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Functional links on coral reefs: urchins and triggerfishes a cautionary tale

Short Title:

Functional links on coral reefs

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25 **Abstract**

26 Urchins are ubiquitous components of coral reefs ecosystems, with significant roles in
27 bioerosion and herbivory. By controlling urchin densities, triggerfishes have been identified as
28 keystone predators. However, the functional linkages between urchins and triggerfishes, in terms of
29 distributional patterns and concomitant effects on ecosystem processes, are not well understood,
30 especially in relatively unexploited systems. To address this we censused urchins and triggerfishes on
31 two cross-shelf surveys on the Great Barrier Reef (GBR) at the same times and locations. We also
32 evaluated the role of urchins in bioerosion. Although urchin abundance and triggerfish biomass varied
33 by 80% and nearly 900% across sites, respectively, this variability was driven primarily by shelf
34 position with no evidence of top-down control on urchins by triggerfishes. Low urchin abundances
35 meant urchins only played a minor role in bioerosion. We highlight the potential variability in
36 functional links, and contributions to ecosystem processes, among regions.

37 **Keywords:**

38 Bioerosion, Ecosystem Processes, Echinoderm, Fish, Great Barrier Reef, Marine Ecology, Predation,
39 Triggerfish, Trophic Cascade

40

41 **1. Introduction**

42 The persistence of ecosystems in particular states is underpinned by the ecosystem processes
43 operating therein (Done et al., 1996). The ecosystem processes are, in turn, dependent on the
44 organisms present (Steneck, 2013; Walker et al., 1981). Some organisms can contribute
45 disproportionately to particular processes due to a high abundance, limited functional redundancy or a
46 high degree of ecological specialization (Bellwood et al., 2003; McWilliam et al., 2018; Mouillot et
47 al., 2014). The latter aspect is particularly clear in keystone species; those species whose effect on an
48 ecosystem is disproportionately large relative to their abundance (Paine, 1969; Power et al., 1996).
49 However, while organisms can be keystone species in certain locations this may not apply in all
50 systems in which they are present. While similar ecosystems often share a similar suit of processes,

51 there can be substantial variability in the species, or organisms which contribute to these processes
52 across biogeographic realms (Hemingson and Bellwood, 2018; McWilliam et al., 2018; Mouillot et
53 al., 2014). Understanding the importance of particular organisms in ecosystem processes among
54 biogeographic realms is essential if we are to understand how different ecosystems will respond to
55 disturbances.

56 Amongst the world's most threatened ecosystems, coral reefs have provided key examples of
57 ecosystem collapse following disturbance events. We have come to realise that coral reefs can exist in
58 a number of different states, depending on their resilience (Bellwood et al., 2004; Graham et al.,
59 2013), with the collapse of many Caribbean reefs to macroalgal-dominated states being a particularly
60 well documented example (Hughes, 1994; Jackson et al., 2014). The transition of these systems is
61 generally believed to involve a disruption of the ecosystem processes that are essential for
62 maintaining their resilience; often due to the direct loss of the organisms responsible for delivering
63 these processes (Bellwood et al., 2004; Hughes et al., 2007). While many coral reefs globally have
64 been degraded, at least in part, due to the overfishing of key functional groups (Berkes et al., 2006;
65 Jackson et al., 2001), the largest reef system in the world, the Great Barrier Reef (GBR) is generally
66 considered to be relatively intact with well managed fisheries (Casey et al., 2017; Cheal et al., 2013;
67 McCook et al., 2010). It therefore offers an exceptional system in which to examine ecosystem
68 processes and explore the extent and nature of key functional groups. Such groups include sea urchins
69 and their key predators, the triggerfishes.

70 Sea urchins have been a key structuring force in shallow water marine ecosystems since the
71 lower Jurassic, when major functional transformations allowed them to bite deeply into calcium
72 carbonate substrata (Steneck, 2013; Steneck et al., 2017). Indeed, sea urchins were the first deep-
73 grazing marine herbivores, with this ability only surpassed by parrotfishes during the Miocene
74 (Cowman et al., 2009; Steneck et al., 2017). On modern day coral reefs, urchins are often the main
75 agents of herbivory and bioerosion. This is particularly marked where overfishing is believed to have
76 released them from top-down predation pressure (Bak, 1994; Carreiro-Silva and McClanahan, 2001;
77 Hay, 1984; but see Cramer et al., 2018; Jackson, 1997). In these systems, urchins can be a major

78 determinant of benthic state and reef development. In a negative way, urchins have the capacity to
79 destroy reefs when bioerosion rates exceed reef accretion rates as urchins can directly erode into the
80 reef matrix, undercut corals, and hinder coral recruit survival (Bellwood et al., 2004; Glynn and
81 Manzello, 2015; Leary et al., 2013; Qiu et al., 2014). On Eastern Tropical Pacific reefs, for example,
82 high urchin abundances have caused significant bioerosion of the reef framework (Glynn, 1988).
83 However, where herbivorous fishes have been removed by fishing, urchins can provide a functional
84 replacement with rates of herbivory high enough to resist transitions to algal-dominated states
85 (Hughes, 1994; Steneck, 2013). For example, in the Caribbean the widespread mortality of *Diadema*
86 *antillarum* revealed the importance of urchins in preventing a transition towards reefs dominated by
87 macroalgae, particularly in areas prone to overfishing of herbivorous fishes (Hughes, 1994; Jackson et
88 al., 2014; Lessios, 2016). Evidently sea urchins can play a major role in marine systems around the
89 globe.

