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

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

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Abstract

Sea urchins are keystone herbivores in many marine benthic habitats. They can significantly influence coral-algae phase shifts and impact on reef carbonate budgets through grazing. Hall Bank reef in Western Australia is unique among other reefs in the region being high latitude with a high hermatypic coral cover but lacking macroalgae and soft corals. Since the reef status is thought to result from high densities of the urchin Centrostephanus tenuispinus limiting the growth of macroalgae, the present study was focused on evaluating their role as bio-eroders. Monthly samples of 26 urchins were collected from 2014-2016 and gut composition was analyzed. Gut evacuation rates were calculated using 50 urchins dissected at time intervals (0, 4, 8, 16, 24, 36, 48, 60, 72 and 96 h). Reworked calcium carbonate was calculated using 30 urchins maintained in five cages in a seagrass bed adjacent to the reef site. Mean percentages for organic component, calcium carbonate and other siliceous components were 86.29 ± 3.23%, 10.32 ± 2.76% and 3.39 ± 1.52% respectively. Gut evacuation rates for autumn, winter, spring and summer were 0.70, 0.24, 0.48 and 0.72 (day⁻¹). Bio-erosion rates were significantly higher in Summer-16 (3.52 g CaCO₃ m⁻² day⁻¹) and lower in winter (1.32 g CaCO₃ m⁻² day⁻¹) (F=101.580, p<0.000). High erosion rates were recorded for large urchins (F= 37.789, P<0.001. Annual urchin bio-erosion was 1017.69 g CaCO₃ m⁻² a⁻¹. Differences in food ingestion rates in response to seawater temperature changes are thought to be the main cause for the significant differences in seasonal bio-erosion rates.

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

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

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

Although coral reef growth has been the focus of many biological studies, reef destruction by bio-erosion has received little attention (Tribollet et al. 2002). Considering the ecological role and impact of urchins on their habitat, quantification of this impact is essential for the management of many marine habitats. Urrchin bio-erosion can equal or exceed reef carbonate production (Bak 1994). Higher average rates of bio-erosion by sea urchins have been reported on reef slopes (0.9 kg CaCO$_3$ a$^{-1}$).
m$^{-2}$ a$^{-1}$) compared to reef flats (0.5 kg CaCO$_3$ m$^{-2}$ a$^{-1}$) (Mokady et al. 1996). Thus, the extent of bio-erosion can vary due to habitat structure. The extent of sea urchin bio-erosion mainly depends on species, test size/diameter and population density (Bak 1994). *Diadema antillarum* has been reported to cause erosion of 4.6 kg CaCO$_3$ m$^{-2}$ a$^{-1}$ in a patch reef at St. Croix, Virgin Islands, US (9 individuals m$^{-2}$), and 5.3 kg CaCO$_3$ m$^{-2}$ a$^{-1}$ in fringing reefs at Barbados (23 individual m$^{-2}$). Carreiro-Silva and McClanahan (2001) stated that, despite similar body sizes, bio-erosion can vary due to different feeding behaviours (species-specific feeding strategies). The outcomes of these studies imply the need for species-specific studies on bio-erosion in unique sea urchin-dominated habitats. Currently, all studies focused on bio-erosion have been centred on tropical reefs, mainly Caribbean and Indo-pacific regions; reefs in higher latitudes have not been studied.

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

2.0 Methodology

2.1 Study Site

Hall Bank reef (32° 2.002' S and 115° 42.957' E) is located 3 km northwest of the Fremantle Harbour in southern Western Australia (Figure 1). It is a small patch of limestone reef (around 2 ha) dominated by scleractinian corals (mostly family Faviidae), depth 7-10 m, which abruptly descends to
the surrounding seagrass bed (depth 15 m). The study was conducted from December 2014 to February 2016.

2.1 Methods

2.1. Analysis of calcium carbonate in urchin gut contents

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

2.2. Determination of newly eroded calcium carbonate

Thirty urchins were caged (1 × 1 × 1 m) in 5 cages (6 urchins per cage) in a seagrass bed adjacent to the Hall Bank reef. Cages were kept underwater for 2 months. After the cage experiment, urchins were collected and transferred on ice to the laboratory, where they were dissected, and gut contents removed into aluminum dishes. The amount of CaCO$_3$ in the guts was analyzed using the methods described above. Newly eroded CaCO$_3$ was calculated as follows:

\[
\text{Newly eroded CaCO}_3 = \frac{\text{Total CaCO}_3 - \text{Reworked CaCO}_3}{1}
\]

