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Title: Quantifying the response of structural complexity and community composition to environmental change in marine communities

Running Head: Measuring change in marine habitat complexity

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Abstract:

Habitat structural complexity is a key factor shaping marine communities. However, accurate methods for quantifying structural complexity underwater are currently lacking. Loss of structural complexity is linked to ecosystem declines in biodiversity and resilience. We developed new methods using underwater stereo-imagery spanning four years (2010-2013) to reconstruct 3D models of coral reef areas, and quantified both structural complexity at two spatial resolutions (2.5 and 25 cm) and benthic community composition to characterise changes after an unprecedented thermal anomaly on the west coast of Australia in 2011. Structural complexity increased at both resolutions in quadrats (4 m^2) that bleached, but not those that did not bleach. Changes in complexity were driven by species-specific responses to warming, highlighting the importance of identifying small-scale dynamics to disentangle ecological responses to disturbance. We demonstrate an effective, repeatable method for quantifying the relationship among community composition, structural complexity and ocean warming, improving predictions of the response of marine ecosystems to environmental change.

Introduction

Habitat complexity is an important predictor of species richness and abundance in numerous marine ecosystems, including kelp forests, seagrass beds and coral reefs (Luckhurst and Luckhurst 1978; Gratwicke and Speight 2005; Kovalenko et al., 2012). Although some complexity may be provided by underlying substrata, a significant and ecologically defining proportion of three-dimensional habitat in many marine communities is provided by ecosystem engineers, such as corals on tropical reefs or seaweeds on temperate reefs. Shifts in habitat-forming taxa and associated changes to structural complexity can have significant and long-lasting effects on marine ecosystems (Steneck et al., 2002; Graham et al., 2006, Roff et al., 2015). Consequently, understanding the relationship between the composition of ecosystem engineer communities and habitat complexity is critical for predicting the response of marine ecosystems to environmental change (Nagelkerken et al., 2000). However, despite the widespread acknowledgement of the importance of structural complexity, quantitative, repeatable methods for measuring complexity in marine systems are either costly (e.g. Airborne LiDAR (Brock et al., 2004)) or infeasible for use over large spatial extents (e.g. manual measurements using diver-based surveys).

Increases in the frequency and severity of disturbances are altering the abundance and distribution of ecosystem engineers, leading to widespread changes in the composition of marine communities. For example, declines in the abundance of seaweeds (on temperate reefs) and corals (on tropical reefs) have precipitated shifts in the composition and body size structure of associated fish assemblages (Halford and Caley 2009; Wernberg et al., 2012; Nash et al., 2015). However, not all coral or seaweed species contribute equally to the provision of structural complexity. Different species also show differential vulnerability to disturbances such as temperature anomalies, disease and storms (Wernberg et al., 2012; Bridge et al., 2014; Madin et al., 2014). Consequently, understanding the relationships between community composition and structural complexity is critical for predicting ecosystem responses to disturbances.

Disturbances such as warm-water induced coral bleaching have resulted in significant shifts in the composition of coral communities and over large spatial scales (Baker et al., 2008; Darling et al. 2013; McClanahan et al. 2014). However, the response of coral assemblages to disturbance events is taxonomically and spatially heterogeneous, particularly at the small but ecologically important spatial extents of 1-10 m (Baker et al., 2008; Madin et al., 2014). Maintaining structural complexity is a key factor determining whether a reef community returns to a coral-dominated or shifts to an algal-dominated state following disturbance (Graham et al., 2015). Consequently, predictions of coral reef vulnerability and recovery potential would be empowered by a greater understanding of the relationship between community composition and structural complexity at small, ecologically relevant spatial extents (Harborne et al., 2012), potentially providing an ‘early-warning’ system for reefs at risk of shifting to alternative, undesirable stable states (Kennedy et al., 2013).

The status and trajectories of coral reefs in many regions is assessed through monitoring programs such as the Global Coral Reef Monitoring Network (see *http://www.icriforum.org/gcrmn*). Despite the clear importance of structural complexity for determining ecosystem resilience, complexity is rarely incorporated into monitoring programs in a quantitative manner. Instead, most monitoring focuses on metrics such as the percent cover of live corals, which cannot account for size-dependent changes in colony morphology (Madin et al., 2014), changes in morphology among habitats (Veron 2000), or additional complexity provided by the underlying substrate. Furthermore, some disturbances may alter the composition of coral communities, thereby influencing structural complexity and coral size distribution, without significantly affecting total coral cover (Berumen and Pratchett 2006, Ferrari et al., 2012b). The relatively weak relationship between live coral cover and structural complexity, combined with the importance of quantifying structural complexity (Graham and Nash 2013) demonstrates the need to develop better metrics for quantifying indicators of coral reef status.

