



# Crown-of-thorns starfish promote additional fine-grained habitat fragmentation in a coral reef ecosystem

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## Abstract

**Context** Species that provide habitat for other organisms are critical for land- and seascape structure. Since coral patch interiors offer different habitats and perform a functionally different role from edges, loss and fragmentation of corals can negatively impact biodiversity. Although processes leading to coral loss have been well documented, their impacts on habitat configuration (arrangement) are poorly documented and understood.

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**Objectives** We asked (1) whether Crown-of-thorns starfish (CoTS) forage preferentially on coral edges; and (2) whether they promote fragmentation by increasing the amount of edge habitat more than might be expected relative to random coral loss.

**Methods** We used two different years (2012 and 2014, pre- and post-CoTS irruption) of classified photographic imagery from 10×10 m transects across 17 different coral reefs in Kimbe Bay, Papua New Guinea.

**Results** Comparisons to standard neutral models at a grain of 15 cm showed that CoTS do not forage preferentially within or on the edges of coral patches. The fine-grained structure of coral patches in the seascape was substantially more fragmented post-CoTS, particularly at intermediate levels of coral cover. Coral cover declined by a relatively high mean of nearly 5% across all sites, with considerable variance in benthic habitat change between reefs.

**Conclusions** CoTS are not preferential edge foragers at this scale of analysis. More broadly, our analysis shows how methods developed in terrestrial systems can offer insights into changes in seascape structure and provides useful detail for further research on the ecological impacts of CoTS on benthic fauna.

**Keywords** Edge · Seascape · Landscape · Habitat configuration · Patch · Predation · Invertebrate

## Introduction

Habitat structure is a critical driver of the community dynamics and interspecific interactions that underpin ecosystem biodiversity and function (Bell et al. 2012; Kovalenko et al. 2012; Loke and Chisholm 2022; Madin et al. 2023). Its relevance extends from broad scales, where biogeographic patterns of dispersal and speciation create filters that maintain local adaptation and biodiversity in populations and communities, through to the much finer scales at which individual events such as herbivory, predation, and reproduction occur (Malmqvist 2002; Cushman and McGarigal 2004). Although ‘habitat’ is often used to describe a single ecosystem type, contemporary ecology understands habitat as a relational, multi-scale network in which such phenomena as dispersal, patch-matrix dynamics, perturbations, successional processes, and subsidies between ecosystems operate as both cause and effect (Saura et al. 2014; Thompson et al. 2017). The many processes that contribute to the loss, degradation and fragmentation of critical habitats are considered to be major causes of declining biodiversity (Brooks et al. 2002; Powers and Jetz 2019). However, in marine systems, the most important drivers of habitat change and their impacts on the spatial arrangement of habitat patches are often unknown. The relative importance of habitat loss versus the additional effects of habitat fragmentation continues to be an issue of particular concern (Miller-Rushing et al. 2019).

Consumers of habitat-forming species are critical in shaping the occurrence and structure of ecosystems across the globe. Herbivory, for example, is a central ecological process in nearly all ecosystems. It is intricately intertwined with habitat structure because plants simultaneously provide both food and key structural habitat elements. In terrestrial ecosystems, the impacts of high densities of browsing megaherbivores (e.g., elephant, black rhinoceros, giraffe) on savanna woodland ecosystems can interact with disturbance regimes and rainfall to shift entire ecosystems between alternate states (e.g., Cumming et al. 1997; Burkepile et al. 2020; Wilson et al. 2021). Large herbivores like elephant and cattle can destroy structural habitat elements (e.g., roosting and nesting sites) that other organisms depend upon. The removal or alteration of habitat structure by herbivory can open new areas for colonisation by weedy and

invasive species and often creates clear interfaces, or edges, between habitats. Edges can in turn facilitate or limit other ecological processes (Fagan et al. 1999). For example, predation on bird nests is higher near forest edges; riparian zones act as dispersal corridors for many species; and the age composition of wooded patches in a habitat mosaic is critical for the spread of fire (Naiman and Decamps 1997; Porensky and Young 2013). Changes in herbivory and edge effects resulting from anthropogenic habitat fragmentation are considered to be among the most critical consequences of anthropogenic impacts in ecosystems globally (Laurance et al. 2007).

As these examples imply, consumers of habitat-forming species have the potential to alter landscape structure in different ways depending on their spatial and temporal patterns of consumption. For example, consumers that focus on early-successional species or feed primarily on habitat edges, such as white-tailed deer, have a different structural impact from consumers that forage inside patches of vegetation or in the matrix between patches (Waller and Alverson 1997). In addition, if edge habitats provide a starting point for self-amplifying ecological feedbacks (e.g., initial colonisation by invasive species, or shifts in the disturbance regime) then their consequences for the functioning of entire ecosystems can reach well beyond their immediate extent (Cumming et al. 2012).

Understanding how consumers alter landscape pattern, and the ways in which removal of structural habitat elements creates feedbacks that further drive landscape pattern, is a vital element of understanding the responses of ecosystems to change. The majority of research into edge effects focuses on terrestrial forests, while marine systems and coral reefs in particular have received comparatively little attention (Boström et al. 2011; Sambrook et al. 2016; Carroll et al. 2019). This does not, however, mean that edges are irrelevant for coral reef ecology. Corals play a plant-like structural and functional role in coral reef ecosystems. The composition and configuration of benthic habitat are relevant for organisms across the size spectrum, influencing (for example) habitat selection for breeding and foraging, predation levels, larval settlement, movement patterns, and competitive interactions between benthic species (e.g., Birrell et al. 2008; Chong-Seng et al. 2012; Robinson et al. 2020). Many disturbances on coral reefs, like

coral predation or disease, are characteristically patchy and selective (Haapkylä et al. 2010; Pratchett 2010; Streit et al. 2019; Dietzel et al. 2021). Their disproportionate and fragmenting impacts can create increased amounts of coral edge. One of the few recent studies to explore edge effects on coral reefs (Sambrook et al. 2016) found strong responses in a majority of reef fish species, suggesting that edge effects may be important in shaping coral reef community responses to environmental change.

Crown-of-thorns starfish (*Acanthaster* spp., CoTS hereafter) are widely considered to be one of the most significant predators of coral in the Indo-Pacific. Like many other invertebrate species that are considered pests (e.g., spruce budworm, locusts), they exhibit episodic population dynamics, with periodic irruptions occurring under favourable conditions (Chesher 1969; Birkeland 1989; Rotjan and Lewis 2008; Pratchett 2019; Pratchett et al. 2014, 2017). High densities of CoTS during an outbreak can have a devastating effect on coral reefs, which may take years to recover (Mellin et al. 2016). CoTS only remove living coral tissue, leaving the coral colony structure intact in early stages post-disturbance. While the exposed skeletons will eventually erode into rubble, this process can take several years, leading to a decline in the structural complexity of reefs and negative consequences for a wide-range of reef-associated organisms (Morais et al. 2022). However, while CoTS are known to quickly drive down coral cover, their influence on habitat fragmentation, including patch number, size and the amount of edge habitat have not been investigated.

