

The Sea Urchin *Centrostephanus Tenuispinus* (Clark, 1914) is an Important Bio-Eroder on a High Latitude (32° S) Coral Reef.

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1 The sea urchin *Centrostephanus tenuispinus* (Clark, 1914) is an important bio-eroder on a high
2 latitude (32° S) coral reef.

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31 Abstract

32 Sea urchins are keystone herbivores in many marine benthic habitats. They can significantly influence
33 coral-algae phase shifts and impact on reef carbonate budgets through grazing. Hall Bank reef in
34 Western Australia is unique among other reefs in the region being high latitude with a high
35 hermatypic coral cover but lacking macroalgae and soft corals. Since the reef status is thought to
36 result from high densities of the urchin *Centrostephanus tenuispinus* limiting the growth of
37 macroalgae, the present study was focused on evaluating their role as bio-eroders. Monthly samples of
38 26 urchins were collected from 2014-2016 and gut composition was analyzed. Gut evacuation rates
39 were calculated using 50 urchins dissected at time intervals (0, 4, 8, 16, 24, 36, 48, 60, 72 and 96 h).
40 Reworked calcium carbonate was calculated using 30 urchins maintained in five cages in a seagrass
41 bed adjacent to the reef site. Mean percentages for organic component, calcium carbonate and other
42 siliceous components were $86.29 \pm 3.23\%$, $10.32 \pm 2.76\%$ and $3.39 \pm 1.52\%$ respectively. Gut
43 evacuation rates for autumn, winter, spring and summer were 0.70, 0.24, 0.48 and 0.72 (day^{-1}). Bio-
44 erosion rates were significantly higher in Summer-16 ($3.52 \text{ g CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$) and lower in winter
45 ($1.32 \text{ g CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$) ($F=101.580$, $p<0.000$). High erosion rates were recorded for large urchins
46 ($F= 37.789$, $P<0.001$). Annual urchin bio-erosion was $1017.69 \text{ g CaCO}_3 \text{ m}^{-2} \text{ a}^{-1}$. Differences in food
47 ingestion rates in response to seawater temperature changes are thought to be the main cause for the
48 significant differences in seasonal bio-erosion rates.

49 Key words: Sea urchin, Grazing, Calcium carbonate, Bio-erosion, Coral reef

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61 1.0 Introduction

62 Sea urchins play a vital role in many marine benthic habitats as grazers, bio-eroders,
63 producers of particulate inorganic matter and habitat providers (Scheibling 1986; Glynn 1988;
64 Andrew and Underwood 1989; Mokady et al. 1996; Tuya et al. 2004; Mamelona and Pelletier 2005;
65 Bluhm et al. 2009; Glynn and Manzello 2015; Glynn et al. 2017). As grazers, the influence of sea
66 urchins can be immense as they prevent the growth of all organisms other than encrusting algae. High
67 densities of sea urchins remove competitive algae, reducing coral mortality due to algal overgrowth
68 and allowing corals to increase in size and abundance (Bluhm et al. 2009). Thus, they significantly
69 contribute to the interplay between seaweed and coral-dominated reefs. Although they are well known
70 to be keystone grazers and studied extensively, their grazing habits and their role as bio-eroders in
71 many habitats is understudied.

72 Sea urchins can weaken carbonate reefs through spine abrasion and through scraping hard
73 carbonate substrate with their tooth-like feeding plates, the Aristotle's lantern (Klinger and Lawrence
74 1985; Ma et al. 2008). These organisms, being one of the major causative agents of bio-erosion play a
75 critical role in shaping reef structure and producing sediments that characterise the reef environment
76 (Scheibling 1986; Glynn 1988; Bak 1994; Mokady et al. 1996; Tuya et al. 2004; Dumont et al. 2013;
77 Glynn and Manzello 2015). Due to this immense impact on their habitats, they are considered "reef
78 engineers". Urchins can exert severe pressure on reefs with shifts from fish bio-eroders to urchin bio-
79 eroders resulting in marked impacts on reef community assemblages because of their grazing pressure,
80 depending on the density of the urchin population (McClanahan et al. 1994). Although they contribute
81 to the balance between reef constructive and destructive processes, overgrazing, with ingestion of
82 large quantities of reef carbonates, can negatively impact reef structure. Glynn (1988) recorded bio-
83 erosion of $40 \text{ kg CaCO}_3 \text{ a}^{-1}$, which exceeded reef accretion rates ($0.3\text{-}12 \text{ kg CaCO}_3 \text{ a}^{-1}$) in tropical
84 reefs. Urchins have been estimated to contribute up to 80% of total erosion of reefs (Scoffin et al.
85 1980).

86 Although coral reef growth has been the focus of many biological studies, reef destruction by
87 bio-erosion has received little attention (Tribollet et al. 2002). Considering the ecological role and
88 impact of urchins on their habitat, quantification of this impact is essential for the management of
89 many marine habitats. Urchin bio-erosion can equal or exceed reef carbonate production (Bak 1994).
90 Higher average rates of bio-erosion by sea urchins have been reported on reef slopes (0.9 kg CaCO_3

91 m⁻² a⁻¹) compared to reef flats (0.5 kg CaCO₃ m⁻² a⁻¹) (Mokady et al. 1996). Thus, the extent of bio-
92 erosion can vary due to habitat structure. The extent of sea urchin bio-erosion mainly depends on
93 species, test size/diameter and population density (Bak 1994). *Diadema antillarum* has been reported
94 to cause erosion of 4.6 kg CaCO₃ m⁻² a⁻¹ in a patch reef at St. Croix, Virgin Islands, US (9 individuals
95 m⁻²), and 5.3 kg CaCO₃ m⁻² a⁻¹ in fringing reefs at Barbados (23 individual m⁻²). Carreiro-Silva and
96 McClanahan (2001) stated that, despite similar body sizes, bio-erosion can vary due to different
97 feeding behaviours (species-specific feeding strategies). The outcomes of these studies imply the need
98 for species-specific studies on bio-erosion in unique sea urchin-dominated habitats. Currently, all
99 studies focused on bio-erosion have been centred on tropical reefs, mainly Caribbean and Indo-pacific
100 regions; reefs in higher latitudes have not been studied.