90 Much of our understanding, however, of the ecosystem function of urchins comes from
91 disturbed systems which have been heavily overfished, including East Africa (Carreiro-Silva and
92 McClanahan, 2001; McClanahan et al., 1994), French Polynesia (Bak, 1990; Done et al., 1991;
93 Peyrot-Clausade et al., 2000), and parts of Asia (Dumont et al., 2013; Goh and Lim, 2015). It has been
94 hypothesised that overfishing released urchins from predation, in turn increasing their relative
95 contribution to ecosystem processes such as grazing and bioerosion (McClanahan and Shafir, 1990;
96 Steneck, 2013). Of all sea urchin predators, the triggerfishes (Balistidae) are considered to be the
97 primary predators; a keystone predator. Triggerfishes are particularly well equipped with powerful
98 mouth structures to prey on hard-shelled benthic invertebrates (Turingan and Wainwright, 1993).
99 They prey on a wide range of urchins and other echinoderms (Hiatt and Strasburg, 1960; McClanahan,
100 2000; Randall et al., 1996; Young and Bellwood, 2012), including the mechanically and chemically
101 defended crown of thorns starfish (CoTS) (Cowan et al., 2017). Indeed, predation experiments
102 suggested that in East Africa *Balistapus undulatus* can be responsible for up to 100% of urchin
103 predation (McClanahan, 2000). On the GBR a similar experiment demonstrated that *Balistoides*
104 *viridescens* and *B. undulatus* together accounted for over 90% of predation with little to no

105 contribution from other nominal echinoderm predators such as large labrids and lethrinids (Young and
106 Bellwood, 2012). However, the paradigm on coral reefs, that urchins are controlled from the top-
107 down by their fish predators, has largely been based on evidence from heavily exploited, degraded,
108 systems comparing areas exposed to, and protected from, fishing.

109 Examining the interrelationship between sea urchins and their key triggerfish predators in a
110 relatively unfished system, the GBR, could provide novel insights into this potentially important
111 functional link. This is because fishing pressure frequently co-varies with other anthropogenic
112 stressors as well as other biotic and abiotic factors (Graham et al., 2013; Hughes et al., 2017a), which
113 could modify the links between urchins and triggerfishes. Yet, the importance of other factors in
114 mediating urchin abundances and distribution patterns might be overlooked if fishing pressure is the
115 sole focus. Indeed, Casey et al., (2017), revealed that when other factors are controlled for, fishing of
116 predators did not lead to trophic cascades, suggesting that top-down forces in complex coral reef
117 systems are weak. The GBR can be considered a relatively unfished system, especially in terms of
118 triggerfishes, because the majority of fishing activity is focused on a few, economically important
119 non-triggerfish species extracted via a targeted line fishery (McCook et al., 2010). Therefore,
120 variation in triggerfish abundance among sites on the GBR is likely to vary because of other
121 ecological and biological factors rather than fishing pressure.

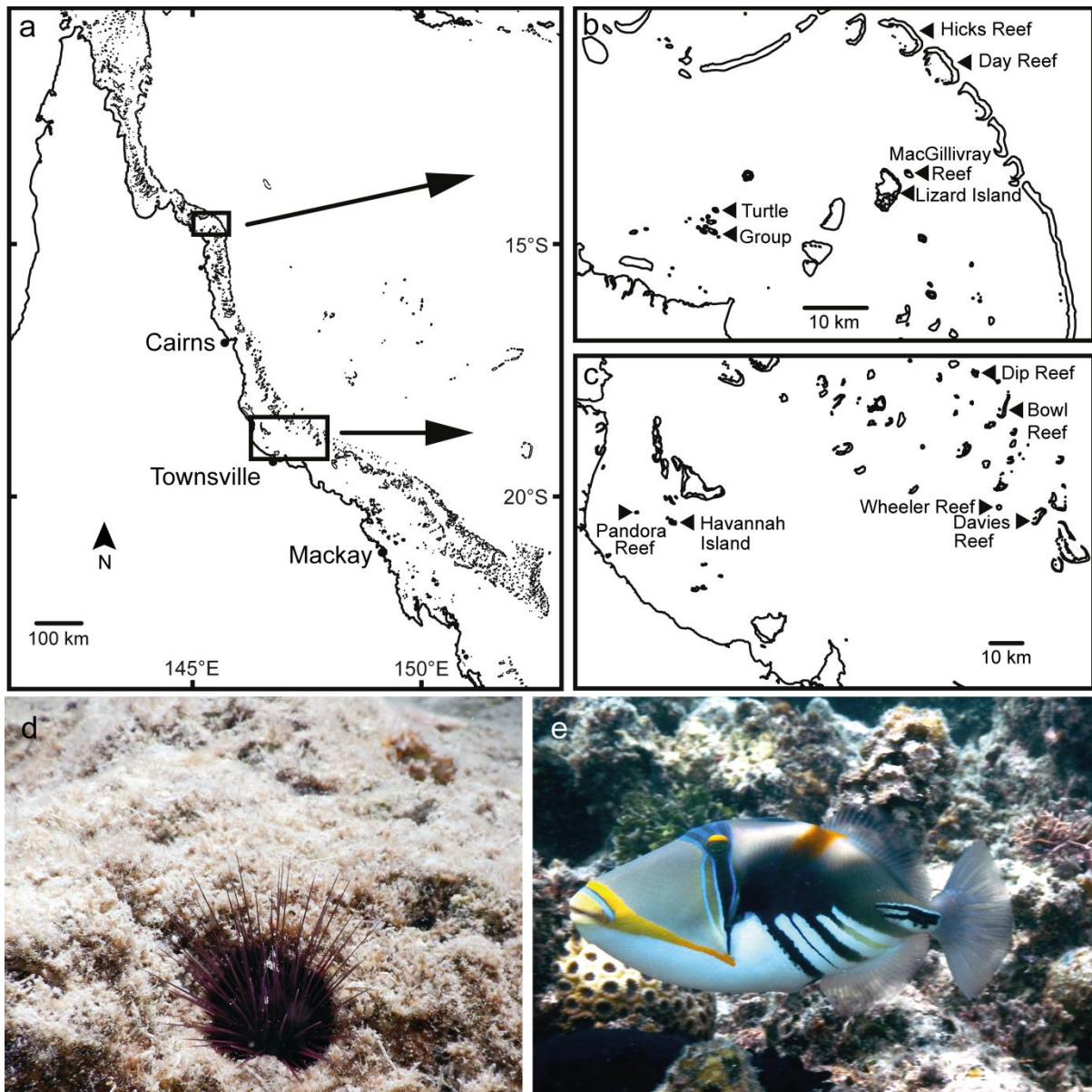
122 Across the GBR distinct gradients in faunal assemblages exist, with a general increase in
123 abundance and diversity further from shore (Cheal et al., 2012; Emslie et al., 2017; Wismer et al.,
124 2009). These ecological gradients follow distinct gradients in abiotic conditions such as
125 hydrodynamic exposure gradients (Bellwood and Wainwright, 2001; Crossman et al., 2001; Fulton et
126 al., 2013) and terrestrial influences on sediment loads and water quality (Fabricius et al., 2014;
127 Tebbett et al., 2017). How sea urchin and triggerfish distributions conform to these previous patterns
128 is unclear. The aim of this study, therefore, was to examine the pattern of urchin and triggerfish
129 distributions across the GBR. Presumably, if a functional linkage exists between urchins and their
130 triggerfish predators, through top-down predation pressure, one would expect their distributions to be
131 negatively correlated. However, this relationship may not hold if other biotic or abiotic factors