In this paper we use data on the impact of a CoTS outbreak on live coral in Kimbe Bay, Papua New Guinea, to evaluate the hypothesis that foraging on corals by one of their most important and voracious predators increases fine-scale fragmentation of coral reef habitat by promoting the amount of edge habitat. While CoTS are one of the primary drivers of coral loss, with characteristically patchy feeding patterns (Pratchett 2010, Castro-Sanguino et al. 2023), no prior studies have explored the spatial implications of CoTS feeding modes and specifically their impact on fine-scale spatial fragmentation on coral reefs. Due to their size (around 40 cm in diameter, on average; Babcock et al. (2016)) and the potential difficulty of accessing the lower regions of dense clusters of coral, we anticipated that adult CoTS should initiate

their foraging activities at the edges of coral patches, rather than starting in the middle (or randomly). If so, CoTS would tend to move edges in space rather than constantly creating new edge habitat.

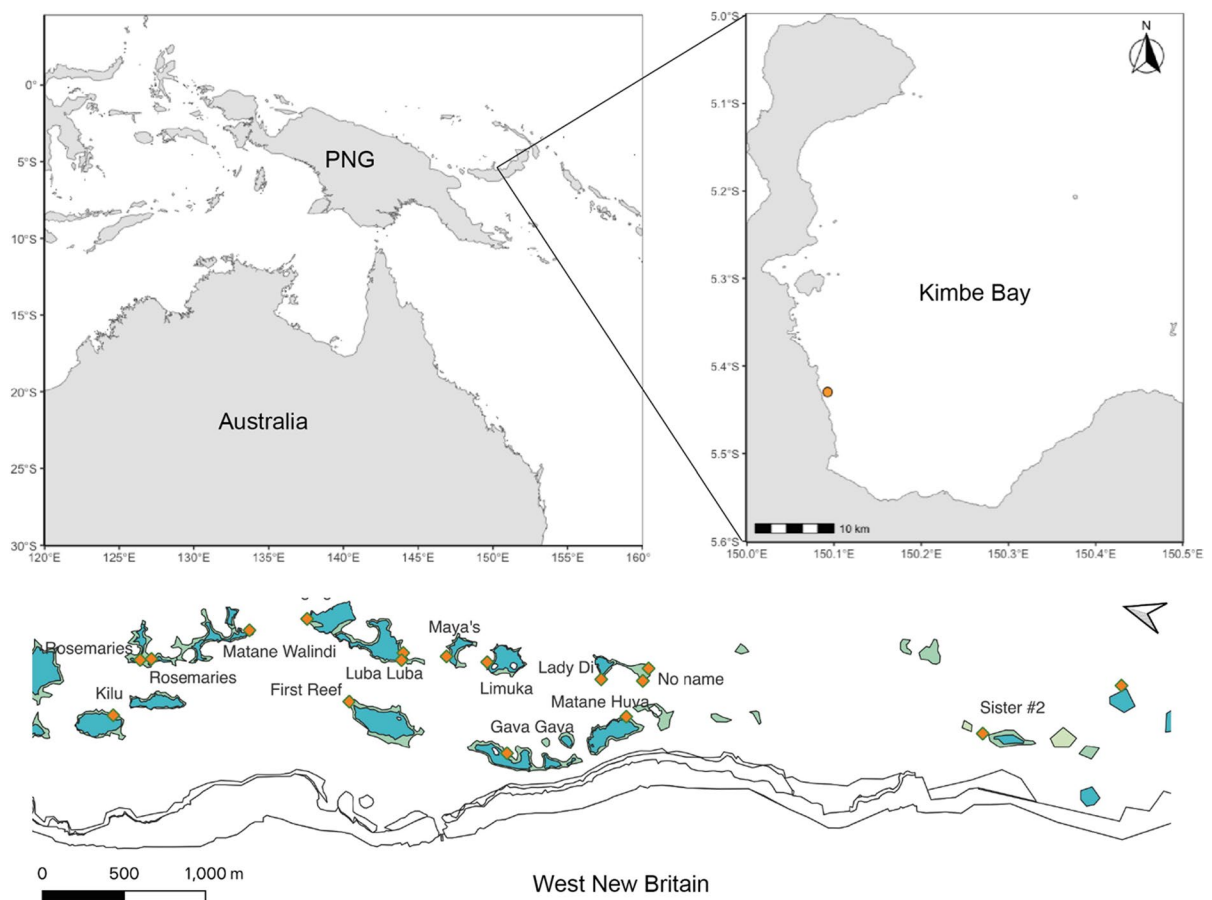
To test this hypothesis, we used a series of detailed photogrammetric benthic habitat maps to describe fine-grained benthic habitat heterogeneity and habitat change and used these to quantify changes in habitat structure before and after a CoTS outbreak. These maps were then analysed to answer three focal questions: (1) What kinds of benthic habitat transitions did we observe at the study sites before and after the outbreak, and how much spatial heterogeneity occurred in these transitions? (2) Did CoTS significantly fragment the coral seascape, in terms of increasing the amount of edge habitat and number of coral patches? And (3), did CoTS forage preferentially at the edges of coral patches?

## Methods

### Study sites

We selected 17 sites on 15 inshore platform reefs along the south-western shore of Kimbe Bay, Papua New Guinea (5°30' S; 150°05' E) (Fig. 1). This location is subject to irregular CoTS outbreaks that have led to substantial declines in coral cover (Jones et al. 2004). Sites were selected with a similar exposure, slope and depth and had a wide range in total coral cover. Together the reefs selected were representative of the live coral cover on inshore reefs of Kimbe Bay, which in the absence of disturbances is largely governed by proximity to rivers and their sediment discharge during the rainy season. Kimbe experienced a significant CoTS outbreak during the period 2012–2015. In 2012, coral cover across all 17 sites was 14.5% to 97.3% with a mean of 58.2%. By 2014 coral cover across all sites had a range of 10.2% to 94.6%, with a mean of 53.7%. Some sites were heavily affected and others were relatively untouched.

It is important to note two details in relation to this data set and analysis. First, no other significant perturbations (e.g., cyclones, floods, bleaching, *Drupella* snail outbreaks) occurred during the period of this study. Thus, we can reasonably attribute the vast majority of observed losses of coral directly to CoTS. Second, the study sites span a gradient from



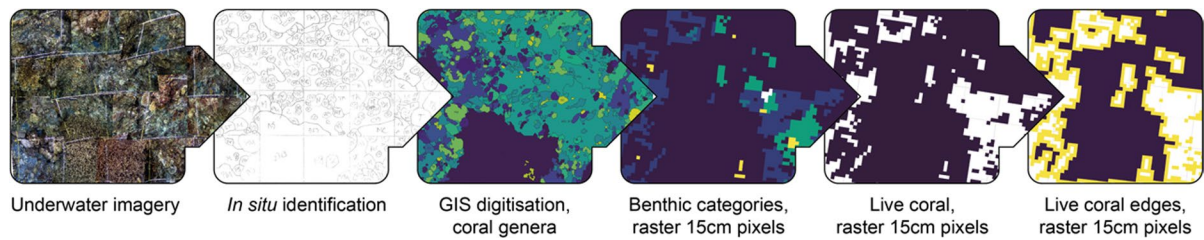
**Fig. 1** Maps showing location of study sites at Kimbe Bay, Papua New Guinea (PNG), at three different scales. The study is located at the orange dot in Kimbe Bay. The lower panel

depicts inshore platform reefs, with shallow reef flats shown blue, reef slopes in green, and orange diamonds at the study sites

highly impacted to un-impacted reefs. Given that CoTS at the study location are mostly active at dawn and dusk, we did not record the numbers of CoTS foraging at each reef, nor were they surveyed between our survey times; so our findings are necessarily inferential. Analysis of CoTS foraging effects over a gradient of impact facilitates some elements of the analysis (e.g., understanding effects of high CoTS densities on seascape fragmentation), but makes others, such as measurements of total coral loss, less clear. The fact that some effects are low on average should not be interpreted as meaning that the effects of CoTS at high densities are small.