101 Among other high latitude temperate reefs, Hall Bank reef (32° 2.002'S, 115° 42.957'E) in
102 southern Western Australia is unique due to its high hermatypic coral cover (mean = 52.6 ± 4.65%),
103 and scarcity of soft coral and macroalgae (Thomson and Frisch 2010). In general, reefs in this area are
104 dominated by kelps and other macro-phaeophytes and grazing herbivores exert little influence
105 (Vanderklift and Kendrick 2004; Vanderklift and Kendrick 2005; Vanderklift et al. 2009) resulting
106 instead on an abundance of drift algae which is the major food sources of large abundant herbivores
107 such as the urchin *Heliocidaris erythrogramma* (Vanderklift and Kendrick; 2005; Vanderklift and
108 Wernberg 2008) and the abalone *Halitois roei* (Wells and Keesing 1989). On the other hand,
109 *Centrostephanus tenuispinus*, the focus of this study, is regarded as a predominantly a grazer rather
110 than a drift feeder (Vanderklift and Kendrick; 2005; Vanderklift and Wernberg 2008). Thomson and
111 Frisch (2010) suggested that the high abundance of herbivorous sea urchin *Centrostephanus*
112 *tenuispinus* (mean density = 5.0 ± 0.81 m⁻²) may contribute to the maintenance of the high cover of
113 corals at Hall Bank. Main objective of this study is to quantify bio- erosion of *C. tenuispinus* and to
114 assess its role in reef structuring process.

115

116 2.0 Methodology

117 2.1 Study Site

118 Hall Bank reef (32° 2.002'S and 115° 42.957'E) is located 3 km northwest of the Fremantle
119 Harbour in southern Western Australia (Figure 1). It is a small patch of limestone reef (around 2 ha)
120 dominated by scleractinian corals (mostly family Faviidae), depth 7-10 m, which abruptly descends to

121 the surrounding seagrass bed (depth 15 m). The study was conducted from December 2014 to
122 February 2016.

123

124 2.1 Methods

125 2.1. Analysis of calcium carbonate in urchin gut contents

126 Sea urchins were collected (26 individuals per month) from December 2014 to February
127 2016. Samples were transported to the laboratory in Murdoch University on ice. Test diameter (± 0.1
128 mm) and wet weight (± 0.001 g) were measured. Urchins were dissected and gut contents extracted to
129 determine the amount of calcium carbonate and organic content using the methods described by
130 Carreiro-Silva and McClanahan (2001). Gut contents were dried to constant weight in a preheated
131 oven set at 70°C for 48 h. Subsamples of 1 g of the gut contents were weighed on a high precision
132 analytical balance (± 0.0001 g) and immediately transferred to a muffle furnace for 5 h at 500 °C to
133 combust the organic matter. Samples were weighed and digested with 5% HCl. Residual matter was
134 filtered with preweighed filter paper under suction, dried (70°C for 8 h) and weighed.

135

136 2.2. Determination of newly eroded calcium carbonate

137 Thirty urchins were caged (1 × 1 × 1 m) in 5 cages (6 urchins per cage) in a seagrass bed
138 adjacent to the Hall Bank reef. Cages were kept underwater for 2 months. After the cage experiment,
139 urchins were collected and transferred on ice to the laboratory, where they were dissected, and gut
140 contents removed into aluminum dishes. The amount of CaCO₃ in the guts was analyzed using the
141 methods described above. Newly eroded CaCO₃ was calculated as follows:

$$142 \text{ Newly eroded CaCO}_3 = \text{Total CaCO}_3 - \text{Reworked CaCO}_3 \text{-----}1$$

143

144 2.3 Determination of gut evacuation rate of *C. tenuispinus*

145 This experiment was carried out in August 2015 (winter) and February 2016 (summer). Gut
146 evacuation rates for autumn and spring were calculated using the values of summer and winter with
147 respect to the mean sea temperature. Fifty sea urchins were collected for each trial. Five urchins were
148 sacrificed at the point of collection (0 hours). The other urchins were transferred to the laboratory and
149 kept in a flow-through seawater aquarium (temperature-controlled 17 °C in winter and 22 °C in
150 summer). These urchins were sacrificed at 4, 8, 12, 16, 24, 36, 48, 72 and 96 hourly intervals. Urchins

151 were dissected and gut contents were carefully removed from the gut and weighed. The gut contents
 152 were dried for 24 h in an oven set at 70°C and weighed. Mean values (n = 5) for dry gut-weight were
 153 plotted against time. The relationship between dry weight and time was defined by the following
 154 regression equation:

$$155 \quad C = C_0 e^{-RT} \text{-----}2$$

156 Where C = gut content weight; C₀ = gut content at time 0; t = time; R = rate of decrease

157

158 Meantime (t) for gut evacuation was calculated using Elliott (1972).

$$159 \quad \bar{t} = \int_0^{\infty} \frac{C_0 e^{-RT} dt}{C_0} = \frac{1}{R} \text{-----}3$$

160 Daily calcium carbonate and algae ingestion were calculated using the below equation.

$$161 \quad F = CR \text{ 24} \text{-----}4$$

162 where F = Food consumption rate

163

164 2. 4 Analysis of sea urchin density

165 Ten haphazard transects (20 ×1 m) were sampled on the reef in each season (autumn 2015,
 166 winter 2015, spring 2015 and summer 2016). The number of urchins in each transect was counted, and
 167 the density was calculated as individuals per square meter.