132 underpin distribution patterns. Furthermore, this study will look beyond potential links in distribution
133 patterns by considering the role that sea urchins play in a key ecosystem process, bioerosion, by
134 comparing and contrasting bioerosion patterns with other key bioeroders.

135 **2. Materials and methods**

136 *2.1 Study sites*

137 Two GBR regions were surveyed in 2004/5: the northern region at approximately 14° 40' S
138 and the central region at approximately 18° 47' S (Fig. 1). In each region two reefs were surveyed in
139 each of the three cross shelf locations (inner-, mid- and outer-shelf). In the northern region two islands
140 in the Turtle group (inner-shelf), MacGillivray Reef and Lizard Island (mid-shelf), and Hicks Reef
141 and Day Reef (outer-shelf) were surveyed. In the central region Pandora Reef and Havannah Island
142 (inner-shelf), Wheeler Reef and Davies Reef (mid-shelf), and Dip and Bowl Reef (outer-shelf) were
143 surveyed. A full site description outlining the nature and state of each site, including dominant benthic
144 cover, is given in Wismer et al., (2009). At each reef, three to four habitats were surveyed. The back
145 reef, flat, crest and slope habitats were surveyed on each of the mid- and outer-shelf reefs. However,
146 as there are no clearly defined crests on inner-shelf reefs the entire seaward slope was surveyed as the
147 crest/slope. Definitions of each habitat can be found in Bellwood and Wainwright, (2001).



148

149 **Fig. 1 a** The Great Barrier Reef (GBR), Australia showing the two regions surveyed. The cross-shelf
 150 census sites in the **b** northern and **c** central regions of the GBR. **d** an *Echinostrephus* sp. urchin and **e**
 151 the picasso triggerfish, *Rhinecanthus aculeatus* both photographed at Lizard Island in the northern
 152 GBR.

153

154 *2.2 Urchin abundance*

155 To quantify sea urchin abundance 12 replicate 10 × 2 m transects were surveyed in each
 156 habitat on each reef ($n = 528$). Transects were haphazardly placed, and laid parallel to the reef crest.

157 Each transect was systematically searched for urchins paying particular attention to examine
158 overhangs and crevices. Urchin abundance and test size (to the nearest 5 mm) was recorded. Urchins
159 were identified to genus and species where possible.

160 *2.3 Contribution of urchins to bioerosion*

161 Bioerosion by urchins was calculated using three equations following Perry et al., (2015) that
162 relate sea urchin test size (diameter in mm) to erosion rate ($\text{kg urchin}^{-1} \text{ year}^{-1}$). *Diadema* sp. and *E.*
163 *mathaei* had their own equations while a general equation was applied to other bioeroding urchins.
164 Bioerosion rates were calculated for each individual urchin, summed within each transect and then
165 divided by transect area (20 m^2) to yield sea urchin bioerosion in $\text{kg m}^{-2} \text{ year}^{-1}$.

166 To explore the differences in bioerosion rates among key bioeroding groups (urchins,
167 parrotfishes and micro/macro boring organisms), we directly compared bioerosion rates among
168 groups in $\text{kg m}^{-2} \text{ year}^{-1}$ across the GBR. Rates of parrotfish bioerosion were sourced from a study
169 conducted in 1998/9 on the northern GBR which quantified erosion rates by 24 parrotfish species
170 (Hoey and Bellwood, 2008). Bioerosion rates of micro- and macro-boring organisms were sourced
171 from a study of bioerosion in 1996-99 across the northern GBR based on *Porites* plates deployed in
172 back reef or similar habitats (Tribollet and Golubic, 2005); these data are converted to bioerosion m^{-2}
173 year^{-1} . As both studies were from the northern GBR (Lizard Island region), only bioerosion rates by
174 urchins from the northern region were used in the among-group comparisons. Therefore, parrotfish
175 and micro/macro boring bioerosion rates were from the same, or nearby study sites, as for urchins.

176 *2.4 Triggerfish abundance and biomass*

177 Triggerfish communities were quantified at the same time and in the same areas as the urchin
178 surveys. Fish were counted on 10-minute timed belt transects equating to approximately 117 m
179 (methods and calibrations following Bellwood and Wainwright, (2001). This census method would
180 have effectively quantified triggerfish densities because triggerfishes are generally site attached (Chen
181 et al., 2001) and have previously been quantified successfully on smaller transects than those used
182 herein (Bean et al., 2002). All fish were identified to species and placed into total length (TL) size

183 classes (for fishes >10 cm size classes with 5 cm intervals were used, while for fishes <10 cm size
184 classes with 2.5 cm intervals were used), and biomass calculated using Bayesian length-weight
185 regression parameters (Froese and Pauly, 2018) (see ESM Table S1 for species recorded).