The four outer corners of a 10×10 m quadrat were marked with permanent markers and floats, and a towed GPS used to record lat/long coordinates. Transect tapes were then laid in a grid pattern

demarcating 2×2 m squares within the larger quadrat. A diver deployed a float attached to a weighted 3 m string in the middle of each square, to ensure pictures were taken over a consistent distance and angle to the reef. Images were then taken of each 2×2 m square in a consistent lawn-mower pattern (deep to shallow, starting bottom left) to simplify post-processing. In the first year (2012), a diver produced a rough map of each 2×2 m square, recording benthic types > 15 cm in situ (Fig. 2). Corals were identified to genus and by growth type (branching, plating, thin plating, massive; free living, attached). To estimate rugosity of each site, a 3-m lightweight chain was deployed five times along the horizontal transect lines in the grid, and the planar distance covered by the chain recorded. This metric was then expressed as ratio of total length, providing a coarse estimate of structural



**Fig. 2** Visualisation of the steps involved in data collection, processing and analysis of one of the 17 study reefs (Hanging Gardens). Underwater imagery was combined with in situ identification to produce vector maps of each reef. These were

then converted to raster format at 15 cm resolution in R software and used to estimate seascape metrics as described in the text

complexity on each site (Luckhurst and Luckhurst 1978). Note that due to challenging field conditions in 2012, rugosity measures from Maya's Reef were not collected during that survey period.

### Image processing

The 17 sites were digitised using ARC GIS and QGIS, producing a georeferenced polygon shapefile of the benthic cover of each site (Fig. 2). Features larger than 15 cm diameter were digitised and classified to coarse taxonomic type for non-coral, and to genera for live coral (noting that for this analysis we used a simple hard coral/non-hard coral classification rather than genus-level data). Standard post-processing procedures to dissolve adjacent polygons and remove slivers were performed to clean the topology of the shapefiles.

Coverages were further checked and validated after digitisation by overlaying digitised versions on the original images, using categorical shading to identify different cover types, and comparing

original estimates of coral cover with results from the analysis to ensure that they were consistent. A few of the lower numbers in our analysis may reflect sampling errors. For example, apparent conversion of small areas of macroalgae to coral may reflect the loss of macroalgae to reveal coral that was underneath the macroalgal canopy. Similarly, field placement of the transects and the nature of identification from photographs may have led to some errors in the exact alignment of individual quadrats between 2012 and 2014. These errors are, however, at overall magnitudes of less than 1% of the total sampled area and so we did not try to correct for them in subsequent analyses.

### Defining benthic cover

Coarse benthic cover types (Table 1) were defined based on field observations undertaken in each quadrat at the time when the photographs were taken.

**Table 1** The different benthic classes considered in this analysis and their definitions

Cover type	Definition	Additional considerations
Live coral	Living coral as evidenced by colour and the presence of polyps	In some cases, live coral may have been masked by algal fronds in the water column above
Abiotic	Bare rock, rubble, sand, dead coral, pavement	Pavement category includes turf algae (which may include juvenile macroalgae < 2 cm) and crustose coralline algae
Sponge	Live sponge	
Macroalgae	Algae > 2 cm tall, with holdfasts (includes coralline and calcifying algae, like <i>Padina</i> spp. and <i>Halimeda</i> spp.)	
Giant clam	Giant clam shell with clearly evident living mantle	
Soft coral	Live soft coral	
Anemone	Live anemone	



## Analysis

All analyses were undertaken in R software (R Core Team 2013). R code and data are provided as a zipped archive in Appendix S1 (supplementary information). Vector data were converted to Rasters using a 0.15 m×0.15 m pixel size and the *rasterize* function in the *Raster* package (Hijmans et al. 2015). The raster images were small enough to work with as columns of matching data for direct comparisons, such as trajectory analysis. We used the *landscapemetrics* package (Hesselbarth et al. 2019) for all estimates of patch, class and landscape attributes. For the analysis we focused on quantifying metrics that have been shown in terrestrial systems to be directly relevant for dispersal and predation.

‘Fine scales’ in most publications about spatial patterns in coral reefs refer to resolutions of 100 m or less, with a 10×10 m pixel as a typical unit of analysis. The recent ‘fine resolution’ Allen Coral Atlas adopts a 5×5 m pixel size. Some studies of individual coral morphology have used very fine scales (e.g., mm to cm) but these analyses have generally focused on coral growth and structure rather than seascape configuration (Zhong et al. 2023). Our analysis uses a 10×10 m extent, for each of a series of repeated quadrats, and a grain (pixel size) of 15×15 cm. The spatially dispersed sampling design coupled with a fine spatial resolution and the inclusion of two rather than one-time steps make this data set unique relative to the vast majority of published analyses of benthic cover on coral reefs.

We used three different approaches to understand changes in coral patch composition and configuration.

1. *Benthic habitat transitions* were quantified by first determining the sequence of transitions between 2012 and 2014 for each pixel in each seascape and then summing these transitions across all 17 different quadrats. We used boxplots and post-hoc statistics to explore changes in individual benthic cover types between 2012 and 2014. We next quantified differences between different quadrats to explore spatial variance in the observed changes. Given the scarcity of seascape analyses at this scale, these descriptive analyses are included because they provide a set of baseline data and expectations for seascape change as measured using this methodology.

2. *Habitat fragmentation* was assessed by comparing coral patch structure and properties

(area, edge, patch cohesion, and number of patches) between 2012 and 2014. Patches are formally defined as contiguous, non-linear surfaces of a single cover type (Turner and Gardner 2015). Fragmentation in its strongest sense should not be confused with habitat loss, although habitat loss can cause fragmentation (Lindenmayer and Fischer 2006). Fragmentation is primarily a problem of seascape configuration (habitat arrangement) rather than of composition (habitat amount or proportion). For example, a landscape in which all remaining habitat is concentrated in a single circle does not become more fragmented if the radius of the circle is reduced. However, in reality, in most cases fragmentation is a result of habitat loss.