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

This experiment was carried out in August 2015 (winter) and February 2016 (summer). Gut evacuation rates for autumn and spring were calculated using the values of summer and winter with respect to the mean sea temperature. Fifty sea urchins were collected for each trial. Five urchins were sacrificed at the point of collection (0 hours). The other urchins were transferred to the laboratory and kept in a flow-through seawater aquarium (temperature-controlled 17 ºC in winter and 22 ºC in summer). These urchins were sacrificed at 4, 8, 12, 16, 24, 36, 48, 72 and 96 hourly intervals.
were dissected and gut contents were carefully removed from the gut and weighed. The gut contents were dried for 24 h in an oven set at 70°C and weighed. Mean values (n = 5) for dry gut-weight were plotted against time. The relationship between dry weight and time was defined by the following regression equation:

\[ C = C_0 e^{-RT} \]

Where \( C \) = gut content weight; \( C_0 \) = gut content at time 0; \( t \) = time; \( R \) = rate of decrease

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

\[ \bar{t} = \frac{1}{R} \]

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

\[ F = CR 24 \]

where \( F \) = Food consumption rate

2.4 Analysis of sea urchin density

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

2.5 Measurements of bio-erosion rates

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

\[ \text{Food ingestion rate} = \text{Daily ingestion rate (day}^{-1}) \times \text{Dry gut content (g)} \]

\[ \text{Bioerosion rate} = \text{Daily ingestion rate (day}^{-1}) \times \text{Newly eroded CaCO}_3 \text{weight (g)} \]

2.6 Statistical Analysis

All sea urchin samples were categorised into three different size classes depending on test diameter: <65 mm, 65-70 mm and >70 mm. CaCO₃ percentages and bio-erosion rates were compared
with respect to seasonal variation and test size using two-way analysis of variance (ANOVA). All statistical tests were carried out in SPSS software (SPSS 24).

3.0 Results

3.1 Analysis of calcium carbonate in urchin gut contents

Gut content composition analysis revealed that urchins ingested $86.29 \pm 3.23\% \text{CaCO}_3$, $10.32 \pm 2.76\%$ organic matter and $3.39 \pm 1.52\%$ other inorganic components (overall mean $\pm$ SD). Mean CaCO$_3$ content ($83.83 \pm 3.73\%$) was significantly lower in summer 2015 than other seasons (ANOVA, $F(4,364) = 17.811$, $P <0.001$). No significant differences in mean CaCO$_3$ content were observed between other seasons. Calcium carbonate content did not vary between test size classes (ANOVA, $F(2,364) = 1.645$, $P = 0.195$) (Figure 2).

3.2 Determination of newly eroded calcium carbonate

The mean percentage composition of CaCO$_3$, organic and other inorganic components of the caged urchins (in seagrass bed) were $64.99 \pm 5.24\%$, $29.75 \pm 4.83\%$ and $5.54 \pm 2.30\%$ respectively (Figure 3). The average newly eroded CaCO$_3$ was $22.38\%$. The organic component of the caged urchins ($29.75 \pm 4.83\%$) was greater than that of the urchin population on the reef ($10.32 \pm 2.76\%$) ($p<0.001$).

3.3 Analysis of gut evacuation rate

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

The mean seasonal dry gut-weight of *C. tenuispinus* was $6.83 \pm 1.69$ g (mean $\pm$ SD). Dry gut-weight of *C. tenuispinus* in spring 2015 ($7.31 \pm 2.02$) was significantly higher than summer 2015 ($6.48 \pm 1.33$) and autumn 2015 ($6.54 \pm 1.37$) (ANOVA, $F(4,364) = 4.485$, $P= 0.002$). No significant differences were observed between other seasons (Table 1). The highest mean dry gut-weight ($7.74 \pm 1.66$) was observed in the large size class ($>70$ mm) and the lowest ($5.81 \pm 1.29$) in the smallest size.
class (<65 mm) (ANOVA, F (2,364) = 55.177, P<0.001). The gut evacuation rate was 0.72 day\(^{-1}\) and 0.24 day\(^{-1}\) for summer and winter respectively (Table 1). Estimated gut turnover rates for autumn and spring were 0.70 day\(^{-1}\) and 0.48 day\(^{-1}\) respectively.

Food ingestion rates were significantly different (ANOVA, F (4,364) =180.999, P<0.001) between all seasons except between summer 2015 and autumn 2015 (P=0.978), summer 2015 and summer 2016 (P=0.073). Differences in food ingestion rates varied among the three size classes independently of the season (ANOVA, F (2,364) =47.460, P<0.001). Mean food ingestion rates for 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 g day\(^{-1}\) respectively.