Effectively quantifying structural complexity requires measurement across multiple spatial extents and resolutions, because individuals of different species and with different body sizes and morphologies influence complexity at different scales (Tews et al., 2004; Bozec et al., 2013; Nash et al., 2013). Many methods have been developed to measure habitat complexity underwater (e.g. Risk 1972; McCormick 1994; Graham and Nash 2013), and considerable interest surrounds the use of high-resolution 3D terrain models of the seascape reconstructed using close-range photogrammetry (Leon et al., 2015; Burns et al., 2015). Close-range photogrammetry provides a powerful tool for examining marine habitat complexity across broad spatial scales. Reconstructions derived from photogrammetry enable precise measurements of structural complexity using area-based analogues of the traditional chain-and-tape method, and provide lower error variance than other methods (Friedman et al., 2013). Reconstructing 3D topographic data also allows structural complexity measurements across multiple spatial resolutions (analogous to the link size in chain-and-tape measurements) by sub-sampling the generated terrain surface (mesh of interconnected triangular faces) at a range of different resolutions. Spatial resolution (or the distance between vertices in the mesh, hereafter referred to as link size) is an important factor in structural complexity measurements (Knudby and LeDrew, 2007) but is rarely reported (Graham and Nash, 2013).

We quantified the spatial and temporal variation in community composition and structural complexity of a coral reef exposed to an unprecedented heat wave that caused a major bleaching event and a subsequent shift in benthic community composition (Bridge et al., 2014). Using precisely-aligned, georeferenced orthomosaics of AUV-derived images, we examined: 1) the effect of coral bleaching and changes in community composition on structural complexity across multiple years; and 2) which taxa contributed to changes in structural complexity at different spatial resolutions/link sizes. We demonstrate the use of new post-processing methods for constructing high-resolution orthomosaics (derived using 2mm per pixel AUV imagery) and 3D terrain reconstructions (Johnson-Roberson et al., 2010) (2.5 cm link size) over 625 m^2 reef areas. We produced Digital Surface Models (DSMs) across multiple surveys over a period of four years, from which the changes of community composition and structural complexity were quantified. We undertook precisely geo-located and repeated measurements (precision ± 5cm), without the need for diver-based data collection or permanent infrastructure to mark site location. For the first time, we quantified the changes in structural complexity across years and over multiple spatial resolutions (from 2.5cm to 25cm), an approach broadly applicable to a wide range of marine ecosystems.

Materials and Methods

Study Site

The study was conducted at Geebank (28.81°S, 113.947°E), a submerged bank in the Houtman Abrolhos Islands (HAI), Western Australia (Fig. 1). In the austral summer of 2010-11, the region experienced an unprecedented 'marine heatwave' associated with strong La Niña conditions (Pearce and Feng, 2013; Zinke et al., 2014). Average sea surface temperatures in February 2011 peaked at 3°C above long-term monthly averages over 12° of latitude of the Western Australian coast (Pearce and Feng, 2013). In the HAI, the average maximum summer (December to May) sea temperatures were ~4.7°C above the previous 30-year average, and 4.3°C above the average for the previous 3 years (22.99°C ± 0.21°C based on HadISST) (Abdo et al., 2012). This marine heatwave resulted in the first documented mass bleaching event in the HAI, and also had detrimental effects on macroalgae, fish and marine invertebrates (Wernberg et al., 2012; Bridge et al., 2014). Additional smaller thermal anomalies occurred during the summer of 2012 and 2013 (see *http://coralreefwatch.noaa.gov/satellite/vs/australia.php*).

Data Collection

Autonomous Underwater Vehicles (AUVs) are increasingly being used for oceanic and seafloor ecology and monitoring to complement traditional approaches involving SCUBA and ship-towed video (Bridge et al., 2011; Smale et al., 2012; Williams et al., 2012). They are well suited to collecting high-resolution optical imagery of the seafloor due to their ability for precise trajectory control and because they provide an ideal platform for mounting stereo-cameras (Yoerger et al., 2007; Williams et al., 2012). Importantly, AUVs allow for repeatable surveying of spatially-precise observational units, owing to precise navigation and the ability to revisit a location with a high degree of accuracy (Williams et al., 2010; Bryson et al., 2013).

Stereo images were collected using the AUV *Sirius* in April of each year from 2010-2013. This allowed comparison among years while minimising the influence of seasonal variability of some taxa (e.g. macroalgae). Maintaining an altitude of 2 m above the seafloor and a speed of approximately 1 m/s using a Doppler velocity log sensor, the AUV captured stereo image pairs with a resolution of 1360-by-1024 pixels and a footprint of approximately 1.5 x 1.2 m at a frame rate of 2 Hz, providing greater than 50% overlap in subsequent images.

