

# Effects of ocean acidification on the dissolution rates of reef corals

Ocean acidification threatens the foundation of tropical coral reefs. This study investigated three aspects of ocean acidification: (i) the rates of dissolution of perforate and imperforate coral colony skeletons at a pH of 7.8, which is predicted to occur globally by 2100, (ii) the rates of coral dissolution with respect to coral-colony surface areas, and (iii) the comparative rates of vertical reef-growth model, incorporating dissolution rates, and predicted sea-level rise. When the ocean pH is 7.8, perforate coral skeletons will lose on average  $15 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ , which is approximately  $-10.5 \text{ mm}$  of vertical reduction of reef framework per year. This rate is three times higher than the average growth rate of modern reefs over the last several millennia and suggests that reefs composed of perforate corals will have trouble keeping up with sea level rise under ocean acidification. Reefs composed of primarily imperforate corals will not likely dissolve, but our model shows they will also have trouble keeping up with sea-level rise by 2050.

2 **Effects of ocean acidification on the dissolution**  
3 **rates of reef corals**

4 R. van Woesik\*<sup>1</sup>, K. van Woesik<sup>2</sup>, L. van Woesik<sup>2</sup>, S. van  
5 Woesik<sup>2</sup>

6 <sup>1</sup>Florida Institute of Technology  
7 150 W. University Blvd., Melbourne FL, 32901 USA

8 ph: +1 321 674 7475; Fax: +1 321 674 7238

9 <sup>2</sup> Melbourne, Florida, USA

10 \* Correspondence to: [rvw@fit.edu](mailto:rvw@fit.edu)

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## Abstract

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14 aspects of ocean acidification: (i) the rates of dissolution of perforate and imperforate coral  
15 colony skeletons at a pH of 7.8, which is predicted to occur globally by 2100, (ii) the rates of  
16 coral dissolution with respect to coral-colony surface areas, and (iii) the comparative rates of  
17 vertical reef-growth model, incorporating dissolution rates, and predicted sea-level rise. When the  
18 ocean pH is 7.8, perforate coral skeletons will lose on average  $15 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ , which is  
19 approximately – 10.5 mm of vertical reduction of reef framework per year. This rate is three  
20 times higher than the average growth rate of modern reefs over the last several millennia and  
21 suggests that reefs composed of perforate corals will have trouble keeping up with sea level rise  
22 under ocean acidification. Reefs composed of primarily imperforate corals will not likely  
23 dissolve, but our model shows they will also have trouble keeping up with sea-level rise by 2050.

## 24 **Introduction**

### 25 *Ocean acidification*

26 As humans continue to burn fossil fuels at an unprecedented rate, the concentration of carbon  
27 dioxide (CO<sub>2</sub>) in the atmosphere is presently higher than it has been for the last 450,000 years  
28 (Hansen et al. 2006; Hoegh-Guldberg et al. 2007). The oceans uptake a large proportion of that  
29 CO<sub>2</sub>, increasing the concentrations of both carbonic acid and bicarbonate ions, and reducing the  
30 concentration of carbonate ions, shifting the ocean's acid-base balance toward a lower pH  
31 (Broecker 1983; Caldeira and Wickett 2003; Silverman et al. 2009). The increase in ocean  
32 acidification directly threatens calcifying marine organisms, such as reef-building corals and the  
33 myriad of species that rely on corals for protection and sustenance (Hoegh-Guldberg et al. 2007;  
34 Rodolfo-Metalpa et al. 2011).

35 The oceanic pH has already decreased by 0.1 pH units since the 18th century, and is expected to  
36 drop by another 0.2 – 0.4 pH units by 2100. Yet the oceans are not homogenous in regard to rates  
37 of reductions in carbonate ions. Thermodynamic principles and Henry's Law tells us that cool  
38 temperate and polar waters absorb asymmetrically more CO<sub>2</sub> than tropical waters, and are  
39 therefore closer to unity than the more super-saturated tropical waters. Yet the tropical oceans are  
40 changing at a more rapid rate and are acidifying more quickly than the cooler waters (Zeebe et al.  
41 2008). Moreover, the Pacific Ocean is more acidic than the Atlantic Ocean, and shoaling  
42 saturation depth is around 500 m in the Pacific and 4500 m in the Atlantic (Feely et al. 2004;  
43 Millero 2007).

44 There is increasing evidence that ocean acidification, through the increase in the partial pressure  
45 of carbon dioxide ( $p\text{CO}_2$ ) and the subsequent changes in the concentration of carbonate and  
46 bicarbonate ions, reduces rates of coral calcification, which are directly proportional to the  
47 saturation state of aragonite (Langdon and Atkinson 2005). Other studies have shown that  
48 calcification rates are proportional to the concentration of carbonate ions in the water column  
49 (Anthony et al. 2008; Marubini et al. 2008). However these studies are essentially synonymous,  
50 because the aragonite and calcite saturation state ( $\Omega$ ) is the product of the concentrations of  
51 calcium and carbonate ions divided by an equilibrium constant. Since the salt concentration,  
52 including calcium ions, stemming from terrestrial weathering hasn't changed in the oceans for  
53 over 1.5 billion years the aragonite saturation state is essentially a measure of carbonate ions in  
54 the oceans.

55 Perhaps more importantly is the strong interaction effects between temperature and ocean  
56 acidification on coral calcification rates (Reynaud et al. 2003; Erez et al. 2010). Indeed, the  
57 optimal window of physiological performance of a given marine species at a given temperature  
58 will be narrowed under acidification (Portner 2010). Calcification of corals under ambient  
59 temperature do not necessarily change with increased  $p\text{CO}_2$ , but calcification decreases when  
60 both temperature and  $p\text{CO}_2$  were elevated (Reynaud et al. 2003). Yet several studies have shown  
61 that many corals are unaffected by external carbonate ion concentrations because they have the  
62 capacity to up-regulate internal pH by actively exchanging internal hydrogen ions for calcium  
63 ions through Ca-ATPase transportation (Al-Horani et al. 2003; Allemand 2004; McCulloch et al.  
64 2012). By modifying their internal chemistry, live corals may buffer themselves from ocean  
65 acidification. Coral skeletons, however, have no internal-buffering capacity because they are not  
66 protected by coral membranes (Rodolfo-Metalpa et al. 2011; Ries 2011). Coral skeletons are

67 instead subjected to the raw and immediate threats of ocean acidification and will be subjected to  
68 dissolution when the ocean's pH declines.

69 *Accretion of coral reefs*

70 The accretion of coral reefs occurs over geological time periods when rates of calcium carbonate  
71 ( $\text{CaCO}_3$ ) production exceed rates of destruction and dissolution (Neumann and MacIntyre 1985;  
72 Buddemeier and Hopley 1988; Glynn 1997; Perry et al. 2013). The interaction between  
73 production and destruction depends on the consistency of coral cover through time. For example,  
74 where coral cover is consistently low, reef accretion is minimal (Neumann and MacIntyre 1985).  
75 Most modern reefs, however, support little more than 28% live coral cover (Bruno and Selig  
76 2007), and are essentially veneers over pre-existing, antecedent foundations of  $\text{CaCO}_3$  (Adey  
77 1978; Hopley 1982).

78 The average modern, shallow seaward coral reef in the Indo-Pacific, with high coral cover, has  
79 been estimated to produce about 4 kilograms of calcium carbonate per square meter of reef per  
80 year, which equates with an upward reef-growth rate of approximately 3 mm per year (Smith and  
81 Kinsey 1976). These estimates were based on alkalinity reduction techniques subjected to a pH of  
82 8.2 of today's oceans. By 2100 the ocean's pH is expected to be 7.8, and we hypothesize that the  
83 destructive processes associated with ocean acidification may outweigh the productive processes.  
84 The rates of dissolution of reef framework may however also depend on the extent of reef  
85 lithification and cementation of reef framework, and on the porosity of corals.