168

169 2.5 Measurements of bio-erosion rates

170 Calcium carbonate and organic matter in gut contents and gut evacuation rate were used to
 171 calculate bio-erosion rates and food ingestion rates for different seasons (Elliott and Persson 1978).

172

$$173 \quad \text{Food ingestion rate} = \text{Daily ingestion rate (day}^{-1}\text{)} \times \text{Dry gut content (g)} \text{....}5$$

$$174 \quad \text{Bioerosion rate} = \text{Daily ingestion rate (day}^{-1}\text{)} \times \text{Newly eroded CaCO}_3 \text{ weight (g)} \text{....}6$$

175

176 2.6 Statistical Analysis

177 All sea urchin samples were categorised into three different size classes depending on test
 178 diameter: <65 mm, 65-70 mm and >70 mm. CaCO₃ percentages and bio-erosion rates were compared

179 with respect to seasonal variation and test size using two-way analysis of variance (ANOVA). All
180 statistical tests were carried out in SPSS software (SPSS 24).

181

182 3.0 Results

183 3.1 Analysis of calcium carbonate in urchin gut contents

184 Gut content composition analysis revealed that urchins ingested $86.29 \pm 3.23\%$ CaCO_3 , 10.32
185 $\pm 2.76\%$ organic matter and $3.39 \pm 1.52\%$ other inorganic components (overall mean \pm SD). Mean
186 CaCO_3 content ($83.83 \pm 3.73\%$) was significantly lower in summer 2015 than other seasons
187 (ANOVA, $F(4,364) = 17.811$, $P < 0.001$). No significant differences in mean CaCO_3 content were
188 observed between other seasons. Calcium carbonate content did not vary between test size classes
189 (ANOVA, $F(2,364) = 1.645$, $P = 0.195$) (Figure 2).

190

191 3.2 Determination of newly eroded calcium carbonate

192 The mean percentage composition of CaCO_3 , organic and other inorganic components of the
193 caged urchins (in seagrass bed) were $64.99 \pm 5.24\%$, $29.75 \pm 4.83\%$ and $5.54 \pm 2.30\%$ respectively
194 (Figure 3). The average newly eroded CaCO_3 was 22.38% . The organic component of the caged
195 urchins ($29.75 \pm 4.83\%$) was greater than that of the urchin population on the reef ($10.32 \pm 2.76\%$)
196 ($p < 0.001$).

197

198 3.3 Analysis of gut evacuation rate

199 The initial mean dry gut-weight in summer and winter was 7.125 ± 2.18 g and 5.198 ± 1.40
200 g, respectively. The gut evacuation experiment revealed that 50% of the gut is emptied within 24 h in
201 summer and 36 h in winter. 86% and 75% of gut contents were emptied within 72 h in summer and in
202 winter respectively (Figure 4). The total time for gut evacuation was 100 h in winter and 33.3 h in
203 summer.

204 The mean seasonal dry gut-weight of *C. tenuispinus* was 6.83 ± 1.69 g (mean \pm SD). Dry
205 gut-weight of *C. tenuispinus* in spring 2015 (7.31 ± 2.02) was significantly higher than summer 2015
206 (6.48 ± 1.33) and autumn 2015 (6.54 ± 1.37) (ANOVA, $F(4,364) = 4.485$, $P = 0.002$). No significant
207 differences were observed between other seasons (Table 1). The highest mean dry gut-weight ($7.74 \pm$
208 1.66) was observed in the large size class (>70 mm) and the lowest (5.81 ± 1.29) in the smallest size

209 class (<65 mm) (ANOVA, F (2,364) = 55.177, P<0.001). The gut evacuation rate was 0.72 day⁻¹ and
210 0.24 day⁻¹ for summer and winter respectively (Table 1). Estimated gut turnover rates for autumn and
211 spring were 0.70 day⁻¹ and 0.48 day⁻¹ respectively.

212 Food ingestion rates were significantly different (ANOVA, F (4,364) =180.999, P<0.001)
213 between all seasons except between summer 2015 and autumn 2015 (P=0.978), summer 2015 and
214 summer 2016 (P=0.073). Differences in food ingestion rates varied among the three size classes
215 independently of the season (ANOVA, F (2,364) =47.460, P<0.001). Mean food ingestion rates for
216 size classes <65 mm, 65-70 mm and >70 mm was 3.33 ± 1.28 g day⁻¹, 3.80 ± 1.46 g day⁻¹, 4.25 ± 1.79
217 g day⁻¹ respectively.

218

219 3.4 Measurements of bio-erosion rates

220 The highest daily bio-erosion rate (1.10 ± 0.36 g CaCO₃ individual⁻¹ day⁻¹) was recorded in
221 summer 2016 and the lowest (0.36 ± 0.09 g CaCO₃ individual⁻¹ day⁻¹) was recorded in winter 2015
222 (Table 2). Differences in daily bio-erosion rates were significant between seasons (ANOVA, F (4,364)
223 =101.580, P<0.000) and urchin size classes (ANOVA, F (2,364) =37.789, P<0.001). Bio-erosion rates
224 were not significantly different between summer 2016 and autumn 2015 (P=0.077).

