

Environmental factors and predator abundance predict the distribution and occurrence of two sympatric urchin species at Ningaloo Reef, Western Australia

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Abstract. Sea urchins can play a critical ecological role in the functioning of marine benthic ecosystems, mediating competitive interactions between corals and algae. Yet, little is known about factors affecting urchin distribution in intact coral reef systems. This study aims to determine the spatial distribution of two sympatric urchin species, *Echinometra mathaei* and *Echinostrephus molaris*, and potential factors contributing to this, within the intact coral reef system of Ningaloo Marine Park, north-western Western Australia. Benthic photographs and surveys were conducted on SCUBA at 126 sites across the Park to determine urchin presence, rugosity, substrate cover, water velocity, and fish predation for each site. Generalised additive models found that *E. mathaei* presence was positively related to algal cover, rugosity and non-sanctuary zones, suggesting that distribution may be driven by foraging behaviour, habitat complexity and predation. *Echinostrephus molaris* presence was positively related to habitat and region, suggesting its distribution may be largely driven by hydrodynamics, feeding strategy and regional variation. This study highlighted species-habitat associations and the complexities of these in structuring urchin communities. Although occupying similar niches, the predominantly non-overlapping feeding preferences, and morphological and behavioural differences between *E. mathaei* and *E. molaris* enable these species to coexist within the intact reef system of Ningaloo Marine Park.

Keywords: sea urchins, distribution, *Echinometra mathaei*, *Echinostrephus molaris*, predation, management zones.

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Introduction

Sea urchins (Class Echinoidea) can play a critical role in the functioning of marine benthic ecosystems (Done *et al.* 1996; Peyrot-Clausade *et al.* 2000; Scheffer *et al.* 2001; Harborne *et al.* 2009). Within temperate reefs, high urchin densities have been responsible for the removal of vast stands of macroalgae (e.g. Lawrence 1975; Lawrence and Sammarco 1982; see also review by Sala *et al.* 1998), subsequently reducing primary productivity and food web complexity (Filbee-Dexter and Scheibling 2014). On tropical coral reefs, substantial increases in urchin densities have been implicated in driving phase shifts from coral- to algal-dominated environments (e.g. Sammarco 1980; Hughes *et al.* 1987; Lessios 1988; Hughes 1994; Dudgeon *et al.* 2010). In addition to their role in mediating competition between coral and algae (Edmunds and Carpenter 2001), urchins are crucial bioeroders (Scoffin *et al.* 1980; Bak 1990), actively eroding reef and dead coral substrata through their feeding and

boring behaviours (Downing and El Zahr 1987; McClanahan and Kurtis 1991; Done *et al.* 1996).

The relationship between urchin abundance and spatial distribution on coral reefs is complex (e.g. McClanahan and Kurtis 1991; McClanahan 1998; Dumas *et al.* 2007; Burt *et al.* 2010; Graham and Nash 2013). The size, composition and distribution of urchin populations are affected by a diverse set of environmental variables, including structural complexity, coral and macroalgal cover, sedimentation, predation and disease (Lessios 1988; Feehan and Scheibling 2014) across multiple scales (Sánchez-Jérez *et al.* 2001; see review by Dumas *et al.* 2007). Additionally, urchin settlement and recruitment patterns (Watts *et al.* 1990), hydrodynamics (Russo 1977; Ogden *et al.* 1989), behavioural processes (Chabanet *et al.* 1997; Lawrence 2001; Dumas *et al.* 2007), and anthropogenic influences such as fishing (e.g. Hay 1984; McClanahan and Shafir 1990) may also play a role in determining urchin abundance and distribution

across local scales. Of these, predation has been identified as a principal regulatory agent affecting urchin presence and density (e.g. Hughes 1994; Sala and Zabala 1996; Harborne *et al.* 2009; Gil Fernández *et al.* 2016).

Marine protected areas (MPAs) may, therefore, indirectly affect urchin distribution. Marine protected areas are management zones that provide varying levels of protection to species and ecosystems, conserve and maintain marine biodiversity and natural and associated cultural resources, and enhance the productivity of fish and marine invertebrate populations (Hoyt 2018). Research on MPAs has shown that a return to hypothetical former predation levels through the exclusion of fishing practices and subsequent restoration of predatory fish numbers may reduce urchin densities (e.g. McClanahan and Muthiga 1989; McClanahan and Shafir 1990) and minimise the negative effects of unregulated urchin populations (Harborne *et al.* 2009). Conversely, a decrease in the abundance of predatory fish, as a result of fishing, may increase sea urchin abundance (Hughes 1994).

Ningaloo Marine Park provides a model system in which to investigate factors affecting urchin distribution both within and outside of MPAs. Ningaloo Marine Park consists of a complex network of multiple-use zones varying in levels of environmental protection and permitted activities, from general use and recreation zones to the more protected special purpose and no-take sanctuary zones (Department of Biodiversity, Conservation and Attractions 2020). Ningaloo Marine Park is considered an intact coral reef system (e.g. Johansson *et al.* 2010, 2013) and is recognised for its outstanding universal value and significant natural habitats for the conservation of biological diversity (United Nations Educational, Scientific and Cultural Organization 2011). The Ningaloo Marine Park extends along ~300 km of coastline and across three degrees of latitude (Kobryn *et al.* 2013). As such, it is influenced by a broad range of environmental variables, making it an ideal location to investigate urchin distribution.