86 *Reef cementation and coral porosity*

87 Reefs vary in porosity depending on both (i) the local rates of sedimentation and the extent to  
88 which those sediments become consolidated, or lithified, within the reef framework, and (ii) the  
89 extent of cementation of the reef framework (MacIntyre and Marshall 1988). Both processes  
90 depend in part on exposure to water-flow rates. High-energy, windward reefs consistently  
91 exposed to large waves are generally more highly cemented than low-wave energy, leeward reefs.  
92 Cementation involves the infilling of intra-skeletal pores with either Mg calcite or aragonite  
93 (MacIntyre and Marshall 1988). While the extent of cementation affects the dislodgment of reef  
94 substrate and the tenacity of corals to remain attached to reefs during storms (Madin et al 2012),  
95 the extent of reef cementation may also affect dissolution rates during ocean acidification because  
96 the infilling of pores by cements decreases the surface area of exposure (Cubillas et al 2005).

97 Similarly, reef corals also vary in porosity (Gladfelter 1982; Hughes 1987). Although, all modern  
98 corals secrete orthorhombic aragonite, as small, 1-3  $\mu\text{m}$ , fusiform crystals, corals vary  
99 considerably in the arrangement of the crystals, which influences their internal surface area  
100 exposed to the bulk water (Fig. 1). Fast-growing corals, such as *Montipora* and *Acropora*, are  
101 mostly perforate corals (Gladfelter 1982), whereas slow growing corals, such as *Pectinia* and  
102 *Symphyllia*, are imperforate (Table 1). An extreme example of imperforate skeletons is evident by  
103 the observation of occasional floating, massive colonies (DeVantier 1992). Because of the fused  
104 nature of the dissepiments and their imperforate skeletons, gases are trapped in the septal  
105 chambers and upon dislodgement from reefs, for example during a storm, the colonies will float.  
106 Not many corals however, have the capacity to isolate septal chambers completely. Walter and  
107 Morse (1984) showed that rates of dissolution of skeletal carbonates were inversely related to  
108 grain size diameter and surface roughness, with fine grained carbonates dissolving faster than  
109 large, rough surfaces. We hypothesize that internal porosity of coral skeletons, at the scale of 0.5

110 —1 mm (Fig. 1), increases the available surface area of chemical exchange and therefore  
111 increases the potential rates of dissolution.

112 This study will examine whether the porosity and the surface area of coral skeletons will  
113 influence their rate of dissolution when the ocean pH is 7.8, which is predicted to occur by 2100.  
114 More specifically, we tested two hypotheses: (1) that perforate *Montipora* coral colonies are more  
115 likely to dissolve than imperforate *Pectinia* corals at a pH of 7.8, and (2) that the rates of  
116 dissolution of coral colonies are proportional to their surface areas. We also approximate whether  
117 future reef accretion rates under ocean acidification will keep up with predicted sea level rise.

## 118 **Materials and Methods**

### 119 *Acidification experiments*

120 In order to test the first hypothesis, perforate *Montipora* colonies (Figure 1) and imperforate  
121 *Pectinia* colonies (Figure 2) were used to make comparisons of weight loss when immersed in  
122 seawater held at a pH of 8.2, equivalent to the pH of today's oceans, and compared with colonies  
123 held at a pH of 7.8, which is predicted to occur globally by 2100. Fifteen skeletal samples ( $\leq 5$   
124 cm) of *Montipora* spp. colonies and fifteen skeletal samples of *Pectinia* spp. were collected from  
125 the fringing reefs of Okinawa, Japan in 2001. In order to test the second hypothesis, we used a  
126 variety of growth forms of *Montipora*, including submassive, branching, encrusting, and foliose.  
127 Colonies of *Pectinia* with different surface areas were used for experimental treatments, but all  
128 samples were foliose because *Pectinia* is only found as foliose colonies on modern coral reefs.

129 Before pH treatments, the samples were placed in a drying oven at 40°C for 48 h and weighed (g)  
130 using a Sartorius Research Balance. Each treatment sample was then placed in a separate  
131 container of seawater that were maintained at a pH of 7.8 by adding diluted acetic acid to match  
132 the predicted pH of the seawater in the year 2100 (Intergovernmental Panel on Climate Change  
133 [IPCC], 2007). The control samples were placed in seawater that was maintained at a pH of 8.2,  
134 to match modern ocean conditions. Seawater was changed every 2 days. After 7 days the samples  
135 were rinsed and dried in a drying oven at 40°C for 48 hours, and re-weighed. The volume of each  
136 coral sample (mL) was calculated using a displacement method and the surface area of each coral  
137 sample (cm<sup>2</sup>) was calculated using a single wax-dipping method (Veal et al. 2010).

### 138 *Data analyses*

139 The difference in dry weight (g) before and after the acid treatment was calculated for each coral  
140 sample. To correct for differences in initial weight, the loss of calcium carbonate was divided by  
141 each coral's initial weight. To compare differences in dissolution rates that may have varied in  
142 accordance with growth form, we undertook an analysis of variance (ANOVA) and a Tukey's  
143 post-hoc test using R (R Development Core Team, 2012). The relationship between the surface  
144 area and volume and the loss of calcium carbonate was examined using curve fitting with  
145 Matlab®.

### 146 *Accretion-dissolution model*

147 The loss of calcium carbonate was extrapolated from the change in calcium carbonate per gram  
148 cm<sup>-2</sup> day<sup>-1</sup>, to the equivalent loss of calcium carbonate per kg m<sup>-2</sup> y<sup>-1</sup>. This loss was compared with

149 the geological literature and converted to the approximate equivalent of vertical reduction of reef  
150 framework in mm per year (Smith and Kinsey 1976). The loss was compared with predicted sea-  
151 level rise (Vermeer and Rahmstorf 2009). In order to achieve this goal, the reef accretion rates  
152 were modeled as an ordinary differential equation:

$$153 \quad dA/dt = (a.A)/A + b.S - (c.D)/A \quad (1),$$

154 where  $A$  is the accretion of a reef relative to time ( $t$ ),  $a$  is the accretion coefficient determined by  
155 coral and coralline algal growth minus the bioerosion rates (input as 7 mm per year for reefs that  
156 accrete the maximum of 10 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ ; 3 mm per year for reefs that accrete 4 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ ;  
157 and 0.75 mm per year for reefs that accrete 1 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ , with a 50% average reef  
158 porosity, after Kinsey 1979 and Smith 1983),  $b$  is a coefficient for sedimentation (S), input as 1  
159 mm per year for consistency, and  $c$  is a coefficient for the dissolution (D) rates, measured in this  
160 study, input as -15 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ , which translates to -10.5 mm per year. The equations were  
161 solved using Runge-Kutta methods using the ode45 solver in Matlab®.

162 The results of dissolution were compared with projections of global sea-level rise, not  
163 considering regional isostatic rebound effects, regional tectonics, and local land-use effects, from  
164 1990 to 2100 following Vermeer and Rahmstorf (2009). The sea-level rise projections used  
165 different IPCC (2007) emission scenarios, including the B1 scenario representing a +1.8°C global  
166 increase in temperature, the A2 scenario representing a +3.4°C global increase in temperature,  
167 and the A1F1 scenario representing a 4°C global increase in temperature.