The impacts of habitat loss on seascape composition must be understood relative to well-established null models. Edge length, which is often used as an index of fragmentation, is determined by both the total area of habitat and the number of patches in the landscape. Any loss of a given habitat will either increase or decrease total edge length within a given area, depending on the starting conditions and specifically on whether habitat area at the starting time is above or below 50% of the total area under consideration (Cumming et al. 2012). In most real-world situations the length of edge over a full range of habitat cover (i.e., 0 to 100% cover) should fit a quadratic relationship. The nature of fragmentation influences the shape of the curve: some kinds of fragmentation may lead to faster or slower changes in edge relative to habitat amount. Previous research suggests that a linear or slightly sigmoidal relationship can be expected between the number of patches and the total area of habitat. Thus, correcting for the total area of habitat, creation of edge by a ‘shrinkage’ process that focuses on patch edges (such as competition, or herbivory on habitat margins) will create fewer new patches than creation of edge by a more stochastic process (e.g., treefall or edge-independent pathogen outbreaks) that randomly removes habitat independently of edge.

To determine whether or not CoTS foraging activities fragment coral-dominated seascapes more than expected, we considered changes in both measures of landscape connectivity (specifically, patch cohesion) and in the relationships between edge length, patch number, and habitat area. The null hypothesis in this instance is that by foraging randomly, CoTS introduce no additional fragmentation beyond what would be

expected from the amount of coral they remove. In practice this would mean that they do not alter the existing relationships of edge and patch number to habitat area, even when habitat area changes. Conversely, if CoTS introduce additional fragmentation then we would expect the slopes of the relationships of both edge and patch number relative to habitat area to become steeper and their overall magnitudes to increase.

To test for an added (i.e., ‘more than expected from a random process’) fragmentation effect, we estimated edge length, patch number and patch area for all coral patches in each quadrat individually in 2012 and 2014. We then fitted curves with the theoretically-expected forms to each data set, using standard linear models, and explored their fit and confidence intervals.

**3. The question of preferential edge foraging by CoTS** was addressed by comparing whether there was a disproportionate loss of edge pixels (defined as those bounding non-coral areas on one or more sides) relative to internal pixels between the two years. Our null hypothesis for this analysis was that there should be no difference in the proportional loss of coral from interior vs edge habitats. We first converted the existing benthic cover data to a  $15 \times 15$  cm resolution raster image with a simple coral-no coral pixel classification scheme. We then used the *boundaries* function in the R *raster* package (Hijmans et al. 2015) to identify the interior edges of each coral patch, creating an ‘edge image’. We converted both the coral image and the corresponding edge image from each of 2012 and 2014 to a data frame with four columns. By summing the frequency of each of the trajectories represented in the data set, we could then quantify the number of pixels for each reef that had stayed as interior or edge or been converted from interior or edge to other types. We calculated the proportions of lost interior pixels to total interior cover in 2012 and lost edge pixels to total edge in 2012 and compared these both visually and using Welch’s two-sample t-test.

## Results

### Overall magnitudes of observed benthic habitat transitions

Since there is a scarcity of research on trajectories of change in benthic cover on coral reefs at fine grains

(cm to m), we first report a series of basic descriptive data to provide a baseline summary of fine-grained change in a tropical coral reef (Fig. 3).

In 2012 there was a total of  $988 \text{ m}^2$  of coral across all 17 quadrats, or 58% coral cover across the sampled area. This declined by just under 5% of the total sampled area to  $908 \text{ m}^2$  (53%) in 2014. The data show that the majority of coral habitat in 2012 remained coral in 2014. Approximately  $688 \text{ m}^2$  of coral persisted (i.e., 40.7% of the total area sampled). A further  $299 \text{ m}^2$  (~17.6% of the surveyed area) was lost to other cover types, particularly abiotic substrata. At the same time,  $220 \text{ m}^2$  (13% of the surveyed area) were converted from other cover types to coral. All other changes were at considerably lower magnitudes (Fig. 4). Despite the ecological relevance of losses of coral habitat, the overall magnitude of coral loss was just under 5% and there was considerable variance among sites; thus, it was unsurprising that a Wilcoxon Test indicated that the only statistically significant ( $p < 0.05$ ) differences in these plots were the increases in patch numbers of soft corals and sponges.

Overall, the decline in coral cover was accompanied by an increase in total edge and number of patches and a decrease in patch cohesion for all cover types, indicating a heterogeneous ‘salt and pepper’ pattern of change rather than a homogeneous clearing or transitioning of large cohesive areas of habitat.

### Spatial heterogeneity in benthic habitat change.

There was considerable variance in the amount of habitat change between individual sites (Fig. 5). Although mean coral cover changed from  $58 \text{ m}^2$  in 2012 to  $53 \text{ m}^2$  in 2014, seven sites experienced a net increase in coral cover and 10 experienced a net decline. Gains in total coral cover were relatively modest, ranging from  $3.9 \text{ m}^2$  (5.5% relative to 2012) to  $11.3 \text{ m}^2$  (78% increase relative to 2012). The largest single decline in coral cover was on Maya’s Reef, where  $55 \text{ m}^2$  of live coral (74.5% relative to 2012) was lost. This reef was heavily impacted by CoTS.

Despite differences in the directions of change of coral cover, the total amount of coral edge habitat increased in all except two locations (Fig. 5). Edge habitat peaks on average at 50% habitat cover and can thus be created by growth or by fragmentation, depending on the starting point. Given the overall decline in coral cover in this data set from 58 to 53%, the observed increase in edge matches theoretical

**Fig. 3** Trajectories of 15×15 cm pixels in each different cover type, in m<sup>2</sup>. This figure summarizes change, or lack of change, by benthic cover type for each individual pixel across all 17 10×10 m quadrats between 2012 (Y2012) and 2014 (Y2014). Darker shades indicate higher numbers. The trajectory of each pixel goes ‘from’ the x axis cover type ‘to’ the y axis cover type

Y2014	anemone	0.09	0.29	0	0	0	0	0.14
	soft_coral	3.98	6.12	0.14	0.09	0	1.06	0
	giant_clam	0.04	0	0	0	0.02	0	0
	macroalgae	5.29	2.05	0.07	5.33	0	0	0
	sponge	15.35	13.34	3.38	0.27	0	0.11	0
	abiotic	274.32	455.38	11.43	17.46	0.02	3.1	0.36
	live coral	688.12	193.57	9.2	15.73	0.14	1.17	0.14
		live coral	abiotic	sponge	macroalgae	giant_clam	soft_coral	anemone
		Y2012						

expectations based on neutral landscape models. Cohesion between patches of coral declined on most reefs, largely mirroring declines in overall coral area, while the number of patches increased (as would be expected from a fragmentation process acting on relatively cohesive areas).

The mean rugosity did not change between the two surveyed years (overall 2012:  $0.63 \pm 0.016\text{SEM}$ ; 2014:  $0.63 \pm 0.018$ , Fig. 6), indicating that the observed changes were primarily in live coral cover.