Nine species of herbivorous urchins commonly inhabit shallow coral reefs of the Indian Ocean (McClanahan 1998). Of these, *Echinometra mathaei* and *Echinostrephus molaris* are widely distributed within the Indo-West Pacific region (Ohgaki *et al.* 2019) and have been identified as common urchin species on the Ningaloo Reef. Both are small-bodied urchins (Cernohorsky *et al.* 2015) and, although considered modest bioeroders compared with other urchin species (Russo 1980; Bak 1990), are important in influencing the structure of the healthy coral reef ecosystem at Ningaloo Reef (Langdon *et al.* 2013). Whereas data on the bioerosion rates of *E. molaris* on the Reef are lacking, *E. mathaei* is considered a significant contributor to this process (Johansson *et al.* 2010; Langdon *et al.* 2013). Furthermore, *E. mathaei* algal grazing studies at Ningaloo Reef have demonstrated the important ecological role this species plays in mediating algal growth and competition (Langdon 2012; Langdon *et al.* 2013).

Although they are identified as sympatric urchin species, *E. molaris* and *E. mathaei* vary in their morphological and behavioural characteristics. *Echinostrephus molaris* is a very small echinometrid, reaching 40-mm test diameter (Campbell *et al.* 1973). It is considered a burrowing urchin, either boring directly into the reef structure or utilising and expanding pre-existing crevices using its spines, large peristome and Aristotle's

lantern (Edmundson 1946; Asgaard and Bromley 2008). Owing to its morphology, it has adapted to a near-complete existence within these. Its test is barrel-shaped, allowing it to rotate within its boring about its oral–aboral axis, and very short ambital spines along each side ensure secure anchorage within and along its boring. It is the only known echinoid genus adapted to 100% suspension feeding, using its long aboral spines to capture drifting algae and suspended particulates (Asgaard and Bromley 2008). By contrast, *E. mathaei* grows slightly larger, up to 50-mm test diameter (McClanahan and Muthiga 1989). It occupies pre-formed crevices and cup-shaped borings (Campbell *et al.* 1973; Clark 1976; Tsuchiya and Nishihira 1984) that it either creates or expands through feeding and spine abrasion (Campbell *et al.* 1973; Russo 1977, 1980; McClanahan 1988). Although being capable of suspension feeding, it is considered to be a grazing echinoid (Khamala 1971; Dart 1972), predominantly scraping the substratum of turf algae (Dart 1972) and augmenting its diet with floating algal particles under stronger hydrodynamic conditions (Campbell *et al.* 1973).

Despite the considerable literature available on urchins and their ecological importance, little is known of the factors affecting the distribution of both *E. mathaei* and *E. molaris* on intact coral reef systems. This study aims to determine the spatial variation and occurrence of two sympatric urchin species, namely *E. mathaei* and *E. molaris*, and the potential factors contributing to this, within the Ningaloo Marine Park. It tests the hypothesis that urchin occurrence is lower within sanctuary zones closed to fishing, owing to increased predation by fish species otherwise targeted by fishers.

Materials and methods

Study site

This study was conducted in the coral reef habitats throughout the Ningaloo Marine Park (Fig. 1), the largest fringing coral reef in Australia. Located along the north-western coast of Western Australia, Ningaloo Marine Park has both State and Commonwealth boundaries and extends latitudes of 21°47'S at Bundeji in the north to 24°00'S at Red Bluff in the south, to the high-water mark. Benthic communities were surveyed during May 2015 and 2016 throughout the northern end of the park on the outer reef slope ($n = 74$; ~8-m depth) and inner reef habitats ($n = 52$; includes bommies ($n = 25$), lagoon ($n = 12$), reef flat ($n = 9$) and inshore ($n = 6$); ~2-m depth). Potential differences in urchin presence among management zones were investigated, with benthic surveys also being conducted within sanctuary (Jurabi, Mangrove and Osprey) and adjacent non-sanctuary zones.