225 Seasonal bio-erosion rates were higher in autumn 2015 and summer 2016 (314.64 g of
226 CaCO₃ m⁻² and 316.80 g of CaCO₃ m⁻² respectively) than that of other seasons (Table 3). *C.*
227 *tenuispinus* was responsible for annual erosion of 1017.69 g of CaCO₃ m^{-2 a-1} at Hall Bank reef.

228

229 4.0 Discussion

230 Sea urchins are considered as reef engineers due to their ability to influence their habitat, in
231 particular destructive grazing of macrophytes and erosion of reefs. The grazing of *C. tenuispinus* on
232 the high latitude coral reef at Hall Bank is believed to exert a structuring influence by excluding the
233 development of a macroalgal canopy and instead favouring a high cover of scleractinian corals
234 (Thomson and Frisch 2010). This study revealed that the gut contents of *C. tenuispinus* were mainly
235 composed of CaCO₃ (86.6 ± 0.96%). Only 10.84 ± 0.52% of the gut contents was organic
236 components. Similar studies in other regions of the world have documented the same outcome, having
237 higher percentages of calcium carbonates (Carreiro-Silva and McClanahan 2001; Brown-Saracino et
238 al. 2007). Carreiro-Silva and McClanahan (2001) stated that *Diadema setosum*, *Diadema savygyi* and

239 *Echinothrix diadema* consumed over 80% calcium carbonate, and only 8% organic components. Hall
240 Bank reef lacks established macroalgal beds, probably due to the competition for space from corals
241 and intensive grazing of any algal recruitment. Urchins therefore totally depend on turf algae and
242 occasional drifting algae. Based on stable isotope analysis, *C. tenuispinus* is an omnivore which feed
243 on both algae and animal matter (Vanderklift et al. 2006). *Centrostephanus tenuispinus* are known to
244 be predominantly grazers (Vanderklift and Kendrick; 2005; Vanderklift and Wernberg 2008) Analysis
245 of gut contents in this study revealed that *C. tenuispinus* on Hall Bank Reef mainly feed on turf algae
246 as well as microinvertebrates (Thilakarathna 2017). Thus, the organic component in the gut
247 corresponds not only to the grazed algae but also to invertebrate tissues. Urchins from the correction
248 factor experiment had a higher percentage of organic components ($29.71 \pm 1.44\%$), than urchins on
249 the reef, mainly due to the availability of seagrass. Most of the CaCO_3 material was derived from
250 encrusting coralline algae and coral substrate. Mollusc shells (snails and bivalves) were also noted
251 during the analysis, although difficult to quantify; a small portion of these mollusc shells might
252 contribute to the total weight of calcium carbonates. Presence of other inorganic substances including
253 calcareous material and rock fragments in *C. tenuispinus* guts is indicative of their active grazing
254 (Vanderklift et al. 2006).

255 Organic components make up one-fifth of the daily calcium carbonate consumption in many
256 studied tropical sea urchins (Carreiro-Silva and McClanahan 2001), yet organic components in *C.*
257 *tenuispinus* from this study was only one-eighth of daily calcium carbonate consumption. The low
258 proportion of organic material in urchin's guts suggests that this herbivore assemblage is food-limited.
259 Hall Bank reef is devoid of macroalgae (Thomson and Frisch 2010). Analysis of organic components
260 in the urchin gut indicates that they mainly depend on turf algae (Thilakarathna 2017).

261 Urchin species, test size, and population density mainly influence grazing and bio-erosion by
262 sea urchins (Bak 1994). Research conducted on *Diadema antillarum* in western Mexico revealed that
263 there is a positive correlation between test diameters and the extent of bio-erosion ($<30\text{mm}$, $0.54 \pm$
264 0.45 g of CaCO_3 / >50 mm, 3.88 ± 0.74 g of CaCO_3) (Herrera-Escalante et al. 2005). Carreiro-Silva
265 and McClanahan (2001) revealed the importance of urchin species and body size on grazing as well.
266 Larger *Echinometra mathaei* (>30 mm) are known to have more impact (166.70 mg day^{-1}) on habitat
267 than smaller individuals (77.78 mg day^{-1}) (Manullang et al. 2014). This study confirms that test size
268 has greater impact on level of bio-erosion as well. Larger individuals had higher erosion rates ($0.932 \pm$

269 0.20 g of CaCO₃ m⁻² day⁻¹) than smaller (0.674 ± 0.022 g of CaCO₃ m⁻² day⁻¹) and medium sized
270 urchins (0.824 ± 0.025 g of CaCO₃ m⁻² day⁻¹) (p=0.000). Large urchins had significantly heavier and
271 larger lanterns (lantern diameter 26.20 ± 2.20mm; lantern height 27.10 ± 2.17 mm, lantern weight
272 10.40 ± 1.78 g) than small urchins (lantern diameter 21.19 ± 1.56 mm; lantern height 21.80 ± 1.61
273 mm, lantern weight 6.10 ± 1.08 g) (p=0.000). The large and heavy lanterns of large urchins enable
274 intense scraping. A positive correlation between test diameters and the extent of feeding rates and bio-
275 erosion has been witnessed for *Echinometra mathaei*, *Tripneustes gratilla*, *Salmacis sphaeroides* and
276 *Strongylocentrotus nudus* (Klumpp et al. 1993; Kawamata 1997; Manullang et al. 2014).

