemistry, *American Zoologist*, 39, 160-183, doi.org/10.1093/icb/39.1.160, 1999.
- 784 Gattuso, J.-P., Epitalon, J.-M., Orr, J., Gentili, B., Hagens, M., Hofmann, A., Mueller, J.-D., Proye,
785 A., Rae, J., and Soetaert, K.: *seacarb:Seawater Carbonate Chemistry*, 2018.
- 786 Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H., and Pratchett, M.S.: Recovery of an Isolated
787 Coral Reef System Following Severe Disturbance, *Science*, 340, 69-71, [doi.org/
788 10.1126/science.1232310](https://doi.org/10.1126/science.1232310), 2013.
- 789 Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., Agrosa, C., Bruno, J.F., Casey,
790 K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T.,
791 Selig, E.R., Spalding, M., Steneck, R., and Watson, R.: A Global Map of Human Impact on Marine
792 Ecosystems, *Science*, 319, 948, [doi.org/ 10.1126/science.1149345](https://doi.org/10.1126/science.1149345), 2008.
- 793 Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F., O'Hara, C., Scarborough, C.,
794 and Selkoe, K.A.: Recent pace of change in human impact on the world's ocean, *Science Reports*, 9,
795 11609, doi.org/10.1038/s41598-019-47201-9, 2019.
- 796 Harborne, A.R., Rogers, A., Bozec, Y.-M. and Mumby, P.J.: Multiple stressors and the functioning of
797 coral reefs. *Annual Review of Marine Science*, 9, 445–468, 2017.
- 798 Harley, C. D., Hughes, A.R., Hultgren, K.M., Miner, B.J., Sorte, C.J.B., Thornber, C.S., Rodriguez,
799 L.F., Tomanek, L., Williams S.L.: The impacts of climate change in coastal marine systems, *Ecology*
800 *Letters*, 9, 228– 241, doi.org/10.1111/j.1461-0248.2005.00871.x, 2006.
- 801 Hart, D.E., and Kench, P.S.: Carbonate production of an emergent reef platform, Warraber Island,
802 Torres Strait, Australia, *Coral Reefs*, 26, 53-68, [doi.org/ 10.1007/s00338-006-0168-8](https://doi.org/10.1007/s00338-006-0168-8), 2007.
- 803 Hatcher, B.G.: Coral reef primary productivity—a hierarchy of patterns and process. *Trends in Ecology*
804 *and Evolution*, 5, 149–155, [doi.org/10.1016/0169-5347\(90\)90221-X](https://doi.org/10.1016/0169-5347(90)90221-X), 1990.
- 805 Hatcher, B.G.: Coral reef ecosystems: How much greater is the whole than the sum of the parts? *Coral*
806 *Reefs*, 16, 77–91, doi.org/10.1007/s003380050244, 1997.

- 807 Hewitt, J.E., Ellis, J.I., and Thrush, S.F.: Multiple stressors, nonlinear effects and the implications of
808 climate change impacts on marine coastal ecosystems, *Global Change Biology*, 2, 2665–2675.
809 doi.org/10.1111/gcb.13176, 2016.
- 810 Heyward, A., Jones, R., Meeuwig, J., Burns, K., Radford, B., Colquhoun, J., Cappo, M., Case, M.,
811 O'Leary, R., Fisher, R., Meekan, M., and Stowar, M.: Monitoring Study S5. Banks and Shoals,
812 Montara 2011 Offshore Banks Assessment Survey Report for PTTEP Australasia (Ashmore Cartier)
813 Pty. Ltd., Australian Institute of Marine Science, Townsville, 253pp, 2011.
- 814 Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell,
815 C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R.,
816 Muthiga, N., Bradbury, R. H., Dubi, A., and Hatziolos, M. E.: Coral reefs under rapid climate change
817 and ocean acidification, *Science*, 318, 1737–1742, doi.org/10.1126/science.1152509, 2007.
- 818 Houlbreque, F., and Ferrier-Pages, C.: Heterotrophy in tropical scleractinian corals, *Biological*
819 *reviews of the Cambridge Philosophical Society*, 84, 1-17, doi.org/10.1111/j.1469-
820 185X.2008.00058.x, 2009.