186 2.5 Analysis

187 The total abundance of triggerfishes across the GBR was examined using a generalised linear
188 mixed effects model (GLMM) with a negative binomial distribution to account for the non-normally
189 distributed and overdispersed nature of the count data. Total triggerfish biomass was examined using
190 a lognormal mixed effects model. In both cases a full model containing the fixed effects of region
191 (central vs. northern), shelf position (inner, mid and outer) and reef habitat (slope, crest, flat, back)
192 was initially fitted, with individual reef as a random factor. The Akaike Information Criterion (AIC)
193 was employed to find the most parsimonious model (ESM Table S2). Model fits were assessed based
194 on residual plots, all of which were satisfactory.

195 We also examined the relationship between mean sea urchin abundance (ind. 100 m⁻²) and
196 mean triggerfish biomass (g 100 m⁻²). Urchin abundance data was used because this is the most
197 commonly reported metric when quantifying urchins (e.g. Table 1), and diameter-weight relationships
198 for urchins from the GBR are not readily available. By contrast, triggerfish biomass estimates were
199 utilised because this is a more functionally relevant metric of potential triggerfish predation compared
200 to abundance data, which overemphasises the importance of the more abundant, smaller triggerfish
201 size classes, that are less likely to be key urchin predators (e.g. Young and Bellwood, 2012).
202 Triggerfish biomass was considered as a predictor variable in two ways: a) the biomass of all
203 triggerfish species known to feed on sea urchins (all urchin predators), and b) only large keystone
204 triggerfish predators (see ESM Table S1 for full details). Mean triggerfish biomass and urchin
205 abundances were compared within each habitat at each reef ($n = 44$). Initially we visualised the
206 relationship between urchin abundance and triggerfish biomass, then considering each potential factor
207 (region, shelf, habitat, reef). These factors were considered because there can be substantial variability
208 in abiotic and biotic processes that influence urchin distributions, such as predation rates, terrestrial

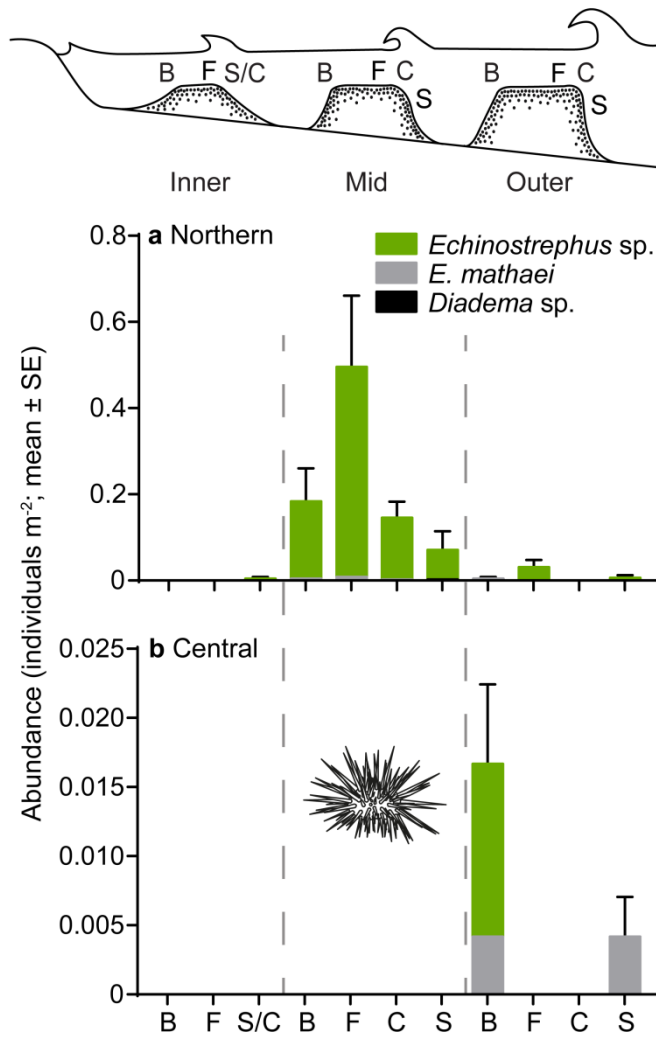
209 influences, and productivity among; regions (latitudinal differences; (Sheppard-Brennand et al.,
210 2017)), shelf positions (Fabricius et al., 2014), habitats (Bellwood et al., 2018) and individual reefs
211 (Browne et al., 2013). Following visual examination, triggerfish biomass (continuous) and shelf
212 position (categorical) were treated as fixed effects in subsequent models comparing the two taxa. Both
213 Gamma distributed generalised linear models (GLM) and lognormal linear models were examined,
214 however, for both urchin predators and keystone triggerfish biomass, the lognormal model was
215 deemed to produce the superior fit based on residual plots. When examining residual plots non-linear
216 relationships were also considered. Statistical modelling was performed in the software R (R Core
217 Team, 2017) using the *lme4* (Bates et al., 2015), *nlme* (Pinheiro et al., 2017), *glmmTMB* (Brooks et
218 al., 2017) and the *AICcmodavg* (Mazerolle, 2017) packages. Due to the nature of the urchin data no
219 formal analysis was conducted on urchin abundance or bioerosion (see below).

220

221 **3. Results**

222 *3.1 Sea urchins*

223 Of the 528 transects, 88.3% had no sea urchins visible with average abundances ranging from
224 0 – 0.5 m⁻² (Fig. 2). A total of 462 sea urchins were recorded across all transects and of these 93.1%
225 were on the two mid-shelf reefs in the northern GBR, with the diminutive *Echinostrephus* sp.
226 accounting for 98.1% of total urchin abundance on these reefs (Fig. 2a, b). There were only 10 urchins
227 recorded across all transects in the central region (Fig. 2b).