## 168 **Results**

169 There was a significant difference ( $p < 0.0258$ ) in coral weight loss that was dependent on coral  
170 colony porosity (Figure 3). Foliose, perforate *Montipora* coral colonies dissolved significantly  
171 (post-hoc Tukey test,  $p < 0.011$ ) faster than foliose, imperforate *Pectinia* coral colonies (Figure  
172 3). Foliose *Montipora* corals also lost more calcium carbonate than other *Montipora* growth  
173 forms (Figure 3). There was a strong negative relationship between the surface area of *Montipora*  
174 corals and the loss of calcium carbonate, suggesting that the larger the surface area of *Montipora*  
175 colonies the more rapidly the corals dissolved (Figure 4). The rate of calcium carbonate loss  
176 followed the equation,  $\text{CaCO}_3 \text{ loss} = -0.005 \times \exp^{0.017 * \text{surface area}}$ . The loss of  $\text{CaCO}_3$  of perforate  
177 *Montipora* was approximately  $0.000042 \text{ g CaCO}_3 \text{ cm}^{-2} \text{ day}^{-1}$  or  $-15.3 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ . This  
178 loss in calcium carbonate is approximately equivalent to  $-10.5 \text{ mm}$  of vertical reduction of reef  
179 framework per year.

180 In contrast, imperforate *Pectinia* colonies showed no consistent dissolution at a pH of 7.8,  
181 suggesting that the loss of weight in low pH treatments was no different than the weight loss in  
182 controls (Figures 3 and 5). There was no significant relationship between the surface area of  
183 *Pectinia* coral colonies and their rate of dissolution (Figure 5). There was also no significant  
184 relationship between dissolution rates and the volume of either *Montipora* or *Pectinia* colonies.

#### 185 *Accretion-dissolution model*

186 The sea-level rise projections from 1990 to 2100 were constructed using different IPCC (IPCC  
187 2007) emission scenarios, including the B1 scenario, representing a  $+1.8^\circ\text{C}$  global increase in  
188 temperature, the A2 scenario representing a  $+3.4^\circ\text{C}$  global increase in temperature, and the A1F1  
189 scenario representing a  $4^\circ\text{C}$  global increase in temperature (Figure 6; Vermeer and Rahmstorf,  
190 2009). These sea-level projections were compared with the reef-building capacity of perforate

191 and imperforate corals under ocean acidification (Figure 6). The perforate corals, even supporting  
192 consistently high coral cover ( $10 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ ) are not expected to keep up with sea level rise  
193 under ocean acidification (Figure 6). By contrast, the imperforate corals could continue to grow  
194 reefs and keep up with sea level rise, but only reefs consistently supporting high coral cover ( $10$   
195  $\text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ ) and only to 2050. Around 2050, the rates of sea level rise are expected to  
196 increase faster than the rates at which even perforate corals could grow reefs (Figure 7).

## 197 **Discussion**

198 Most recent studies have investigated live corals and examined whether they continue to calcify  
199 in reduced pH environments (Fine & Tchernov 2007; Kroeker et al. 2010). Yet coral reefs are  
200 primarily extensive carbonate surfaces supporting, on average, a relatively low percentage of live  
201 coral coverage not exceeding on average 28% (Bruno & Selig 2007; Perry et al. 2013). For  
202 example, the Florida Keys only supported, on average, 2-3% of live coral cover in 2011 (Office  
203 of National Marine Sanctuaries 2011). Therefore, reefs with high carbonate cover and few corals  
204 are particularly vulnerable to ocean acidification.

205 This study examined whether the destructive processes of calcium carbonate dissolution on coral  
206 reefs will over-ride the accretionary processes when the oceans pH drops to 7.8, which is  
207 predicted to occur by 2100. We examined the rates of skeletal dissolution of two common Indo-  
208 Pacific corals, *Montipora* and *Pectinia*, subjected to a pH of 7.8. Rates of dissolution were  
209 directly proportional to the surface area of corals, but only for *Montipora*. The average loss of  
210 *Montipora*  $\text{CaCO}_3$  per surface area was  $15.3 \text{ kg m}^{-2} \text{ y}^{-1}$ , which was 3 times more than the average

211 growth rates of modern corals ( $4 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ ) and 1.5 times faster than the maximum rate of  
212 reef growth ( $9.6 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) over the last several millennia (Smith 1983; Smith and  
213 Kinsey 1976; Kinsey 1979).

214 Kinsey (1979) measured the maximum rate of modern reef growth ( $9.6 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ) on a  
215 back-reef of Johnston Atoll ( $16^\circ\text{N}$ ,  $169^\circ\text{W}$ ), that supported "heavy" coral cover, but the  
216 percentage coral cover was not provided in the original publication. Yet these estimates, by Smith  
217 and Kinsey and co-workers, of calcium carbonate production, were all originally calculated using  
218 alkalinity reduction techniques. Other estimates using X-radiographs and extrapolation  
219 techniques showed similar results, ranging from  $9 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  for reefs in the Caribbean  
220 with uncharacteristically high coral cover (38%) (Stearn et al. 1977), to less than  $1 \text{ kg CaCO}_3 \text{ m}^{-2}$   
221  $\text{y}^{-1}$  for reefs with low coral cover (Dullo 2005).

222 Rates of carbonate dissolution will depend on not only the surface area of calcium carbonate  
223 ( $\text{CaCO}_3$ ), as shown in the present study, but will also depend on the type of coral assemblages  
224 present on reefs. Globally, approximately 404 coral species are perforate and 432 imperforate  
225 (Table 1), yet most Indo-Pacific reefs are dominated by *Acropora*, *Montipora*, *Porites*, and  
226 faviids, and Caribbean reefs are dominated by *Porites*, *Siderastrea*, and faviids (Veron 1995).  
227 Therefore, most modern reefs are primarily supporting perforate corals, and these corals have  
228 been largely responsible for vertical reef accretion through the Holocene (Veron 1995, Wood  
229 1999). Although only around 50% of the corals globally are perforate, these perforate corals  
230 disproportionately contribute to modern reef-building frameworks.

231 Hiatuses in coral-reef accretion have frequently occurred through the geological past (Veron  
232 1995; Wood 1999) and have been recently linked to high concentrations of  $p\text{CO}_2$  (Hautmann  
233 2004; Veron 2008). Still, changing the pH of seawater is only one of the changes that will occur  
234 to reefs subjected to climate change. Warmer waters will increase the reaction rates of coral  
235 dissolution, but ocean acidification is more likely in colder waters than in warmer waters,  
236 because high-latitude waters absorb more  $\text{CO}_2$  from the atmosphere than low-latitude waters  
237 (Broecker 1983). Sea level will also rise with increasing global temperature (Smith and  
238 Buddemeier 1992; Vermeer and Rahmstorf 2009). The conservative estimates from the IPCC  
239 (2007), which did not consider ice-sheet dynamics, showed that sea level will increase 20-60 cm  
240 by 2100 (approximately 4 mm a year). More recent estimates by Vermeer and Rahmstorf (2009)  
241 predict a sea level increase of 75-90 cm by 2100 (approximately 9 mm a year). The average  
242 growth rate of a healthy reef with high coral cover is approximately 4 kg calcium carbonate per  
243 year, which translates to 3 mm per year of upward growth (Buddemeier and Hopley 1988). Our  
244 predictive model showed that coral reefs composed of perforate assemblages will have trouble  
245 keeping up with sea level rise under ocean acidification (Figure 3). Therefore research on ocean  
246 acidification should not only focus on quantifying effects of live corals, but also hierarchically  
247 quantifying the production versus dissolution rates of reefs in relation to: (i) coral cover, (ii)  
248 coral-community composition, (iii) habitat type, and (iv) the oceanography of the region.