- 821 Houlbreque, F., Tambutte, E., Allemand, D. and Ferrier-Pages, C.: Interactions between zooplankton
822 feeding, photosynthesis and skeletal growth in the Scleractinian coral *Stylophora pistillata*, *Journal of*
823 *Experimental Biology*, 207, 1461–1469, doi.org/10.1242/jeb.00911, 2004.
- 824 Hudson, J.H.: Growth rate and carbonate production in *Halimeda opuntia*: Marquesas Keys, Florida.
825 In *Paleoalgology: contemporary research and applications*, edited by Toomey, D.F. and Nitecki,
826 M.H., Springer-Verlag: Berlin, 1985.
- 827 Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H.,
828 Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., Bridge, T.C., Butler, I.R., Byrne, M.,
829 Cantin, N.E., Comeau, S., Connolly, S.R., Cumming, G.S., Dalton, S.J., Diaz-Pulido, G., Eakin, C.M.,
830 Figueira, W.F., Gilmour, J.P., Harrison, H.B., Heron, S.F., Hoey, A.S., Hobbs, J.A., Hoogenboom,
831 M.O., Kennedy, E.V., Kuo, C.-Y., Lough, J.M., Lowe, R.J., Liu, G., McCulloch, M.T., Malcolm,
832 H.A., McWilliam, M.J., Pandolfi, J.M., Pears, R.J., Pratchett, M.S., Schoepf, V., Simpson, T.,
833 Skirving, W.J., Sommer, B., Torda, G., Wachenfeld, D.R., Willis, B.L. and Wilson, S.K.: Global
834 warming and recurrent mass bleaching of corals, *Nature*, 543, 373–377, doi.org/10.1038/nature21707,
835 2017a.
- 836 Hughes, T.P., Barnes, M.L, Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., Kleypas,
837 J., van de Leemput, I.A., Lough, J.M., Morrison, T.H., Palumbi, S.R., van Nes, E.H. and Scheffer, M.:
838 Coral reefs in the Anthropocene, *Nature*, 546, 82-90, doi:10.1038/nature22901, 2017b.
- 839 IPCC: Climate Change 2014: Impacts, Adaptation, and Vulnerability, Part A: Global and Sectoral
840 Aspects, Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental
841 Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York,
842 2014.
- 843 Jokiel, P.L.: Ocean Acidification and Control of Reef Coral Calcification by Boundary Layer
844 Limitation of Proton Flux, *Bulletin of Marine Science*, 87, 639-657, doi.org/10.5343/bms.2010.1107,
845 2011.
- 846 Kangwe, J., Semesi, I.S., Beer, S., Mtolera, M., and Björk, M.: Carbonate Production by Calcareous
847 Algae in a Seagrass-Dominated System: The Example of Chwaka Bay, CHAPTER 8, In *People,*
848 *Nature and Research in Chwaka Bay, Zanzibar, Tanzania*, edited by de la Torre-Castro, M. and
849 Lyimo, T.J., WIOMSA: Zanzibar, 2012.
- 850 Kayanne, H., Suzuki, A., and Saito, H.: Diurnal changes in the partial pressure of carbon dioxide in
851 coral reef water, *Science*, 269, 214—216, doi.org/ 10.1126/science.269.5221.214, 1995.

- 852 Kayanne, H., Hata, H., Kudo, S., Yamano, H., Watanabe, A., Ikeda, Y., Nozaki, K., Kato, K., Negishi,
853 A., and Saito, H.: Seasonal and bleaching-induced changes in coral reef metabolism and CO₂ flux,
854 *Global Biogeochemical Cycles*, 19, 1–11, doi.org/10.1029/2004GB002400, 2005.
- 855 Kinsey, D.W.: Metabolism, calcification and carbon production: I: System level studies, paper
856 presented at 5th International Coral Reef Congress, Int. Coral Reef Soc., Tahiti, 1985.
- 857 Kleypas, J.A., and Yates, K.K.: Coral reefs and ocean acidification, *Oceanography*, 22, 108–117,
858 <https://doi.org/10.5670/oceanog.2009.101>, 2009.
- 859 Kleypas, J.A., Anthony, K.R.N., and Gattuso, J.P.: Coral reefs modify their seawater carbon
860 chemistry—case study from a barrier reef (Moorea, French Polynesia), *Global Change Biology*, 17,
861 3667–3678, doi.org/10.1111/j.1365-2486.2011.02530.x, 2011.
