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2 Limited cross-shelf variation in the growth of three 3 branching corals on Australia's Great Barrier Reef.

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9

10 **Abstract:** Pronounced differences exist in the biodiversity and structure of coral reef assemblages 11 with increasing distance from shore, which may be expected given marked cross-shelf gradients in 12 environmental conditions. Cross-shelf variation in the abundance of coral reef organisms is likely 13 to be caused, at least in part, by differences in demography (e.g., growth and survival), though this 14 has rarely been tested. This study quantified growth of three distinct coral taxa (*Acropora nasuta*, 15 *Pocillopora* spp., and *Stylophora pistillata*) at 6 sites on Australia's Great Barrier Reef (GBR), 16 encompassing inshore, mid-shelf and outer-shelf reefs. Replicate colonies (up to 15 colonies per 17 species, per reef) were stained using Alizarin red in December 2015 and retrieved 1-year later to 18 quantify linear extension on replicate branches for each colony. Annual linear extension varied 19 within and among coral taxa, with pronounced differences among reefs. For *A. nausta.* and *S.* 20 *pistillata*, growth rates were highest at Orpheus Island, which is an inner shelf reef. However, inter- 21 reef differences in coral growth were not explained by shelf position. Based on differences in skeletal 22 density, which did vary according to shelf position, branching corals at the inshore sites may 23 actually have higher rates of calcification compared to conspecifics on mid- and outer-shelf reefs. 24 This study shows that growth of branching corals is not lower at inshore sites (and perhaps even 25 higher) compared to sites at mid-shelf and outer reefs, despite generally higher levels of 26 sedimentation and turbidity.

27 **Keywords:** annual linear extension; calcification; coral reefs; environmental gradients; growth; 28 turbidity

29

30 1. Introduction

31   Reef building, scleractinian ("hard") corals have specific environmental tolerances (Kleypas et 32 al. 1999 [1]), such that individual demography, population dynamics and community structure vary 33 markedly along environmental gradients (e.g., Done 1982 [2]; Harriot 1999 [3]; Anderson et al. 2017 34 [4]). Most notably, there are clear and well-defined latitudinal limits to growth and abundance of 35 scleractinian corals, and therefore, reef accretion (Buddemeier and Kinzie 1976 [5]; Kleypas et al. 1999 36 [1]; Muir et al. 2015 [6]), which are constrained at high latitudes by lower temperature, aragonite 37 saturation and light levels. Even within the latitudinal limits of coral reef accretion, there are declines 38 in diversity of coral assemblages with increasing latitude (Bellwood and Hughes, 2001 [7]). For those 39 coral species that are distributed over a wide latitudinal extent, there are also differences in 40 demography linked to differences in local environmental conditions (e.g., Anderson et al. 2015 [8]). 41 In general, corals grow more slowly at high latitude locations, which is largely attributed to thermal 42 constraints on coral growth (e.g., Harriot, 1999 [3], Anderson et al. 2015 [8], Pratchett et al. 2015 [9]), 43 and this may in turn, lead to lower population turnover and reduced resilience (Hoey et al. 2011 [10]). 44   Despite considerable research on large-scale (biogeographical) patterns in coral assemblages, 45 and the various factors that contribute to these patterns (Bellwood and Hughes, 2001 [7]; Connolly et 46 al. 2003 [11]; Keith et al. 2013 [12]), variation in coral populations and communities is often very