228

229 **Fig. 2** The abundance of sea urchins across the Great Barrier Reef in **a** the northern and **b** the central
 230 regions (note the difference in scales on the y-axis). B = back reef, F = Flat, S/C = combined slope
 231 crest habitat, S = Slope, C= Crest

232

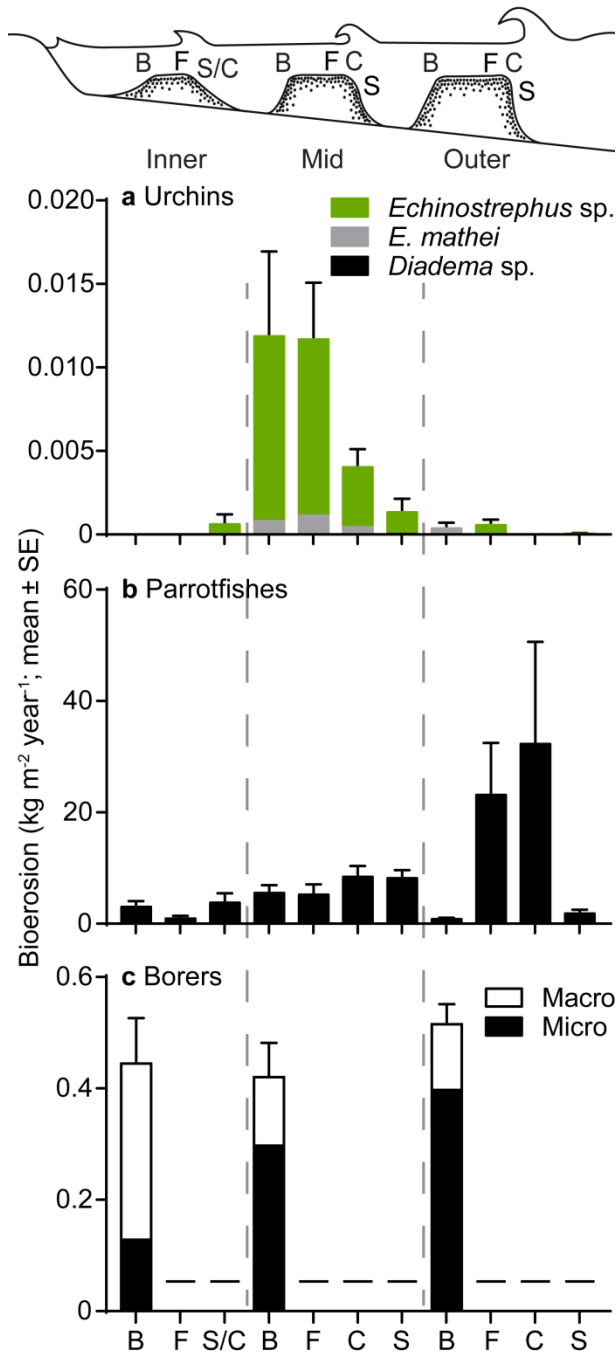
233 3.2 Bioerosion patterns

234 The low urchin abundances in turn meant that urchin bioerosion rates were very low across
 235 the GBR (0 – 0.01 kg m⁻² year⁻¹; Fig. 3a). Even where urchin bioerosion rates were highest (on
 236 northern mid-shelf back reef habitats [Fig. 3a]) they only accounted for 0.2% of total external
 237 bioerosion (0.01 kg m⁻² year⁻¹ urchin erosion compared to 5.5 kg m⁻² year⁻¹ by parrotfishes) (Figs 3a,
 238 b). In all locations, parrotfishes accounted for over 99% of external bioerosion with total values

239 increasing in an offshore direction; urchin bioerosion peaked on mid-shelf reefs. In terms of total
240 bioerosion (parrotfishes, urchins and borers) parrotfishes accounted for 61 - 93%. Urchins accounted
241 for just 0 - 0.2% ($0 - 0.01 \text{ kg m}^{-2} \text{ year}^{-1}$). Both microborers and macroborers also contributed far more
242 to bioerosion than sea urchins ($0.13 - 0.4 \text{ kg m}^{-2} \text{ year}^{-1}$, [4 - 30%] and $0.1 - 0.3 \text{ kg m}^{-2} \text{ year}^{-1}$, [2 - 9%]
243 respectively) (Fig. 3).

244

245



246

247 **Fig. 3** Bioerosion rates by **a** urchins, **b** parrotfishes and **c** boring organism across the northern Great
 248 Barrier Reef. B = back reef, F = Flat, S/C = combined slope crest habitat, S = Slope, C= Crest. Data
 249 on parrotfish erosion from Hoey and Bellwood (2008); borer erosion from Tribollet and Golubic
 250 (2005) available from back reef habitats only. Note the difference in scales: parrotfish bioerosion is
 251 orders of magnitude higher than the invertebrates.