Benthic surveys

Urchin presence was determined by evaluating benthic photographs taken by SCUBA divers along a 25-m transect at each site. Photographs were taken parallel to, and at a height of ~0.3 m from, the substrate, at 0.5-m intervals along the transect. The transect start location was chosen haphazardly within the site and the tape laid out following the depth contour. A subset of 30 randomly selected photographs was used at each site to avoid any autocorrelation issues arising from analysing multiple consecutive images. The area represented by each photograph was estimated using the average length and width of

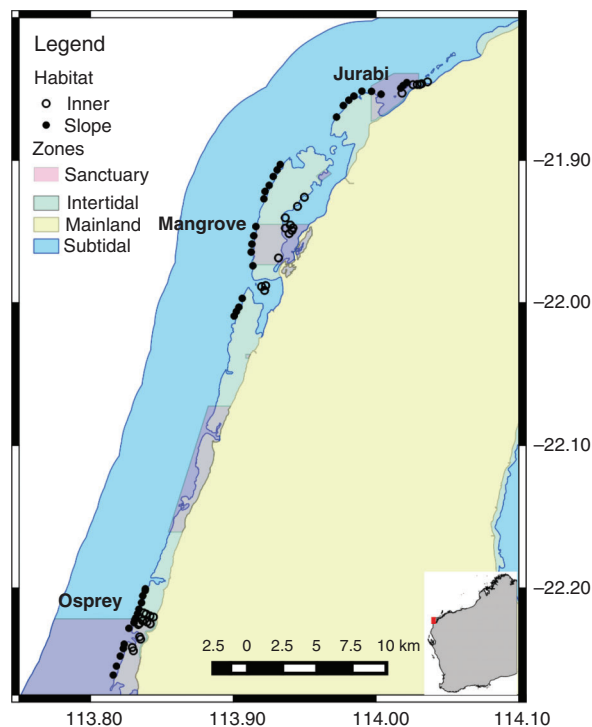


Fig. 1. Location of benthic survey sites throughout the Ningaloo Marine Park, northern Western Australia.

photographs containing sections of transect tape and determined to be $\sim 0.35 \text{ m}^2$ ($0.7 \times 0.5 \text{ m}$). From each site, a total of 30 images, representing an area of 10.5 m^2 per transect, were used to quantify the two most abundant sea urchin species, namely, *Echinometra mathaei* (Blainville, 1825) and *Echinostrephus molaris* (Blainville, 1825). Urchin presence was determined following the positive identification of a representative feature, such as a spine protruding from the burrow. If some part of the urchin was not visible, despite the presence of a characteristic urchin burrow, the presence of that urchin could not be confirmed and was therefore not included.

Structural complexity at each site was estimated using an index of rugosity obtained by laying a 10-m length of chain (chain link $22 \times 12 \text{ mm}$) over the substrate alongside a transect tape. The chain was allowed to extend over coral and within the gaps and grooves of the substrate. The distance the chain extended along the transect tape was recorded, and the index of rugosity determined as 10 m divided by the recorded distance of the chain along the transect tape (modified from Risk 1972). Therefore, a high index of rugosity was associated with structurally complex habitat, whereas low values corresponded with smoother, less complex habitat.

Substrate cover (as a percentage) at each site was determined from 30 benthic photographs randomly selected from a total of 50 images. By using TransectMeasure (SeaGIS, Bacchus Marsh, Australia, see <https://www.seagis.com.au/transect.html>; Abdo *et al.* 2006), six points were overlaid on each image, and the broad cover class (algae, hard coral, soft coral, sponge, seagrass, abiotic, other, indeterminate, or unknown) beneath each point was recorded. Percentage cover of algae (turving and macroalgae)

Table 1. Teleost species identified through the literature as predators of *Echinometra mathaei* and included in the index of predatory fish

Family	Scientific name	Reference
Balistidae	<i>Balistapus undulatus</i>	McClanahan and Shafir 1990
	<i>Pseudobalistes fuscus</i>	Johansson <i>et al.</i> 2013
	<i>Pseudobalistes</i> spp.	McClanahan 1998
	<i>Rhinecanthus aculeatus</i>	McClanahan and Shafir 1990
Labridae	<i>Cheilinus trilobatus</i>	Johansson <i>et al.</i> 2013
	<i>Choerodon cauteroma</i>	McClanahan and Shafir 1990
	<i>Choerodon cyanodus</i>	McClanahan and Shafir 1990
	<i>Choerodon monostigma</i>	McClanahan and Shafir 1990
	<i>Choerodon schoenleinii</i>	McClanahan and Shafir 1990
	<i>Coris aygula</i>	Johansson <i>et al.</i> 2013
Lethrinidae	<i>Lethrinus atkinsoni</i>	Johansson <i>et al.</i> 2013
	<i>Lethrinus laticaudis</i>	McClanahan 1998
	<i>Lethrinus miniatus</i>	McClanahan 1998
	<i>Lethrinus nebulosus</i>	McClanahan 1998
	<i>Lethrinus olivaceus</i>	McClanahan 1998
	<i>Lethrinus</i> spp.	McClanahan 1998
Tetraodontidae	<i>Arothron</i>	Johansson <i>et al.</i> 2013
	<i>caeruleopunctatus</i>	
	<i>Arothron manilensis</i>	Johansson <i>et al.</i> 2013
	<i>Arothron mappa</i>	Johansson <i>et al.</i> 2013
	<i>Arothron meleagris</i>	Johansson <i>et al.</i> 2013
	<i>Arothron reticularis</i>	Johansson <i>et al.</i> 2013
	<i>Arothron</i> spp.	Johansson <i>et al.</i> 2013

was then used as an index of food availability for urchins, whereas percentage hard coral cover was used as an index of competition for space with corals.

