Investigating sea-urchin densities critical to macroalgal control on degraded coral reefs

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KEYWORDS

Sea urchin grazing, habitat predictors, functional importance, *Echinotrix calamaris*, Seychelles, penning, *Sargassum*

SUMMARY

There is an assumption that tropical sea urchins are macroalgal grazers with the ability to control macroalgal expansion on degraded coral reefs. We surveyed abundances of *Echinothrix calamaris*, an urchin species common in the western Indian Ocean, on 21 reefs the inner Seychelles and predicted their density using habitat predictors in a modelling approach. Urchin densities were greatest on patch-reef habitat types and declined with increasing macroalgal cover. Next, we experimentally investigated the macroalgae-urchin relationship by penning two sea urchin densities on macroalgal fields. Over six weeks, the highest density treatment (4.44 urchins m^{-2}) cleared 13 % of macroalgal cover. This moderate impact leads us to conclude that controlling macroalgal expansion is not likely to be one of the main functions of *E. calamaris* in the inner Seychelles given the current densities we found in our surveys (mean: 0.02 urchins m^{-2}, maximum: 0.16 urchins m^{-2}).

INTRODUCTION

Tropical coral reefs are changing under recent anthropogenic pressures such as overfishing, near-shore pollution, and climate change (Norström et al. 2016). There are cases where overfished coral reefs do not recover from acute disturbances, such as thermally induced mass bleaching, and undergo a regime shift to dominance of benthic states alternative to coral, such as of macroalgae (Graham et al. 2015). One of the key ecological controls of macroalgal expansion is herbivory (Bellwood et al. 2004), and sea urchins are widely assumed to perform that function (McClanahan 1992; Carpenter & Edmunds 2006). However, the dominant species of sea urchin varies among locations, and whether this macroalgae-controlling role is true for all species of sea urchin is uncertain.

Our knowledge regarding the role of sea urchins on degraded coral reefs is limited in geographical extent (Caribbean: Carpenter & Edmunds 2006; Kenya: McClanahan & Shafir 1990; Western Australia: Johansson, Bellwood & Depczynski 2010; Great Barrier Reef: Young & Bellwood 2011) and is based on very few species (McClanahan 1992; Young & Bellwood 2011). Especially prevalent in this literature is a single Caribbean species, *Diadema antillarum* (Maciá, Robinson & Nalevanko 2007; Hughes et al. 2010). *D. antillarum* became the main controllers of macroalgal cover in the Caribbean in the early 1980s with mean densities of 7.7 urchins m^{-2} (Hughes 1994). The urchins' macroalgae-controlling role was assumed to be critical on overfished Caribbean reefs. However, the macroalgae-controlling impact of *D. antillarum* was virtually erased following mass die-off from disease (Hughes et al. 2010). More recent recovery of *D. antillarum* populations in the Caribbean has been correlated with some returns in coral cover in the region (Carpenter & Edmunds 2006). In a large-scale model, some urchin species (Caribbean: *D. antillarum*, *Tripneustes ventricosus*, *Tripneustes esculentes;* Western Indian Ocean: *Echinometra mathaei*) have been suggested to be especially important for controlling algae in heavily fished areas (McClanahan 1992). While knowledge of the ecological dynamics associated with these urchin species is fairly extensive, the densities at which other urchin species in other geographic locations have notable macroalgae-controlling impact is poorly studied.

The macroalgae-controlling role of sea urchins may be useful to coral reef management interventions, yet few studies have attempted to actively utilise urchin grazing in a focussed area. Whether urchins can be used to effectively control algal expansion or even clear algal patches and thereby aid coral recovery is yet to be determined. Maciá et al. (2007) conducted experiments transplanting urchins to high algal density areas. While the urchins were recorded to graze on algae, they rapidly vacated the area. The potential for urchin transplanting to focus urchin grazing thus remains understudied.