249 In conclusion, calcifying marine organisms, such as corals, are particularly vulnerable to changes  
250 in pH (Langdon and Atkinson 2005), particularly coral skeletons with no buffering capacity (Ries  
251 2011). Perforate reef corals will most likely dissolve under ocean acidification, whereas reefs  
252 composed of imperforate skeletons will not likely dissolve. When the ocean pH is 7.8, which is  
253 expected by 2100, perforate coral skeletons will lose calcium carbonate, the reef's primary

254 framework, in proportion to the surface area exposed to seawater. That loss of skeletal mass is on  
255 average -  $15.3 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ , which is approximately – 10.5 mm of vertical reduction of  
256 reef framework per year. This rate is three times the average growth rate of modern reefs.  
257 Therefore, coral reefs composed mainly of perforate corals will have trouble accreting and  
258 keeping up with sea level rise when the pH of the oceans is 7.8, which is expected by 2100.

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264 **References**

- 265 Adey W.H. (1987) Coral reef morphogenesis: A multi-dimensional model, *Science* 202: 831-837
- 266 Al-Horani F.A., Al-Moghrabi S.M., de Beer D. (2003) The mechanism of calcification and its  
267 relation to photosynthesis and respiration in the scleractinian coral *Galaxea fascicularis*, *Marine*  
268 *Biology* 142: 419-426
- 269 Allemand D., Ferrier-Pagès C., Furla P., Houlbrèque F., Puverel S., Reynaud S., Tambutté E.,  
270 Tambutté S., Zoccola D. (2004) Biomineralisation in reef-building corals: from molecular  
271 mechanisms to environmental control, *Comptes Rendus Palevol* 3: 453–467
- 272 Anthony K.R.N., Kline D.I., Diaz-Pulido G., Dove S., Hoegh-Guldberg O. (2008) Ocean  
273 acidification causes bleaching and productivity loss in coral reef builders, *Proceedings of the*  
274 *National Academy of Science* 105: 17442–17446
- 275 Broecker W.S (1983) The Ocean, *Scientific American* 249: 146-48
- 276 Bruno J.F., Selig E.R (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent,  
277 and subregional comparisons, *PLoS ONE*, 2, 8, e711. doi:10.1371/journal.pone.0000711
- 278 Buddemeier R.W., Hopley D (1988) Turn-ons and turn offs: Causes and mechanisms of the  
279 initiation and termination of coral reef growth, *Proceedings of the 6<sup>th</sup> International Coral Reef*  
280 *Symposium*, Townsville, Australia, 8-12 August 1988, 1988, 1, 253-261
- 281 Caldera K., Wickett M.E. (2003) Anthropogenic carbon and ocean pH, *Nature* 425: 365
- 282 Cubillas P, Kohler S, Prieto M, Chairat C, Oelkers EH (2005) Experimental determination of the  
283 dissolution rates of calcite, aragonite, and bivalves. *Chemical Geology* 216: 59-77
- 284 DeVantier L.M (1992) Rafting of tropical marine organisms on buoyant coralla, *Mar. Ecol. Prog.*  
285 *Ser.* 86, 301-302
- 286 Dullo W.C. (2005) Coral growth and reef growth: a brief review, *Facies* 51: 33-48
- 287 Erez J, Reynaud S, Silverman J, Schneider K, Allemand D (2010) Coral calcification under ocean  
288 acidification and global change. In, Editors, Z. Dubinsky & N Stambler, *Coral reefs: an*  
289 *ecosystem in transition*, Springer, New York, 551 pp
- 290 Feely RA, Christopher L. Sabine CL, Lee K, Will Berelson W, Kleypas J, Fabry VJ, Frank J.  
291 Millero FJ (2004) Impact of Anthropogenic CO<sub>2</sub> on the CaCO<sub>3</sub> System in the Oceans.  
292 *Science* 305: 362–366
- 293 Fine M., Tchernov D (2007) Scleractinian coral species survive and recover from decalcification,  
294 *Science* 315: 1811

- 295 Gladfelter EH (1982) Skeletal development in *Acropora cervicornis*: I. patterns of calcium  
296 carbonate accretion in the axial corallite. *Coral Reefs* 1:45-51
- 297 Glynn P.W (1997) Bioerosion and coral-reef growth: a dynamic balance, In Birkeland, C. (Ed.),  
298 Life and Death of coral reefs, Chapman & Hall, 68-95
- 299 Hansen L., Sato M., Ruedy R., Lo K., Lea D.W., Medina-Elizade M. (2006) Global temperature  
300 change, *PNAS* 103: 14288-14293
- 301 Hoegh-Guldberg O., Mumby P., Hooten A.J., Steneck R.S., Greenfield P., Gomez E., Harvell  
302 C.D., Sale P.F., Edward A.J., Caldiera K., Knowlton N., Eakin C.M., Iglesias-Prieto R., Muthiga  
303 N., Bradbury R.H., Dubi A., Hatziolos M.E (2007) Coral reefs under rapid climate change and  
304 ocean acidification, *Science* 318: 1737-1742
- 305 Hautmann M (2004) Effect of End-Triassic CO<sub>2</sub> maximum on carbonate sedimentation and  
306 marine mass extinction. *Facies* 50:257–261
- 307 Hopley D (1982) The geomorphology of the Great Barrier Reef: Quaternary development of  
308 coral reefs, John Wiley-Interscience, New York, pp 453
- 309 Hughes TP (1987) Skeletal density and growth form of corals. *Marine Ecology Progress Series*  
310 35: 259-266
- 311 Intergovernmental Panel on Climate Change (IPCC 2007), *Climate Change 2007: the physical  
312 science basis, Contribution of Working Group 1 to the Fourth Assessment Report of the  
313 Intergovernmental Panel on Climate Change*, Cambridge Univ. Press, Cambridge, p 793
- 314 Kinsey D.W (1979) Carbon turnover and accumulation by coral reefs, PhD Dissertation thesis,  
315 University of Hawaii, 284
- 316 Kroeker K.J., Kordas R.L., Crim R.N., Singh G.G (2010) Meta-analysis reveals negative yet  
317 variable effects of ocean acidification on marine organisms, *Ecology Letters* 13: 1419–1434
- 318 Langdon C., Atkinson M.J (2005) Effect of elevated pCO<sub>2</sub> on photosynthesis and calcification of  
319 corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment, *J.  
320 Geophys. Res.* 110, C09S07, doi:10.1029/2004JC002576
- 321 MacIntyre I., Marshall J.F (1988) Submarine lithification in coral reefs: same facts and  
322 misconceptions, *Proc 6th Int. Coral Reef Symp., Australia*, 1, 263-272
- 323 Madin JS, Hughes TP, Connolly SR (2012) Calcification, storm damage, and population  
324 resilience of tabular corals under climate change. *PLOS ONE* 10.1371/journal.pone.0046637
- 325 Manzello D.P., Kleypas J.A., Budd D.A., Eakin C.M., Glynn P.W., Langdon C. (2008)  
326 *Proceedings of the National Academy of Sciences* 105: 10450-10455