Georeferencing, accurate to ±0.5 cm (accuracy determined by visual re-identification of seafloor features), was conducted using a combination of ship-based GPS at the surface, an Ultra-Short BaseLine (USBL) acoustic positioning system, Doppler velocity log and depth sensors to determine the vehicle's location in real-time. These tools enabled repeated surveys of the same geographical location each year without the need for fixed infrastructure on the reef (Williams et al., 2012). Data were collected over three 625 m^2 (25 x 25 m) plots, each consisting of overlapping stereo image pairs that allowed for three contiguous sections of the reef to be mapped in 3D at high-resolution in each year. The three plots were 50 – 100 m apart to ensure spatial independence and capture spatial heterogeneity within each site (Hurlbert, 1984).

Post Processing and Precisely Aligned 'Virtual Quadrats'

In order to evaluate the effect of bleaching on changes in habitat complexity we selected 61 'virtual quadrats' (2 x 2 m) from each plot. Each quadrat was analysed from imagery taken in 2010, 2011 and 2013 to identify temporal changes in community composition and structural complexity over the three-year period. The quadrat size was selected to be similar to but slightly larger than spatial extents used in past coral reef studies (e.g. 0.5 to 2.0 m) in order to encapsulate effects that occurred directly on top of coral colonies and the immediate spatial region around colonies. Quadrats were selected based on the presence of bleached corals in 2011 to ensure an equivalent number of both bleached corals and 'control' quadrats with no bleaching to enable robust statistical comparisons. Quadrats with no bleaching included unbleached colonies of bleaching-sensitive taxa (e.g. *Montipora*) to ensure that any observed differences between bleached and unbleached quadrats were not simply due to the presence of different taxa. Each quadrat was extracted from the 625 m^2 meshes using a series of post-processing steps (described below), and precisely spatially-aligned to ensure high spatial precision among years. Each quadrat contained an orthographically-projected colour photomosaic layer with a resolution of 2 mm per pixel and a 3D topographic surface model layer (composed of a regular grid of vertices and triangular surface elements) with a link size of 2.5 cm per grid cell. Post-processing consisted of a bundle adjustment algorithm (Bryson et al., 2012) for highly accurate estimation and refinement of stereo camera poses and lens distortion calibration parameters, a 3D terrain reconstruction and texturing algorithm (Johnson-Roberson et al., 2010) and an inter-year precision spatial alignment technique (Bryson et. al, 2013). The multi-year spatial alignment of the virtual quadrats was performed first by using an automated technique (Bryson et al., 2013) to provide a coarse alignment, followed by an additional correction step in which common features in the quadrats were annotated by hand (using up to 10 points) and used to precisely align the plots to an accuracy of ±5cm (based on residual analysis of the annotated features).

Benthic Community Composition and Bleaching

We estimated the areal coverage of the five most abundant coral (branching *Acropora* [AcBr], tabulate *Acropora* [AcTb] and plating *Montipora spp*. [Mon]) and algal (simple algae with canopy height less than 5 cm [MAs] and complex algae with canopy height > 5 cm [MAc]) morphotypes in each quadrat using a polygonal region-based labelling scheme in ImageJ (version 1.47, *http://imagej.nih.gov/ij/*). Photomosaics for each quadrat were divided into hand-annotated regions, with each region assigned to one of the five morphotypes which together accounted for ~95% of epibenthic taxa in the quadrats. The areal (m^2) and percent coverage of each taxon was estimated in all quadrats for 2010 and 2013 to evaluate change over the period and data collected during the bleaching event in 2011 was used to identify the occurrence of bleaching in each quadrat.

Structural Complexity

To examine change in structural complexity over the study period, we quantified structural complexity as surface rugosity *sensu* (Friedman et al., 2012). Surface rugosity was calculated by dividing the actual surface area of the 3D terrain by the area of the terrain projected onto a flat plane, which can be either the plane of best fit or the horizontal plane. We used the plane of best fit in order to decouple structural complexity from the effect of slope. A plane-of-best-fit algorithm, based on a least-squares fit to the vertices of the topographic model, was used to transform the surface model of each quadrat into its own coordinate system. Surface rugosity (SR) was calculated for each quadrat in 2010 and 2013, at both 2.5 cm ($SR_{2.5}$) and 25 cm (SR_{25}) link sizes. Measurements of $SR_{2.5}$ were derived from the original DSMs for $SR_{2.5}$, while values for SR_{25} were obtained by downscaling the original layers to a 25cm grid size. The 2.5 cm scale was selected based on the maximum consistently derived topographic resolution achievable from the AUV images used in this study, and is similar to chain link lengths used in previous studies on structural complexity of coral reefs (Knudby and LeDrew, 2007; Graham and Nash, 2013). The 25 cm scale was selected as one order of magnitude greater, and is a scale likely to be relevant as shelter for small and medium-sized reef fish (Caley and St. John, 1996; Rogers et al., 2014). Link sizes greater than 25 cm required a level of 3D surface sub-sampling that resulted in a high degree of measurement error within the 2 x 2 m quadrats used in this study, and hence were not used. The maximum achievable link size is dependant on the spatial extent over which measurement are made; in practice we found that link sizes could be derived up to approximately one tenth of the spatial measurement unit (quadrat size) considered. Surface rugosity was calculated as:

$$SR = \sum_{N}^{i=1} \frac{a_i}{a_{proj,i}} \qquad \text{Equation 1.}$$

Where a_i is the actual area of a surface face element i, i=1 to N, and $a_{proj,i}$ is the orthographically projected area of face i, corresponding to the coordinate system based on the plane-of-best-fit. Change in SR (CSR) was calculated as the difference in SR measurements made in 2013 to those made in 2010 in a given quadrat, and was computed at both the 2.5cm and 25cm link sizes separately.

Statistical analyses

We used multivariate Generalised Linear Models (GLMs) to investigate the relationship between benthic community composition and two categorical explanatory variables: year (2010, 2013) and bleaching incidence, a binary response depending on whether bleaching was observed in a quadrat ('bleached') or not ('not bleached'). A negative binomial distribution was applied to all models to account for over-dispersion, and 999 pit-trap re-sampling iterations were run for each model to account for correlation in testing and calculate model term p-values using the R package *mvabund* (Wang et al., 2013). Data were also examined using distance-based multivariate data (e.g. PERMANOVA; Anderson et al., 2008), which produced parsimonious results. We present only the results of the multivariate GLMs, which are considered more statistically robust, given that in contrast to the negative binomial distribution, transforming raw data and distance-based methods can potentially confound the effects of explanatory variables and thus inflate p-values, leading to incorrectly rejecting the null hypothesis (Warton et al., 2012). Residual plots were used to verify that model assumptions were not violated. The results were visualised using non-metric multidimensional scaling (nMDS) plots produced using the *vegan* package in R (Oksanen et al., 2015)

We used hierarchical linear mixed-effects models (GLMMs) to investigate the effect of bleaching on the change in surface rugosity over time for both $SR_{2.5}$ and SR_{25}. The models used change in surface rugosity $CSR_{2.5}$ or CSR_{25} as the response variable and bleaching state in 2011 (bleached or not bleached), percent cover of benthic taxa in each quadrat in 2011 and changes in the percent coverage from 2011 to 2013 as explanatory variables (Table 1). In all models, ‘plot’ was originally included as a random effect, but was subsequently removed because it did not improve model fit (Zuur et al., 2009). Model fit was evaluated using Aikaike Information Criterion, Bayesian Information Criterion and Maximum Likelihood, with all three metrics agreeing on the best-fitting model in all cases. Residual plots were used to verify assumptions of normality, independence and heteroscedasticity. All GLMMs were run using the package *lme4* (Bates et al., 2013) in R.

Results and Discussion

Using high-resolution spatial models, we detected and quantified shifts in community composition and structural complexity at both link sizes ($SR_{2.5}$ and SR_{25}). Importantly, our results showed that changes in surface rugosity were dependent on the occurrence of bleaching, identified which taxa were responsible for driving changes in surface rugosity and showed the link sizes at which changes in rugosity occurred. Our results demonstrate that three-dimensional terrain reconstructions can be used to quantify disturbance-mediated shifts in both community composition and surface rugosity, and provides a basis for predicting the impact of ocean warming on habitat structural complexity, a key attribute of marine ecosystems.

Change in community composition

Community composition of the most abundant epibenthic taxa changed significantly between 2010 and 2013, and among bleached and unbleached quadrats (Table 2). The interaction between year and bleaching was significant, meaning that the multiplicative effect of year on the mean abundance of the morphospecies present in each quadrat differed between quadrats that bleached in 2011 and quadrats that did not. Differences in community composition between years were primarily due to changes in the abundance of plating *Montipora*, branching *Acropora* and complex macroalgae (Fig. 2). The 2011 bleaching event had a significant effect on the subsequent composition of quadrats in 2013. There were greater declines in *Montipora* and increases in branching *Acropora* in quadrats where bleaching was observed in 2011 (Fig. 3).