277 It is evident that the density of the urchin population has an immense impact on structuring
278 benthic communities and the extent of reef bio-erosion (Hereu et al. 2004; Ling and Johnson 2009).
279 High densities of urchins can cause higher levels of bio-erosion (Glynn 1988; McClanahan and Kurtis
280 1991; Bak 1994; Eakin 1996). *Eucidaris galapagensis* in reef flats of Floreana Islands and Galapagos
281 Islands is known to contribute to reef erosion of 3.320 kg CaCO₃ m⁻² a⁻¹ and 22.332 kg CaCO₃ m⁻² a⁻¹
282 with population densities of 4.6 individuals m⁻² and 30.8 individuals m⁻² respectively (Glynn 1988).
283 High densities of small urchins can have a larger bio-erosion impact than low densities of larger
284 individuals (Griffin et al. 2003). *C. tenuispinus* had a mean density ranging from 3.20 ± 0.23 m⁻² to
285 3.73 ± 0.33 m⁻² throughout the year. Annual bio-erosion caused by a density of 3.2-3.7 m⁻² *C.*
286 *tenuispinus* was 1.017 kg CaCO₃ m⁻² a⁻¹.

287 Most previously conducted studies on bio-erosion focused on tropical urchins; mainly
288 *Diadema*, *Echinometra* and *Echinothrix* species, and these species are considered to be the most
289 impacting bio-eroding agents in tropical reefs (Bak 1990; Mokady et al. 1996). Environmental
290 conditions, specifically water temperature, impact the urchins' physiology, directly influencing
291 ingestion and gut evacuation rates. Since there were no significant differences in dry gut-weight
292 across the seasons sampled in this study, differences in ingestion rate are critical for determining the
293 rate of bio-erosion. Significant differences in seasonal ingestion rates are mainly in response to the
294 changes in seawater temperatures, from 17°C in winter to 22°C in summer. The gut evacuation rate
295 was highest in summer and lowest in winter. Calculations based on mean seawater temperatures in
296 autumn and spring indicated gut evacuation rates were 0.70 day⁻¹ and 0.48 day⁻¹. Food ingestion rates
297 were higher in summer due to increased metabolism at higher temperatures; thus the erosion rates
298 were higher as well. *Centrostephanus tenuispinus* in the current study were subjected to lower water

299 temperatures (17°C) in winter than in summer (23°C). A difference of 6°C directly impacted on
300 physiology and activity levels, and therefore changes in ingestion rates between winter and summer.
301 The highest ingestion rate recorded in this study was 5.02 ± 1.33 gut dry weight individual⁻¹ day⁻¹ in
302 summer 2016, which is higher than *Diadema savygyi* from tropical waters with a mean ingestion
303 rate of 3.11 ± 0.70 g gut dry weight individual⁻¹ day⁻¹ (Carreiro-Silva and McClanahan 2001). At the
304 same time *D. setosum* has shown an ingestion rate of 8.36 ± 1.16 g day⁻¹ (Carreiro-Silva and
305 McClanahan 2001). Most urchin species in the tropics experience water temperatures over 25°C all
306 round year, and therefore have consistently high ingestion rates. Since the rate of bio-erosion is based
307 on food ingestion rates, any factor affecting food intake indirectly affects the bio-erosion rate as well.
308 The influence of water temperature on feeding has been recorded for other diadematoids as well
309 (Coppard and Campbell 2005).

310 Bio-erosion calculations for both summers (2015 /2016) in this study were based on a gut
311 evacuation rate of 0.72 day⁻¹. Mean seawater temperature was lower in summer 2015 (22.5°C) than in
312 summer 2016 (23.5°C). The percentage of calcium carbonate in the guts of urchins was lower in
313 summer 2015 than in summer 2016. The significant difference in CaCO₃ ingestion rates (and hence
314 bio-erosion) between summers may be attributed to temperature differences.

315 Many studies suggest that urchin feeding is affected by reproductive periods (Muthiga 2003).
316 Some urchin species feed less during spawning periods; *Strongylocentrotus intermedius* rarely feed
317 during their reproductive season (Fuji 1962). *C. tenuispinus* spawns during the winter
318 (Thilakarathna,2017). Although no significant seasonal differences of dry gut weights were observed,
319 food ingestion rate was low (0.24 day⁻¹) in winter compared to the other seasons. The lowest
320 percentage of organic components was recorded in winter ($8.74 \pm 1.77\%$), when urchins were
321 spawning. Higher percentages of organic components were observed in autumn and summer when
322 urchin gonads are resting and initiating gametogenesis of the next cycle.

323 The highest mean dry gut-weight for *C. tenuispinus* was 7.31 ± 2.02 g, recorded in spring
324 2015. *Diadema setosum* has a similar range of test diameter and had a dry gut-weight of (7.05 ± 0.98
325 g) (Table 4). On the other hand, *Diadema savygyi*, which is in the same range of test diameters, had a
326 mean dry gut-weight of 3.48 ± 0.78 g (Carreiro-Silva and McClanahan 2001).

327 The gut evacuation rate for *Centrostephanus tenuispinus* in this study is nearly 100 h in
328 winter, which is longer than other sea urchin species, reducing to 33.3 h in summer. Carreiro-and

329 McClanahan (2001) reported that the common tropical diadematoids *Diadema setosum*, *D. savynyi*
330 and *Echinothrix diadema* take 20.29, 26.86 and 21.10 h respectively to empty their guts. *Echinometra*
331 *mathaei* takes 13.94 h to empty all gut contents (Carreiro-Silva and McClanahan 2001). The slower
332 body physiology recorded for *C. tenuispinus* in this study may be associated with low winter
333 temperatures.