47 pronounced even at relatively small spatial scales (e.g., with depth, aspect, and distance from shore),
48 associated with steep gradients in environmental conditions (Done 1982 [2]; Cleary et al. 2005 [13]).
49 Cross-shelf variation in the abundance, biodiversity, and composition of benthic reef assemblages is
50 particularly pronounced (e.g., Done 1982 [2]; Wilkinson and Cheshire 1989 [14]; Fabricius and De'Ath
51 2001 [15], Wismer et al. 2009 [16]). In general, near shore (or inshore) reef habitats have higher
52 abundance of fleshy macroalgae and coral assemblages are dominated by stress-tolerant species,
53 whereas offshore reef habitats have higher cover of crustose coralline algae and higher diversity of
54 corals (but see Lirman and Fong 2007 [17]). There are also marked differences in the abundance and
55 composition of fish assemblages between inshore and offshore reefs (e.g., Williams 1982 [18];
56 Williams and Hatcher 1983 [19]; Russ 1984 [20]; Hoey and Bellwood 2008 [21]; Emslie et al. 2010 [22]),
57 with possible consequences for the structure and functioning of reef ecosystems.
58   Cross-shelf variation in the abundance, biodiversity and composition of coral reef organisms
59 may be ascribed to natural and inherent gradients in environmental conditions, such as depth and
60 wave exposure (Bellwood and Wainwright 2001 [23]). However, anthropogenic transformation of
61 coastal environments, involving land clearing, coastal development, and dredging, are causing
62 increasing sedimentation, eutrophication, and pollution (Hughes et al. 2015 [24]; Kroon et al. 2016
63 [25]), which have disproportionate impacts on near shore systems. Increasing levels of both
64 suspended sediment and sediment deposition have generally negative consequences for corals (Loya,
65 1976 [26]; Riegl and Branch 1995 [27]; Fabricius 2005 [28]; Weber et al. 2012 [29]), causing light
66 attenuation and reduced photosynthesis versus tissue abrasion and smothering, respectively. Some
67 coral species are capable of withstanding increased exposure to sedimentation by actively feeding on
68 particulate matter (Anthony & Fabricius, 2000 [30]), though increased levels of sedimentation often
69 have catastrophic impacts on established coral assemblages (Dodge & Vaisnys, 1977 [31]) if not
70 sublethal effects such as suppressed coral growth (Fabricius 2005 [28]).
71   The purpose of this study was to quantify cross-shelf variation in annual linear extension (ALE)
72 for three different taxa of branching corals; *Acropora nasuta*, *Pocillopora* spp., and *Stylophora pistillata*.
73 The focus on branching corals was intended to complement previous studies (e.g., Lough and Barnes
74 2000 [32], Carricart-Ganivet & Merino, 2001 [33]) that have explored spatial variation (at a wide range
75 of different scales) in growth of massive corals, for which growth can be retrospectively measured
76 from skeletal features (Pratchett et al. 2015 [9]). Estimating growth of branching corals meanwhile,
77 requires real time measurements of changes in weight or external dimensions. Branching corals also
78 make disproportionate contributions to the structure and topographic complexity of reef habitats,
79 which supports high abundance and diversity of reef organisms (Messmer et al., 2011 [34]).
80 Moreover, branching corals are amongst the fastest growing corals (Pratchett et al. 2014 [9]), but are
81 also very susceptible to environmental change (Hughes et al. 2018 [35]). Given the sustained and
82 ongoing degradation of near shore environments (Kroon et al. 2016 [25]), as well as the sensitivity of
83 branching corals to sedimentation (Fabricius 2005 [28]; Weber et al. 2012 [29]), we expected to find
84 markedly lower rates of growth on inshore reefs (located within 20 km of the coastline) compared to
85 corals growing at reefs located up to >35 km offshore.

2. Materials and Methods

2.1. Field sampling

88   Annual linear extension (ALE) of three coral taxa (*Acropora nasuta*, *Pocillopora* spp., and
89 *Stylophora pistillata*) was quantified at six reefs (Orpheus Island, Pelorus Island, Bramble Reef, Trunk
90 Reef, Pith Reef, and Unnamed Reef) in the central Great Barrier Reef (GBR), near Townsville (Fig. 1).
91 *Pocillopora* colonies were selected based on their fine branching structure, and were ostensibly *P.*
92 *damicornis* (Schmidt-Roach et al. 2014 [36]), though it is possible that some colonies were actually *P.*
93 *acuta*. Reefs were specifically selected to represent inshore (Orpheus and Pelorus Islands), mid-shelf
94 (Bramble and Trunk reefs) and offshore reefs (Pith and Unnamed reefs), though cross-shelf
95 differences were confounded by reef type; nearshore reefs (Orpheus and Pelorus Islands) were
96 fringing reefs associated with continental islands whereas mid- and offshore reefs are submerged

97   platform reefs. Sites were established on the western margin of each reef, to allow for moderate water
98   flow, but minimize more devastating effects of south-easterly swells. Sites selected at the near shore
99   reefs (Orpheus and Pelorus Islands) were located 20 km from the coastline, compared to 35-50 km for
100 sites on mid-shelf sites (Bramble and Trunk reefs). The outermost site, at Pith Reef, was located 75
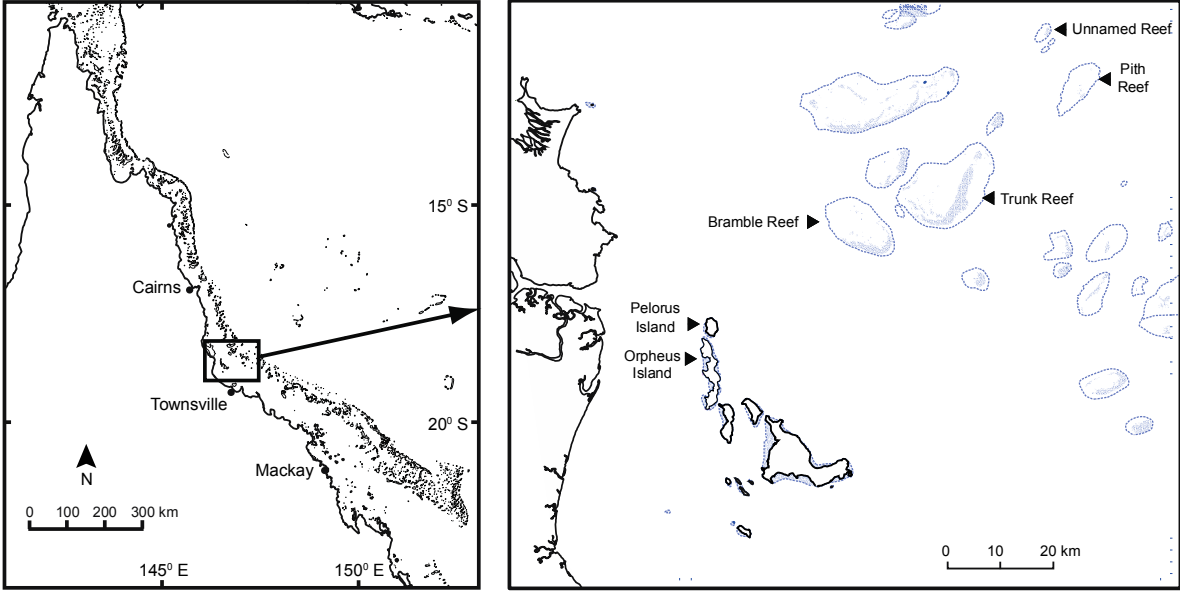101 km from the nearest coastline.
102