#### CoTS impacts and fragmentation

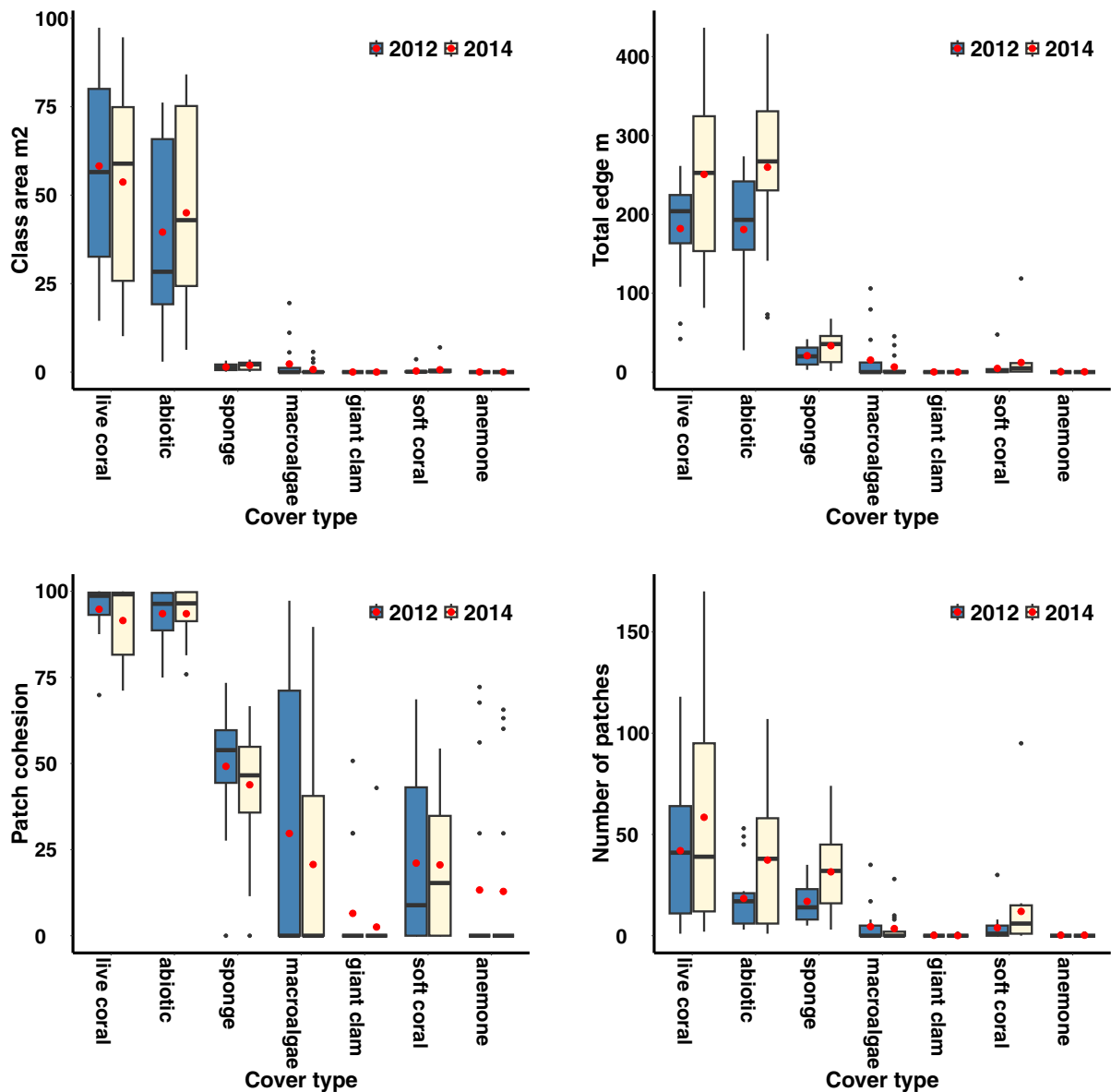
In 2014 the shape of the coral area-edge function was different from that of 2012 (Fig. 7). As expected, the 2012 data were well-fitted by a quadratic curve  $y = -1.695x^2 + 280.65$ , where  $y$  is the total edge of coral in 2012 and  $x$  is the total area. For this relationship, the intercept  $\text{SE} = 28.12$ ,  $t = 9.8$ ,  $p < 0.000$ ; for  $x$ ,  $\text{SE} = 0.44$ ,  $t = -3.84$ ,  $p < 0.0016$ ;  $\text{AIC} = 183$ , 16 df. However, the length of coral edge in 2014 for quadrats with cover in the range of roughly 15–95 m<sup>2</sup> (15% to 95%) was considerably greater than in 2012 and the expected

quadratic relationship was no longer significant due to the high variance introduced by the heterogeneous foraging activities of CoTS. For the 2014 data, coral edge ( $y$ ) related to coral area ( $x$ ) as  $y = -0.655x^2 + 285.84$  with intercept  $\text{SE} = 52.79$ ,  $t = 5.4$ ,  $p < 0.000$ ; and for  $x$ ,  $\text{SE} = 0.87$ ,  $t = -0.75$ ,  $p < 0.46$ ; overall  $\text{AIC} = 209$ , 16 df.

When we treated the total edge of coral in 2014 as a mixed function of coral area in 2012, coral area in 2014, and total edge in 2012, total edge in 2012 was the most significant predictor ( $p < 0.0006$ ) of coral edge in 2014; but coral area in 2014 also became statistically significant ( $p < 0.034$ ). Correcting for starting conditions by including edge length from 2012 pushed the conformity of the 2014 edge data closer to what we had expected.

As indicated in Fig. 7, the confidence intervals for these two curves did not overlap in their central and most relevant portions. The higher and steeper curve in the 2014 data indicates that CoTS altered landscape pattern in such a way as to introduce more edge proportional to area than the process that had previously generated area-edge relationships in this seascape.