334 Sea urchin feeding, and hence bio-erosion rate, is influenced by space, nature of habitat,
335 habitat structure and water temperature. Interaction of these factors causes higher bio-erosion in some
336 habitats. It is also essential to calculate annual reef accretion rates to determine the impact of bio-
337 erosion on reef carbonate budgets.

338 Hall Bank reef is dominated by massive corals (Thomson and Frisch 2010) and the reef
339 accretion rate of Hall Bank reef has not been quantified. Coral calcification rates are known to depend
340 on seawater temperatures (Kleypas et al. 1999). Since Marmion reef is in close proximity (25 km) to
341 Hall Bank reef and having similar seawater temperature ranges (22 - 23°C), the calcification rate in
342 Marmion reef assumed to be similar to Hall Bank reef. The highest calcification rates were recorded
343 for Marmion for winter 2011 (7.3 g m⁻² day⁻¹) after a marine heatwave event (Foster et al. 2014) which
344 is higher than daily bio-erosion rates in Hall Bank reef. However, calcification rates at Marmion reef
345 for summer 2012, winter 2012 and summer 2013 were (1-2.5 g m⁻² day⁻¹) lower than daily bio-erosion
346 rates of Hall Bank reef in both summer and autumn. Mean annual growth rates recorded for *G. aspera*
347 / *palauensis* and *G. australensis* in Hall Bank reef are 5.4 ± 0.9 mm a⁻¹ and 10.9 mm a⁻¹ (Antipas
348 2013). Higher growth rates of these corals at Hall Bank reef despite its near-shore location and
349 compared to other tropical/subtropical location could be attributed to increasing trends of seawater
350 temperature. Lack of seasonality in calcification rates and slower growth of branching coral compared
351 to massive coral is known to cause by temperature anomalously occurred in 2010-2011 (Foster et al.
352 2014). Since bio-erosion is positively correlated with seawater temperature, increase in seawater
353 temperature could also lead to conditions where reef erosion rates exceed reef accretion rates, which
354 can affect the coral cover in Hall Bank reef. The absence of any measurements of calcification rates
355 on Hall Bank precludes determining a reef carbonate budget for Hall Bank reef.

356 This study only examined bio-erosion due to grazing; bio-erosion from spine abrasion has
357 not been accounted for in this study. Similarly, bio-erosion caused by other herbivores has not been
358 accounted for since *C. tenuispinus* is the main bio-eroder in this system. The difference in food

359 ingestion rates in response to seawater temperature changes is the main cause for the significant
360 differences in seasonal bio-erosion rates on Hall Bank reef and the high rates of bio-erosion likely
361 contribute to the absence of macroalgae and the maintenance of high coral cover on Hall Bank.

362

363 **Compliance with Ethical Standards**

364 None of the authors does have any conflict of interests associated with this publication, and there has
365 been no significant financial support for this work that could have influenced its outcome. All
366 applicable international, national and/or institutional guidelines for sampling, care and experimental
367 use of organisms for the study have been followed and all necessary approvals have been obtained.

368

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375

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377 **Conflicts of Interest/Competing Interests:** None of the authors does have any conflict of interests
378 associated with this publication, and there has been no significant financial support for this work that
379 could have influenced its outcome.

380

381 **Ethical approval:** No approval of research ethics committees was required to accomplish the goals of
382 this study because experimental work was conducted with an unregulated invertebrate species.

383

384 **Consent to participate:** Not applicable.

385

386 **Consent for Publication:** There is no conflict of interest to report.

387

388 **Availability of Data and Material:** Not applicable

389 **Code availability:** Not applicable

390 **Author contributions:** All authors, RMGN Thilakarathna, Mike van Keulen and John K. Keesing
391 contributed to the study conception and design. Material preparation, data collection and analysis were
392 performed by RMGN Thilakarathna under the supervision of Mike van Keulen and John K. Keesing.
393 The first draft of the manuscript was written by RMGN Thilakarathna, and all authors commented on
394 previous versions of the manuscript. All authors read and approved the final manuscript.