Figure 1. Reefs in the central section of Australia's Great Barrier Reef used to explore cross-shelf variation
in the growth of 3 branching corals.

106   Replicate colonies of each species were collected from the reef flat and crest (>4m depth) at one
107 site per reef and then stained and tagged *ex situ*. Corals were stained onboard the RV James Kirby,
108 where individual colonies were tagged with numbered cattle tags and then placed in large (200L)
109 plastic containers containing Alizarin Red mixed in sea water at a concentration of 12 mg.l^{-1}, following
110 Oliver et al. (1983). Water exchange in these tanks was stopped for four hours (during staining) to
111 prevent dilution of the stain. Temperature of the tanks was carefully monitored during staining, and
112 where necessary partial water exchanges (with additional Alizarin Red stain added to maintain
113 concentrations) were used to prevent temperature increasing to more than 2°C above ambient. After
114 four hours, the tanks were flushed with fresh seawater and the corals were held with constant flow
115 for up to 12 hours (overnight). Corals were then returned to collection locations and reattached to the
116 reef using UV stabilized plastic cable ties.
117   In December 2016 (12 months after staining), stained coral colonies were retrieved to quantify
118 annual linear extension. Only colonies that were firmly attached, upright, clearly tagged, and living
119 were considered and retrieved (Table 1). Collected colonies were bleached, by completely
120 submerging them in mild (5%) hypochlorite solution for up to 4 hours until all tissue was removed,
121 washed with freshwater and dried in the sun. Annual linear extension was measured as the minimum
122 distance (mm) from the point of staining to tip of relevant branch. Where possible, twelve
123 measurements were taken for each colony recording the minimum growth on each of 12 distinct
124 branches. For colonies with fewer than 12 distinct branches, or where staining was not clear, the
125 maximum possible number of independent measures was used.
126   To account for potential cross-shelf differences in skeletal density (more specifically, bulk
127 density; Buchere et al. 1998 [38]), which may confound estimates of linear extension (Pratchett et al.
128 2015 [9]), skeletal densities of entire, intact coral colonies were also quantified. The bulk density is the
129 ratio of the colony weight to volume, whereby the volume is measured by comparing the weight of
130 entire dry skeletons to the buoyant weight of the same skeleton when fully submerged in fresh water.
131 Based on Archimedes' principal the skeletal volume is equal to the difference in the dry versus

132 buoyant weight, assuming that the density of the water (freshwater) is equal to 1g. cm^{-3} (Hughes 1987
133 [39]).

2.2. Data analyses

135 To test whether shelf position (inner, mid, versus outer reefs) had a significant effect on the
136 growth of each of the three focal coral species (*Acropora nasuta*, *Pocillopora* spp. and *Stylophora*
137 *pistillata*) we compared between General Linear Models (GLMs) that did or did not account for the
138 shelf position of individual reefs. In all cases, we included a random factor to account for intra-colony
139 and / or inter-colony differences. Independent analyses were run for each coral taxa, comparing i)
140 annual linear extension (measured for up to 12 branches on each of 3-15 colonies for each species)
141 and ii) skeletal density (measured for individual colonies). All analyses were conducted in R, and
142 model comparisons were conducted using Second-order Akaike Information Criterion (AICc), to
143 account for small sample sizes (Burnham and Anderson 2002 [40]). After selecting the best model, we
144 then used model summaries to explore where significant differences actually occurred.

3. Results

146 A total of 129 out of 198 (65.1%) stained colonies were successfully retrieved in December 2016,
147 contributing to exploration of cross-shelf differences in annual linear extension (Table 1). We concede
148 from the outset, that sample sizes are very limiting in some instances, but this reflects inherent risks
149 associated with staining and re-deploying coral colonies for the necessary period (up to 1 year) to
150 effectively quantify and resolve colony-level rates and patterns of linear extension. Moreover, the
151 specific study species that were selected for their abundance on mid-shelf reefs, did not occur in
152 sufficient abundance across all study sites. Notably, this is our third attempt to compare demography
153 of branching corals among reefs at increasing distance from shore on the Great Barrier Reef; In
154 previous attempts, corals were stained at 6 reefs in the vicinity of Lizard Island, but virtually all
155 stained colonies (especially on nearshore reefs) were lost due to successive years of severe cyclones
156 (Cyclone Ita - 2014, and Cyclone Nathan - 2015).