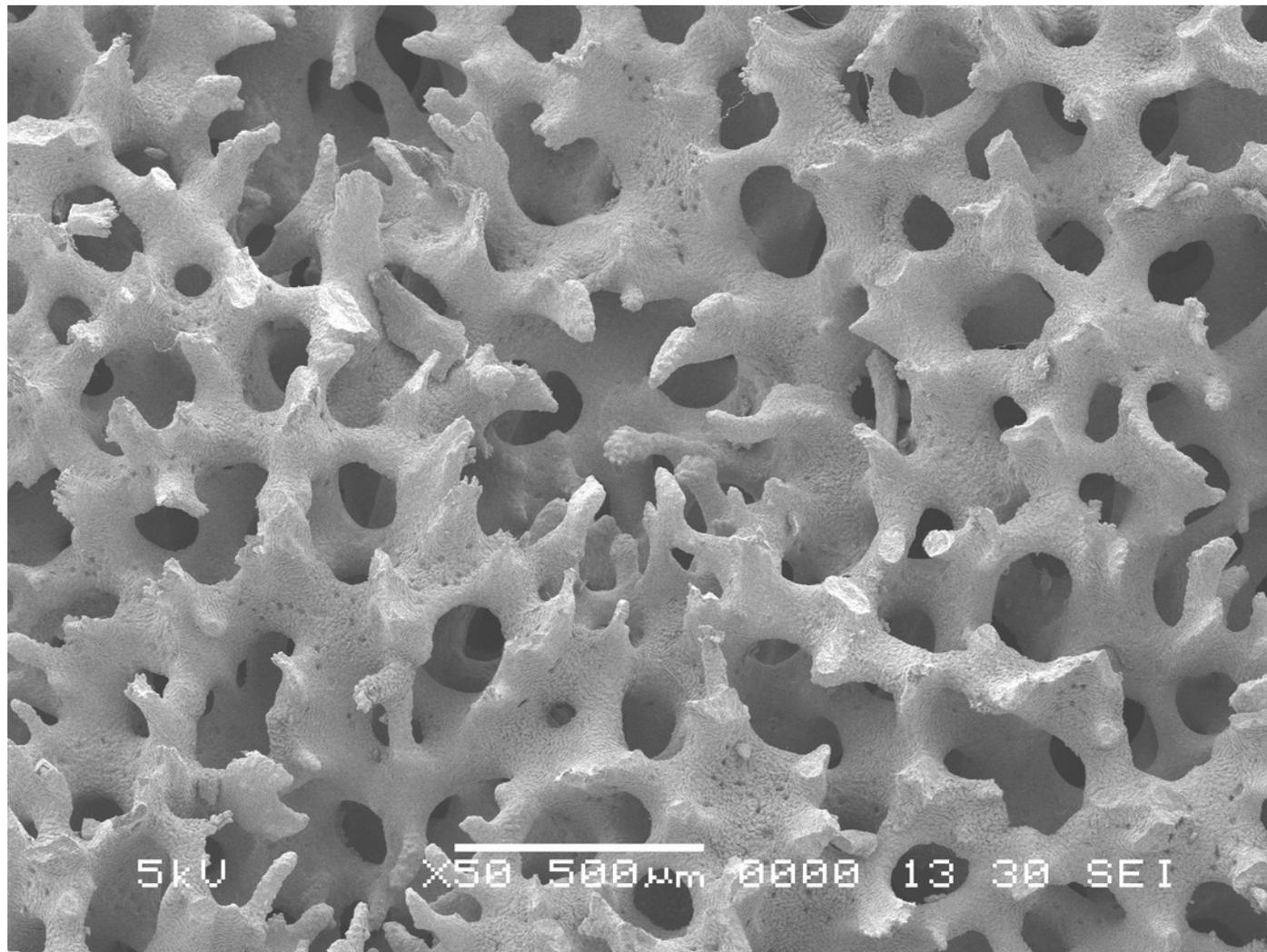
- 327 Marubini F., Ferrier-Pages C., Furla P., Allemand D (2008) Coral calcification responds to  
328 seawater acidification: a working hypothesis towards a physiological mechanism, *Coral Reefs* 7:  
329 491–499
- 330 McCulloch M., Falter J., Trotter J., Montagna P (2012) Coral resilience to ocean acidification  
331 and global warming through pH up-regulation, *Nature Climate Change*, 2012, doi:  
332 10.1038/NCLIMATE1473
- 333 Millero FJ (2007). The marine inorganic carbon cycle. *Chem. Rev.* 2007, 107, 308-341
- 334 Morse JW, Arvidson, RS, Luttge A (2007) Calcium Carbonate Formation and Dissolution. *Chem.*  
335 *Rev.* 107: 342-381
- 336 Neumann A.C., MacIntyre I (1985) Reef response to sea level rise: keep-up, catch-up or give-  
337 up, *Proc. 5th International Coral Reef Congress*, 3: 105-110
- 338 Office of National Marine Sanctuaries, Florida Keys National Marine Sanctuary Condition  
339 Report 2011, U.S. Department of Commerce, National Oceanic and Atmospheric Administration,  
340 Office of National Marine Sanctuaries, Silver Spring, MD, 2011, 105
- 341 Perry CT, Murphy GN, Kench PS, Smithers SG, Edinger EN, Steneck RS, Mumby PJ (2013).  
342 Caribbean-wide decline in carbonate production threatens coral reef growth. *Nature*  
343 *Communications* 4:1402. doi:10.1038/ncomms2409
- 344 Portner H.-O (2010) Oxygen- and capacity-limitation of thermal tolerance: a matrix for  
345 integrating climate-related stressor effects in marine ecosystems. *J Exp Biol* 213:881-893
- 346 Reynaud S, Leclercq N, Romaine-Lioud S, Ferrier-Pagès C, Jaubert J, Gattuso J-P (2003)  
347 Interacting effects of CO<sub>2</sub> partial pressure and temperature on photosynthesis and calcification in  
348 a scleractinian coral. *Glob Change Biol* 9:1660–1668
- 349 Ries J. (2011) Acid ocean cover up, *Nature Climate Change* 1: 294-295
- 350 Rodolfo-Metalpa R., Houlbrèque F., Tambutté E., Boisson F., Baggini C., Patti F.P., Jeffrey R.,  
351 Fine M., Foggo A., Gattuso J.P., Hall-Spencer J.M. (2011) Coral and mollusc resistance to  
352 ocean acidification adversely affected by warming, *Nature Climate Change*, doi:  
353 10.1038/NCLIMATE1200
- 354 R Development Core Team (2012). R: A language and environment for statistical computing. R  
355 Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL  
356 <http://www.R-project.org>.
- 357 Silvermann J., Lazor B., Cao L., Caldiera K., Erez J. (2009) Coral reefs may start dissolving  
358 when atmospheric CO<sub>2</sub> doubles, *Geophysical Research Letters* 36: L05606,  
359 doi:10.1029/2008GL036282
- 360 Smith S.V. (1983) Coral reef calcification, In Barnes, D.G. (Ed.), *Perspectives on coral reefs*,  
361 Brian Clouston Publisher, 240-247

- 362 Smith S.V., Kinsey D.W. (1976) Calcium carbonate production, coral reef growth, and sea level  
363 change, *Science* 194, 937-939
- 364 Smith S.V., Buddemeier R.W. (1992) Global change and coral reef ecosystems, *Annual Review*  
365 *of Ecology and Systematics* 23: 89-118
- 366 Stearn C.W., Scoffin T.P., Martindale W. (1977) Calcium carbonate budget of a fringing reef on  
367 the west coast of Barbados, *Bull. Marine Science* 27: 479-510
- 368 Veal C.J., Carmi M., Fine M. (2010) Increasing the accuracy of surface area estimation using  
369 single wax dipping of coral fragments. *Coral Reefs* 29: 893-897
- 370 Vermeer M., Rahmstorf S. (2009) Global sea level linked to global temperature, *Proceedings of*  
371 *the National Academy of Sciences* 106, 21527-21532
- 372 Veron JEN (1995) *Corals in space and time: the biogeography and evolution of the Scleractinia.*  
373 University of New South Wales Press, Sydney, pp 321
- 374 Veron JEN (2008) Mass extinctions and ocean acidification: biological constraints on geological  
375 dilemmas. *Coral Reefs* 27: 459-472
- 376 Walter L.M., Morse J.W. (1984) Reactive surface area of skeletal carbonates during dissolution:  
377 effect of grain size, *J. of Sedimentary Petrology* 54: 1081-1090
- 378 Wood R (1999) *Reef evolution.* Oxford University Press, Oxford, pp 414
- 379 Zeebe RE, JC Zachos, Caldira K, Tyrrell T (2008) Carbon emissions and acidification. *Science*  
380 321: 51-52

# Figure 1

*Montipora*.