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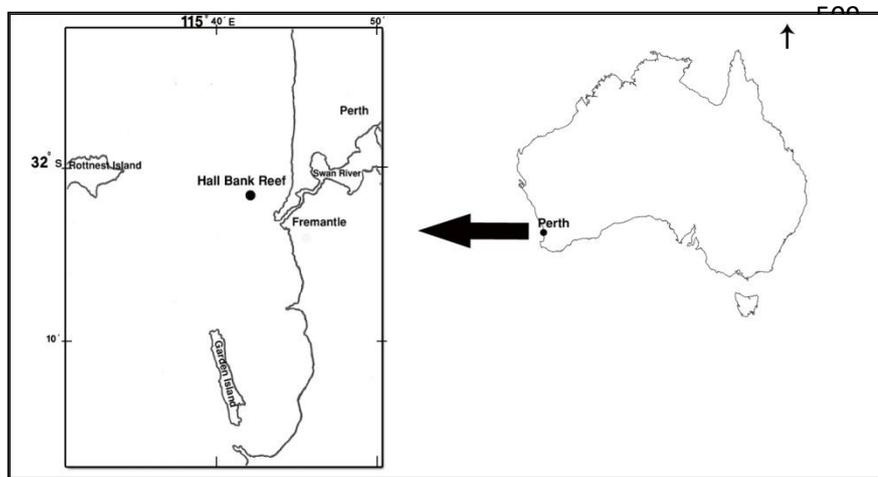
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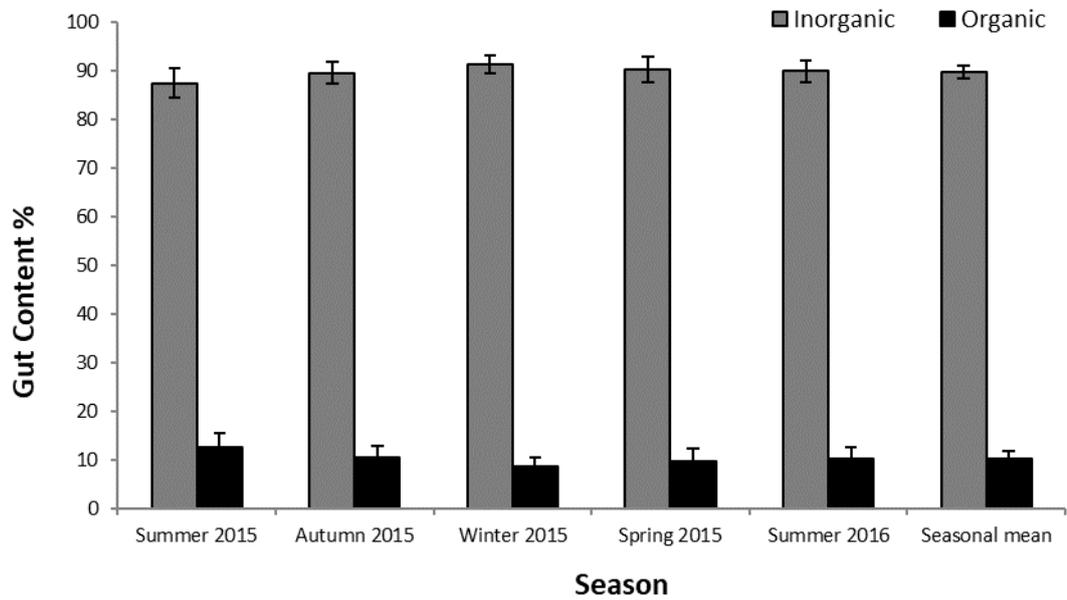
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Figure 1. Map showing location of the Hall Bank reef in Western Australia.

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540 Figure 2. Seasonal mean proportions of inorganic (mean \pm SD) and organic (mean \pm SD)
541 dry gut components in sampled *C. tenuispinus* population (n = 364).
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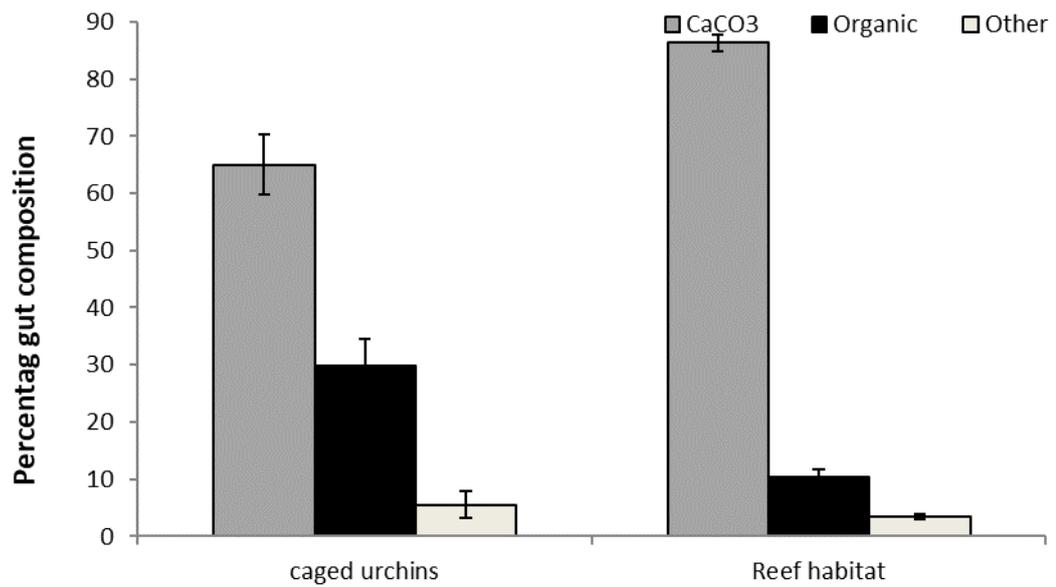
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562 Figure 3. Composition of *C. tenuispinus* mean dry gut components in sampled population (n=364) and
563 caged population (n=30).
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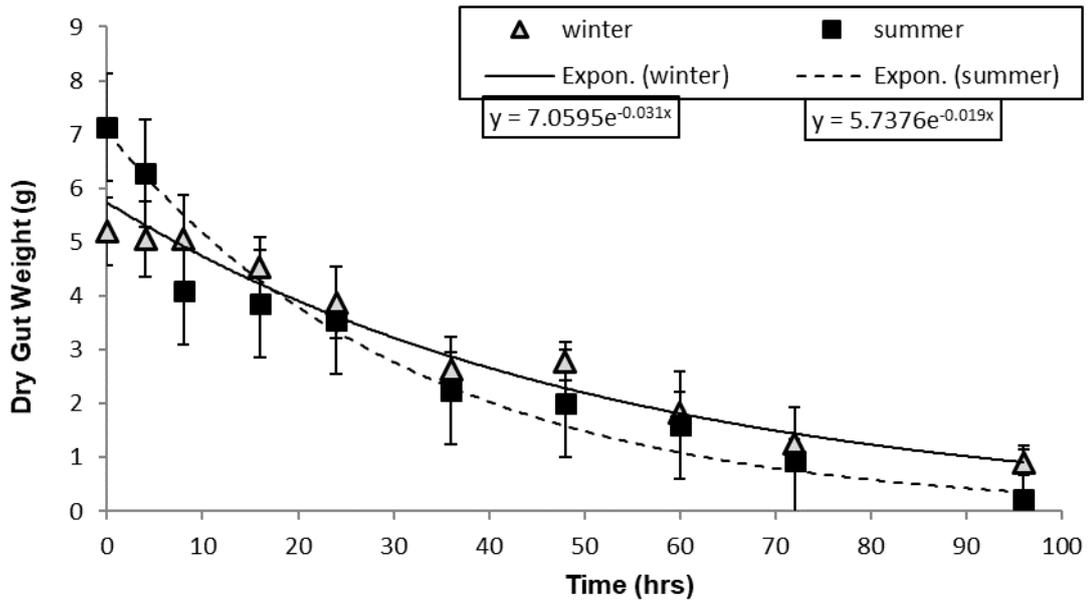
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578 Figure 4. Gut evacuation of *C. tenuispinus* over 96 h in winter (n = 50) 2015 and summer 2016 (n =
 579 50), Exponential curve fitted by least regression on the natural logarithms of dry gut
 580 weight with time.
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598 Table 1. Mean density, mean test diameter, mean gut weight, gut turnover rate and food ingestion rate
 599 of *C. tenuispinus* (mean \pm SD, n=364).