- 862 Lesser, M.P., Weis, V.M., Patterson, M.R., and Jokiel, P.L.: Effects of morphology and water motion
863 on carbon delivery and productivity in the reef coral, *Pocillopora damicornis*: diffusion barriers,
864 inorganic carbon limitation, and biochemical plasticity, *Journal of Experimental Marine Biology and*
865 *Ecology*, 178, 153–179, doi.org/10.1016/0022-0981(94)90034-5, 1994.
- 866 Lewis, J. B.: Process of organic production on coral reefs, *Biological Reviews*, 52, 305–347,
867 doi.org/10.1111/j.1469-185X.1977.tb00836.x, 1977.
- 868 Lowe, R.J., Leon, A.S., Symonds, G., Falter, J.L., and Gruber, R.: The intertidal hydraulics of tide-
869 dominated reef platforms, *J. Geophys. Res.-Oceans*, 120, 4845–4868,
870 <https://doi.org/10.1002/2015jc010701>, 2015.
- 871 Madin, J.S., Anderson, K.D., Andreasen, M.H., Bridge, T.C.L., Cairns, S.D., Connolly, S.R., Darling,
872 E.S., Diaz, M., Falster, D.S., Franklin, E.C., Gates, R.D., Harmer, A.M.T., Hoogenboom, M.O.,
873 Huang, D., Keith, S.A., Kosnik, M.A., Kuo, C.-Y., Lough, J.M., Lovelock, C.E., Luiz, O., Martinelli,
874 J., Mizerek, T., Pandolfi, J.M., Pochon, X., Pratchett, M.S., Putnam, H.M., Roberts, T.E., Stat, M.,
875 Wallace, C.C., Widman, E. and Baird, A.H.: The Coral Trait Database, a curated database of
876 trait information for coral species from the global oceans. *Scientific Data*, 3, 160017.
877 <https://doi.org/10.1038/sdata.2016>.
- 878 Mass, T., Genin, A., Shavit, U., Grinstein, M., and Tchernov, D.: Flow enhances photosynthesis in
879 marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water,
880 *Proceedings of the National Academy of Sciences USA*, 107, 2527–2531,
881 doi.org/10.1073/pnas.0912348107, 2010.
- 882 McLaughlin M.J., Lourey M.J., Hanson C.E., Cherukuru N, Thompson P.A., and Pattiaratchi C.:
883 Biophysical oceanography of tidally-extreme waters of the southern Kimberley coast, Western
884 Australia, *Continental Shelf Research*, 173, 1-12, doi.org/10.1016/j.csr.2018.12.002, 2019.
- 885 Meyer, J.L., Schultz, E.T. and Helfman, G.S.: Fish schools—an asset to corals, *Science* 220, 1047–
886 1049, doi.org/10.1126/science.220.4601.1047, 1983.
- 887 Moberg F., and Folke C.: Ecological goods and services of coral reef ecosystems, *Ecological*
888 *Economics*, 29, 215–233, doi.org/10.1016/S0921-8009(99)00009-9, 1999.
- 889 Montaggioni, L.F., and Braithwaite, C.J.R.: Quaternary coral reef systems. Elsevier, p 532, 2009.
- 890 Murru, M., and Sandgren, C.D.: Habitat matters for inorganic carbon acquisition in 38 species of red
891 macroalgae (Rhodophyta) from Puget Sound, Washington, USA, *Journal of Phycology*, 40, 837–845,
892 doi.org/10.1111/j.1529-8817.2004.03182.x, 2004.
- 893 Nelson, W.A.: Calcified macroalgae – critical to coastal ecosystems and vulnerable to change: a
894 review, *Marine and Freshwater Research*, 60, 787–801, doi.org/10.1071/MF08335, 2009.

- 895 Niggel, W., Haas, A.F., and Wild, C.: Benthic community composition affects O₂ availability and
896 variability in a Northern Red Sea fringing reef, *Hydrobiologia*, 644, 401–405,
897 doi.org/10.1007/s10750-010-0200-4, 2010.