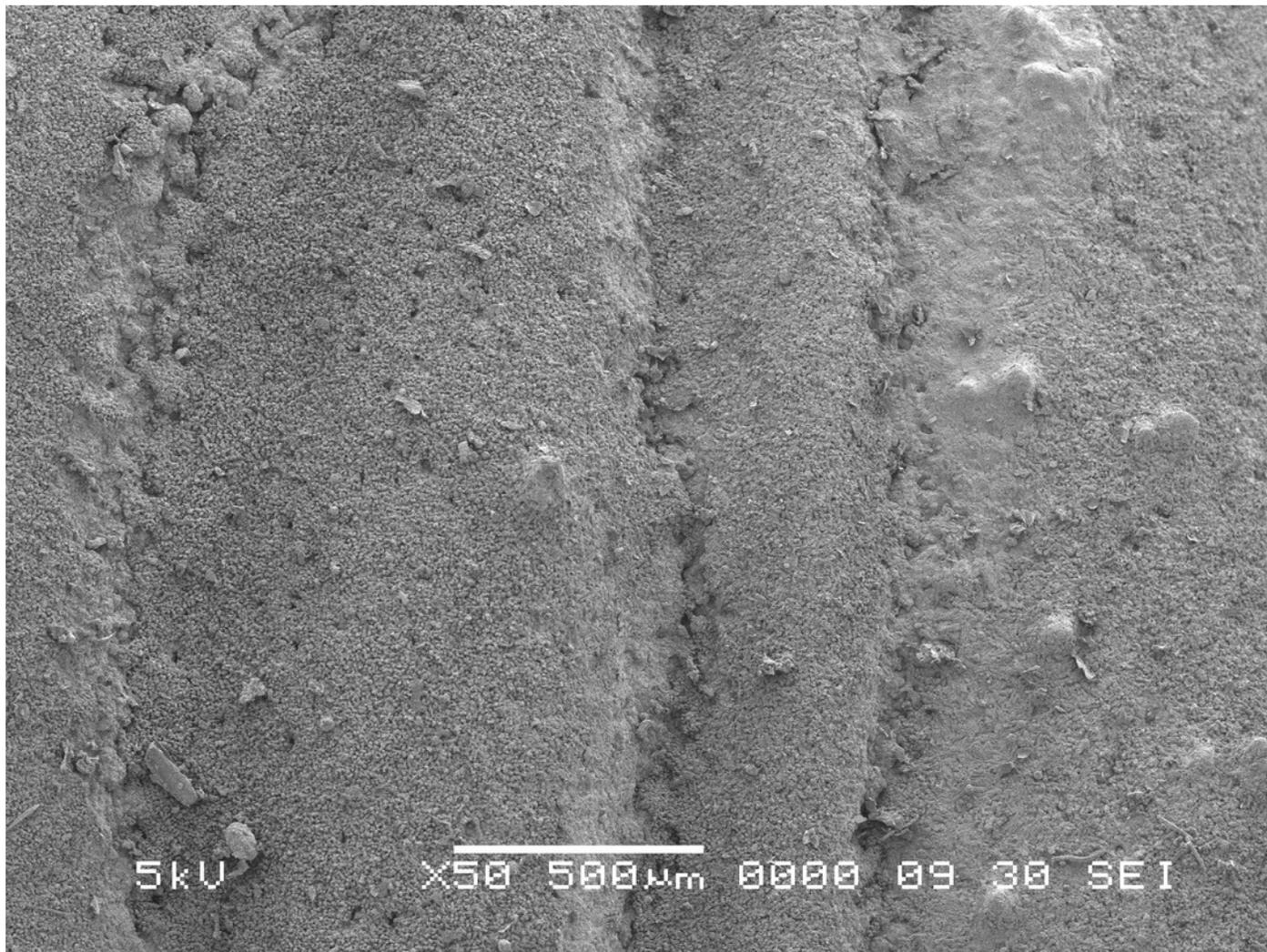
Scanning electron microscope image of *Montipora*; scale bar is 500 micrometer.



# Figure 2

*Pectinia*.

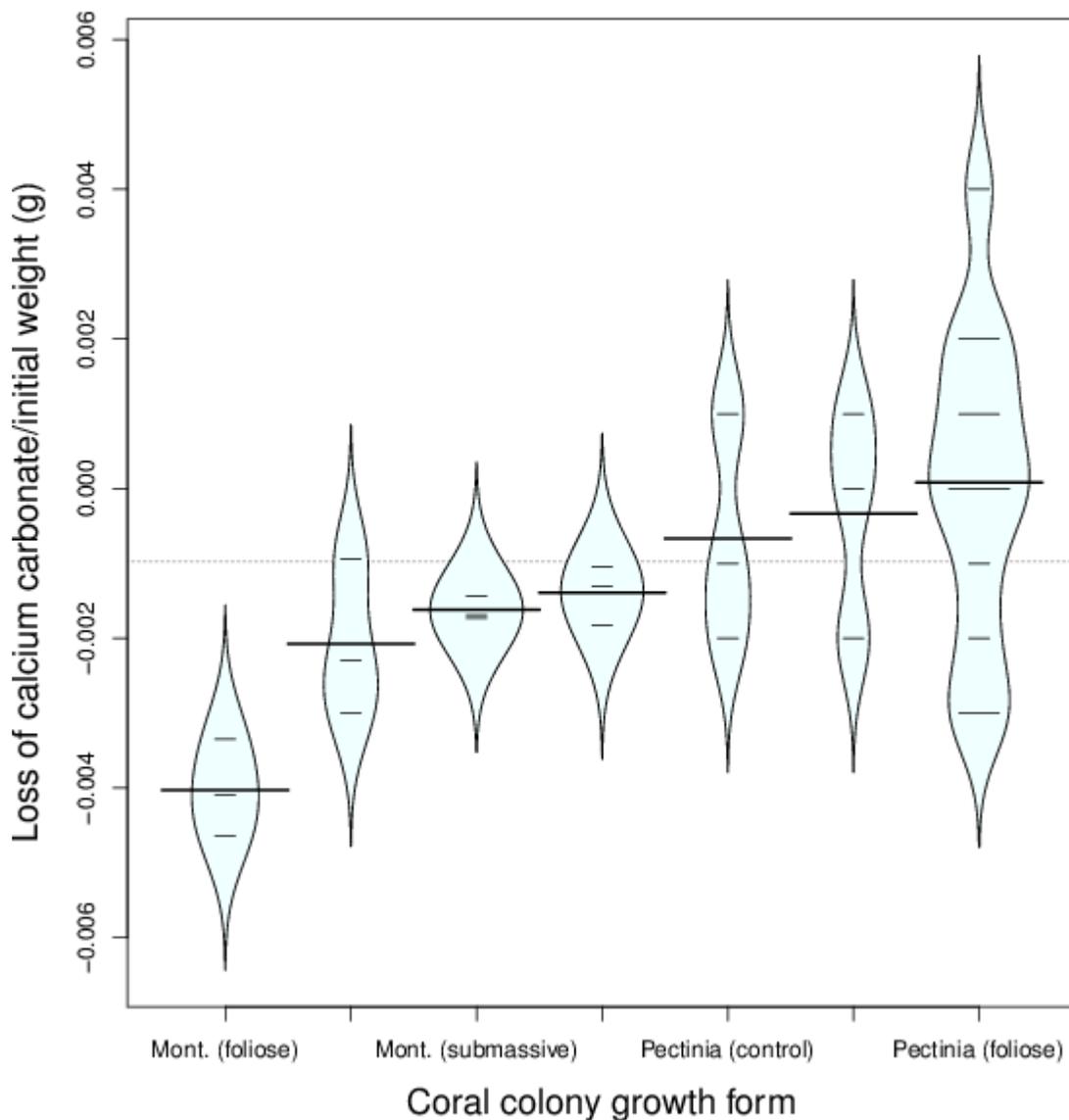
Scanning electron microscope image of *Pectinia*; scale bar is 500 micrometer.



