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

Short Title:

Functional links on coral reefs

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Abstract

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

Keywords:
Bioerosion, Ecosystem Processes, Echinoderm, Fish, Great Barrier Reef, Marine Ecology, Predation, Triggerfish, Trophic Cascade

1. Introduction

The persistence of ecosystems in particular states is underpinned by the ecosystem processes operating therein (Done et al., 1996). The ecosystem processes are, in turn, dependent on the organisms present (Steneck, 2013; Walker et al., 1981). Some organisms can contribute disproportionately to particular processes due to a high abundance, limited functional redundancy or a high degree of ecological specialization (Bellwood et al., 2003; McWilliam et al., 2018; Mouillot et al., 2014). The latter aspect is particularly clear in keystone species; those species whose effect on an ecosystem is disproportionately large relative to their abundance (Paine, 1969; Power et al., 1996). However, while organisms can be keystone species in certain locations this may not apply in all systems in which they are present. While similar ecosystems often share a similar suit of processes,
there can be substantial variability in the species, or organisms which contribute to these processes
across biogeographic realms (Hemingson and Bellwood, 2018; McWilliam et al., 2018; Mouillot et al., 2014). Understanding the importance of particular organisms in ecosystem processes among biogeographic realms is essential if we are to understand how different ecosystems will respond to disturbances.

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

Sea urchins have been a key structuring force in shallow water marine ecosystems since the lower Jurassic, when major functional transformations allowed them to bite deeply into calcium carbonate substrata (Steneck, 2013; Steneck et al., 2017). Indeed, sea urchins were the first deep-grazing marine herbivores, with this ability only surpassed by parrotfishes during the Miocene (Cowman et al., 2009; Steneck et al., 2017). On modern day coral reefs, urchins are often the main agents of herbivory and bioerosion. This is particularly marked where overfishing is believed to have released them from top-down predation pressure (Bak, 1994; Carreiro-Silva and McClanahan, 2001; Hay, 1984; but see Cramer et al., 2018; Jackson, 1997). In these systems, urchins can be a major
determinant of benthic state and reef development. In a negative way, urchins have the capacity to destroy reefs when bioerosion rates exceed reef accretion rates as urchins can directly erode into the reef matrix, undercut corals, and hinder coral recruit survival (Bellwood et al., 2004; Glynn and Manzello, 2015; Leary et al., 2013; Qiu et al., 2014). On Eastern Tropical Pacific reefs, for example, high urchin abundances have caused significant bioerosion of the reef framework (Glynn, 1988). However, where herbivorous fishes have been removed by fishing, urchins can provide a functional replacement with rates of herbivory high enough to resist transitions to algal-dominated states (Hughes, 1994; Steneck, 2013). For example, in the Caribbean the widespread mortality of Diadema antillarum revealed the importance of urchins in preventing a transition towards reefs dominated by macroalgae, particularly in areas prone to overfishing of herbivorous fishes (Hughes, 1994; Jackson et al., 2014; Lessios, 2016). Evidently sea urchins can play a major role in marine systems around the globe.

Much of our understanding, however, of the ecosystem function of urchins comes from disturbed systems which have been heavily overfished, including East Africa (Carreiro-Silva and McClanahan, 2001; McClanahan et al., 1994), French Polynesia (Bak, 1990; Done et al., 1991; Peyrot-Clausade et al., 2000), and parts of Asia (Dumont et al., 2013; Goh and Lim, 2015). It has been hypothesised that overfishing released urchins from predation, in turn increasing their relative contribution to ecosystem processes such as grazing and bioerosion (McClanahan and Shafir, 1990; Steneck, 2013). Of all sea urchin predators, the triggerfishes (Balistidae) are considered to be the primary predators; a keystone predator. Triggerfishes are particularly well equipped with powerful mouth structures to prey on hard-shelled benthic invertebrates (Turingan and Wainwright, 1993). They prey on a wide range of urchins and other echinoderms (Hiatt and Strasburg, 1960; Mcclanahan, 2000; Randall et al., 1996; Young and Bellwood, 2012), including the mechanically and chemically defended crown of thorns starfish (CoTS) (Cowan et al., 2017). Indeed, predation experiments suggested that in East Africa Balistapus undulatus can be responsible for up to 100% of urchin predation (Mcclanahan, 2000). On the GBR a similar experiment demonstrated that Balistoides viridescens and B. undulatus together accounted for over 90% of predation with little to no
contribution from other nominal echinoderm predators such as large labrids and lethrinids (Young and Bellwood, 2012). However, the paradigm on coral reefs, that urchins are controlled from the top-down by their fish predators, has largely been based on evidence from heavily exploited, degraded, systems comparing areas exposed to, and protected from, fishing.