Change in Surface Rugosity

Across all quadrats, there was a significant increase in surface rugosity at both $SR_{2.5}$ (12% mean ± 2.9% SE) and SR_{25} (4.1% mean ± 0.7% SE) over 2010-2013 (Table 3). However, changes in complexity varied significantly between quadrats where bleaching was observed in 2011 versus quadrats with no bleaching. At both link sizes, structural complexity increased significantly from 2010 to 2013 in quadrats with bleaching, but not in quadrats that did not bleach (Table 3, Fig. 4).

Changes in surface rugosity were related to shifts in the relative abundances of the three dominant coral morphospecies at smaller link sizes ($SR_{2.5}$), but not at the larger link size (SR_{25}). For $SR_{2.5}$, changes in the abundance of branching and tabulate *Acropora* had significant but opposing effects. Quadrats with a higher abundance of branching *Acropora* in

2010 showed a significant increase in $SR_{2.5}$, due to increased abundance of branching *Acropora* over the three-year period. Increases in complexity at $SR_{2.5}$ were more frequent in quadrats where bleaching occurred in 2011 than quadrats with no bleaching. In contrast, increased abundance of tabulate *Acropora* from 2010-2013 was related to a significant decrease in $SR_{2.5}$, which was also more frequently observed in bleached quadrats (Table 3, Fig. 4).

Bleaching incidence was the only significant predictor of increase in SR_{25}. However, initial cover of branching *Acropora* was related to an increase of SR_{25} but only in unbleached quadrats and so improved model fit, and was therefore retained in the final model (Table 3, Fig. 5).

Implications for quantifying changes in benthic marine communities

Habitat complexity is important for maintaining resilience of coral-dominated reefs (Graham et al., 2015). The mechanisms by which complexity increases resilience are not fully understood, but may involve processes such as coral recruitment or because complexity increases cross-scale redundancy of important functional groups such as herbivores (Nash et al., 2015). Despite the increasing importance of quantifying structural complexity for coral reef management and monitoring (Graham and Nash, 2013), techniques for quantifying structural complexity in marine ecosystems, particularly at small spatial resolutions (1s to 10s of centimetres) are rudimentary, labour-intensive, and/or subjective and are not easily repeatable (Friedman et al., 2013). Here, we demonstrate the novel insights that can be gained through use of precisely-aligned, multi-temporal 3D image reconstructions to quantify structural complexity across multiple time points and different spatial resolutions. This approach provides a framework to link changes in community composition to structural complexity and identify which taxa are most critical to coral reef recovery. The total increase in complexity observed in our study was small, yet we were able to detect this increase consistently and identify links between bleaching history and changes in complexity. Attributing these differential responses among quadrats to changes in specific taxa would not be possible with traditional methods of quantifying structural complexity. Combined with information on the vulnerability to disturbances, understanding the contribution of different taxa to structural complexity across multiple scales will enable better predictions of ecosystem trajectories, and could potentially provide an ‘early-warning’ system for reefs at risk of shifting ecological states.

Disturbances such as coral bleaching commonly show high spatial and taxonomic variability (Baker et al., 2008; Guest et al., 2012; Bridge et al., 2014), but the effects of such heterogeneity on coral reef recovery and resilience are poorly understood. In the HAI, our counter-intuitive finding that complexity increased at sites where bleaching occurred was caused by the greater vulnerability of plating taxa (*Montipora* and tabulate *Acropora*) than branching *Acropora* (Bridge et al., 2014). At smaller link sizes ($SR_{2.5}$), higher abundance of plating corals reduced complexity, but branching *Acropora* increased complexity (Fig. 6). Complexity also increased at larger link sizes (SR_{25}), but the change could not be attributed to a particular taxon. Understanding the relationships between community composition and structural complexity, particularly in the context of taxonomic variability in vulnerability to disturbance, is critical for predicting the responses of reef biodiversity to environmental change (Ferrari et al., 2012a, Madin et al., 2014).

The abundance of branching corals has been shown to influence the richness and diversity of fish assemblages (e.g. Chabanet et al., 1997), and an increase in branching corals may mitigate bleaching-related shifts in the fish assemblage in the HAI (Halford and Caley, 2009; Emslie et al., 2014). However, it is important to consider how different coral reef fishes utilise complexity at different scales, depending on factors such as body size, ontogeny or species identity (e.g. Caley and St John, 1996; Harborne et al., 2011; Wen et al., 2013; Nash et al., 2013; Rogers et al., 2014). For species with known habitat preferences, our method can be used to identify key habitat areas for different taxa by examining entire image mosaics over multiple spatial scales, enabling rapid assessments of habitat suitability for a wide range of species at different life history stages (Harborne et al., 2012; Ferrari et al., 2012b). Changes in habitat quality through time can also be quantified through identification of changes in community composition and/or complexity at specific spatial resolutions (Fig. 2). The use of multiple spatial resolutions also potentially allows for the calculation of scale-invariant complexity indices which may provide good explanations of benthic composition (Leon et al., 2015). By decoupling changes in community composition from changes in complexity, we were able to identify critical changes in habitat complexity not detectable using traditional metrics such as coral cover or semi-quantitative metrics of complexity averaged across an entire transect.