- 898 Odum, H. T., and Odum, E. P.: Trophic structure and productivity of a windward coral reef
899 community on Eniwetok Atoll, *Ecological Monographs*, 25, 291–320, 1955.
- 900 Olsen, Y.S., Bessey, C., McLaughlin, J., and Keesing, J.K.: Annual Report: Patterns in primary
901 producers, herbivory and reef metabolism around Browse Island, Milestone Report for Shell/INPEX
902 Applied Research Program, 2017.
- 903 Overholtzer, K.L. and Motta, P.J.: Comparative resource use by juvenile parrotfishes in the Florida
904 Keys, *Marine Ecology Progress Series*, 177, 177–187, 1999.
- 905 Panchang, R. and Ambokar, M.: Ocean acidification in the Northern Indian ocean : A review, *Journal*
906 *of Asian Earth Sciences*, doi.org/10.1016/j.jseaes.2021.104904, 219, (104904), 2021.
- 907 Pandolfi, J. M., Connolly, S. R., Marshall, D. J., and Cohen, A. L.: Projecting coral reef futures under
908 global warming and ocean acidification, *Science*, 333, 418–422, doi.org/10.1126/science.1204794,
909 2011.
- 910 Payri, C.E.: *Halimeda* contribution to organic and inorganic production in a Tahitian reef system,
911 *Coral Reefs*, 6, 251-262, doi.org/10.1007/BF00302021, 1988.
- 912 Perry, C.T., Spencer, T., and Kench, P.: Carbonate budgets and reef production states: a geomorphic
913 perspective on the ecological phase-shift concept, *Coral Reefs*, 27, 853–866, doi.org/10.1007/s00338-
914 008-0418-z, 2008.
- 915 Perry, C.T., Edinger, E.N., Kench, P.S., Murphy, G.N., Smithers, S.G., Steneck, R.S., and Mumby,
916 P.J.: Estimating rates of biologically driven coral reef framework production and erosion: a new
917 census-based carbonate budget methodology and applications to the reefs of Bonaire, *Coral Reefs*, 31,
918 853–868, doi.org/ 10.1007/s00338-012-0901-4, 2012.
- 919 Perry, C.T., Alvarez-Filip, L., Graham, N.A.J., Mumby, P.J., Wilson, S.K., Kench, P.S., Manzello,
920 D.P., Morgan, K.M., Slangen, A.B.A., Thomson, D.P., Januchowski-Hartley, F., Smithers, S.G.,
921 Steneck, R.S., Carlton, R., Edinger, E.N., Enochs, I.C., Estrada-Saldívar, N., Haywood, M.D.E.,
922 Kolodziej, G., Murphy, G.N., Pérez-Cervantes, E., Suchley, A., Valentino, L., Boenish, R., Wilson,
923 M., and Macdonald, C.: Loss of coral reef growth capacity to track future increases in sea level.
924 *Nature*, 558, 396–400, doi.org/10.1038/s41586-018-0194-z, 2018.
- 925 Pomeroy, L.R.: The ocean's food web, a changing paradigm. *Bioscience* 24, 9,
926 doi.org/10.2307/1296885, 1974.
- 927 Price, N.N., Hamilton, S.L., Tootell, J.S., and Smith, J.E.: Species-specific consequences of ocean
928 acidification for the calcareous tropical green algae *Halimeda*, *Marine Ecology Progress Series*, 440,
929 67–78, doi.org/10.3354/meps09309, 2011.
- 930 Purcell, S.W., and Bellwood, D.R.: Spatial patterns of epilithic algal and detrital resources on a
931 windward coral reef, *Coral Reefs*, 20, 117– 125, doi.org/10.1007/s003380100150, 2001.
- 932 R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical
933 Computing, Vienna, Austria. URL <https://www.R-project.org/>. 2018.
- 934 Raven, J.A., Walker, D.I., Johnston, A.M., Handley, L.L., and Kübler, J.E.: Implications of ¹³C
935 natural abundance measurements for photosynthetic performance by marine macrophytes in their
936 natural environment, *Marine Ecology Progress Series*, 123, 193-205, doi.org/ 10.3354/meps123193,
937 1995.