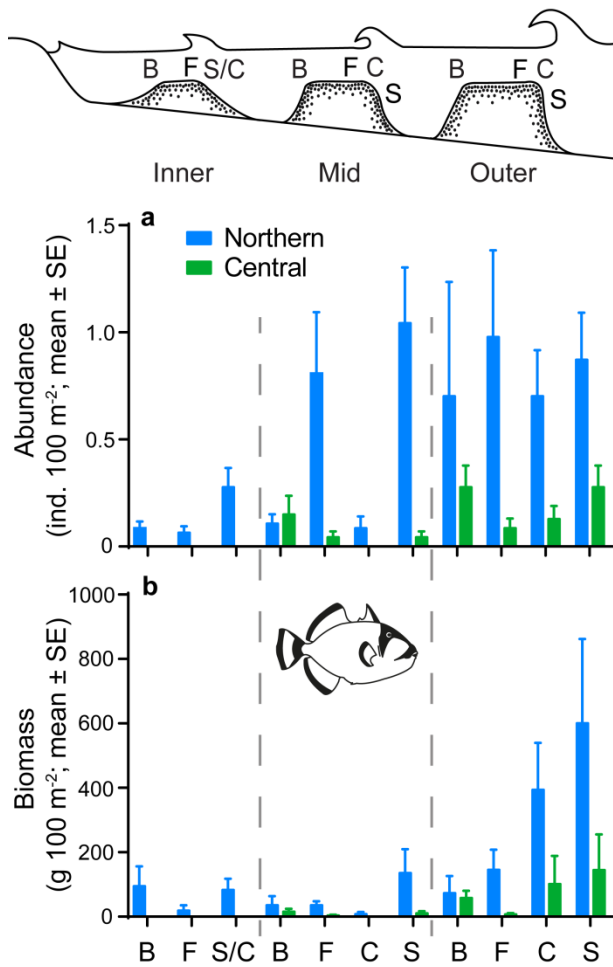
252

253 3.3 Triggerfishes

254 In general the abundance and biomass of triggerfishes increased across the shelf and was far
255 higher in the northern region compared to the central region (Fig. 4). Based on the GLMM the AIC
256 suggested that the interaction between region and shelf position played an influential role in the
257 abundance patterns of triggerfishes (ESM Table S2), however, this was not significant in the final
258 model (ESM Table S3). The biomass of triggerfishes was significantly higher on outer-shelf reefs
259 compared to inner-shelf reefs (LME; $p < 0.001$; ESM Table S3), and in the northern region compared
260 to the central region (LME; $p < 0.001$; ESM Table S3). The only significant differences in triggerfish
261 biomass among habitats occurred between back reef and slope habitats (LME; $p < 0.01$; ESM Table
262 S3).

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264



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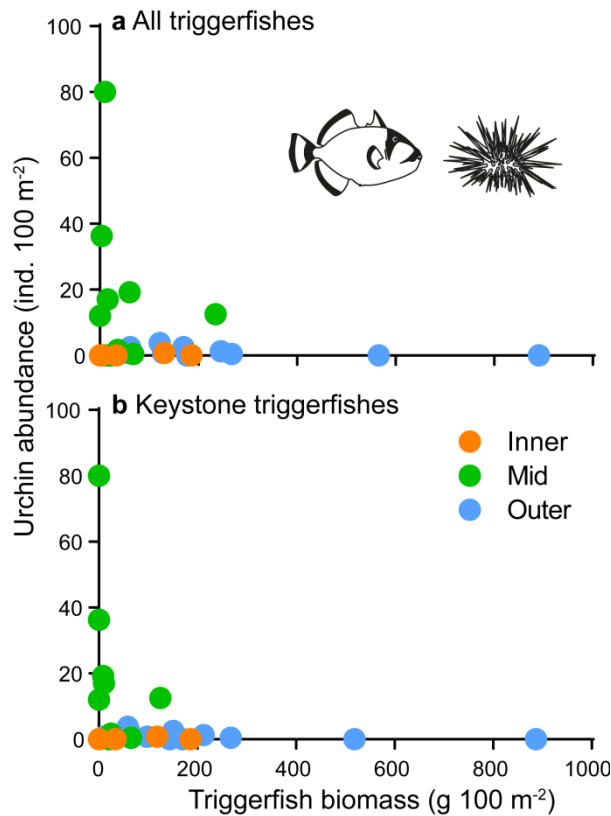
266 **Fig. 4** The **a** abundance and **b** biomass of all triggerfishes observed across the Great Barrier Reef. B =
 267 back reef, F = Flat, S/C = combined slope crest habitat, S = Slope, C= Crest.

268

269 *3.4 Interrelationship between urchins and triggerfishes*

270 On first inspection, there is a distinct relationship between urchin abundance and the biomass
 271 of both all triggerfishes and keystone triggerfishes, with high variability of urchins at low triggerfish
 272 biomass, and limited urchins where triggerfishes occurred (Fig. 5). Indeed, urchin abundances varied
 273 by up to 80%, and triggerfish biomass varied by nearly 900% (Fig. 5). However, there was a marked
 274 spatial component to this relationship. If the role of shelf position is considered, all urchin variability
 275 is largely constrained to the mid-shelf, while triggerfish biomass primarily varies on the outer-shelf
 276 (Fig. 5). As such, the factor shelf position is significant in both the models (ESM Table S4), while

277 triggerfish biomass was not significantly related to urchin abundances in either model (ESM Table
 278 S4). Nor was there a non-linear relationship. We therefore found no evidence of any significant
 279 correlation between urchin abundances and the biomass of triggerfishes, the key urchin predators on
 280 the GBR.



281
 282 **Fig. 5** The relationship between urchin abundance and the biomass of **a** all triggerfishes considered
 283 urchin predators, and **b** triggerfishes considered keystone urchin predators across the Great Barrier
 284 Reef ($n = 44$). Note at ‘face value’ the apparent exponentially declining relationship between urchin
 285 abundance and triggerfish biomass. However, this variability is chiefly driven by differences in urchin
 286 abundance and triggerfish biomass related to shelf location.

287
 288 **4. Discussion**

289 This study examined the interrelationship and ecosystem function of sea urchins and their
 290 triggerfish predators across the GBR. Both are often considered to be keystone organisms. Although

291 an area of more than $>10\ 500\ \text{m}^2$ was surveyed for urchins, very few were detected, supporting
 292 findings from previous smaller scale studies on the GBR which found mean abundances ranged from
 293 $0 - 1.06$ individuals m^{-2} (Browne et al., 2013; Done et al., 1991; Mallela, 2018; Sammarco, 1985;
 294 Young and Bellwood, 2011). However, these low densities on the GBR contrast markedly with the far
 295 higher urchin densities reported from most major coral reef regions globally (Table 1). These
 296 differences across biogeographic scales may support the common paradigm that urchins are naturally
 297 not major contributors to reef ecosystem processes when predatory fish communities remain intact
 298 (McClanahan and Muthiga, 2016; Sheppard-Brennand et al., 2017; Steneck, 2013). Yet, on the GBR
 299 we also recorded a nearly 900% variation in the biomass of the triggerfishes considered to be
 300 keystone urchin predators (Fig. 5). Despite this background variability there was no evidence for
 301 urchins being released from predation pressure, with a distinct spatial mismatch between triggerfish
 302 and urchin densities. This cautions against the assumption of functional linkages outside the systems
 303 in which they were established.