Repeated measurements of sessile marine biota at spatially-fixed sample locations (in this case quadrats) yield lower error-variance in estimates of change compared to measurements where sample locations vary in subsequent years, even within the same site (Van der Meer, 1997; Ryan and Heyward, 2003). Furthermore, repeated measures have been used to disentangle important ecological processes driving underwater ecosystem trajectories, such as coral-algal competition at different levels of herbivory (Ferrari et al., 2012a). Consequently, our method will provide more accurate values for the change in complexity than other commonly-used methods, such as contour-chain or semi-quantitative visual estimates (e.g. Wilson et al., 2007) owing to the use of precisely repeated spatial units, which are difficult to achieve using other methods. Repeated surveys of fixed sample locations in sub-tidal habitats typically require the presence of fixed markers (such as permanent stakes), which can limit the number of samples and spatial scale of data collection, and are also vulnerable to dislodgement from storms. The use of AUVs and the development of post-processing tools demonstrated here enable high-precision spatially-repeated measurements (±5cm) of key variables (benthic community composition and structural complexity) without the need for permanent markers. In addition, our method identifies which taxa explain changes in complexity, providing greater insight into mechanisms by which structural complexity is generated and maintained. Although AUVs provide an ideal platform for large-scale repeat monitoring, photogrammetry-derived DSMs are also possible using manually-operated underwater camera systems (Leon et al., 2015), allowing for the techniques described here to be potentially used when AUVs are not available.

Importantly, spatially repeated measurements derived from three-dimensional image reconstructions allow analysis of *distribution of changes* in these variables rather than just the *change in distribution*, and can be measured over a range of small to intermediate spatial scales. Given the importance of both community composition and habitat complexity to biodiversity and ecosystem processes, our method provides an effective means of identifying changes in marine habitats and predicting key habitat changes likely to affect marine communities in the face of global change.

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Data availability

All imagery collected by the AUV and used in this study are freely available through the Australian Ocean Data Network Portal at *https://auv.aodn.org.au/auv/* and the Integrated Marine Observing System Data Portal at *http://imos.org.au/auv_data.html*.

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Table 1 Explanatory variables tested to explain the change is surface rugosity at two link sizes (2.5 and 25 cm). Plot was also tested as a random effect but not needed.

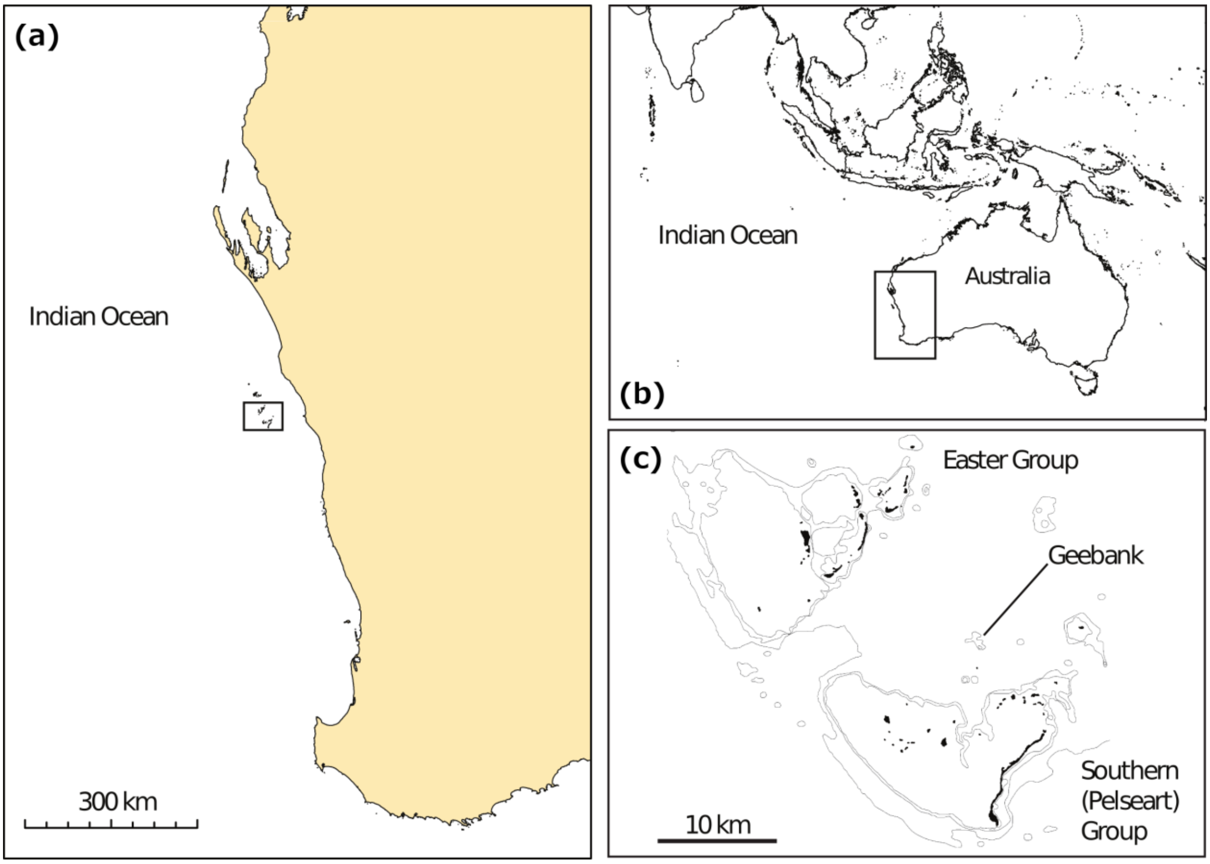
Explanatory variable	**Type and levels**
Bleaching per quadrat	Not totally bleached colonies, totally bleached colonies.
Benthic areal cover in 2010	Branching *Acropora* spp., tabulate *Acropora* spp., plating *Montipora* spp., complex macroalgae and simple macroalgae
Change benthic areal cover between 2010 and 2013	Change in branching *Acropora* spp., tabulate *Acropora* spp., plating *Montipora* spp., complex macroalgae and simple macroalgae