Season	Mean sea urchin density (individuals m ⁻²)	Mean test diameter (mm)	Mean gut weight (g)	Gut turnover rate (g day ⁻¹)	Food ingestion rate gut dry weight (g individual ⁻¹ day ⁻¹).
Summer 2015	3.20 \pm 0.23	67.70 \pm 5.95	6.48 \pm 1.33	0.72	4.67 \pm 0.96
Autumn 2015	3.45 \pm 0.29	67.79 \pm 2.94	6.54 \pm 1.37	0.70	4.58 \pm 0.96
Winter 2015	3.65 \pm 0.30	68.61 \pm 6.47	6.75 \pm 1.63	0.24	1.62 \pm 0.39
Spring 2015	3.73 \pm 0.33	67.46 \pm 5.75	7.31 \pm 2.02	0.48	3.51 \pm 0.97
Summer 2016	3.20 \pm 0.23	68.06 \pm 5.37	6.98 \pm 1.95	0.72	5.02 \pm 1.33

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621 Table 2. Herbivory rate, CaCO₃ ingestion rate, percentage newly eroded CaCO₃ and bio-erosion rate
 622 of *C. tenuispinus* (mean± SD, n=364).

Season	Herbivory rate (g individual ⁻¹ day ⁻¹)	CaCO ₃ ingestion rate (g CaCO ₃ individual ⁻¹ day ⁻¹)	Newly eroded percentage of CaCO ₃ in gut	Bio-erosion rate (g CaCO ₃ individual ⁻¹ day ⁻¹)
Summer2015	0.58±0.18	3.92±0.83	18.83±3.73	0.88±0.26
Autumn2015	0.47±0.14	3.97±0.85	21.60±2.36	0.99±0.24
Winter2015	0.14±0.05	1.41±0.34	22.30±2.69	0.36±0.09
Spring2015	0.34±0.14	3.06±0.85	22.19±2.73	0.78±0.24
Summer2016	0.50±0.13	4.36±1.18	21.67±2.97	1.10±0.36

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646 Table 3: Mean seasonal bio-erosion and annual bio-erosion in Hall Bank reef

Season	Daily bio-erosion g of CaCO ₃ m ⁻² day ⁻¹	Seasonal erosion g of CaCO ₃ m ⁻²	Annual bio-erosion g of CaCO ₃ m ⁻² a ⁻¹
Autumn 2015	3.42	314.64	1017.69
Winter 2015	1.32	121.44	
Spring 2015	2.91	264.81	
Summer 2016	3.52	316.80	

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671 Table 4. Test diameter, mean dry gut weight, food ingestion rates, gut turnover rates, daily bio-erosion
 672 rates of sea urchins *Diadema setosum*, *D. savygyi*, *Echinothrix diadema* and *C. tenuispinus* (mean \pm
 673 SD).

Species	<i>Diadema setosum</i> Carreiro-Silva and McClanahan (2001)	<i>Diadema savygyi</i> Carreiro-Silva and McClanahan (2001)	<i>Echinothrix diadema</i> Carreiro-Silva and McClanahan (2001)	<i>Centrostephanus tenuispinus</i> (This study/summer)
Test diameter (mm)	67.74 \pm 0.88	69.86 \pm 0.98	103.96 \pm 1.02	69.06 \pm 0.61
Mean gut weight (g)	7.05 \pm 0.98	3.48 \pm 0.78	18.54 \pm 3.10	6.98 \pm 0.21
Food ingestion rate (gut dry weight individual ⁻¹ day ⁻¹)	8.34 \pm 1.16	3.11 \pm 0.70	21.09 \pm 3.52	5.02 \pm 0.15
Gut turnover rate (day ⁻¹)	1.18	0.89	1.14	0.72
Bio-erosion rate (g CaCO ₃ individual ⁻¹ day ⁻¹)	1.79 \pm 0.25	0.72 \pm 0.16	5.49 \pm 0.91	1.10 \pm 0.04

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