3.1. Annual linear extension (ALE)

158 To quantify cross-shelf variation in ALE, 1,479 branches were measured from 129 colonies across
159 the three coral taxa (*A. nasuta*, *Pocillopora* spp. and *S. pistillata*) and six reefs. *Pocillopora* spp. exhibited
160 highest rates of average annual linear extension (23.56 mm.y^{-1} ±0.86 SE), which were 1.36 times faster
161 than recorded for *A. nasuta* (17.22 mm.y^{-1} ±0.86 SE), and nearly twice that of *S. pistillata* (11.81 mm.y^{-1}
162 ±0.73 SE). For all three of the coral taxa (*A. nasuta*, *Pocillopora* spp. and *S. pistillata*) considered in this
163 study, spatial variation in ALE was most apparent at the level of reefs, rather than shelf position (Fig.
164 2; Table 1). For *A. nasuta*, variation in ALE was most apparent between Bramble Reef and Trunk Reef
165 (coef. = -12.73, SE = 2.64, p <0.01). Otherwise, ALE was generally higher at near shore sites (19.03
166 mm.y^{-1} ±1.29 SE), compared to mid-shelf (14.47 mm.y^{-1} ±4.54 SE), or offshore sites (15.87 mm.y^{-1} ±0.87
167 SE).
168

Table 1. Sample sizes for both the number of colonies actually stained and re-deployed at each location, and the number and percentage recovered (in brackets) that were used to quantify linear extension for each of the three taxa.

Shelf position - Reef	*Acropora nasuta*	*Pocillopora spp.*	*Stylophora pistillata*	Total
Inshore – Orpheus Island	15/ 15 (100%)	10/ 12 (83%)	1/ 3* (33%)	26/ 30 (87%)
Inshore – Pelorus Island	6/ 13 (46%)	12/ 12(100%)	0/0*	18/ 25 (72%)
Mid-shelf – Bramble Reef	2/ 12 (17%)	13/ 13 (100%)	0/11 (0%)	15/ 36 (42%)
Mid-shelf – Trunk Reef	2/ 12 (17%)	11/ 12 (92%)	4/ 11 (36%)	17/ 35 (49%)
Offshore – Pith Reef	9/ 12 (75%)	9/ 12 (75%)	10/ 13 (77%)	28/ 37 (76%)
Offshore – Unnamed Reef	9/ 11 (82%)	10/12 (83%)	6/12 (50%)	25/ 35 (71%)
TOTAL	43/ 75 (57%)	65/ 73 (89%)	21/ 50 (42%)	129/ 198 (65%)

* Could not find sufficient colonies within the specific study location.

Growth rates (ALE) recorded for *Pocillopora* spp. varied greatly among colonies, ranging from a mean of just 4.5 mm.y^{-1}(±0.44 SE) for a colony from Trunk Reef, up to 35.10 mm.y^{-1}(±2.24 SE) for a colony at the outer reef site at Unnamed Reef. However, the average ALE recorded at each site was remarkably consistent between reefs and shelf positions; The only significant difference in ALE was between Bramble Reef where average ALE was 20.35 mm.y^{-1}(±1.71 SE) and Pelorus Island (coef. = 5.78, SE = 2.15, $p < 0.01$) and inter-reef differences were explained by shelf position (Table 2).

For *S. pistillata*, the limited data (especially at inshore sites) greatly constrains any conclusions regarding spatial patterns in coral growth (Fig. 1). Relevant data are included here for completeness, and though the GLM detected a significant effect of reef, we are not prepared to read too much into apparent patterns.

3.2. Skeletal Density

Whole-colony densities (or bulk densities) of the 198 coral colonies used to measure annual linear extension were relatively consistent across the different taxa, but were slightly higher for *Pocillopora* spp. (1.94 g.cm^{-3} ±0.05 SE) compared to *A. nasuta* (1.87 g.cm^{-3} ±0.05 SE) and *S. pistillata* (1.77 g.cm^{-3} ±0.06 SE).

Within taxa, there was marked spatial variation in bulk density (Fig. 3), which was best explained by shelf position (rather than reef) for both *Pocillopora* spp. and *A. nasuta* (Table 2). For *Pocillopora* spp. bulk density was highest at inner shelf locations (2.17 g.cm^{-3} ±0.04 SE), and significantly lower at both mid-shelf (coef. = -0.38, SE = 0.10, $p = <0.01$) and outer shelf locations (coef. = -0.31, SE = 0.11, $p = <0.01$). Within site variation in the density of *Pocillopora* spp. was greatest at mid-shelf and offshore locations (Fig. 2), though most colonies for these locations had much lower density compared to colonies from inshore reefs. Similarly, for *A. nasuta*, bulk density was highest at inner shelf locations (2.02 g.cm^{-3} ±0.04 SE), and significantly lower at both mid-shelf (coef. = -0.44, SE = 0.16, $p = 0.01$) and outer shelf locations (coef. = -0.22, SE = 0.10, $p = 0.03$). Within site variation in the density of *A. nasuta* was greatest at the near shore location at Orpheus Island, though there was only one colony (out of 18 colonies) from inshore reefs, for which bulk density was <1.7 g.cm^{-3}. The lowest average bulk density for *A. nasuta* (1.57 g.cm^{-3} ±0.10 SE) was recorded at mid-shelf reefs (Fig. 3), but was even lower at Trunk Reef (1.50 g.cm^{-3}) compared to Bramble Reef (1.64 g.cm^{-3}), though these estimates are based on very small sample sizes (n = 2).