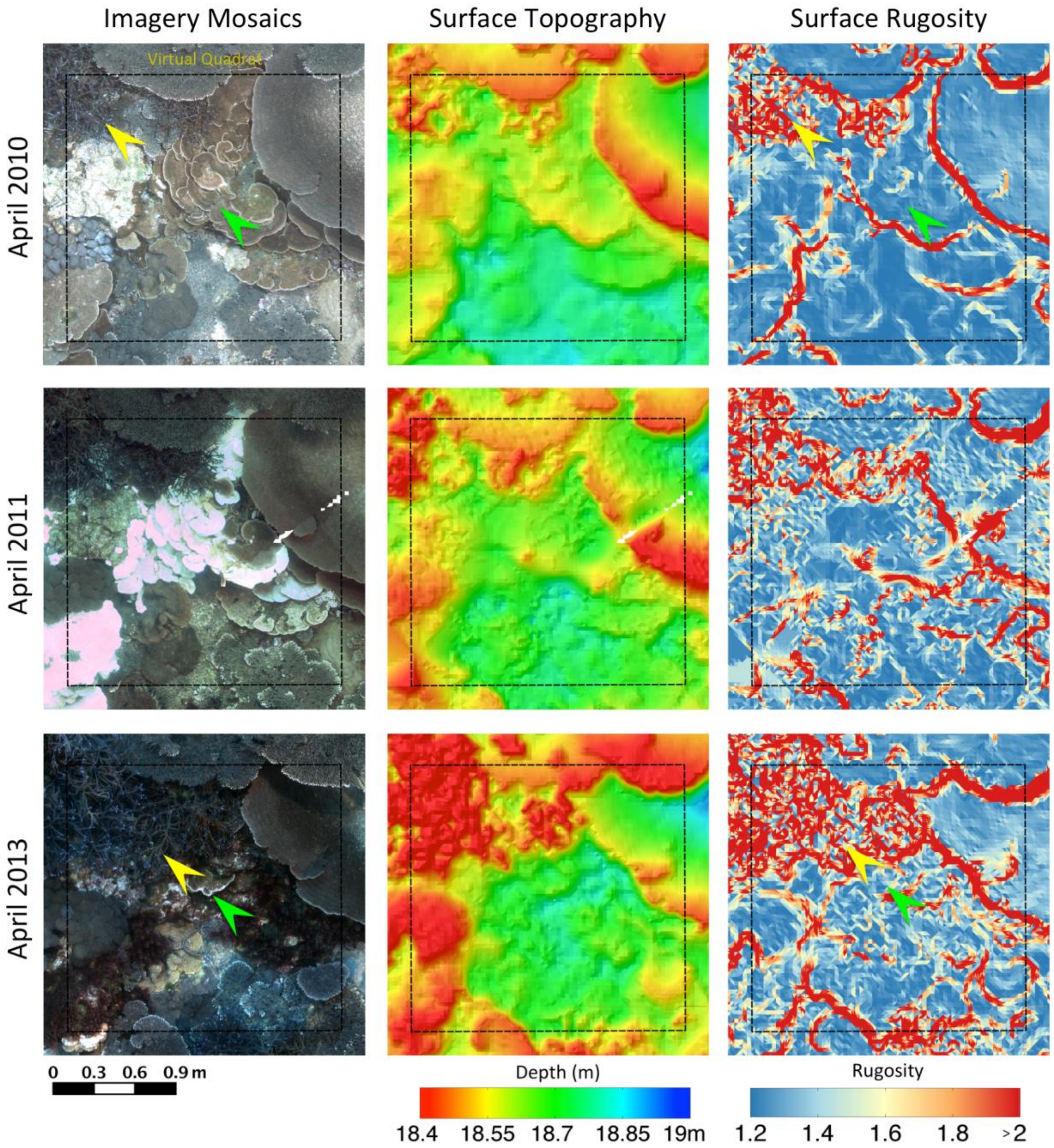
Table 2 Analysis of deviance table for the negative binomial model on the effect of year, bleaching and their interaction on the multivariate abundance of the community composition. P-values calculated using 999 resampling iterations via pit-trap resampling. Values are deviance, in parentheses p-values and residual degrees of freedom. For the PERMANOVA values are sums of squares, F-statistics, (r-squared, p-values).