Estimates of wave-induced water velocity were derived using 'simulating waves near shore' (SWAN) model predictions (Booij *et al.* 1999). These were based on the mean orbital seafloor velocity at each site on a $30 \times 30\text{-m}$ grid encompassing the study area from 1 January to 31 December 2007.

An index of fish predation on *E. mathaei* was determined using data from underwater visual fish surveys conducted by SCUBA divers along a $100 \times 10\text{-m}$ belt transect at each site. These were conducted concurrently with benthic surveys. Teleost species observed along each transect were identified, quantified and the total length was estimated (Babcock *et al.* 2008). Predatory fish biomass was then determined for each transect by summing the biomass of all observed predators of *E. mathaei* (identified through the literature; see Table 1) that were $\geq 35 \text{ cm}$ in total length. In total, 22 predatory fish species were included in this index (Table 1). Because little is known of predatory fish species of *E. molaris*, no index was determined for this species.

Statistical analysis

A full set of generalised additive models (GAMS) was constructed, fit and compared using the FSSgam R package (R. Fisher, see https://github.com/beckyfisher/FSSgam_package; Fisher *et al.* 2018), so as to evaluate which ecological predictors best explained sea urchin occurrence (response variable). These GAMS were fit using a binomial distribution on the presence or absence of urchins on each transect, with a logit link function. Presence or absence was modelled rather than abundance because the data were highly zero inflated, with zeros

making up nearly 50% of observations at the transect level for both species (52 and 48% for *E. mathaei* and *E. molaris* respectively). Predictor variables included (i) habitat (slope and inner reef habitats, e.g. indicator of shelter, hydrodynamic effects), (ii) region (indicator of spatial distribution), (iii) zone (sanctuary and non-sanctuary, e.g. indicator of predation), (iv) rugosity (index of structural complexity), (v) percentage cover of algae (index of food availability), (vi) percentage cover of hard coral (index of competition for space with corals), and (vii) water velocity (e.g. indicator of food transport, sedimentation), as well as interaction terms. All models with pairs of variables with a Pearson correlation above a covariance cut-off limit of 0.28 were removed, and only models containing up to three predictors were allowed, ensuring that the resulting model fits remained ecologically interpretable (Fisher *et al.* 2018). The resulting 74 models for each species were compared using Akaike information criteria for small sample sizes (AICc), as described in Fisher *et al.* (2018). For brevity, only the top-performing models (within 2AICc) for each urchin species are presented, with plots constructed only for that with the lowest AICc. Complete model results for all models within 2AICc are contained in Table S1 of the Supplementary material.

To account for incidences of high predatory fish abundances, non-parametric statistics (Kruskal–Wallis test) were used to compare predatory fish biomass in sanctuary and non-sanctuary zones. All graphics and statistical analyses were run using R (ver. 4.0.0, R Foundation for Statistical Computing, Vienna, Austria, see <https://www.R-project.org/>).

Results

Generalised additive models of the presence or absence of urchins on transects showed that the predictor variables contained in the model with the lowest AICc value were different for each urchin species. The top-performing model for predicting *E. mathaei* occurrence contained the variables algal cover, management zone and rugosity, whereas only habitat and region were the variables in the top-performing model for *E. molaris* (Table 2). The deviance explained by the top-performing model of *E. molaris* was 0.48, compared with only 0.24 for the top-performing model of *E. mathaei*.

Echinometra mathaei occurrence had a positive relationship with both percentage cover of algae and rugosity (Fig. 2a, c) and were higher in non-sanctuary (2; median individuals per 10.5 m²) than in sanctuary (0; median individuals per 10.5 m²) zones (Fig. 2b). Interestingly, predatory fish biomass was significantly higher in sanctuary (2249; median kilograms per 1000 m²) than in non-sanctuary (698; Kruskal–Wallis $\chi^2 = 5.68$, d.f. = 1, $P = 0.017$) zones (Fig. 3).

By contrast, *E. molaris* occurrence was highest on the outer reef slope (29; median individuals per 10.5 m²), with negligible urchins present in inner reef habitats (0; median individuals per 10 m²) across all regions (Fig. 4). For slope habitats, the most northern sites (Jurabi) contained the highest occurrence of *E. molaris* (29; median individuals per 10.5 m²), whereas the most southern sites (Osprey) contained the lowest (1; median individuals per 10.5 m²; Fig. 4). The interaction between rugosity and region was significant in the third-top model, although this was relatively weak and of lower weight than the model where this interaction is excluded (Table 2).

Discussion

This study highlighted the differing spatial distributions of two urchin species within Ningaloo Marine Park and the potential drivers of variation. Although *E. mathaei* and *E. molaris* are considered sympatric echinoids, the distribution of each species in this study can be associated with different variables. *Echinometra mathaei* occurrence typically increased with percentage algal cover and structural complexity and was lower in protected areas. *Echinostrephus molaris*, in contrast, showed greater presence within reef-slope habitats and northern sites.