As for growth (ALE), there were apparent inter-reef differences in bulk density for *S. pistillata* (Fig. 2), though apparent differences were based on the relatively high density (2.15) recorded for the one colony sampled from inshore sites.
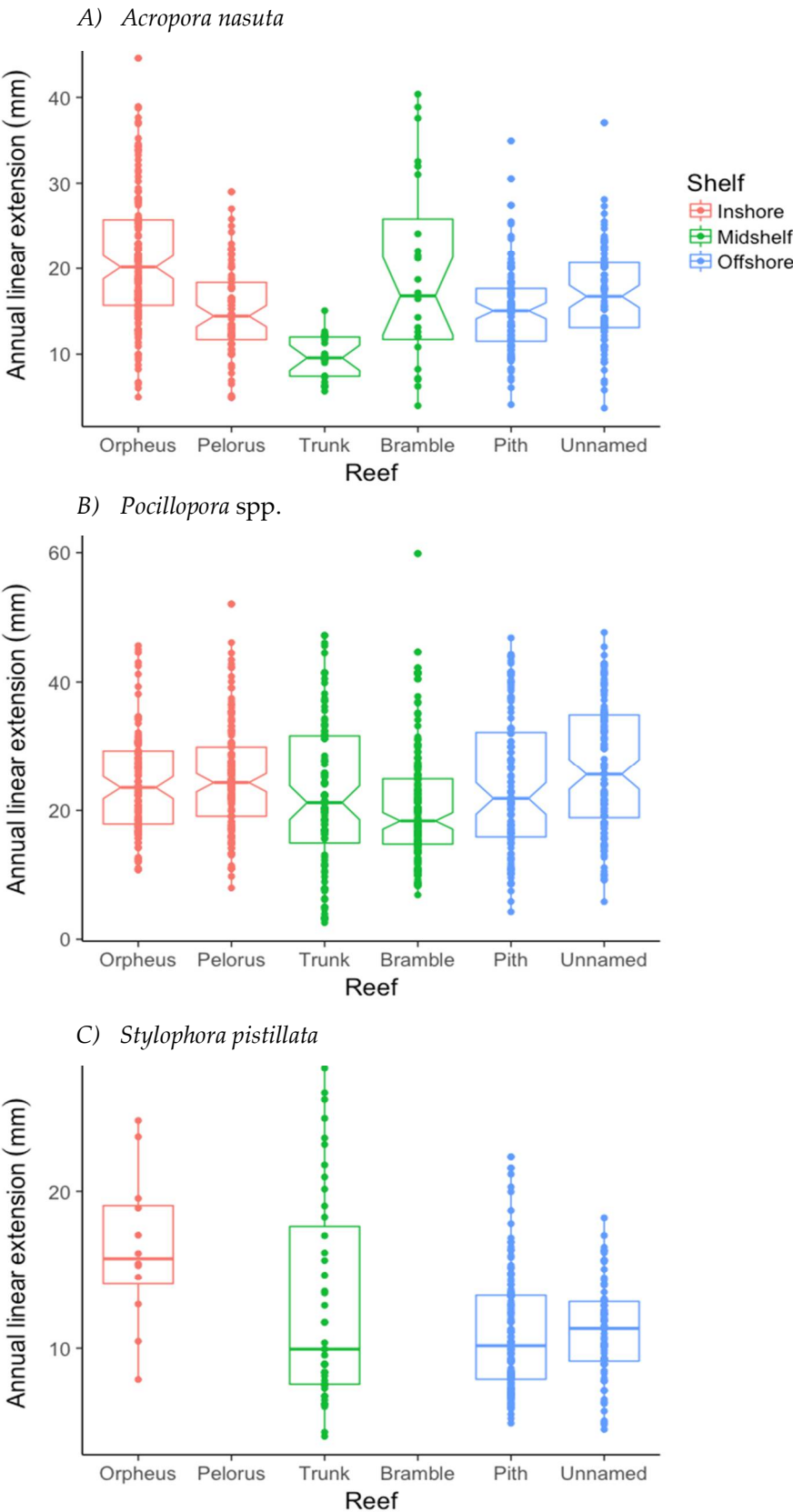
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Figure 2. Inter-reef differences