- 938 Rees, S.A., Opdyke, B.N., Wilson, P.A., and Henstock, T.J.: Significance of Halimeda bioherms to
 939 the global carbonate budget based on a geological sediment budget for the Northern Great Barrier
 940 Reef, Australia, *Coral Reefs*, 26, 177-188, doi.org/10.1007/s00338-006-0166-x, 2007.
- 941 Richards, Z.T., Garcia, R.A., Wallace, C.C., Rosser, N.L., and Muir, P.R.: A diverse assemblage of
 942 reef corals thriving in a dynamic intertidal reef setting (Bonaparte Archipelago, Kimberley, Australia),
 943 PLoS ONE, 10, e0117791, doi.org/10.1371/journal.pone.0117791, 2015.
- 944 Rueden, C.T., Schindelin, J., Hiner, M.C., DeZonia, B.E., Walter, A.E., Arena, E.T., and Eliceiri,
 945 K.W.: ImageJ2: ImageJ for the next generation of scientific image data, *BMC Bioinformatics*, 18,
 946 529, doi.org/10.1186/s12859-017-1934-z, 2017.
- 947 Schneider, K. and Erez, J.: The effect of carbonate chemistry on calcification and photosynthesis in
 948 the hermatypic coral *Acropora eurystroma*, *Limnology and Oceanography*, 51, 1284–1293,
 949 doi.org/10.4319/lo.2006.51.3.1284, 2006.
- 950
 951 Schindler, D.W.: Recent advances in the understanding and management of eutrophication,
 952 *Limnology and Oceanography*, 51, 356– 363, doi.org/ 10.4319/lo.2006.51.1_part_2.0356, 2006.
- 953
 954 Shamberger, K.E.F., Feely, R.A., Sabine, C.L., Atkinson, M.J., DeCarlo, E.H., Mackenzie, F.T.,
 955 Drupp, P.S., and Butterfield, D.A.: Calcification and organic production on a Hawaiian coral reef,
 956 *Marine Chemistry*, 127, 64–75. doi.org/10.1016/j.marchem.2011.08.003, 2011.
- 957 Shashar, N., Cohen, Y., and Loya, Y.: Extreme diel fluctuations of oxygen in diffusive boundary
 958 layers surrounding stony corals, *Biological Bulletin*, 185, 455–461, doi.org/ 10.2307/1542485, 1993.
- 959 Shaw, E.C., Hamylton, S.M., and Phinn, S.R.: Incorporating benthic community changes into
 960 hydrochemical-based projections of coral reef calcium carbonate production under ocean
 961 acidification, *Coral Reefs*, 35, 739-750, doi.org/10.1007/s00338-016-1407-2, 2016.
- 962 Silverman, J., Lazar, B., Cao, L., Caldeira, K., and Erez, J.: Coral reefs may start dissolving when
 963 atmospheric CO₂ doubles, *Geophysical Research Letters*, 36, L05606, doi:10.1029/2008gl036282,
 964 2009.
- 965 Smith, J.E., Hunter, C.L., Conklin, E.J., Most, R., Sauvage, T., Squair, C., and Smith, C.M.: Ecology
 966 of the Invasive Red Alga *Gracilaria salicornia* (Rhodophyta) on O'ahu, Hawai'i, *Pacific Science*, 58,
 967 325-343, doi.org/ 10.1353/psc.2004.0023, 2004.
- 968 Smith, J.E., Price, N.N., Nelson, C.E., and Haas, A.F. Coupled changes in oxygen concentration and
 969 pH caused by metabolism of benthic coral reef organisms, *Marine Biology*, 160, 2437-2447,
 970 doi.org/10.1007/s00227-013-2239-z, 2013.
- 971 Smith, S.V., and Key, G.S.: Carbon dioxide and metabolism in marine environments, *Limnology and*
 972 *Oceanography*, 20, 493-495, doi.org/10.4319/lo.1975.20.3.0493, 1975
- 973 Smith, S.V.: Reflections on the measurement and significance of carbon metabolism on coral reefs,
 974 Kansas Geological Survey Open-File Report 95-96a, Kansas Geological Survey, Lawrence, Kansas,
 975 1995.
- 976 Smith, T.B., Nemeth, R.S., Blondeau, J., Calnan, J.M., Kadison, E., and Herzlieb S.: Assessing coral
 977 reef health across onshore to offshore stress gradients in the US Virgin Islands, *Marine Pollution*
 978 *Bulletin*, 56, 1983–1991, doi.org/10.1016/j.marpolbul.2008.08.015, 2008.