304

Location	Urchin	Density (ind. m^{-2})	Bioerosion (kg $\text{m}^{-2}\ \text{year}^{-1}$)	Study
Panama	<i>Diadema mexicanum</i> & <i>Toxopneustes roseus</i>	0.1 - 150	0.0073 – 10.4	Glynn, 1988
La R�union (West Indian Ocean)	Total	3.8 – 73.6	0.4 – 8.3	Peyrot-Clausade et al., 2000
Puerto Rico	<i>Echinometra viridis</i>	0.8 - 62	0.11 - 4.14	Griffin et al., 2003
Belize	Total	0.8 - 40	0.2 – 2.7	Brown-Saracino et al., 2007
Galapagos Islands	<i>Eucidaris thouarsii</i>	1.1 – 32.7	0.8 – 23.65	Glynn, 1988
Zanzibar	Total	0 – 20.28	0 – 6.91	Bronstein and Loya, 2014
United Arab Emirates	<i>Echinometra mathaei</i>	0 - 14	-	Bauman et al., 2016
New Caledonia	Total	0 - 13	-	Dumas et al., 2007
Moorea	Total	7.12 – 10.10	0.6 – 7.5	Peyrot-Clausade et al., 2000
Mexico (East Pacific)	<i>Diadema mexicanum</i>	1 - 6.8	0.17 - 3.28	Herrera-Escalante et al., 2005

Kenya	Total	0.06 – 6.2	0.05 – 1.18	Carreiro-Silva and McClanahan, 2001
Tanzania	Total	0.08 – 5.02	-	McClanahan et al., 1999
Hong Kong	<i>Diadema setosum</i>	0.5 – 4.4	0.12 – 0.66	Dumont et al., 2013
Singapore	<i>Diadema setosum</i>	0 - 4	-	Goh and Lim, 2015
Western Australia (Ningaloo Reef)	<i>Echinometra mathaei</i>	0.001 – 2.2	-	Johansson et al., 2013
Great Barrier Reef	Total	0 – 0.5	0 – 0.01	Present study

305

306 **Table 1.** Mean urchin densities and bioerosion rates on natural coral reef substrata reported from reefs
307 around the world.

308

309 The strongest evidence for a relationship between triggerfishes and urchins was established
310 on the coral reefs along the East coast of Africa (McClanahan, 2000; McClanahan et al., 1999;
311 McClanahan and Muthiga, 2016; McClanahan and Shafir, 1990). These studies related variation in
312 triggerfish biomass/density and predation pressure, inside and outside marine reserves, to urchin
313 densities (McClanahan et al., 1999; McClanahan and Muthiga, 2016; McClanahan and Shafir, 1990).
314 They also linked a decline in urchins to the recovery of *B. undulatus* inside marine reserves
315 (McClanahan, 2000). Interestingly, triggerfish densities on the GBR mirrored those in East Africa.
316 Where the abundance of triggerfishes was highest on the GBR (northern mid- and outer-shelf reefs),
317 triggerfish densities (0.09 - 1.04, 100 m⁻²) were comparable to areas protected from fishing in Kenya
318 (0.33 – 0.92, 100 m⁻²) (McClanahan and Shafir, 1990) and Tanzania (0.16 - 1.02, 100 m⁻²)
319 (McClanahan et al., 1999). While, triggerfish densities on GBR northern inner-shelf reefs (0.06 –
320 0.28, 100 m⁻²) and across the entire central region (0 – 0.28, 100 m⁻²) were comparable to fished areas
321 in Kenya (0.04 – 0.12, 100 m⁻²) (McClanahan and Shafir, 1990) and Tanzania (0 – 0.06, 100 m⁻²)
322 (McClanahan et al., 1999). Yet, despite this similarity, we did not detect any significant correlation
323 between triggerfishes and urchins.

324 Ningaloo Reef, in Western Australia, provides another example of a coral reef system in
325 which the relationship between urchins and triggerfishes has been examined. Here, moderate-high
326 densities of the sea urchin *E. mathaei* exist, despite intact communities of nominal urchin predators,
327 with no evidence that predation-controls urchin populations (Johansson et al., 2013). Johansson et al.,
328 (2013) hypothesised that because the predator assemblage was composed chiefly of large labrids (the
329 large triggerfishes considered to be keystone urchin predators were conspicuously absent or rare) this
330 may have allowed for the higher densities of *E. mathaei*. Interestingly, a similar situation existed in
331 our GBR dataset, with few triggerfishes recorded from the central region despite surveying
332 approximately 5 hectares of reef. Unlike on Ningaloo Reef, however, these reefs also had the lowest
333 abundances of sea urchins with only 10 specimens recorded on surveys. Clearly, the urchin –
334 triggerfish paradigm does not hold in all locations.

335 If the evidence from East Africa, Ningaloo Reef and the GBR are taken together, they suggest
336 that the functional linkage between urchins and their predators, especially triggerfishes is far more
337 complex than often assumed. The lack of clear relationships between urchins and predators in systems
338 that are considered to be relatively undisturbed, such as the GBR, could highlight the role of both
339 bottom-up and top-down processes in mediating urchin populations. The abundance of echinoderms
340 in general, are heavily influenced by bottom-up factors such as food supply, larval supply, water flow
341 and settlement cues (Metaxas, 2013; Uthicke et al., 2009). Variations in densities within the
342 echinoderms is exemplified best by the CoTS, and indeed, the role of both bottom-up and top-down
343 factors in underpinning these outbreaks is still actively debated, with outbreaks potentially being a
344 result of influences from both directions (Pratchett et al., 2017). The limited number of urchins on
345 inner-shelf reefs may point to bottom-up control. These reefs lack the diversity and abundance of
346 nominal echinoid predators (Emslie et al., 2017; Williams and Hatcher, 1983), including triggerfishes
347 (Fig. 4). They are also considered to be more disturbed than reefs further offshore (Fabricius et al.,
348 2014; Goatley et al., 2016) and exhibit high sediment loads both in the water column (Browne et al.,
349 2013; Fabricius et al., 2014) and within algal turfs (Goatley et al., 2016; Tebbett et al., 2017).
350 Previously, urchin abundances have been negatively correlated with higher loads of fine sediments

351 (Dumas et al., 2007; Sangil and Guzman, 2016) and it has been suggested that long sediment-laden
352 algal turfs hinder urchin recruitment (Lessios, 2016). Perhaps high sediment loads, rather than
353 predation, are the main driver of urchin settlement dynamics on inner-shelf reefs.