3.4 Measurements of bio-erosion rates

The highest daily bio-erosion rate (1.10 ± 0.36 g CaCO\(_3\) individual\(^{-1}\) day\(^{-1}\)) was recorded in summer 2016 and the lowest (0.36 ± 0.09 g CaCO\(_3\) individual\(^{-1}\) day\(^{-1}\)) was recorded in winter 2015 (Table 2). Differences in daily bio-erosion rates were significant between seasons (ANOVA, F (4,364) =101.580, P<0.000) and urchin size classes (ANOVA, F (2,364) =37.789, P<0.001). Bio-erosion rates were not significantly different between summer 2016 and autumn 2015 (P=0.077).

Seasonal bio-erosion rates were higher in autumn 2015 and summer 2016 (314.64 g of CaCO\(_3\) m\(^{-2}\) and 316.80 g of CaCO\(_3\) m\(^{-2}\) respectively) than that of other seasons (Table 3). C. tenuispinus was responsible for annual erosion of 1017.69 g of CaCO\(_3\) m\(^{-2}\) a\(^{-1}\) at Hall Bank reef.

4.0 Discussion

Sea urchins are considered as reef engineers due to their ability to influence their habitat, in particular destructive grazing of macrophytes and erosion of reefs. The grazing of C. tenuispinus on the high latitude coral reef at Hall Bank is believed to exert a structuring influence by excluding the development of a macroalgal canopy and instead favouring a high cover of scleractinian corals (Thomson and Frisch 2010). This study revealed that the gut contents of C. tenuispinus were mainly composed of CaCO\(_3\) (86.6 ± 0.96%). Only 10.84 ± 0.52% of the gut contents was organic components. Similar studies in other regions of the world have documented the same outcome, having higher percentages of calcium carbonates (Carreiro-Silva and McClanahan 2001; Brown-Saracino et al. 2007). Carreiro-Silva and McClanahan (2001) stated that Diadema setosum, Diadema savignyi and
Echinothrix diadema consumed over 80% calcium carbonate, and only 8% organic components. Hall Bank reef lacks established macroalgal beds, probably due to the competition for space from corals and intensive grazing of any algal recruitment. Urchins therefore totally depend on turf algae and occasional drifting algae. Based on stable isotope analysis, C. tenuispinus is an omnivore which feed on both algae and animal matter (Vanderklift et al. 2006). Centrostephanus tenuispinus are known to be predominantly grazers (Vanderklift and Kendrick; 2005; Vanderklift and Wernberg 2008) Analysis of gut contents in this study revealed that C. tenuispinus on Hall Bank Reef mainly feed on turf algae as well as microinvertebrates (Thilakarathna 2017). Thus, the organic component in the gut corresponds not only to the grazed algae but also to invertebrate tissues. Urchins from the correction factor experiment had a higher percentage of organic components (29.71 ± 1.44%), than urchins on the reef, mainly due to the availability of seagrass. Most of the CaCO₃ material was derived from encrusting coralline algae and coral substrate. Mollusc shells (snails and bivalves) were also noted during the analysis, although difficult to quantify; a small portion of these mollusc shells might contribute to the total weight of calcium carbonates. Presence of other inorganic substances including calcareous material and rock fragments in C. tenuispinus guts is indicative of their active grazing (Vanderklift et al. 2006).

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

Urchin species, test size, and population density mainly influence grazing and bio-erosion by sea urchins (Bak 1994). Research conducted on Diadema antillarum in western Mexico revealed that there is a positive correlation between test diameters and the extent of bio-erosion (<30mm, 0.54 ± 0.45 g of CaCO₃ / >50 mm, 3.88 ± 0.74 g of CaCO₃) (Herrera-Escalante et al. 2005). Carreiro-Silva and McClanahan (2001) revealed the importance of urchin species and body size on grazing as well. Larger Echinometra mathaei (˃30 mm) are known to have more impact (166.70 mg day⁻¹) on habitat than smaller individuals (77.78 mg day⁻¹) (Manullang et al. 2014). This study confirms that test size has greater impact on level of bio-erosion as well. Larger individuals had higher erosion rates (0.932 ±
0.20 g of CaCO$_3$ m$^{-2}$ day$^{-1}$) than smaller (0.674 ± 0.022 g of CaCO$_3$ m$^{-2}$ day$^{-1}$) and medium sized urchins (0.824 ± 0.025 g of CaCO$_3$ m$^{-2}$ day$^{-1}$) (p=0.000). Large urchins had significantly heavier and larger lanterns (lantern diameter 26.20 ± 2.20mm; lantern height 27.10 ± 2.17 mm, lantern weight 10.40 ± 1.78 g) than small urchins (lantern diameter 21.19 ± 1.56 mm; lantern height 21.80 ± 1.61 mm, lantern weight 6.10 ± 1.08 g) (p=0.000). The large and heavy lanterns of large urchins enable intense scraping. A positive correlation between test diameters and the extent of feeding rates and bio-erosion has been witnessed for *Echinometra mathaei*, *Tripneustes gratilla*, *Salmacis sphaeroides* and *Strongylocentrotus nudus* (Klumpp et al. 1993; Kawamata 1997; Manullang et al. 2014).