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

Across the GBR distinct gradients in faunal assemblages exist, with a general increase in abundance and diversity further from shore (Cheal et al., 2012; Emslie et al., 2017; Wismer et al., 2009). These ecological gradients follow distinct gradients in abiotic conditions such as hydrodynamic exposure gradients (Bellwood and Wainwright, 2001; Crossman et al., 2001; Fulton et al., 2013) and terrestrial influences on sediment loads and water quality (Fabricius et al., 2014; Tebbett et al., 2017). How sea urchin and triggerfish distributions conform to these previous patterns is unclear. The aim of this study, therefore, was to examine the pattern of urchin and triggerfish distributions across the GBR. Presumably, if a functional linkage exists between urchins and their triggerfish predators, through top-down predation pressure, one would expect their distributions to be negatively correlated. However, this relationship may not hold if other biotic or abiotic factors
underpin distribution patterns. Furthermore, this study will look beyond potential links in distribution patterns by considering the role that sea urchins play in a key ecosystem process, bioerosion, by comparing and contrasting bioerosion patterns with other key bioeroders.

2. Materials and methods

2.1 Study sites

Two GBR regions were surveyed in 2004/5: the northern region at approximately 14° 40′ S and the central region at approximately 18° 47′ S (Fig. 1). In each region two reefs were surveyed in each of the three cross shelf locations (inner-, mid- and outer-shelf). In the northern region two islands in the Turtle group (inner-shelf), MacGillivray Reef and Lizard Island (mid-shelf), and Hicks Reef and Day Reef (outer-shelf) were surveyed. In the central region Pandora Reef and Havannah Island (inner-shelf), Wheeler Reef and Davies Reef (mid-shelf), and Dip and Bowl Reef (outer-shelf) were surveyed. A full site description outlining the nature and state of each site, including dominant benthic cover, is given in Wismer et al., (2009). At each reef, three to four habitats were surveyed. The back reef, flat, crest and slope habitats were surveyed on each of the mid- and outer-shelf reefs. However, as there are no clearly defined crests on inner-shelf reefs the entire seaward slope was surveyed as the crest/slope. Definitions of each habitat can be found in Bellwood and Wainwright, (2001).
Fig. 1 a The Great Barrier Reef (GBR), Australia showing the two regions surveyed. The cross-shelf census sites in the b northern and c central regions of the GBR. d an *Echinostrephus* sp. urchin and e the picasso triggerfish, *Rhinecanthus aculeatus* both photographed at Lizard Island in the northern GBR.

2.2 Urchin abundance

To quantify sea urchin abundance 12 replicate 10 × 2 m transects were surveyed in each habitat on each reef (*n* = 528). Transects were haphazardly placed, and laid parallel to the reef crest.
Each transect was systematically searched for urchins paying particular attention to examine overhangs and crevices. Urchin abundance and test size (to the nearest 5 mm) was recorded. Urchins were identified to genus and species where possible.

2.3 Contribution of urchins to bioerosion

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

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

2.4 Triggerfish abundance and biomass

Triggerfish communities were quantified at the same time and in the same areas as the urchin surveys. Fish were counted on 10-minute timed belt transects equating to approximately 117 m (methods and calibrations following Bellwood and Wainwright, 2001). This census method would have effectively quantified triggerfish densities because triggerfishes are generally site attached (Chen et al., 2001) and have previously been quantified successfully on smaller transects than those used herein (Bean et al., 2002). All fish were identified to species and placed into total length (TL) size
classes (for fishes >10 cm size classes with 5 cm intervals were used, while for fishes <10 cm size classes with 2.5 cm intervals were used), and biomass calculated using Bayesian length-weight regression parameters (Froese and Pauly, 2018) (see ESM Table S1 for species recorded).

2.5 Analysis

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

We also examined the relationship between mean sea urchin abundance (ind. 100 m\(^{-2}\)) and mean triggerfish biomass (g 100 m\(^{2}\)). Urchin abundance data was used because this is the most commonly reported metric when quantifying urchins (e.g. Table 1), and diameter-weight relationships for urchins from the GBR are not readily available. By contrast, triggerfish biomass estimates were utilised because this is a more functionally relevant metric of potential triggerfish predation compared to abundance data, which overemphasises the importance of the more abundant, smaller triggerfish size classes, that are less likely to be key urchin predators (e.g. Young and Bellwood, 2012).