## Figure 3

Comparative loss of Calcium carbonate.

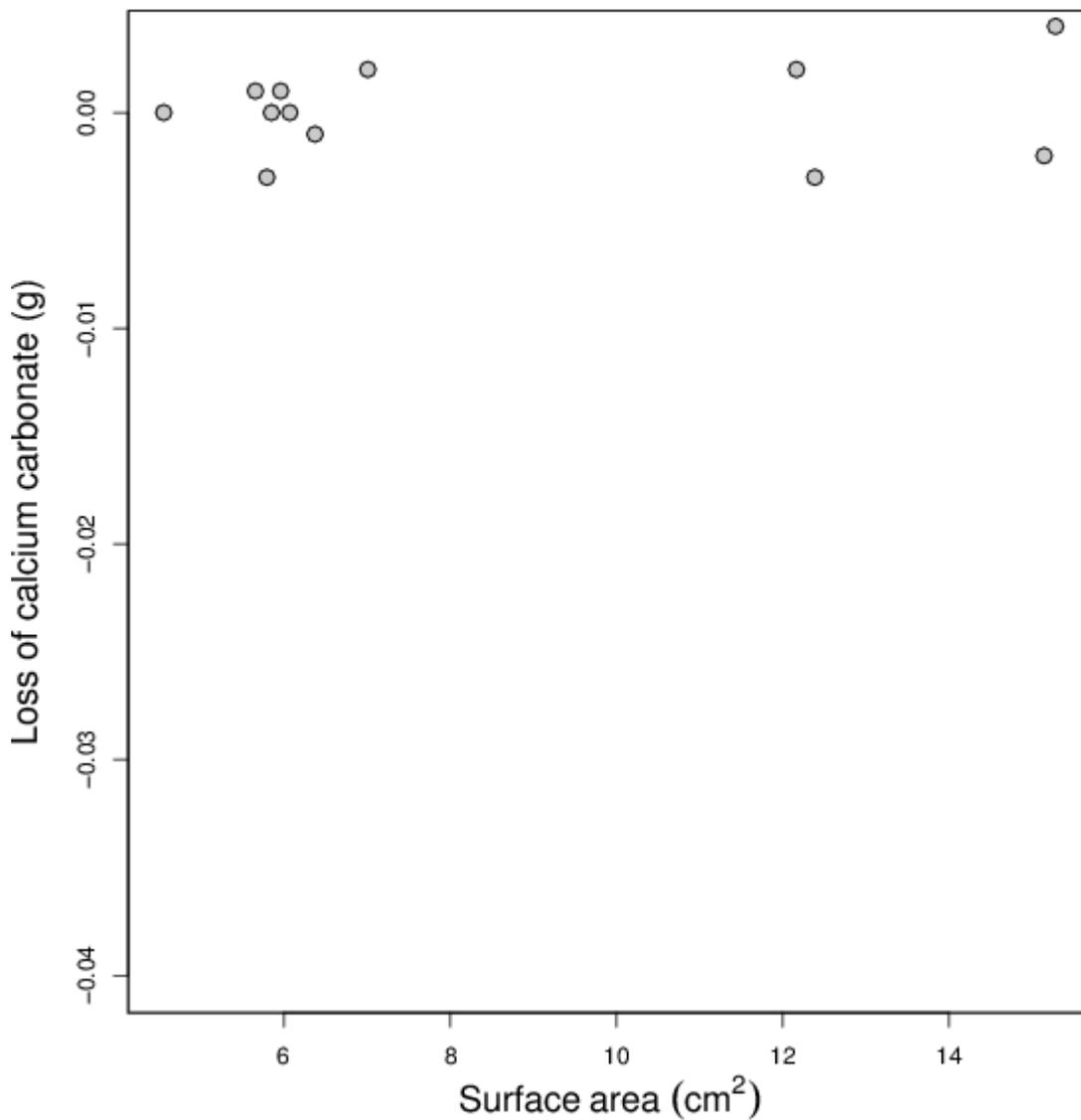
Loss of calcium carbonate, divided by the initial weight (g), of four different coral growth forms of *Montipora* coral skeletons, and one growth form of *Pectinia* coral skeleton, when exposed to pH 7.8 seawater for 7 days. The graph also depicts the controls for *Montipora* and *Pectinia* coral skeletons, which were exposed to present-day seawater, at a pH of 8.2, for 7 days. The dashes are the data points, the horizontal lines on each 'bean' show the means, and each 'bean' shape follows the general the distribution of the data relative to density.



# Figure 4

*Pectinia* dissolution.

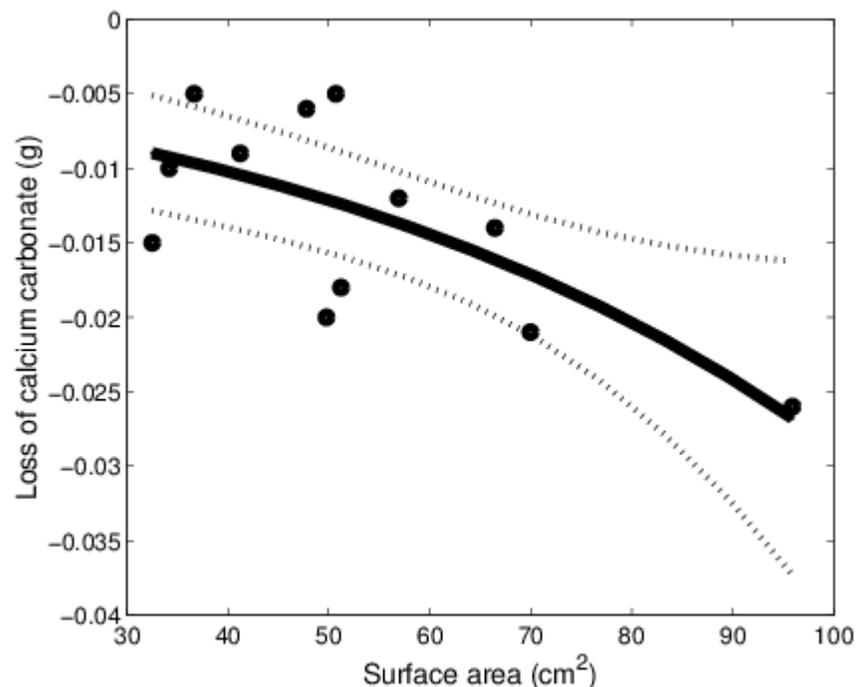
The relationship between the surface area of the *Pectinia* coral skeletons (cm<sup>2</sup>) and the loss of calcium carbonate (CaCO<sub>3</sub>) (g) over 7 days.