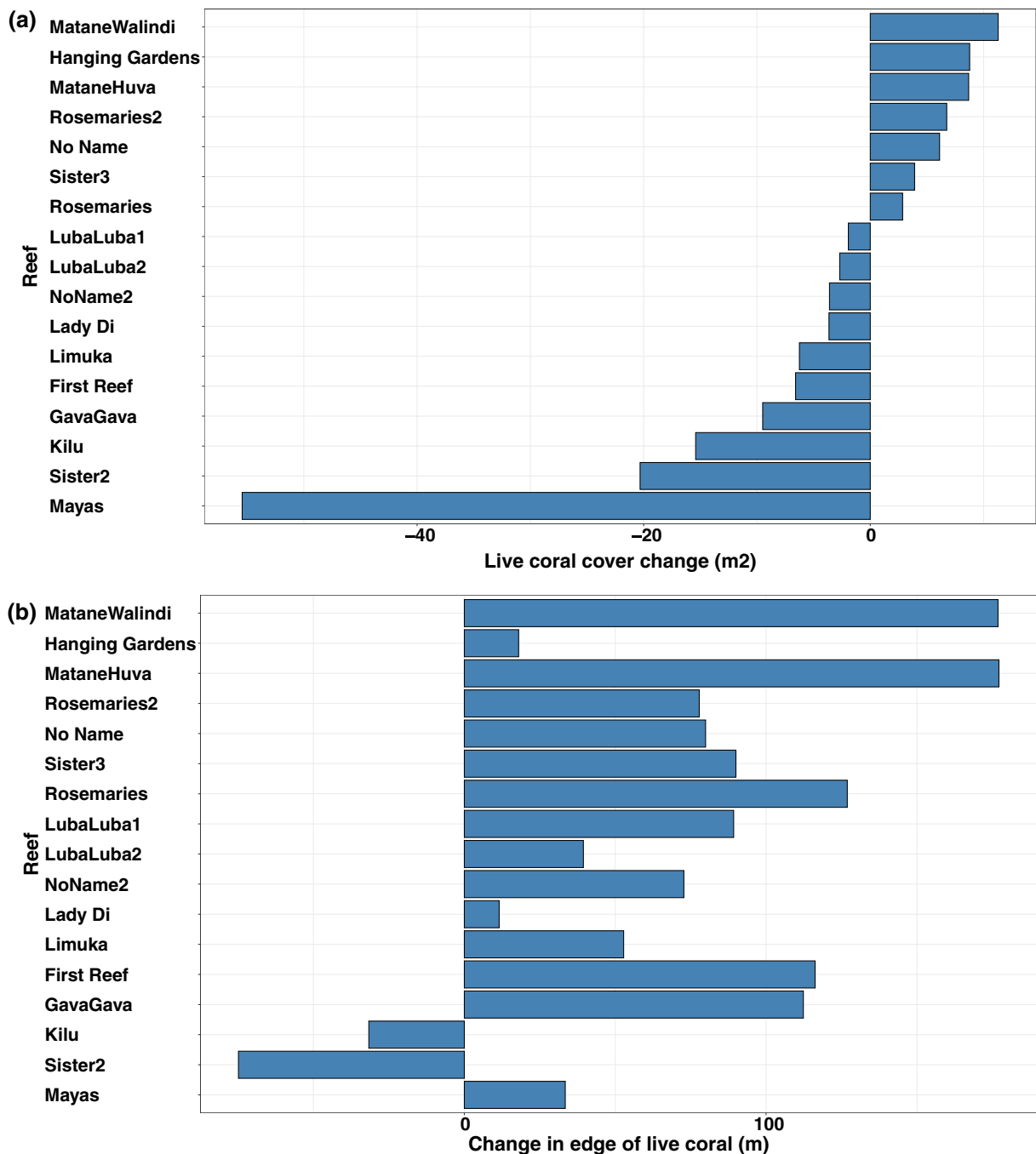


**Fig. 4** Boxplots showing median, mean and variance in **a** class area (m<sup>2</sup>), **b** total edge (m), **c** patch cohesion and **d** number of patches for each benthic cover type for 2012 (blue) and 2014 (cream) for all seventeen 10×10 m quadrats. Horizontal

black lines in the boxes indicate medians; red dots represent means; error bars represent standard deviations. None of these changes were statistically significant except the increases in patch number of sponges and soft corals

The number of patches relative to coral area was higher in many locations, and the relationship had a steeper slope, in 2014 than in 2012. For 2012,  $y = -1.36x + 121$  where  $x$  = coral area and  $y$  = number of coral patches. For this relationship the intercept had  $SE = 7.05$ ,  $t = 17.17$ ,  $p < 0.000$ ; and the coefficient,  $SE = 0.11$ ,  $t = -12.27$ ,  $p < 0.000$ ;

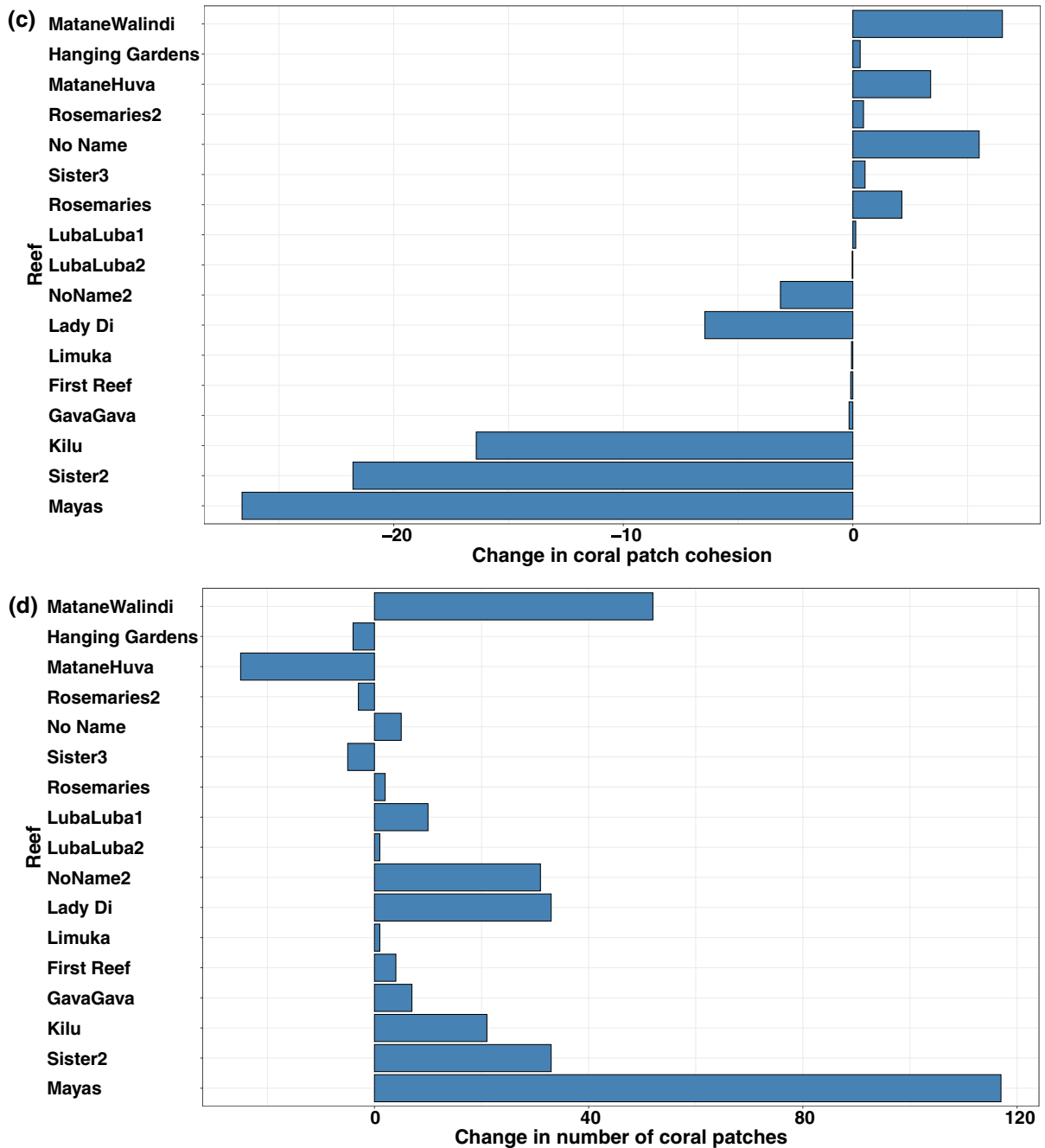
AIC 136.11,  $df = 16$ . For 2014,  $y = -1.66x + 147.5$ ; intercept  $SE = 13.43$ ,  $t = 10.98$ ,  $p < 0.000$ ; coefficient  $SE = 0.22$ ,  $t = -7.48$ ,  $p < 0.000$ ; AIC 162,  $df = 16$ . The number of patches in 2014 was not significantly different from the number of patches in 2012 according to a Welch's two-sample t-test ( $t = -1.03$ ,  $df = 28.73$ ,  $p < 0.31$ ) although divergence between