Triggerfish biomass was considered as a predictor variable in two ways: a) the biomass of all triggerfish species known to feed on sea urchins (all urchin predators), and b) only large keystone triggerfish predators (see ESM Table S1 for full details). Mean triggerfish biomass and urchin abundances were compared within each habitat at each reef (\(n = 44\)). Initially we visualised the relationship between urchin abundance and triggerfish biomass, then considering each potential factor (region, shelf, habitat, reef). These factors were considered because there can be substantial variability in abiotic and biotic processes that influence urchin distributions, such as predation rates, terrestrial...
influences, and productivity among regions (latitudinal differences; (Sheppard-Brennand et al., 2017)), shelf positions (Fabricius et al., 2014), habitats (Bellwood et al., 2018) and individual reefs (Browne et al., 2013). Following visual examination, triggerfish biomass (continuous) and shelf position (categorical) were treated as fixed effects in subsequent models comparing the two taxa. Both Gamma distributed generalised linear models (GLM) and lognormal linear models were examined, however, for both urchin predators and keystone triggerfish biomass, the lognormal model was deemed to produce the superior fit based on residual plots. When examining residual plots non-linear relationships were also considered. Statistical modelling was performed in the software R (R Core Team, 2017) using the lme4 (Bates et al., 2015), nlme (Pinheiro et al., 2017), glmmTMB (Brooks et al., 2017) and the AICcmodavg (Mazerolle, 2017) packages. Due to the nature of the urchin data no formal analysis was conducted on urchin abundance or bioerosion (see below).

3. Results

3.1 Sea urchins

Of the 528 transects, 88.3% had no sea urchins visible with average abundances ranging from 0 – 0.5 m² (Fig. 2). A total of 462 sea urchins were recorded across all transects and of these 93.1% were on the two mid-shelf reefs in the northern GBR, with the diminutive Echinostrephus sp. accounting for 98.1% of total urchin abundance on these reefs (Fig. 2a, b). There were only 10 urchins recorded across all transects in the central region (Fig. 2b).
The abundance of sea urchins across the Great Barrier Reef in a the northern and b the central regions (note the difference in scales on the y-axis). B = back reef, F = Flat, S/C = combined slope crest habitat, S = Slope, C= Crest

3.2 Bioerosion patterns

The low urchin abundances in turn meant that urchin bioerosion rates were very low across the GBR (0 – 0.01 kg m$^{-2}$ year$^{-1}$; Fig. 3a). Even where urchin bioerosion rates were highest (on northern mid-shelf back reef habitats [Fig. 3a]) they only accounted for 0.2% of total external bioerosion (0.01 kg m$^{-2}$ year$^{-1}$ urchin erosion compared to 5.5 kg m$^{-2}$ year$^{-1}$ by parrotfishes) (Figs 3a, b). In all locations, parrotfishes accounted for over 99% of external bioerosion with total values
increasing in an offshore direction; urchin bioerosion peaked on mid-shelf reefs. In terms of total bioerosion (parrotfishes, urchins and borers) parrotfishes accounted for 61 - 93%. Urchins accounted for just 0 - 0.2% (0 – 0.01 kg m\(^{-2}\) year\(^{-1}\)). Both microborers and macroborers also contributed far more to bioerosion than sea urchins (0.13 - 0.4 kg m\(^{-2}\) year\(^{-1}\), [4 – 30%] and 0.1 – 0.3 kg m\(^{-2}\) year\(^{-1}\), [2 – 9%] respectively) (Fig. 3).
Fig. 3 Bioerosion rates by a urchins, b parrotfishes and c boring organism across the northern Great Barrier Reef. B = back reef, F = Flat, S/C = combined slope crest habitat, S = Slope, C= Crest. Data on parrotfish erosion from Hoey and Bellwood (2008); borer erosion from Tribollet and Golubic (2005) available from back reef habitats only. Note the difference in scales: parrotfish bioerosion is orders of magnitude higher than the invertebrates.
3.3 Triggerfishes

In general the abundance and biomass of triggerfishes increased across the shelf and was far higher in the northern region compared to the central region (Fig. 4). Based on the GLMM the AIC suggested that the interaction between region and shelf position played an influential role in the abundance patterns of triggerfishes (ESM Table S2), however, this was not significant in the final model (ESM Table S3). The biomass of triggerfishes was significantly higher on outer-shelf reefs compared to inner-shelf reefs (LME; \( p < 0.001 \); ESM Table S3), and in the northern region compared to the central region (LME; \( p < 0.001 \); ESM Table S3). The only significant differences in triggerfish biomass among habitats occurred between back reef and slope habitats (LME; \( p < 0.01 \); ESM Table S3).
Fig. 4 The a abundance and b biomass of all triggerfishes observed across the Great Barrier Reef. B = back reef, F = Flat, S/C = combined slope crest habitat, S = Slope, C = Crest.