We investigate the role of the short-spined sea urchin (*Echinothrix calamaris*) as potential macroalgal herbivores in the inner Seychelles. First, we conducted field surveys of urchin densities and modelled the habitat predictors of urchin abundance. Second, we experimentally relocated varying densities of *E. calamaris* into standardised pens located on dense, continuous fields of macroalgae to focus their grazing impact.

MATERIAL & METHODS

Study organism and site

The short-spined sea urchin *Echinothrix calamaris* is a common urchin species in the western Indian Ocean and in our study area, the inner Seychelles (McClanahan & Sharif 1990). The inner Seychelles (4°30'S, 55°30'E) are granitic islands with well-developed carbonate fringing reefs that have been increasingly fragmented by large-scale disturbances. In particular, two major coral-bleaching events caused by thermal anomalies (in 1998: ~ 90 % coral loss [Goreau et al. 2000]; and 2016: ~ 70 % coral loss [Wilson et al. 2019]) have led to habitat fragmentation of coral reefs and regime shifts to macroalgae-dominated habitat (average macroalgae cover of 42 %) on many reefs in the Seychelles (Graham et al. 2015).

Ecological surveys

We surveyed 21 sites of the inner Seychelles in April 2017 that were randomly selected for a long-term monitoring program that started in 1994 (Jennings, Grandcourt & Polunin 1995, Fig. S1). Sites were independent, separated by at least a kilometre, and stratified among three habityat types: continuous, well developed fringing reef with limestone framework (carbonate); continuous reef with granitic base (granite); or fragmented reef (patch). Eight replicate circular areas (7 m radius), 15 m apart, were surveyed along the reef slope base (3-9 m). Cover of macroalgae and corals was estimated visually, and structural complexity was estimated on a 5-point scale, both of which strongly correlate with a range of other methods for capturing benthic cover and structural complexity of coral reefs (Wilson, Graham & Polunin 2007). We counted *E. calamaris* within each replicate area, along with the abundances and size (total length) of 134 diurnally active, non-cryptic, reef-associated fish species. Fish size estimation was calibrated be estimating and confirming the lengths of pre-sized plastic pipes at the start of each sampling day (Graham et al. 2007). Large mobile fish in the cylinder were recorded first, followed by a systematic search for smaller site-attached fish. We converted estimated fish lengths from the resulting dataset into biomass using published length-weight relationships

(Letourneur, Kulbicki & Labrosse 1998; Froese & Pauly 2011) and assigned recorded species to feeding groups based on their diet and feeding behaviour (Wilson et al. 2008).

Experimental sea urchin penning

The second part of our study was conducted from January to March 2018 on the degraded reefs of Anse Papaie (4.28°S, 55.73°E), Curieuse Island, one of the 21 sites surveyed in the first part of the study (Fig. S1). We chose the bay because it is a marine park, minimising disturbance to our experiment and because it is almost universally covered by continuous macroalgal fields. Canopy and overstorey are primarily made up of *Sargassum* spp and some *Turbinaria* spp, while the understorey is primarily *Lobophora* spp and *Dictyota* spp. *Sargassum* in particular often shows strong seasonality, mainly driven by temperature changes and nutrient limitation (McCourt 1984), and in the inner Seychelles this appears to be tied to the prevailing seasonal winds and currents (Bijoux 2013). *Sargassum* appears to senesce during the peak of the cloudier season (May-October) and regrow (likely from leftover holdfasts) during the predominantly clear-sky season (December-March; Bijoux 2013), leading to our choice of experimental timing (January to March).