It is evident that the density of the urchin population has an immense impact on structuring benthic communities and the extent of reef bio-erosion (Hereu et al. 2004; Ling and Johnson 2009). High densities of urchins can cause higher levels of bio-erosion (Glynn 1988; McClanahan and Kurtis 1991; Bak 1994; Eakin 1996). *Euclidaris galapagensis* in reef flats of Floreana Islands and Galapagos Islands is known to contribute to reef erosion of 3.320 kg CaCO$_3$ m$^{-2}$ a$^{-1}$ and 22.332 kg CaCO$_3$ m$^{-2}$ a$^{-1}$ with population densities of 4.6 individuals m$^{-2}$ and 30.8 individuals m$^{-2}$ respectively (Glynn 1988).

High densities of small urchins can have a larger bio-erosion impact than low densities of larger individuals (Griffin et al. 2003). *C. tenuispinus* had a mean density ranging from 3.20 ± 0.23 m$^{-2}$ to 3.73 ± 0.33 m$^{-2}$ throughout the year. Annual bio-erosion caused by a density of 3.2-3.7 m$^{-2}$ *C. tenuispinus* was 1.017 kg CaCO$_3$ m$^{-2}$ a$^{-1}$.

Most previously conducted studies on bio-erosion focused on tropical urchins; mainly *Diadema*, *Echinometra* and *Echinothrix* species, and these species are considered to be the most impacting bio-eroding agents in tropical reefs (Bak 1990; Mokady et al. 1996). Environmental conditions, specifically water temperature, impact the urchins’ physiology, directly influencing ingestion and gut evacuation rates. Since there were no significant differences in dry gut-weight across the seasons sampled in this study, differences in ingestion rate are critical for determining the rate of bio-erosion. Significant differences in seasonal ingestion rates are mainly in response to the changes in seawater temperatures, from 17°C in winter to 22°C in summer. The gut evacuation rate was highest in summer and lowest in winter. Calculations based on mean seawater temperatures in autumn and spring indicated gut evacuation rates were 0.70 day$^{-1}$ and 0.48 day$^{-1}$. Food ingestion rates were higher in summer due to increased metabolism at higher temperatures; thus the erosion rates were higher as well. *Centrostephanus tenuispinus* in the current study were subjected to lower water
temperatures (17°C) in winter than in summer (23°C). A difference of 6°C directly impacted on physiology and activity levels, and therefore changes in ingestion rates between winter and summer. The highest ingestion rate recorded in this study was 5.02 ± 1.33 gut dry weight individual\(^{-1}\) day\(^{-1}\) in summer 2016, which is higher than *Diadema savygni* from tropical waters with a mean ingestion rate of 3.11 ± 0.70 g gut dry weight individual\(^{-1}\) day\(^{-1}\) (Carreiro-Silva and McClanahan 2001). At the same time *D. setosum* has shown an ingestion rate of 8.36 ± 1.16 g day\(^{-1}\) (Carreiro-Silva and McClanahan 2001). Most urchin species in the tropics experience water temperatures over 25°C all round year, and therefore have consistently high ingestion rates. Since the rate of bio-erosion is based on food ingestion rates, any factor affecting food intake indirectly affects the bio-erosion rate as well. The influence of water temperature on feeding has been recorded for other diadematoids as well (Coppard and Campbell 2005).

Bio-erosion calculations for both summers (2015 /2016) in this study were based on a gut evacuation rate of 0.72 day\(^{-1}\). Mean seawater temperature was lower in summer 2015 (22.5°C) than in summer 2016 (23.5°C). The percentage of calcium carbonate in the guts of urchins was lower in summer 2015 than in summer 2016. The significant difference in CaCO\(_3\) ingestion rates (and hence bio-erosion) between summers may be attributed to temperature differences.