Differences in the distribution of species are often related to their ecological niche, defined as the set of environmental conditions within which a species can survive and persist (Hutchinson 1957). Numerous studies have investigated the association among urchin distribution, abundance and habitat (e.g. McClanahan and Kurtis 1991; McClanahan 1998; Dumas *et al.* 2007; Burt *et al.* 2010; Graham and Nash 2013), each highlighting the complexities relating to urchin spatial distribution on coral reefs. Here, we discuss the unique factors that may contribute to the sympatry observed in these two urchin species.

Table 2. All best GAMs for probability of occurrence of *Echinometra mathaei* and *Echinostrephus molaris*

Only models within 2AICc of that with the lowest AICc are shown. Included are difference in AICc (d.AICc = AICc – min AICc), AICc-based model weights (*wi* AICc), explained deviance (Dev.) and the estimated degrees of freedom from the GAM fits (d.f._e)

Model	d.AICc	<i>wi</i> AICc	Dev.	d.f. _e
<i>Echinometra mathaei</i>				
Algae + Rugosity + Zone	0	0.2	0.24	4
Algae + Rugosity × Zone + Zone	0.44	0.16	0.26	5.39
Algae + Zone	1.2	0.11	0.22	3
Algae × Zone + Rugosity + Zone	1.23	0.11	0.26	5.77
Algae × Zone + Rugosity × Zone + Zone	1.52	0.09	0.27	6.49
<i>Echinostrephus molaris</i>				
Habitat × Region	0	0.42	0.48	6
Habitat + Region	1.38	0.21	0.45	4
Habitat + Region + Rugosity × Region	1.68	0.18	0.49	7

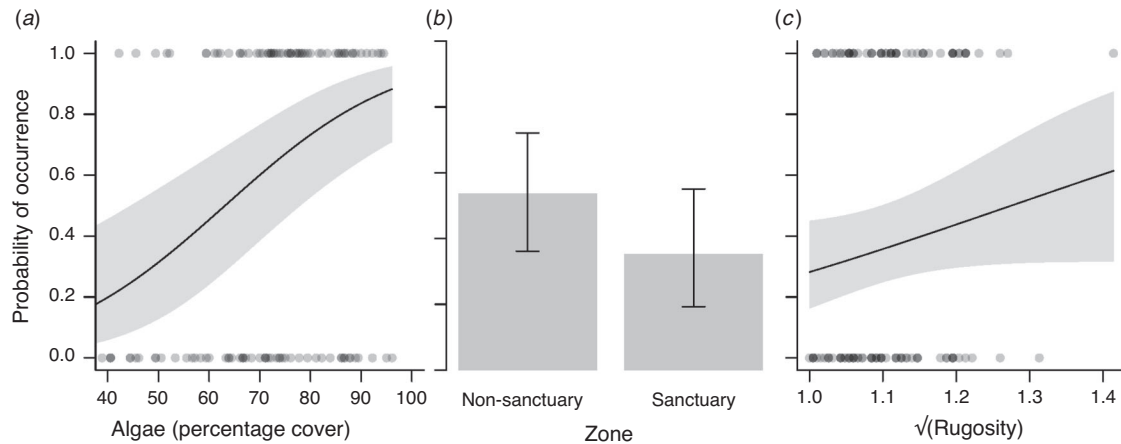


Fig. 2. Probability of *Echinometra mathaei* occurring on transects as a function of (a) percentage algae cover, (b) management zone (sanctuary and non-sanctuary) and (c) rugosity. Round symbols indicate the presence or absence of urchins on each transect, with model predictions (solid lines) and 95% confidence intervals (shaded bands) based on the best-fit GAM model (see Table 2).

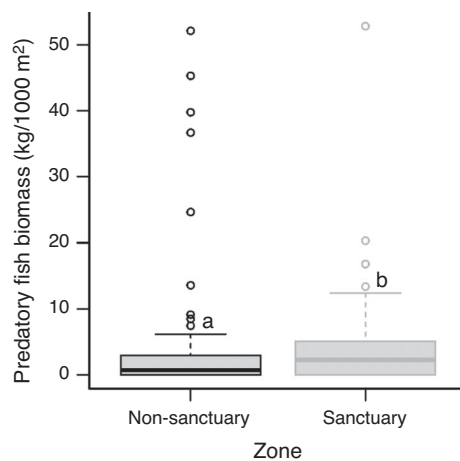


Fig. 3. Distribution of predatory fish biomass by management zone (sanctuary and non-sanctuary). Different letters indicate a significant difference as determined by a Kruskal–Wallis test ($\chi^2 = 5.68$, d.f. = 1, $P = 0.017$).