In early January 2018, we built 13 individual experimental pens (2.25 m^2 area, each fenced with chicken wire and built with open top) on continuous macroalgal fields that grew on relatively flat surfaces to ensure the fences were flush with the sea floor. We stocked five pens each with 10 *E. calamaris* (4.44 urchins m^{-2}), five pens with 4 *E. calamaris* (1.78 urchins m^{-2}), and three pens without urchins as controls. These stocking densities were the logistically highest attainable given the surrounding natural urchin abundances, and balanced between natural densities in Seychelles, and the very high densities of urchins once seen in the Caribbean (Hughes et al. 2010). The pens were dispersed randomly within the same macroalgal field, although we kept a minimum distance of 1 m between each treatment pen and 5 m between control and treatment pens. On 28 January (0 days), we took HD-photographs of each pen from above before placing the urchins into the pens. We repeated the process on 18 February (21 days) and 11 March (42 days). On day 42 we removed the pens. We compared the photographs using CPCe software (Kohler & Gill 2006) to estimate change in macroalgal cover over time. The mean cover of macroalgae prior to sea urchins being introduced in pens was 79.3 % (± 4.7 % [95% confidence interval]) for control pens, 80.4 % (± 7.5 %) for 4 urchin pens, and 92.4 % (± 4.2 %) for 10 urchin pens. These initial differences were induced by natural variation and random placement; they were not by design.

We fitted a zero-inflated negative binomial regression (with a presence-absence ‘zero’ component, and a ‘count’ component with true zeros removed) to assess habitat predictors of urchin densities from the surveys, and a generalised linear mixed model to analyse the urchin penning experiment. A detailed desciption of our statistical analyses can be found in the Supplementary Material.

RESULTS

Benthic predictors of sea urchin abundance

Our model’s zero component indicated a strong positive correlation of patch-reef type with sea urchin abundance, as well as weak positive correlation of the macroalgae-structural complexity interaction and structural complexity (Fig. 1 A). Macroalgae displayed a strong negative correlation on urchin abundance in the zero component. The count component of our model showed a strong positive correlation for patch-reef type, and a weak positive correlation for macroalgae (Fig. 1 B), and a weak negative correlation of structural complexity with urchin abundance. The macroalgae-structural-complexity interaction displayed a strong negative correlation with urchin abundance in the count-component of our model. The sizes of the confidence intervals (thin lines) weaken the inferences that can be drawn from the trends.

The predictor trends resulting from the count component of our model predict a steady decline in urchin abundance with increasing macroalgal cover (Fig. 2 A). Our model predicted ~ 3 urchins per replicate (0.019 urchins m^{-2}) when macroalgae were absent, but ~ 2 urchins (0.013 urchins m^{-2}) when macroalgal cover extended to 5 %. Further interpretation of this trend was not warranted due to large standard errors resulting from few occurrences of macroalgal cover values above 5 %. Our model suggested that no urchins were found in replicates with > 90 % algal cover, while over 20 replicates were found where there were urchins present. The predictor trend of structural complexity predicted a slight increase of urchin abundances with increasing structural complexity (Fig. 2 B). In replicates with structural complexity of 2, the model trend predicted abundances of ~ 2.5 urchins (0.02 urchins m^{-2}) that increased to ~ 3 urchins (0.02 urchins m^{-2}) at a structural complexity of 4. Continuous reefs of granitic or carbonate base predicted abundances of ~ 1.5 urchins (0.01 urchins m^{-2}) while fragmented patch habitats predicted abundances of ~ 6.5 urchins (0.04 urchins m^{-2}, Fig. 2 C). With increasing structural complexity, macroalgae correlated with a more severe decrease of urchin abundances (Fig. 2 D). As macroalgal cover increases from 0 % to 7.5 % per replicate, urchin abundances decreased with structural complexity.

Experimental sea urchin penning

Macroalgal cover declined from day 0 to day 21 (Fig. 3, 13 % reduction: Tukey pair-wise comparison z-Δ10 = 3.074, p = 0.054, Suppl. table 1 & 2) and declined significantly from day 0 to day 42 in pens stocked with 10 *E. calamaris* (Fig. 3, 16 % reduction: Tukey pair-wise comparison z-Δ10 = 4.293, $p < 0.001$, Suppl. table 1 & 2). Pens stocked with 4 urchins as well as control pens displayed no notable differences in macroalgal cover over time (Fig. 3, Suppl. table 1 & 2).