# Figure 5

*Montipora* dissolution.

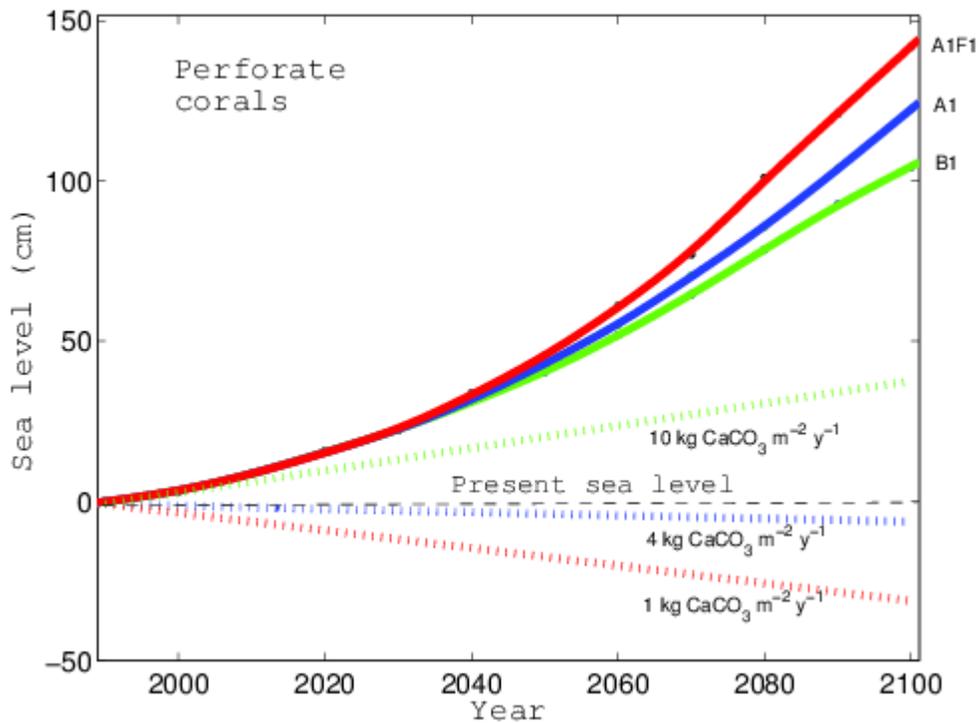
The relationship between the surface area of the *Montipora* coral skeletons ( $\text{cm}^2$ ) and the loss of calcium carbonate ( $\text{CaCO}_3$ ) (g) over 7 days follows the equation  $\text{loss} = -0.005 \times \exp(0.017 \cdot \text{surface area})$ . The dots are the data points, the thick, black line represents the equation, and the dotted lines represent the 95% confidence intervals.



## Figure 6

Perforate corals and predicted sea level rise.

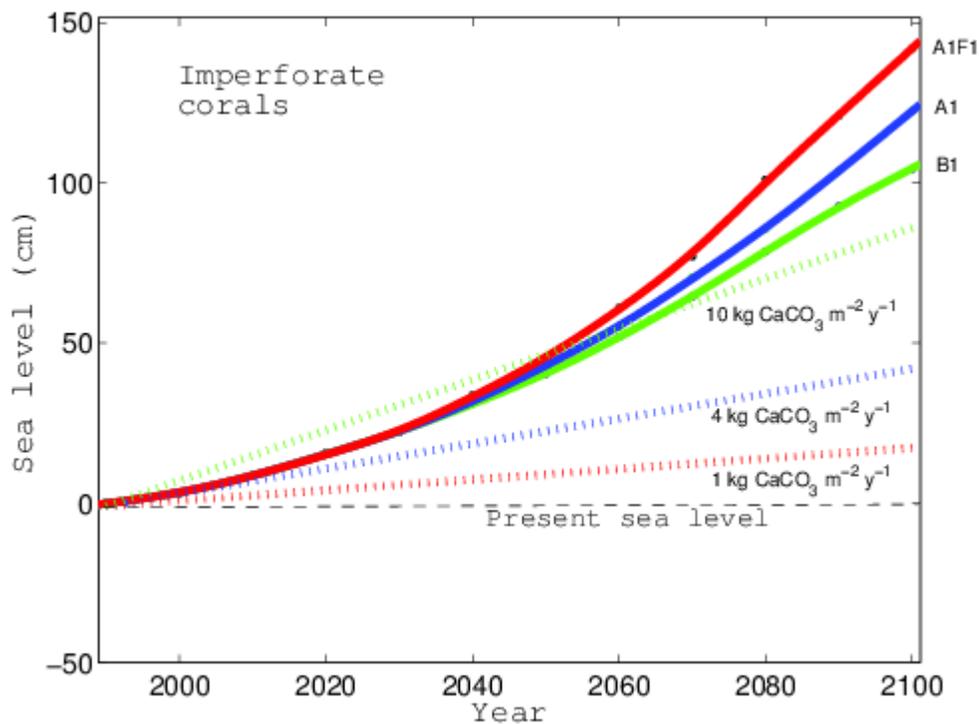
The projections of expected rates of coral-reef accretion relative to rates of dissolution of reefs composed of mainly perforate corals, with 3 different densities of corals (low, medium and high modeled as 1, 4, and 10 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ ), along with projections of global sea-level rise (not considering regional isostatic rebound effects, regional tectonics, and local land-use effects) and potential reef-accretion rates from 1990 to 2100 following Vermeer and Rahmstorf (2009, Figure 6) for different IPCC (2007) emission scenarios, where the B1 scenario is green and represents a  $+1.8^\circ\text{C}$  global increase in temperature; the A2 scenario is blue and represents a  $+3.4^\circ\text{C}$  global increase in temperature; the A1F1 scenario is red and represents a  $4^\circ\text{C}$  global increase in temperature.



# Figure 7

Imperforate corals and predicted sea level rise.

The projections of expected rates of coral-reef accretion relative to rates of dissolution of reefs composed of mainly imperforate perforate corals, with 3 different densities of corals (low, medium and high modeled as 1, 4, and 10 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$ ), along with projections of global sea-level rise (as in Figure 6).



**Table 1** (on next page)

Porosity of scleractinian corals.

Scleractinian coral families, the number of species in each family, and the general porosity of the coral skeletons. Classifications were based on the porosity of the colony walls, the coenosteum, and the collumellae at the scale of 1 mm<sup>2</sup>. There are approximately 404 perforate species and 432 imperforate coral species, globally.

	<b>Family</b>	<b>Number of species</b>	<b>Porosity</b>
2			
3	Acroporidae	271	Perforate
4	Agariciidae	45	Imperforate
5	Astrocoeniidae	15	Imperforate
6	Caryophylliidae	7	Imperforate
7	Dendrophylliidae	19	Imperforate
8	Euphyllidae	17	Imperforate
9	Faviidae	130	Imperforate
10	Fungiidae	46	Imperforate
11	Meandrinidae	12	Imperforate
12	Merulinidae	12	Imperforate
13	Mussidae	52	Imperforate
14	Oculinidae	16	Imperforate
15	Pectiniidae	29	Imperforate
16	Pocilloporidae	31	Imperforate
17	Poritidae	101	Perforate
18	Siderastreidae	32	Perforate
19	Trachphylliidae	1	Imperforate