Echinometra mathaei

Foraging behaviour

On Ningaloo Reef, the presence of *E. mathaei* was positively related to percentage algal cover. *Echinometra mathaei* is considered a grazing echinoid (Khamala 1971; Dart 1972) and systematically scrapes the substratum of turf algae (Dart 1972). Large fractions of calcium carbonate sediments have been identified in the gut contents of *E. mathaei* (Downing and El Zahr 1987; McClanahan and Kurtis 1991), supporting the conclusion that benthic epi- and endolithic algae are the major components of *Echinometra* spp. diet (McClanahan and Muthiga 2013). Furthermore, *Echinometra* spp. allocate energy resources to growth, reproduction and maintenance, depending on food availability (Gadgil and Bossert 1970; Muthiga 1996; Brown-Saracino *et al.* 2007), specifically algae. Observations of

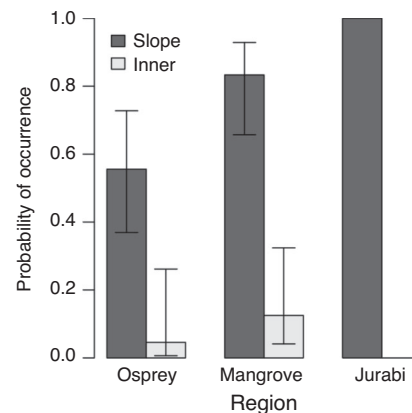


Fig. 4. Probability of *Echinostrephus molaris* occurring on transects within each habitat, and region. Estimates are based on model predictions (bar height) and 95% confidence intervals (error bars).

smaller urchin sizes under low algal-cover conditions (Brown-Saracino *et al.* 2007) and energy-based simulation models (McClanahan 1992, 1995) have highlighted the importance of turf algae as an energy source for *E. mathaei*. Over half of all benthic cover on Ningaloo Reef is composed of macroalgal and turfing algal communities (Kobryn 2018). This high algal cover and subsequent food availability in some areas of the Reef may, therefore, be a significant contributing factor to increased urchin presence.

Marine protected areas and predation

The presence of *E. mathaei* was higher in non-sanctuary areas than within sanctuary zones. Conversely, predatory fish abundance was greater within sanctuary zones, suggesting the role of predation in mediating urchin occurrence. Sanctuary zones and MPAs are created to protect and conserve biodiversity, and marine habitats, along with areas and species of high conservation value (Roberts *et al.* 2005; Edgar *et al.* 2007; Kirkman

2013). Although responses to protection are highly variable among fish taxa (Côté *et al.* 2001), MPAs have been shown to effectively increase abundance and biomass of larger fish species vulnerable to fishing practices (e.g. Russ 1985, 2002; García-Rubies and Zabala 1990; Harmelin *et al.* 1995; Letourneur 1996; Rakitin and Kramer 1996; Côté *et al.* 2001). This was observed at Ningaloo Reef, with predatory fish biomass being significantly higher in sanctuary than in non-sanctuary zones.

Yet, the increased presence of *E. mathaei* outside of sanctuary areas compared with that within sanctuary zones, adds support to suggestions that non-target species may respond negatively to protection, which has been attributed to greater predator pressure within sanctuary areas (Letourneur 1996; McClanahan *et al.* 1999).

Ningaloo Reef is a hotspot for recreational fishing, with the unusually narrow continental shelf and proximity to land making the oceanic waters, reef and coastal communities highly accessible to fishers. Of the >500 species of fish that inhabit the reef and deeper offshore waters (Department of Biodiversity, Conservation and Attractions 2019), many, including balistids, labrids and lethinids, are identified as predatory species of urchins (McClanahan and Shafir 1990; McClanahan 1998; Johansson *et al.* 2013), with numerous species of the latter two families being targeted by recreational fishers (Ryan *et al.* 2017). Whereas conflicting reports of urchin abundances within MPAs at Ningaloo Reef exist (e.g. Westera 2003; Webster 2008; Langdon 2012), recreational line fishing alone may be sufficient to alter the composition of targeted fish (Westera *et al.* 2003) and, subsequently, urchin populations.

Marine protected areas that provide refuge for species of urchin predators have shown lower urchin densities than have reefs with depauperate predator populations (McClanahan and Muthiga 1989; McClanahan and Kurtis 1991; Hughes 1994; Sala and Zabala 1996; McClanahan *et al.* 1999; Carreiro-Silva and McClanahan 2001; Harborne *et al.* 2009; Bronstein and Loya 2014; Gil Fernández *et al.* 2016). Additionally, the size and biomass of predatory species within MPAs may also adversely affect urchin abundances (Gil Fernández *et al.* 2016). Larger-bodied fish are able to predate more successfully on urchins than are smaller individuals (Harborne *et al.* 2009; Johansson *et al.* 2013). Thus, a greater abundance of larger predatory fish may act as a regulatory agent affecting urchin presence, and account for lower urchin densities (McClanahan and Kurtis 1991; Westera *et al.* 2003), within sanctuary zones of Ningaloo Marine Park.