DISCUSSION

In our penning experiment, *Echinothrix calamaris* was associated with some macroalgal reduction within six weeks. While the experimental densities (4.44 urchins m^{-2}) required to achieve this reduction were far above mean and maximum densities observed in surveys across the inner Seychelles (mean: 0.02 urchins m^{-2}, maximum: 0.16 urchins m^{-2}), there are studies that have recorded even higher densities of sea urchins in the Caribbean between 1970 and 1983 (mean: 7.7 urchins m^{-2}, maximum: > 20 urchins m^{-2}) before the die-off (Hughes et al. 2010). A study that relocated *Diadema antillarum* achieved reductions in macroalgal cover by about 15 % before the urchins left the un-penned area (Maciá, Robinson & Nalevanko 2007). When we relocated similar densities of *E. calamaris* into pens, we did not observe a significant reduction of macroalgal cover.

At lower densities, closer to those that we found naturally in the Seychelles, our model suggests that urchin abundance correlates positively with patch reefs and negatively with macroalgae. We also found a weak positive correlation of structural complexity with urchins, although the negative correlation with macroalgae appeared to outweigh the positive correlation with structural complexity, leading to a more drastic reduction of urchin abundances on complex reefs as macroalgal cover expanded. The relationship between urchins and structural complexity in the wider literature is multi-facetted, which might be why our results did not show clear patterns. Some studies report a positive relationship between urchins and structural complexity (Hereu et al. 2004; Lee 2006) while others, including a meta-analysis, report a negative relationship (Weil, Torres & Ashton 2005; Graham & Nash 2013). These discrepancies could stem from behaviours such as substrate-eroding and protection from predators, which vary among urchin species. Some urchins, such as the substrate-boring urchin *E. mathaei*, tend to use crevices for protection (Khamala 1971), while other species such as *D. antillarum* display gregarious behaviour in open areas (Graham & Nash 2013). We observed both hiding in crevices and gregarious behaviour in open areas by *E. calamaris* during our study (JCD, pers. obs.).

It is not clear whether the high densities of urchins we observed at lower macroalgal cover is due to grazing of macroalgae, or actively searching in open areas. Our combined experimental and observational evidence suggests the latter. In our penning experiment, only unnaturally high densities of urchins had an effect on algal densities (4.44 urchins m^{-2} vs 0.16 urchins m^{-2}), and locally common macroalgal genera like *Sargassum* were not heavily grazed. As a whole, our findings align with the literature in that notable sea urchin grazing impacts on macroalgae appear to scale with local urchin densities (Carpenter & Edmunds 2006; Hughes et al. 2010). *E. calamaris* could have a macroalgal controlling effect like its Caribbean relative, but this is only likely if mean densities that we recently observed in the Seychelles were to rise over 200-fold.

The penning technique as we used it is unlikely to lend itself as an effective method for controlling macroalgal expansion on degraded coral reefs. This is mainly because of the large number of urchins that need to be transported into the pens in order to achieve macroalgal reduction. The technique may be enhanced by including structural elements into the pens, given the partly positive relationship between structural complexity and urchins (Hereu et al. 2004; Lee 2006). A longer penning time at higher stocking densities (minimum of 4.44 urchins m^{-2}) could also prove effective in clearing the entire pen of macroalgae.

It is notable that the penning experiments with stocking densities of 4 urchins commenced with an average of ~ 81 % initial macroalgal cover, while pens with 10 urchins commenced with ~ 92 % (Fig. 3). This difference was induced by a combination of the random placement of treatments and is compounded by the low number of pens per treatment (n = 5); we believe that further replication would have rectified this irregularity. We therefore refrained from analysing our data across treatments and only compared each experimental week with the starting point of the same treatment. Macroalgal cover declined from day 21 (week 3) to day 42 (week 6) almost uniformly across all treatments, including controls. We propose that the onset of south-easterly winds in March (see methods) towards the end of our experiment may have increased wave energy to the extent that similar amounts of macroalgae got removed by increased wind force rather than by urchin feeding in week 6. However, we believe the strong decline in macroalgal cover in the first three weeks only occurring in the 10-urchin treatment indicates that higher densities of sea urchins had greater potential to reduce algal cover.