3.4 Interrelationship between urchins and triggerfishes

On first inspection, there is a distinct relationship between urchin abundance and the biomass of both all triggerfishes and keystone triggerfishes, with high variability of urchins at low triggerfish biomass, and limited urchins where triggerfishes occurred (Fig. 5). Indeed, urchin abundances varied by up to 80%, and triggerfish biomass varied by nearly 900% (Fig. 5). However, there was a marked spatial component to this relationship. If the role of shelf position is considered, all urchin variability is largely constrained to the mid-shelf, while triggerfish biomass primarily varies on the outer-shelf (Fig. 5). As such, the factor shelf position is significant in both the models (ESM Table S4), while
triggerfish biomass was not significantly related to urchin abundances in either model (ESM Table S4). Nor was there a non-linear relationship. We therefore found no evidence of any significant correlation between urchin abundances and the biomass of triggerfishes, the key urchin predators on the GBR.

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

### 4. Discussion

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

<table>
<thead>
<tr>
<th>Location</th>
<th>Urchin</th>
<th>Density (ind. m$^{-2}$)</th>
<th>Bioerosion (kg m$^{-2}$ year$^{-1}$)</th>
<th>Study</th>
</tr>
</thead>
<tbody>
<tr>
<td>Panama</td>
<td><em>Diadema mexicanum</em> &amp; <em>Toxopneustes roseus</em></td>
<td>0.1 - 150</td>
<td>0.0073 – 10.4</td>
<td>Glynn, 1988</td>
</tr>
<tr>
<td>La Rèunion (West Indian Ocean)</td>
<td>Total</td>
<td>3.8 – 73.6</td>
<td>0.4 – 8.3</td>
<td>Peyrot-Clausade et al., 2000</td>
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<td>Puerto Rico</td>
<td><em>Echinometra viridis</em></td>
<td>0.8 - 62</td>
<td>0.11 - 4.14</td>
<td>Griffin et al., 2003</td>
</tr>
<tr>
<td>Belize</td>
<td>Total</td>
<td>0.8 - 40</td>
<td>0.2 – 2.7</td>
<td>Brown-Saracino et al., 2007</td>
</tr>
<tr>
<td>Galapagos Islands</td>
<td><em>Eucidaris thouarsii</em></td>
<td>1.1 – 32.7</td>
<td>0.8 – 23.65</td>
<td>Glynn, 1988</td>
</tr>
<tr>
<td>Zanzibar</td>
<td>Total</td>
<td>0 – 20.28</td>
<td>0 – 6.91</td>
<td>Bronstein and Loya, 2014</td>
</tr>
<tr>
<td>United Arab Emirates</td>
<td><em>Echinometra mathaei</em></td>
<td>0 - 14</td>
<td>-</td>
<td>Bauman et al., 2016</td>
</tr>
<tr>
<td>New Caledonia</td>
<td>Total</td>
<td>0 - 13</td>
<td>-</td>
<td>Dumas et al., 2007</td>
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<tr>
<td>Moorea</td>
<td>Total</td>
<td>7.12 – 10.10</td>
<td>0.6 – 7.5</td>
<td>Peyrot-Clausade et al., 2000</td>
</tr>
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<td>Mexico (East Pacific)</td>
<td><em>Diadema mexicanum</em></td>
<td>1 - 6.8</td>
<td>0.17 - 3.28</td>
<td>Herrera-Escalante et al., 2005</td>
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</tr>
<tr>
<td></td>
<td>Total</td>
<td>0.06 – 6.2</td>
<td>0.05 – 1.18</td>
<td>Carreiro-Silva and McClanahan, 2001</td>
</tr>
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<td>Kenya</td>
<td>Total</td>
<td>0.08 – 5.02</td>
<td>-</td>
<td>McClanahan et al., 1999</td>
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<tr>
<td>Tanzania</td>
<td>Total</td>
<td>0.5 – 4.4</td>
<td>0.12 – 0.66</td>
<td>Dumont et al., 2013</td>
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<td>Hong Kong</td>
<td><em>Diadema setosum</em></td>
<td>0 - 4</td>
<td>-</td>
<td>Goh and Lim, 2015</td>
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<td>-</td>
<td>Johansson et al., 2013</td>
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<td>Western Australia (Ningaloo Reef)</td>
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<td>0.0 – 0.5</td>
<td>0 – 0.01</td>
<td>Present study</td>
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<td>Great Barrier Reef</td>
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<td>0.28, 100 m²</td>
<td>0.06 – 0.28, 100 m²</td>
<td>Carreiro-Silva and McClanahan, 2001</td>
</tr>
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</table>