Habitat complexity

At Ningaloo Reef, *E. mathaei* presence was greater in areas of increased rugosity. Structural complexity and coral cover have been recognised as important factors influencing epifaunal mobile invertebrate communities, including urchin populations (Ogden 1976; Weil *et al.* 2005; Lee 2006; Dumas *et al.* 2007; Clemente and Hernández 2008; Labbé-Bellas *et al.* 2016). Additionally, small-scale habitat heterogeneity (e.g. crevices, pits, cracks) has been implicated in urchin recruitment and retention, morphology and behaviour (Hereu *et al.* 2005; Hernández and Russell 2010; Clemente *et al.* 2013). This is indicative of the importance of reef structure because of the services provided, including refuge from

predation, shelter and food resources (Ogden 1976; McClanahan and Kurtis 1991; Benedetti-Cecchi and Cinelli 1995; McClanahan 1998).

Echinometra mathaei is highly susceptible to predation when outside of its burrow (McClanahan 1988). As such, the availability of shelter is a key factor in determining predator rates (e.g. Roberts and Ormond 1987; Beck 1995) and influencing urchin distribution and abundance (Carpenter 1984; McClanahan and Kurtis 1991; Sala *et al.* 1998). *Echinometra mathaei* lives in crevices and cup-shape borings (Campbell *et al.* 1973; Clark 1976; Tsuchiya and Nishihira 1984) that alone may not provide sufficient protection from predators. However, urchins are capable of accessing concealed microhabitats, burrowing directly into the reef matrix (Done *et al.* 1991; Bellwood *et al.* 2004; Glynn and Manzello 2015; Perry and Harborne 2016) and, subsequently, gaining shelter (Labbé-Bellas *et al.* 2016). Whereas some fishes, e.g. larger triggerfish, are highly efficient predators of concealed urchins (Fricke 1971), other fish families, including labrids and lethinids, are restricted to predating on solitary exposed urchins.

The role of habitat complexity may also assist reproduction through reducing energy expenditure. *Echinometra* spp. have low energy requirements because of the reduced amount of organic matter within their bodies (McClanahan and Muthiga 2013). Much of this energy expenditure is dedicated to reproduction, allowing *E. mathaei* to dominate in low-predation, high environmental-stress conditions (McClanahan and Muthiga 2013). Although described as a burrowing echinoid, Gray (1990) suggested that burrowing behaviour is related to unfavourable environmental conditions, with energy being expended only on such when inhospitable conditions prevail. Lowering energetic demands by reducing the need for burrow formation may allow *E. mathaei* to direct energy, instead, to reproduction. As a result, an increase in rugosity and structural complexity may provide greater protection from predation and increase the availability of refuges (Johansson *et al.* 2013), limiting the energy expended on burrow formation.

Echinostrephus molaris

Site specificity

Echinostrephus molaris presence was higher on the outer reef slope than in other areas of the reef. Gradients in the physical environment, including exposure to wave action (Ebert 1982), sedimentation (Dumas *et al.* 2007; Sangil and Guzman 2016), and habitat structural complexity (Graham and Nash 2013), influence echinoid community structure, abundance and distribution in coral reef ecosystems (Andrew 1993; Clemente and Hernández 2008). The outer reef slope of Ningaloo Reef is structurally complex, being characterised by distinct spur and groove structures (Collins *et al.* 2011). Spur communities are dominated by encrusting coralline algae, robust-branching and tabular-branching coral assemblages and associated domal, arborescent, foliaceous and encrusting corals (Collins *et al.* 2011). It is subject to high wave energy, water movement and tidal run-off (Department of Environment, Water, Heritage and the Arts 2008), and decreased sedimentation.

Although introducing a level of stress, hydrodynamics may play an important role in influencing predation, foraging and

sedimentation. *Echinostrephus molaris* has a well-adapted morphology that allows it to occupy longitudinal borings that provide a high level of protection from dislodgement and predation (Campbell *et al.* 1973). Individuals inhabiting borings have been found in habitats dominated by hydrodynamic forces, including groove structures dominated by off-shore flow (Rogers *et al.* 2013; C. Bessey and D. Thomson, CSIRO, pers. comm.), whereas those within crevices or on bare substrates dominate more sheltered areas (Tsuchiya and Nishihira 1984; Prince 1995). This morphology and use of borings in habitats dominated by hydrodynamic forces, in addition to its preference to feed on drift algae, allow efficient exploitation of food resources and reduce competition from other organisms (Asgaard and Bromley 2008), making it ideally suited to the increased energy and water-flow conditions of the outer reef environment (Johansson *et al.* 2013).

Echinostrephus is the only known echinoid genus adapted completely to suspension feeding (Asgaard and Bromley 2008), using its spines to catch drifting algae (Campbell *et al.* 1973; Russo 1977, 1980). In sheltered inner reef flat areas, the quantity of drift algae is far lower than at exposed sites (Russo 1977), owing to decreased current speeds and an absence of macroalgae inhabiting this area (Russo 1977; Neill 1988). Thus, the greater current velocities on the outer exposed reef slope may increase the availability and accessibility of food (Bronstein and Loya 2014). The consumption of drift algae may be especially advantageous when mobile foraging behaviour is hazardous, such as, for example, where the risk of dislodgement or predation is high, enabling *E. molaris* to persist in otherwise stressful environments (Vanderklift *et al.* 2009).