In conclusion, *E. calamaris* in the Seychelles does not appear to be controlling macroalgal expansion given the natural densities we found in our study. It is likely that a drastic elevation of species' density on degraded coral reefs could make the controlling effect on macroalgae measurable. Our model suggests that *E. calamaris* are most likely to congregate on patch reefs, especially if these patch reefs feature structurally complex elements and are low in macroalgal cover. Future studies should investigate these habitats to narrow down the function of *E. calamaris* in the western Indian Ocean. Our study provides insights to the species' function as macroalgal controllers that add to our knowledge of degraded coral reef dynamics.

CONFLICT OF INTERESTS

On behalf of all authors, the corresponding author states that there is no conflict of interest.

REFERENCES

Bates, D, Maechler, M, Bolker, B, Walker, S (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*: 67, 1-48.

Bellwood, DR, Hughes, TP, Folke, C, Nyström, M (2004) Confronting the coral reef crisis. *Nature*: 429, 827-833.

Bijoux, JP (2013) Reef fish spawning aggregation sites: the ecology of aggregating and resident species. PhD thesis, Université de la Méditerranée Aix-Marseille II.

Brooks, ME, Kristensen, K, van Benthem, KJ, Magnusson, A, Berg, CW, Nielsen, A, Skaug, HJ, Machler, M, Bolker, BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R journal*: 9, 378-400.

Carpenter, RC, Edmunds, PJ (2006) Local and regional scale recovery of Diadema promotes recruitment of scleractinian corals. *Ecology Letters*: 9, 271-280.

Dajka, JC, Wilson, SK, Robinson, JPW, Chong-Seng, KM, Harris, A, Graham, NAJ (2019) Uncovering drivers of juvenile coral density following mass bleaching. *Coral Reefs*: 38, 637-649.

Froese, R, Pauly, D (2011) FishBase (http://www.fishbase.org).

Goreau, T, McClanahan, TR, Hayes, R, Strong, A (2000) Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology*: 14, 5-15.

Graham, NAJ, Jennings, S, MacNeil, MA, Mouillot, D, Wilson, SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*: 518, 94-97.

Graham, NAJ, Nash, KL (2013) The importance of structural complexity in coral reef ecosystems. *Coral Reefs*: 32, 315-326.

Graham, NAJ, Wilson, SK, Jennings, S, Polunin, NVC, Robinson, JAN, Bijoux, JP, Daw, TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conservation Biology*: 21, 1291-1300.

Hereu, B, Zabala, M, Linares, C, Sala, E (2004) The effects of predator abundance and habitat structural complexity on survival of juvenile sea urchins. *Marine Biology*: 146, 293-299.

Hughes, TP (1994) Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science*: 265, 1547-1551.

Hughes, TP, Graham, NAJ, Jackson, JBC, Mumby, PJ, Steneck, RS (2010) Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution*: 25, 633-642.

Jennings, S, Grandcourt, EM, Polunin, NVC (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs*: 14, 225-235.

Johansson, C, Bellwood, D, Depczynski, M (2010) Sea urchins, macroalgae and coral reef decline: a functional evaluation of an intact reef system, Ningaloo, Western Australia. *Marine Ecology Progress Series*: 414, 65-74.

Khamala, C (1971) Ecology of *Echinometra mathaei* (Echinoidea: Echinodermata) at Diani Beach, Kenya. *Marine Biology*: 11, 167-172.

Kohler, KE, Gill, SM (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences*: 32, 1259-1269.

Lee, SC (2006) Habitat complexity and consumer-mediated positive feedbacks on a Caribbean coral reef. *Oikos*: 112, 442-447.

Lenth, R, Singmann, H, Love, J, Buerkner, P, Herve, M (2019) Estimated Marginal Means, aka Least-Squares Means. *R package version 1.3.2*.