- 979 Sorokin, Y.: in *Coral Reef Ecology*, 102, 215–249, edited by: Heldmaier, G., Lange, O.L., Mooney,
 980 H.A., and Sommer, U., Springer: Berlin, Heidelberg, 1995.

- 981 Sreeush, M.G., Valsala, V., Santanu, H., Pentakota, S., Prasad, K.V.S.R., Naidu, C.B., and
982 Murtugudde, R.: Biological production in the Indian Ocean upwelling zones – Part II: Data based
983 estimates of variable compensation depths for ocean carbon models via Cyclostationary Bayesian
984 Inversion, *Deep Sea Research Part II*, 179, doi.org/10.1016/j.dsr2.2019.07.007, 2020.
- 985 Stuart-Smith, R.D., Brown, C.J., Ceccarelli, D.M. and Edgar, G.J.: Ecosystem restructuring along the
986 Great Barrier Reef following mass coral bleaching, *Nature*, 560, 92–96, 2018.
- 987 Szmant, A.M.: Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? *Estuaries*
988 25, 743–766, doi.org/10.1007/BF02804903, 2002.
- 989 Trapon, M.L., Pratchett, M.S., and Hoey, A.S.: Spatial variation in abundance, size and orientation of
990 juvenile corals related to the biomass of parrotfishes on the Great Barrier Reef, Australia, *PLoS One*,
991 8, e57788, doi.org/10.1371/journal.pone.0057788, 2013.
- 992 Veal, C.J., Carmi, M., Fine, M., and Hoegh-Guldberg, O.: Increasing the accuracy of surface area
993 estimation using single wax dipping of coral fragments, *Coral Reefs*, 29, 893–897,
994 doi.org/10.1007/s00338-010-0647-9, 2010.
- 995 Vecsei, A.: A new estimate of global reefal carbonate production including the fore-reefs. *Global*
996 *Planet Change*, 43, 1–18, doi.org/10.1016/j.gloplacha.2003.12.002, 2004.
- 997 Venn, A. A., Tambutté, E., Holcomb, M., Laurent J., Allemand, D. and Tambutté, S.: Impact of
998 seawater acidification on pH at the tissue–skeleton interface and calcification in reef corals,
999 *Proceedings of the National Academy of Sciences*, 110, 1634–1639,
1000 doi.org/10.1073/pnas.1216153110, 2013.
- 1001 Walther, G-R.: Community and ecosystem responses to recent climate change, *Philosophical*
1002 *Transactions of the Royal Society B: Biological Sciences*, 365, 2019– 2024, doi.org/
1003 0.1098/rstb.2010.0021, 2010.
- 1004 Watson, R.J., Butler, E.C.V., Clementson, L.A., and Berry, K.M.: Flow-injection analysis with
1005 fluorescence detection for the determination of trace levels of ammonium in seawater, *Journal of*
1006 *Environmental Monitoring*, 7, 37–42, doi.org/10.1039/b405924g, 2005.
- 1007 Ware, J. R., Smith, S.V., and Reaka-Kudla, M.L.: Coral reefs: Sources or sinks of atmospheric CO₂?
1008 *Coral Reefs*, 11, 127–130, doi.org/10.1007/BF00255465, 1992.
- 1009 Wild, C., Niggel, W., Naumann, M.S., and Haas, A.F.: Organic matter release by Red Sea coral reef
1010 organisms—potential effects on microbial activity and in situ O₂ availability, *Marine Ecology*
1011 *Progress Series*, 411, 61–71, doi.org/10.3354/meps08653, 2010.
- 1012 WillyWeather 2022, Browse Island Sunrise / Sunset Times website, accessed 02 November 2022,
1013 <https://sunrisesunset.willyweather.com.au/wa/kimberley/browse-island.html>.
- 1014 Zeebe, R.E., Wolf-Gladrow, D.A., and Jansen, H.: On the time required to establish chemical and
1015 isotopic equilibrium in the carbon dioxide system in seawater, *Marine Chemistry*, 65, 135–153,
1016 doi.org/10.1016/S0304-4203(98)00092-9, 1999.
- 1017