**Fig. 5** Changes in **a** live coral cover, **b** live coral edge, **c** coral patch cohesion, and **d** number of coral patches in each 10×10 m quadrat for all 17 study reefs. Reefs in all panels are sorted vertically based on the magnitude of change in coral cover

the two curves with decreasing coral area is obvious from inspection of Fig. 7. Overall, the more fragmented appearance of the 2014 seascape, with its proportionally higher number of patches

and proportionally more edge per unit habitat area,



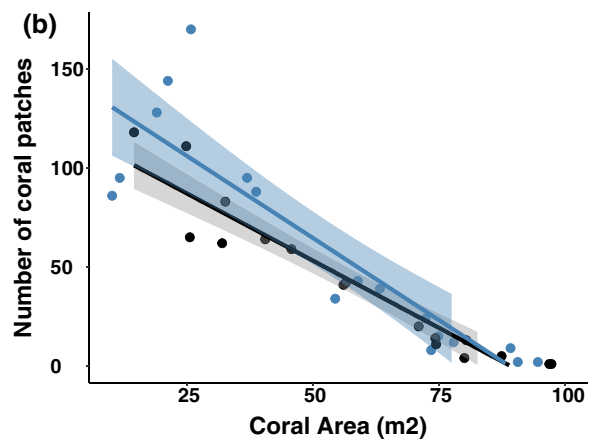
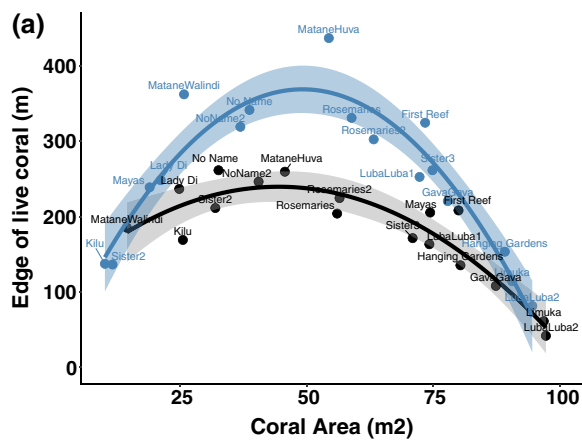
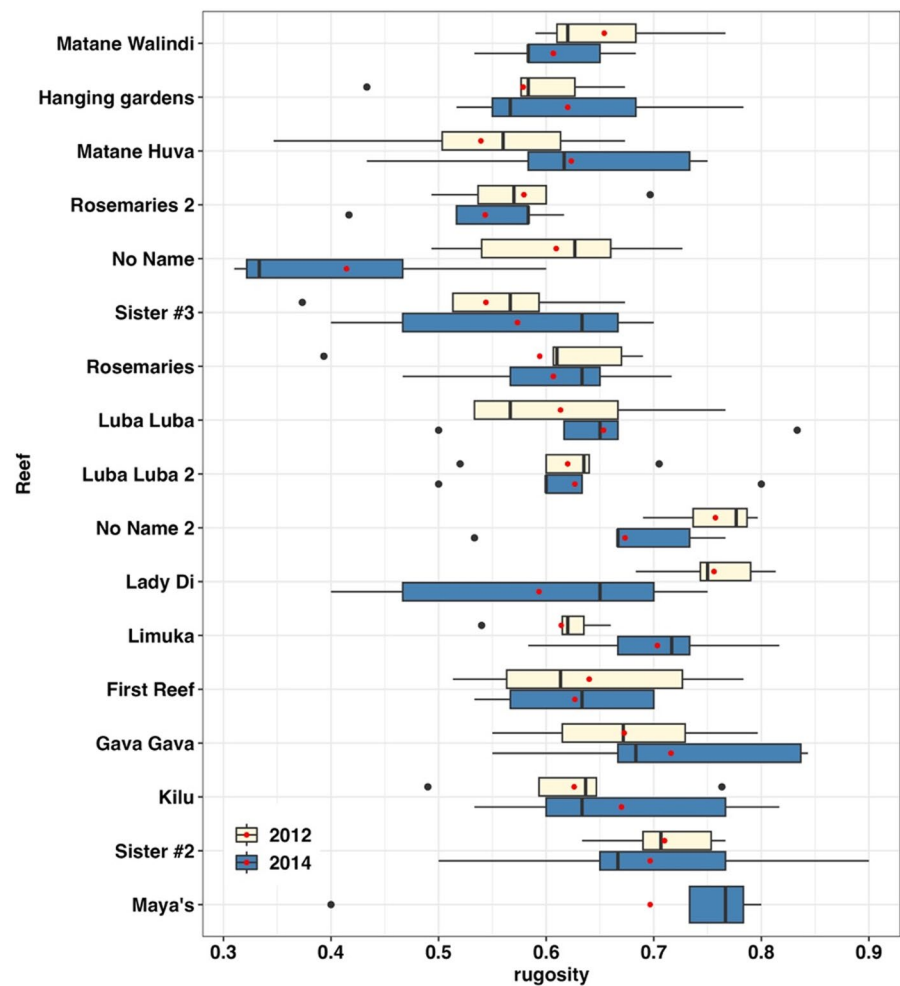
**Fig. 5** (continued)

consistently suggests a different underlying process of edge creation relative to the 2012 seascape.

Do CoTS forage preferentially on coral patch edges?

Our analysis showed a close relationship between loss of interior and loss of edge pixels across all reefs (Fig. 8). The Welch's two-sample t-test suggested

**Fig. 6** Changes in the rugosity of the 17 study reefs, estimated using the chain method, where a ratio of 1 (planar length:chain length) represents a flat reef with no structural complexity and lower values indicate higher complexity. No data were available for Maya's Reef in 2012



**Fig. 7** Comparison between 2012 (black points and line) and 2014 (blue points and line) for the relationships between **a** coral edge (m) and area ( $\text{m}^2$ ); and **b** number of coral patches

and coral area ( $\text{m}^2$ ). Shading indicates 95% confidence intervals (grey is 2012, blue is 2014)

that there was no significant difference between the proportional rates of loss ( $t = -1.48$ ,  $df = 31.65$ ,  $p = 0.15$ ), indicating that coral loss (and by inference, CoTS foraging) was not concentrated either on the edges of coral patches or in the interiors of patches.