in annual linear extension for A) *Acropora nasuta*, B) *Pocillopora* spp.
and C) *Stylophora pistillata*. Notched boxplots (where possible) show the 95% confidence interval, the
first and third quartiles, and range. Limited and missing data for *S. pistillata* (see Table 1) prevent the
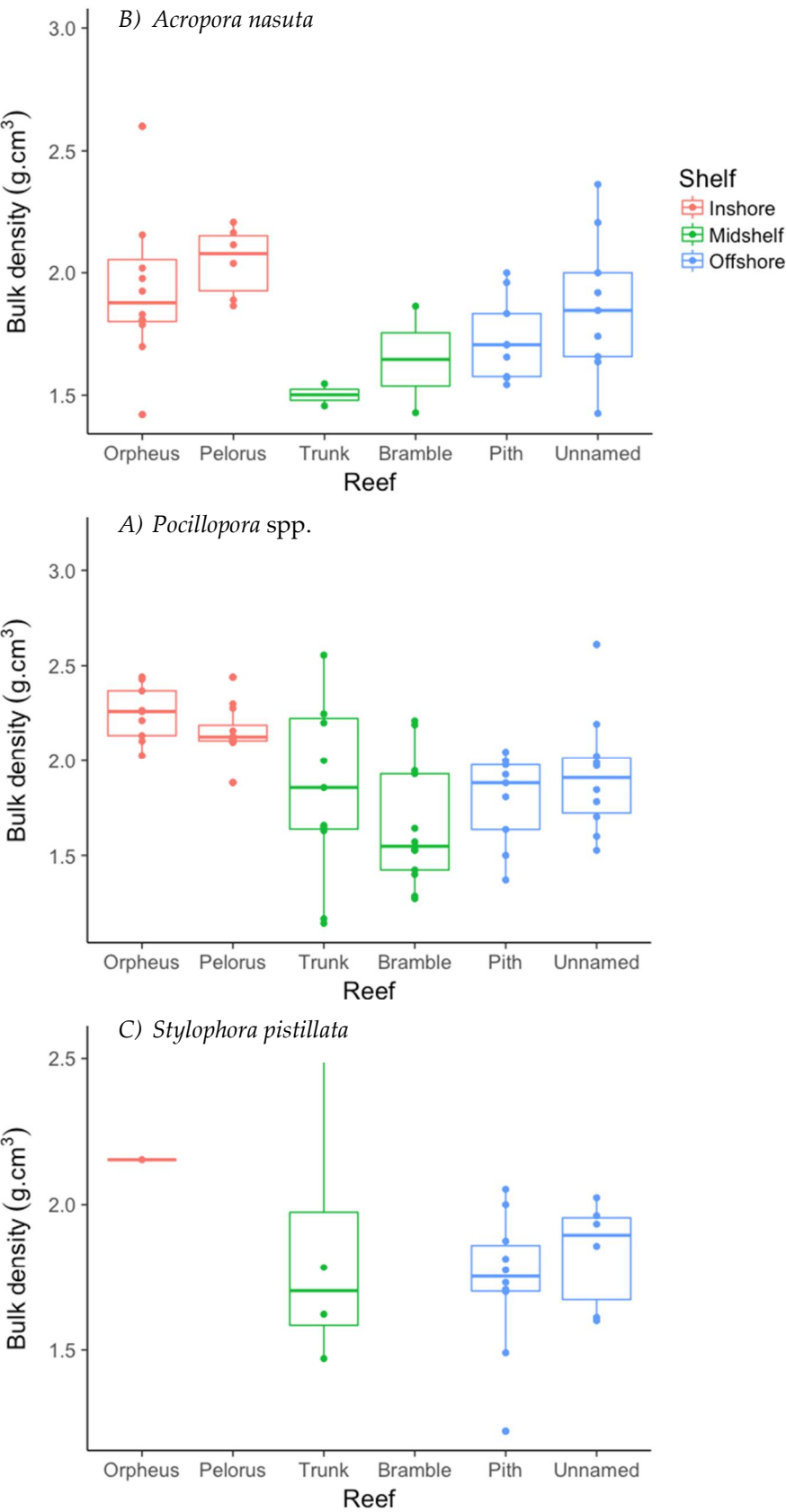meaningful estimates of confidence limits.