Urchin abundance has previously been negatively correlated with increased sedimentation of fine particulates (Dumas *et al.* 2007; Sangil and Guzman 2016), with high sedimentation negatively affecting grazing rates (Traiger 2019), settlement and early life stages (Walker 2007; Traiger 2019). As a result, it is possible that lower suspended sediment loads resulting from the topographic and hydrodynamic characteristics of the reef slope, compared with sheltered lagoonal and back reef habitats (Browne *et al.* 2013; Fabricius *et al.* 2014; Goatley *et al.* 2016; Tebbett *et al.* 2017), may contribute to differences in *E. molaris* presence between these habitats.

Regional variation

The highest occurrence of *E. molaris* was found at northern sites and it decreased towards southerly sites. Variation in urchin densities has been observed across global, regional, local and within-reef scales (Pearse and Phillips 1968; Kelso 1970; Glynn *et al.* 1979; McClanahan 1988; McClanahan and Muthiga 2001; Dumas *et al.* 2007; Johansson *et al.* 2010). Ningaloo Marine Park extends for 300 km from Bundegi in the north to Red Bluff in the south. Mapping of the marine habitat of Ningaloo Reef has highlighted clear differences in biodiversity among regions (Kobryn 2018) with distinction between the northern and southern regions being attributed to local environmental conditions and the habitat preferences of specific organisms (Kobryn 2018). Within the northern region, extensive macroalgae and higher coral cover transition to sparse and patchy macroalgal and coral communities in the south beyond Yardie Creek (Kobryn *et al.* 2013; Kobryn 2018). Structurally, substrates transition from spur

and groove structures in the north to limestone pavement in the south. As a result, increased *E. molaris* presence at northern sites may be due to a combination of preferred environmental factors, including greater food availability and increased protection from predation (Sheppard-Brennand *et al.* 2017) afforded by greater structural complexity.

Yet, the spatial patchiness displayed by urchin populations remains difficult to explain in terms of environmental factors alone (McClanahan and Muthiga 2001; Langdon 2012). Anthropogenic effects of fishing and area use may facilitate differences in urchin densities among regions. Ningaloo Reef, although remote, is easily accessed from the coast, with some areas of reef within 100 m of the shore. Boat ramps and main access points to Ningaloo Reef are located to the north, with the main ramps at Exmouth, Bundegi and Tantabiddi near the tip of the Exmouth Peninsula. The northern Jurabi sites surveyed in this study are located close to the Tantabiddi boat ramp, one of the largest boat ramps in the area, providing direct access to Ningaloo Reef. Sites further south, between Mandu and Osprey, are located on a more remote section of the Reef, further away from access points. Additionally, within this section of Ningaloo Reef, a complex system of marine protected zones and open access areas exists. No-take zones prohibiting fishing practices and special purpose zones are interspersed with recreation and general-purpose areas open to fishing. A large area prohibiting spearfishing extends from Tantabiddi Well, south of Jurabi, to Winderabandi Point, encompassing all southern sites (Mangrove and Osprey). Consequently, the higher occurrence of urchins present at the northern (Jurabi) sites may also be attributed to more extensive fishing areas, and increased access to and fishing of predatory species in this area.

Conclusions

This study has highlighted the related but differing abiotic and biotic factors controlling the distribution of two sympatric urchin species at a small spatial scale. By investigating urchin occurrence and distribution over a range of sites and reef zones, this study has highlighted the species-habitat associations, and emphasises the complexities of these, in determining urchin community structure.

Urchin species have been shown to coexist generally because of the variation in the niche of each species. The relationships between echinoderms and habitat are species-specific and most likely attributed to preferences in resources, predation risk and reproduction (Labbé-Bellas *et al.* 2016), food preferences, foraging behaviour and morphological adaptations (McClanahan 1988; Bonaviri *et al.* 2011).

Yet, understanding the mechanisms that control the distribution and abundance of different urchin populations is challenging. Different morphological adaptations, and spatial specialisations to avoid predation and competition (e.g. different burrow types and locations; McClanahan 1988), lead to differences in spatial resource utilisation (McClanahan and Muthiga 1989). Although occupying similar niches in reef communities, the predominantly non-overlapping feeding preferences, and morphological and behavioural differences between *E. molaris* and *E. mathaei* may enable these two species to coexist within the intact coral reef system of Ningaloo Marine Park.

Author contributions

E. L. Westlake interpreted data and wrote the paper; C. Bessey conceived the initial project idea and experimental design; C. Bessey and R. Fisher developed the experimental concept, conducted statistical analyses, generated graphics and contributed to manuscript writing; D. P. Thomson and M. D. E. Haywood contributed to data collection. All authors contributed to manuscript revisions.

Compliance with ethical standards

This work was undertaken before the inclusion of observational research in CSIRO ethics requirements. However, this work aligned with current CSIRO Wildlife, Livestock and Laboratory Animal Animal Ethics Committee (CWLLA AEC) approval for the use of free-living wildlife for research (current permit 2019-07).

Conflicts of interest

The authors declare that they have no conflicts of interest.

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