Letourneur, Y, Kulbicki, M, Labrosse, P (1998) Length-weight relationship of fishes from coral reefs and lagoons of New Caledonia: an update. *Naga*: 21, 39-46.

Maciá, S, Robinson, MP, Nalevanko, A (2007) Experimental dispersal of recovering *Diadema antillarum* increases grazing intensity and reduces macroalgal abundance on a coral reef. *Marine Ecology Progress Series*: 348, 173-182.

McClanahan, TR (1992) Resource utilization, competition, and predation: a model and example from coral reef grazers. *Ecological Modelling*: 61, 195-215.

McClanahan, TR, Shafir, SH (1990) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia,* 83, 362-370.

McCourt, RM (1984) Seasonal patterns of abundance, distributions, and phenology in relation to growth strategies of three *Sargassum* species. *Journal of Experimental Marine Biology and Ecology*: 74, 141-156.

Norström, AV, Nyström, M, Jouffray, JB, Folke, C, Graham, NAJ, Moberg, F, Olsson, P, Williams, GJ (2016) Guiding coral reef futures in the Anthropocene. *Frontiers in Ecology and the Environment*: 14, 490-498.

R-Core-Team (2019) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Schielzeth, H (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*: 1, 103-113.

Weil, E, Torres, JL, Ashton, M (2005) Population characteristics of the sea urchin *Diadema antillarum* in La Parguera, Puerto Rico, 17 years after the mass mortality event. *Revista de biología tropical*: 53, 219-231.

Wilson, SK, Dolman, AM, Cheal, AJ, Emslie, MJ, Pratchett, MS, Sweatman, HPA (2008) Maintenance of fish diversity on disturbed coral reefs. *Coral Reefs*: 28, 3-14.

Wilson, SK, Graham, NAJ, Polunin, NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. *Marine* Biology: 151, 1069-1076.

Wilson, SK, Robinson, JPW, Chong-Seng, K, Robinson, JAN, Graham, NAJ (2019) Boom and bust of keystone structure on coral reefs. *Coral Reefs*: 38, 625–635.

Young, M, Bellwood, D (2011) Diel patterns in sea urchin activity and predation on sea urchins on the Great Barrier Reef. *Coral Reefs*: 30, 729-736.

Zeileis, A, Kleiber, C, Jackman, S (2008) Regression models for count data in R. *Journal of statistical software*: 27, 1-25.

Zuur, A, Ieno, E, Walker, N, Saveliev, A, Smith, G (2009) Mixed effects models and extensions in ecology with R. Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, editors. *New York, NY: Spring Science and Business Media*.

Zuur, AF, Ieno, EN, Elphick, CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*: 1, 3-14.

Zuur, AF, Saveliev, AA, Ieno, EN (2012) *Zero Inflated Models and Generalized Linear Mixed Models with R*. Highland Statistics Ltd., Newburgh, UK.

FIGURE LEGENDS

Figure 1. Effect size estimates of predictor coefficients in zero model with standard error (thick lines) and 95% confidence intervals (thin lines); zero-model component: positive coefficient estimates predict urchin absences (0) and negative coefficient estimates predict urchin presence (1), stronger negative values indicate stronger positive effect on urchin abundance (A); count-model component: negative coefficient estimates predict lower urchin abundance, positive coefficients predict higher abundance (B).

Figure 2. Model prediction trends of macroalgae (A), structural complexity (B), and patch-reef type (C), and for the interaction of macroalgae * structural complexity (D) for the count component of the

zero-inflated negative binomial model, panels show the fitted effect (line) and 95 % confidence intervals (shaded bands) for each variable.

Figure 3. Macroalgal cover (in %) changes observed in three-week intervals inside the penned experimental plots for stocking densities of 10 & 4 Echinothrix calamaris, as well as controls; central line: mean, boxplot boundaries: interquartile range, outside dot: value is > 1.5 times and < 3 times the interquartile range beyond either end of the box, whiskers: ± standard error.