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

The strongest evidence for a relationship between triggerfishes and urchins was established on the coral reefs along the East coast of Africa (McClanahan, 2000; McClanahan et al., 1999; McClanahan and Muthiga, 2016; McClanahan and Shafir, 1990). These studies related variation in triggerfish biomass/density and predation pressure, inside and outside marine reserves, to urchin densities (McClanahan et al., 1999; McClanahan and Muthiga, 2016; McClanahan and Shafir, 1990). They also linked a decline in urchins to the recovery of *B. undulatus* inside marine reserves (McClanahan, 2000). Interestingly, triggerfish densities on the GBR mirrored those in East Africa. Where the abundance of triggerfishes was highest on the GBR (northern mid- and outer-shelf reefs), triggerfish densities (0.09 - 1.04, 100 m²) were comparable to areas protected from fishing in Kenya (0.33 – 0.92, 100 m²) (McClanahan and Shafir, 1990) and Tanzania (0.16 - 1.02, 100 m²) (McClanahan et al., 1999). While, triggerfish densities on GBR northern inner-shelf reefs (0.06 – 0.28, 100 m²) and across the entire central region (0 – 0.28, 100 m²) were comparable to fished areas in Kenya (0.04 – 0.12, 100 m²) (McClanahan and Shafir, 1990) and Tanzania (0 – 0.06, 100 m²) (McClanahan et al., 1999). Yet, despite this similarity, we did not detect any significant correlation between triggerfishes and urchins.
Ningaloo Reef, in Western Australia, provides another example of a coral reef system in which the relationship between urchins and triggerfishes has been examined. Here, moderate-high densities of the sea urchin *E. mathaei* exist, despite intact communities of nominal urchin predators, with no evidence that predation-controls urchin populations (Johansson et al., 2013). Johansson et al. (2013) hypothesised that because the predator assemblage was composed chiefly of large labrids (the large triggerfishes considered to be keystone urchin predators were conspicuously absent or rare) this may have allowed for the higher densities of *E. mathaei*. Interestingly, a similar situation existed in our GBR dataset, with few triggerfishes recorded from the central region despite surveying approximately 5 hectares of reef. Unlike on Ningaloo Reef, however, these reefs also had the lowest abundances of sea urchins with only 10 specimens recorded on surveys. Clearly, the urchin–triggerfish paradigm does not hold in all locations.

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

Previously, urchin abundances have been negatively correlated with higher loads of fine sediments...
and it has been suggested that long sediment-laden algal turfs hinder urchin recruitment (Lessios, 2016). Perhaps high sediment loads, rather than predation, are the main driver of urchin settlement dynamics on inner-shelf reefs.

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

The diurnal survey techniques used may also have resulted in urchins being undercounted resulting in no clear relationship between triggerfishes and urchins. Two studies on the GBR have found that urchins are predominantly nocturnal, presumably to avoid high predation rates during the day (Sammarco, 1985; Young and Bellwood, 2011). Indeed, the urchin counts in the present study were dominated by *Echinostrephus* sp. which are readily visible during the day in their burrows. However, while urchin abundances may be conservative estimates, the maximum mean nocturnal urchin density recorded by the two previous studies was just 1.06 m$^{-2}$, which is still far lower than other coral reef regions (Table 1). Due to the largescale nature of the surveys in the present study it would make nocturnal counts logistically challenging and as most sea urchin counts are performed during the day, our diurnal counts are directly comparable with previous studies. Furthermore, localised high-densities of diurnally-active *Diadema* sp. have been observed on the GBR such as in the lagoon at Brampton Island (20°48′2.3292″S, 149°16′46.9518″ E) (pers. obs. SBT, DRB; Fig. S1)
and on the back reefs of Magnetic Island (19°9′38.2962″S, 146°51′28.152″ E) (pers. obs. SBT, DRB).

As such, if urchins were present and free from predation they would be easily detected during diurnal surveys. Why densities of urchins in general are so low is currently unclear, but it is likely to result from a complex interaction between bottom-up and top-down factors.

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

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

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

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