Figure 3. Cross-shelf variation in bulk density for A) *Acropora nasuta*, B) *Pocillopora* spp. and C) *Stylophora pistillata*. Data is presented for each reef separately (to allow for comparisons with Figure 2), though spatial variation bulk density were best explained by shelf position (rather than reef) for both *A. nasuta* and *Pocillopora* spp. Box plots show first and third quartiles

Table 2. Model comparisons for GLMs used to test whether shelf position (inshore, mid-shelf of offshore) effectively accounts for inter-reef differences in growth and density of three distinct branching corals. Models selected (based on Akaike Information Criterion (AICc) and degrees of freedom (df)) are shown in bold.

Coral Taxa	Parameter	Model	AICc	df
Acropora nasuta	Growth	~Shelf + Colony	3029.63	5
		~Reef + Colony	**2875.40**	**8**
	Density	**~Shelf**	**21.66**	**4**
		~Reef	28.56	7
Pocillopora spp.	Growth	~Shelf + Colony	5597.42	5
		~Reef + Colony	**5424.05**	**8**
	Density	**~Shelf**	**51.19**	**4**
		~Reef	51.34	7
Stylophora pistillata	Growth	~Shelf + Colony	1568.08	5
		~Reef + Colony	**1427.73**	**6**
	Density	**~Shelf**	**15.75**	**4**
		~Reef	16.33	5

4. Discussion

Growth rates of corals vary taxonomically, spatially and temporally, and have an important role in structuring coral assemblages and reef habitats (Pratchett et al. 2015 [9]). Average ALE recorded for scleractinain ranges from <2 mm.y^{-1} for *Siderastrea* spp. up to 172 mm.y^{-1} for *Acropora pulchra*, and is generally higher for branching versus massive corals (Pratchett et al. 2015 [9]). In this study, average ALE was highest (23.56 mm.y^{-1} ±0.86 SE) for *Pocillopora* spp. Though we are not certain of the taxonomic identity of these corals, nor whether there were possibly more than one species considered within this complex (Schmidt-Roach et al. 2014 [36]), our growth rates correspond with growth rates recorded previously for colonies nominally considered to be *P. damicornis* (Anderson et al. 2015 [8]) that used the same teechniques. Notably, growth rates recorded for *Pocillopora* colonies exceeded that of *A. nasuta*. In general, *Acropora* corals exhibit the highest growth rates, and previous estimates of ALE for *A. nasuta* (39.2-52.8 mm.y^{-1}) are much higher than were recorded herein (Pratchett et al. 2015 [9]), even within reef habitats (shallow, obliquely exposed, reef crests on mid-shelf and outermost reefs) where these corals predominate. Similarly, published growth rates for S. *pistillata* are generally much higher (15.05-24.61 mm.y^{-1}; Pratchett et al. 2015 [9]) than were recorded in this study (11.81 mm.y^{-1} ±0.73 SE). Intraspecific variation in the growth rates of corals, especially among widely separated geographic locations, is often attributed to differences in environmental conditions, and especially temperature (Carricart-Ganivet 2004 [41]; Lough 2008 [42]). In particular, growth rates of corals may be constrained at both low and high temperatures (Pratchett et al. 2015 [9]). Low rates of ALE recorded in this study, relative to growth rates reported for the same species in other locations, cannot be attributed to low temperatures, but may reflect higher than normal temperatures that occurred across much of the GBR in 2016 (Hughes et al. 2017 [43]). Elevated temperatures may have accounted for the poor survival of *A. nasuta* and *S. pistillata* at mid-shelf sites, while also suppressing coral growth and calcification more broadly (Anderson et al. 2018 [44]).

Although species-specific growth rates recorded in this study are lower than reported previously, there were no apparent differences in ALE between inner-, mid-shelf and outer-shelf sites. Many studies have reported comparatively low rates of coral growth or calcification in near shore environments linked to high or elevated levels of suspended sediments (e.g., Tomascik & Sander 1985 [45]; Guzmán et al. 2008 [46]; Sowa et al. 2014 [47]). We'd expect, therefore, that coral growth would be highest at offshore locations, which are furthest removed from land-based sources of sediment, nutrients and other pollutants. However, the few studies that have explicitly studied cross-shelf variation in growth rates of select coral species (massive *Porites*; Scoffin et al. 1992 [48], Lough and Barnes 2000 [32], and *Montasrea annularis*; Carricart-Ganivet & Merino, 2001 [33]), reveal