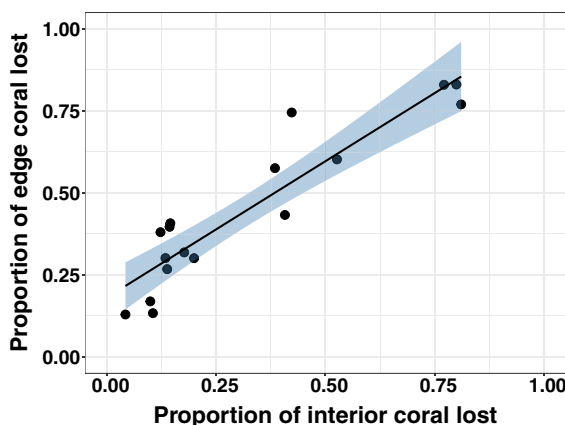
## Discussion

We found considerable spatial and temporal heterogeneity at fine scales in the marine benthic ecosystem of Kimbe Bay. Substantial changes in coral reef habitat amount and arrangement were observed between 2012 and 2014, with a majority of reefs losing live coral area. Our results suggest that the foraging activities of CoTS during population irruptions alter the spatial structure of coral communities, promoting fragmentation by increasing the proportional number of patches and the amount of edge habitat relative to pre-2012 coral community structuring processes (presumably, recruitment and competition). After correction for the non-linear influence of the reduction in habitat area on edge length, the fragmentation effect of CoTS foraging is strong. There was no evidence that CoTS primarily forage at either edge or interior sites; instead, the data suggest that CoTS begin foraging at random locations independent of patch characteristics, but create

heterogeneity at finer scales than that resulting from pre-irruption processes. This is demonstrated by data from the reefs near the middle of Fig. 7; for example, the two Rosemaries Reefs exhibit a much higher edge length post-outbreak despite showing only a small change in area.

The area of coral removed by CoTS during the irruption, as measured using our dispersed quadrats, averaged less than 5% of the total habitat area. This led to insignificant statistical differences among years for most groups of benthic organisms. The degree of seascape change required to produce classical statistical significance is relatively extensive. Others have, however, argued that fine-grained studies of coral cover have to be interpreted in their spatial and temporal context (Madin and Madin 2015). Hard corals are relatively slow-growing by comparison to many terrestrial species. For example, sequential declines in coral cover at an average rate of loss of just 1.25% of the original area per year or 0.34% of the current total per year over the Great Barrier Reef led to a decline of nearly 25% in total coral area over 20 years (Hughes et al. 2011). In the Caribbean, loss of 80% of coral cover over three decades occurred at an average decline of just 2.6% of the original area of coral per year (Gardner et al. 2003). Thus, the decline in coral cover at our study sites over two years was considerably higher than baseline rates of loss that have been of high concern to experts, further supporting our argument that statistical significance in this case is a poor indication of ecological relevance.

Many of our findings are further influenced by our choice of scale and the decision to include all sites in our analyses. The lack of fit of simpler theoretical expectations to the 2014 data may be due to the mixture of heavily and lightly impacted sites, for which two different processes (respectively, competition and predation) were driving qualitatively different spatial patterns. While CoTS impacts on coral cover were high at some of the study sites, as indicated by marked declines in coral, other sites were relatively untouched. If we had restricted our analysis to heavily impacted sites (e.g., by working only on reefs that have showed coral loss, as depicted in Fig. 5) or reduced resolution further to increase sample sizes of pixels, we would almost certainly have found statistical significance in changes in seascape metrics.



**Fig. 8** Relationship between the proportion of edge coral lost and the proportion of interior coral lost across all 17 study reefs. Shading indicates 95% confidence interval. The slope of this line is close to one; if CoTS were unambiguously choosing to forage on either edges or interiors, it would be either much steeper or much shallower



The primary direct threats to coral reefs globally (predation, disease, and coral bleaching) share a characteristic effect in that they often disproportionately target some species over others, creating a patchwork effect of more or less degradation across a reef or seascape (Baird and Marshall 2002; Pratchett 2010; Stuart-Smith et al. 2018). This uneven impact on resources can have cascading consequences to other organisms in reef communities, by disrupting established competitive hierarchies and successional sequences (Emslie et al. 2011; Ford et al. 2024). Further, during recovery, areas that have been recently cleared of coral and contain coral rubble, coralline algae, or other scleractinian corals are potential locations for the settlement of coral larvae, particularly those of either highly competitive or weedy, fast-growing species (Randall et al. 2024; Whitman et al. 2025). Competitive corals include ‘large, branching and plating species that grow quickly, occur at shallow depths and reproduce by broadcast spawning’ (Darling et al. 2012); weedy species are typically brooding spawners that may gain an advantage at low densities by producing higher numbers of large, locally abundant propagules (Darling et al. 2012; Cant et al. 2021). Together, these processes can play a major role in restructuring coral reef communities by removing and favouring the regrowth of some species more than others.

While we did not measure the responses of benthic organisms directly, edge habitats on coral reefs are known to be used by a wide range of marine organisms, including algae (Barott et al. 2012), macroinvertebrates (Dumas et al. 2013), and fish (Acosta and Robertson 2002; Sambrook et al. 2016). Invertebrates and smaller benthic species are likely to be strongly affected by the creation of edges, given their need for shelter and the influence of edges on the abundance and distribution of potential predators. For coral-associated fish on reefs it has been shown that fragmentation can have positive effects (via a mechanism of reduced competition, given that many species feed at coral edges or rely on them for shelter), while net habitat loss has consistently negative effects (Bonin et al. 2011; Jones et al. 2020). The feedbacks from changes in fish distributions to coral cover are, however, poorly understood.

When CoTS prey on corals, they often create a mosaic of disturbance by selectively feeding on

certain coral species above others. Our results suggest that their effects may cross scales, impacting reef composition at between-reef scales as well as on individual reefs. Seascape spatial pattern may predict regime shifts in coral reef ecosystems (Génin et al. 2024). As terrestrial ecologists have found, teasing apart the relative influences of changes in composition and changes in configuration on animal communities will require a substantial amount of evidence from different locations and contexts (Fletcher Jr et al. 2018; Fahrig et al. 2019). Given the high diversity of many coral reef ecosystems, and the relatively high mobility of many fish and invertebrate species, coral reef ecology has the potential to contribute new and valuable perspectives to this ongoing debate.

Our application of more intensive analytical methods for analysing benthic pattern in coral reef ecosystems (i.e., moving beyond simple characterisations of changes in coral area) shows how methods that were originally developed in terrestrial landscape ecology to understand the impacts of herbivory and other perturbations on vegetation can contribute to understanding the impacts of processes that are relevant to marine organisms. We focused on CoTS foraging as a potential driver of seascape pattern, but similar analyses of other kinds of impact on corals (e.g., cyclones, changes in densities of coral-eating fishes, or tourist visitation in relation to moorings) would contribute additional information about the relative effects of different disturbances on coral reef structure and the feedbacks that we hypothesise exist between pattern and process in coral reef ecosystems. Thus, although we disproved our original hypothesis that CoTS forage preferentially at the edges of coral patches, our results show how detailed analyses of benthic structure can provide useful insights into the causes and consequences of changes in seascape habitat configuration.

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**Data availability** Data are provided in the supplementary information.

## Declarations

**Competing interests** The authors declare no competing interests.

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