354 The lack of a relationship between triggerfishes and urchins could also be a result of other
355 nominal urchin predators (primarily labrids and lethrinids) playing important roles in urchin predation
356 on the GBR. The available evidence suggests this is unlikely, with the triggerfishes *B. viridescens* and
357 *B. undulatus* contributing disproportionately to urchin predation compared to both labrids and
358 lethrinids (Young and Bellwood, 2012). Furthermore, Fricke, (1971) showed that larger triggerfishes
359 were far more efficient urchin predators, that could consume concealed urchins, while labrids and
360 lethrinids were restricted to feeding on solitary exposed urchins. Nevertheless, there is the potential
361 that a high density of labrids or lethrinids could maintain low urchin abundances even in the absence
362 of triggerfish predators. It should be noted that macro- and/or micro- invertebrates can play important
363 roles as predators of urchins (Ling and Johnson, 2012), urchin recruits (Bonaviri et al., 2012), as well
364 as other echinoderm recruits (Cowan et al., 2016), and could have the potential to mediate urchin
365 densities on GBR reefs.

366 The diurnal survey techniques used may also have resulted in urchins being undercounted
367 resulting in no clear relationship between triggerfishes and urchins. Two studies on the GBR have
368 found that urchins are predominantly nocturnal, presumably to avoid high predation rates during the
369 day (Sammarco, 1985; Young and Bellwood, 2011). Indeed, the urchin counts in the present study
370 were dominated by *Echinostrephus* sp. which are readily visible during the day in their burrows.
371 However, while urchin abundances may be conservative estimates, the maximum mean nocturnal
372 urchin density recorded by the two previous studies was just 1.06 m⁻², which is still far lower than
373 other coral reef regions (Table 1). Due to the largescale nature of the surveys in the present study it
374 would make nocturnal counts logistically challenging and as most sea urchin counts are performed
375 during the day, our diurnal counts are directly comparable with previous studies. Furthermore,
376 localised high-densities of diurnally-active *Diadema* sp. have been observed on the GBR such as in
377 the lagoon at Brampton Island (20°48'2.3292"S, 149°16'46.9518" E) (pers. obs. SBT, DRB; Fig. S1)

378 and on the back reefs of Magnetic Island (19°9'38.2962"S, 146°51'28.152" E) (pers. obs. SBT, DRB).
379 As such, if urchins were present and free from predation they would be easily detected during diurnal
380 surveys. Why densities of urchins in general are so low is currently unclear, but it is likely to result
381 from a complex interaction between bottom-up and top-down factors.

382 By directly controlling urchin densities, top-down control is often believed to indirectly affect
383 ecosystem processes, particularly in terms of the relevant contribution of urchins to bioerosion.
384 However, clearly this is only possible if urchins are controlled by top-down predation and if they
385 increase to substantial numbers. On the GBR we found no evidence for top-down control, with
386 generally low urchin densities. Concomitantly, urchin bioerosion rates were very low ($0 - 0.01 \text{ kg m}^{-2}$
387 year^{-1} ; Fig. 3a) and were only a fraction of the bioerosion rates that have been reported elsewhere
388 (Table 1), which reach up to $23.65 \text{ kg m}^{-2} \text{ year}^{-1}$ (Glynn, 1988). Our results support those of Browne et
389 al., (2013) who estimated urchin bioerosion rates on two nearshore reefs in the central GBR to be <
390 $0.1 \text{ kg m}^{-2} \text{ year}^{-1}$. On the GBR bioerosion is predominantly by parrotfishes (Fig. 3). This comparison
391 was made across back reefs, where parrotfish bioerosion rates are lowest (Hoey and Bellwood, 2008),
392 yet parrotfishes still accounted for 61 - 93% of total bioerosion compared to $0 - 0.2\%$ for urchins.

393 Unfortunately, the large parrotfishes which contribute disproportionately to bioerosion are
394 often heavily exploited and rapidly overfished (Bellwood et al., 2012), and in such systems
395 herbivorous fishes can be replaced by urchins (Graham et al., 2017). As such, the relative
396 contributions to bioerosion reported herein are likely to reflect more natural levels from relatively
397 unfished systems (but see Johansson et al., 2010). While both sea urchins and parrotfishes are
398 considered external bioeroders on coral reefs they contribute to bioerosion in markedly different
399 ways. Bioeroding parrotfishes are believed to feed on the surface of the reef targeting endolithic
400 cyanobacteria within the reef matrix (Clements et al., 2017). By contrast, urchins access more
401 concealed microhabitats and can burrow directly into the reef matrix undercutting and dislodging
402 massive corals (Bellwood et al., 2004; Done et al., 1991; Glynn and Manzello, 2015; Perry and
403 Harborne, 2016) and rendering coral colonies more vulnerable to hydrodynamic disturbances (Perry
404 and Harborne, 2016). When present in high numbers, the more destructive bioerosion delivered by

405 urchins may therefore hinder reef development, and place the long-term survival of reefs in jeopardy
406 (Bellwood et al., 2004).

407 In this study we have highlighted that functional linkages may not operate across similar
408 systems, and that the contributions that organisms make to ecosystem processes can also differ
409 markedly. Essentially, on the GBR, we found no evidence that triggerfishes control urchin
410 distributions, triggerfish and urchin distributions appear to be unrelated. Furthermore, urchins are not
411 important players in ecosystem processes such as bioerosion. Notably this study was performed on the
412 GBR prior to recent upheavals which included back-back mass coral bleaching events (Hughes et al.,
413 2017b). As such, it may provide a valuable insight into the functioning of this system prior to these
414 disturbances. However, coral reefs are now changing fast, with new, transitional, reef configurations
415 emerging unlike anything we have experienced previously (Hughes et al., 2017a). Assessing the
416 applicability of commonly held paradigms to these new, transitional, coral reef systems will be a rich
417 area of investigation for future research that will be vital to understand and preserve the functioning of
418 these ecosystems.

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