257 the opposite relationship, with decreasing ALE with distance from shore. There was evidence of a
258 similar trend in ALE for *A. nasuta* and *S. pistillata* in this study, though all we can really conclude is
259 that growth rates of all three branching coral taxa were not any lower at sites on inshore reefs
260 (Orpheus and Pelorus Islands), compared to sites at mid-shelf (Bramble Reef and Trunk Reef) and
261 outer-shelf reefs (Pith Reef and Unnamed Reef). Although we did not explicitly measure
262 environmental conditions, the distance between the innermost and outermost sites was >65 km and
263 inner shelf reefs were located on the landward side of high continental islands that had conspicuously
264 higher levels of sedimentation and turbidity compared to sites at mid-shelf and offshore reefs.
265   Environmental constraints on coral growth, which is ultimately determined by overall rates of
266 carbonate deposition (calcification), are not always manifest as changes in ALE (Brown et al. 1990
267 [49]). Scleractinian corals are indeed capable of maintaining or increasing linear extension, despite
268 reductions in calcification, by sacrificing skeletal density (Carricart-Ganivet & Merino 2001 [33];
269 Hoegh-Guldberg et al. 2007 [50]), which presumably impacts on skeletal integrity and resistance to
270 physical disturbances. When comparing cross-shelf variation in growth process, both Lough and
271 Barnes (2000 [32]) and Carricart-Ganivet & Merino (2001 [33]) found that skeletal density increases
272 with distance from shore. This may be a necessary response to increase skeletal integrity and
273 persistence in the face of increased wave exposure and hydrodynamic forcing. Conversely, lower
274 levels of wave action on inshore reefs may allow corals to persist with comparably lower skeletal
275 densities, allowing for faster rates of linear extension. Risk and Sammarco (1991 [51]) suggested that
276 the low densities of *Porites* corals at inshore sites on the GBR reflect inhibition of calcification by
277 elevated nutrients, though overall rates of calcification for massive *Porites* are actually higher on
278 inshore reefs (Lough & Barnes 1992 [52]), which combined with reduced skeletal density, result in
279 higher rates of ALE. As with previous studies, we found differences in the skeletal density of corals
280 growing on different reefs, which were related to shelf position. However, skeletal density was higher
281 on inshore, rather than offshore reefs (Fig. 3). As such, differences in skeletal densities do not account
282 for (but compound upon) differences in linear extension. This suggests that overall rates of
283 calcification for the branching corals considered in this study (*A. nasuta*, *Pocillopora* spp. and *S.
284 pistillata*) may actually be higher at sites on the inshore reefs, compared to colonies growing at sites
285 on mid- and outer-shelf reefs.
286   It is incontrovertible that elevated sedimentation and eutrophication can have adverse effects on
287 the growth, reproduction and demography of scleractinain corals, as shown in experimental studies
288 (Humphrey et al. 2008 [53]) as well as highly perturbed environments (Dodge & Vaisnys, 1977 [31]).
289 However, most experimental studies use extreme levels of sedimentation (Jones et al. 2016 [54]) that
290 poorly reflect predominant conditions that occur even on fringing coastal reefs. These unrealistic
291 treatment levels were justified based on erroneous early estimates of sedimentation in the field (Jones
292 et al. 2016 [53]) that failed to account for sediment resuspension and flux. While sedimentation is a
293 prominent feature of near shore reefs and one of the major factors that differentiates inshore reefs
294 from offshore systems (Wolanski et al., 2005 [55]), extreme levels of sediment resuspension and
295 turbidity are often short-lived (Browne et al. 2013 [56]). Moreover, high levels of sedimentation are
296 restricted to specific habitats, where coral assemblages are dominated by species (e.g., *Goniopora* and
297 *Turbinara*) that are predominantly heterotrophic and can withstand prolonged turbidity and
298 sediment deposition (Browne et al. 2012 [56]). Ultimately, fine-scale heterogeneity in environmental
299 conditions do enable branching corals (e.g., *Acropora*) to grow at some sites (Browne et al. 2013 [56]),
300 even if this is more restrictive than occurs on reefs further offshore. In this study, for example, we
301 compared growth rates of corals in very shallow environments (1-3 m), reflecting where we found
302 highest abundance of the specific study species. It is likely however, that these corals might be much
303 more restricted in their depth distribution on near shore reefs due to higher levels of turbidity and
304 light attenuation.
305   The results and conclusions of this study are limited by inherent constraints in the method used
306 to measure coral growth. Although ALE is among the most commonly used metric to measure coral
307 growth and is broadly comparable across different types of corals (Pratchett et al. 2015 [9]), it does
308 not fully account for complexities in the way that corals (especially, branching corals species) actually

309 deposit calcium carbonate, which is the main rate limiting process for coral growth. This study also
310 used the vital stain (Alizarin red), requiring corals to be sacrificed to record change in physical
311 dimensions, which provides only a single time-averaged estimate of coral growth across the period
312 between staining and subsequent collection (Morgan & Kench 2012 [57]). Recent advances in
313 underwater photogrammetry enable 3D reconstructions from images of individual coral colonies,
314 which when compared over time, can provide much more holistic, precise, and higher resolution
315 measures of growth (Ferrari et al. 2017 [58]). Moreover, 3D photogrammetry does not require that
316 corals be manipulated or ultimately collected (Ferrari et al. 2017 [58]), which otherwise imposes
317 considerable risks and inherent constraints on the sample size and design. This study provides the
318 first test of cross-shelf variation in growth rates of branching corals, though much more expansive
319 sampling (making use of new methods to better represent the size and shape of individual coral
320 colonies) is still warranted.

5. Conclusions

322 This study shows that growth rates of branching corals (specifically, *A. nasuta*, *Pocillopora* spp.
323 and *S. pistillata*) are comparable between sites at inshore, mid-shelf and offshore reefs, questioning
324 whether inshore reefs of the GBR are necessarily degraded or lacking resilience (Browne et al. 2012
325 [59]). Browne et al. (2012 [59]) explored the contemporary condition of inshore reefs along the length
326 of the GBR, and while recognizing that many of these reef systems are subject continual or episodic
327 sedimentation, they showed that many turbid inshore reefs have high cover of scleractinian corals
328 and that the corals are regrowing and calcifying at sufficient rate to sustain positive reef accretion.
329 Also, even within individual reefs there is considerable heterogeneity in environmental conditions
330 and corresponding differences in coral assemblages (Browne et al. 2013 [56]). In this study, care was
331 taken to ensure that study sites were broadly comparable among the different reefs, but the specific
332 sites selected (within very shallow and obliquely exposed habitats) may have had relatively minimal
333 differences in environmental conditions across inshore, mid-shelf and offshore reefs.

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