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

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

The gut evacuation rate for *Centrostephanus tenuispinus* in this study is nearly 100 h in winter, which is longer than other sea urchin species, reducing to 33.3 h in summer. Carreiro-and
McClanahan (2001) reported that the common tropical diadematoids Diadema setosum, D. savygni and Echinothrix diadema take 20.29, 26.86 and 21.10 h respectively to empty their guts. Echinometra mathaei takes 13.94 h to empty all gut contents (Carreiro-Silva and McClanahan 2001). The slower body physiology recorded for C. tenuispinus in this study may be associated with low winter temperatures.

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

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

This study only examined bio-erosion due to grazing; bio-erosion from spine abrasion has not been accounted for in this study. Similarly, bio-erosion caused by other herbivores has not been accounted for since C. tenuispinus is the main bio-eroder in this system. The difference in food...
ingestion rates in response to seawater temperature changes is the main cause for the significant
differences in seasonal bio-erosion rates on Hall Bank reef and the high rates of bio-erosion likely
contribute to the absence of macroalgae and the maintenance of high coral cover on Hall Bank.

Compliance with Ethical Standards
None of the authors does have any conflict of interests associated with this publication, and there has
been no significant financial support for this work that could have influenced its outcome. All
applicable international, national and/or institutional guidelines for sampling, care and experimental
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this study because experimental work was conducted with an unregulated invertebrate species.

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

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Figure 1. Map showing location of the Hall Bank reef in Western Australia.
Figure 2. Seasonal mean proportions of inorganic (mean ± SD) and organic (mean ± SD) dry gut components in sampled *C. tenuispinus* population (n = 364).
Figure 3. Composition of *C. tenuispinus* mean dry gut components in sampled population (n=364) and caged population (n=30).
Figure 4. Gut evacuation of *C. tenuispinus* over 96 h in winter (n = 50) 2015 and summer 2016 (n = 50), Exponential curve fitted by least regression on the natural logarithms of dry gut weight with time.
Table 1. Mean density, mean test diameter, mean gut weight, gut turnover rate and food ingestion rate of *C. tenuispinus* (mean ± 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±0.23                                      | 67.70±5.95              | 6.48±1.33           | 0.72                            | 4.67±0.96                                                    |
| Autumn 2015  | 3.45±0.29                                      | 67.79±2.94              | 6.54±1.37           | 0.70                            | 4.58±0.96                                                    |
| Winter 2015  | 3.65±0.30                                      | 68.61±6.47              | 6.75±1.63           | 0.24                            | 1.62±0.39                                                    |
| Spring 2015  | 3.73±0.33                                      | 67.46±5.75              | 7.31±2.02           | 0.48                            | 3.51±0.97                                                    |
| Summer 2016  | 3.20±0.23                                      | 68.06±5.37              | 6.98±1.95           | 0.72                            | 5.02±1.33                                                    |
Table 2. Herbivory rate, CaCO$_3$ ingestion rate, percentage newly eroded CaCO$_3$ and bio-erosion rate 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                                               |
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                                 |                                                  |
Table 4. Test diameter, mean dry gut weight, food ingestion rates, gut turnover rates, daily bio-erosion rates of sea urchins *Diadema setosum*, *D. savignyi*, *Echinothrix diadema* and *C. tenuispinus* (mean ± SD).

| Species | *Diadema setosum* Carreiro-Silva and McClanahan (2001) | *Diadema savignyi* Carreiro-Silva and McClanahan (2001) | *Echinothrix diadema* Carreiro-Silva and McClanahan (2001) | *Centrostephanus tenuispinus* (This study/summer) |
|---------|-------------------------------------------------|-------------------------------------------------|-------------------------------------------------|-----------------------------------------------|
| Test diameter (mm) | 67.74 ±0.88 | 69.86±0.98 | 103.96±1.02 | 69.06±0.61 |
| Mean gut weight (g) | 7.05±0.98 | 3.48±0.78 | 18.54±3.10 | 6.98±0.21 |
| Food ingestion rate (g dry weight individual⁻¹ day⁻¹) | 8.34±1.16 | 3.11±0.70 | 21.09±3.52 | 5.02±0.15 |
| Gut turnover rate (day⁻¹) | 1.18 | 0.89 | 1.14 | 0.72 |
| Bio-erosion rate (g CaCO₃ individual⁻¹ day⁻¹) | 1.79±0.25 | 0.72±0.16 | 5.49±0.91 | 1.10±0.04 |