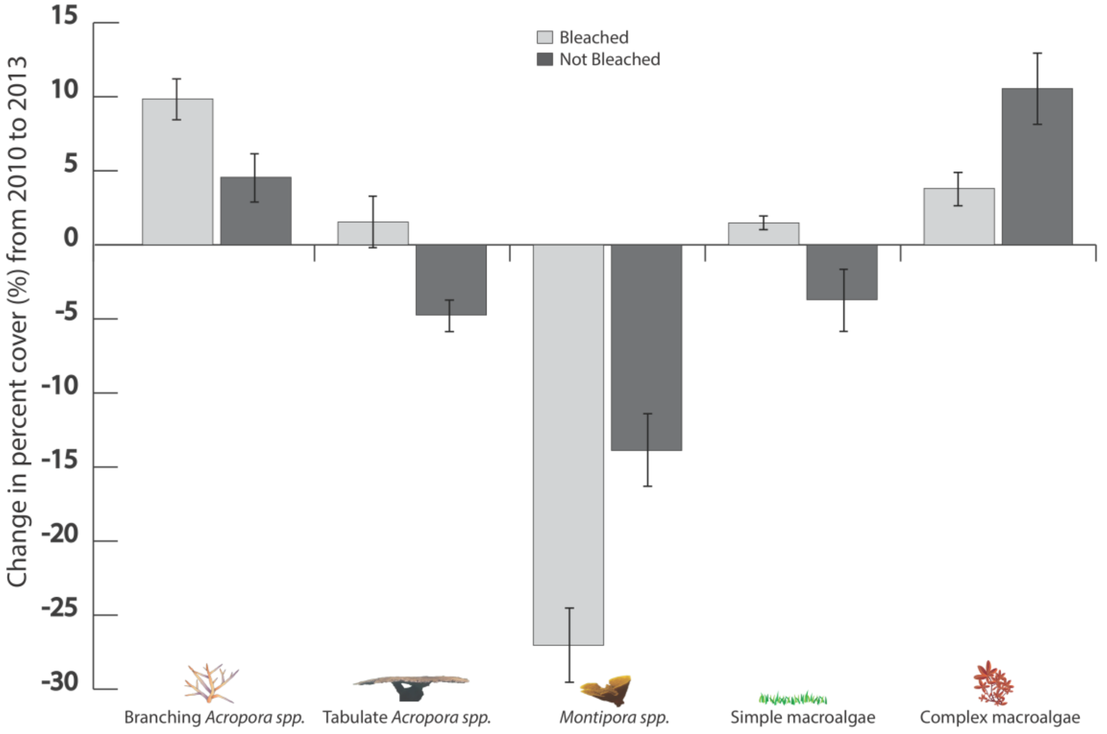
	Change in benthic community composition	
	Negative binomial GLM Test statistic =13.71 (p = 0.001)	*Non-parametric Multivariate Analyses of Variance (Bray-Curtis)*
Bleaching	100.44 (p = 0.001, 120)	1.182, 13.20, (R2 = 0.08, p = 0.001)
Year	43.64 (p = 0.001, 119)	4.48, 32.55 (R2 = 0.19, p = 0.001)
Bleaching : Year	3.445 (p = 0.043, 118)	Not tested

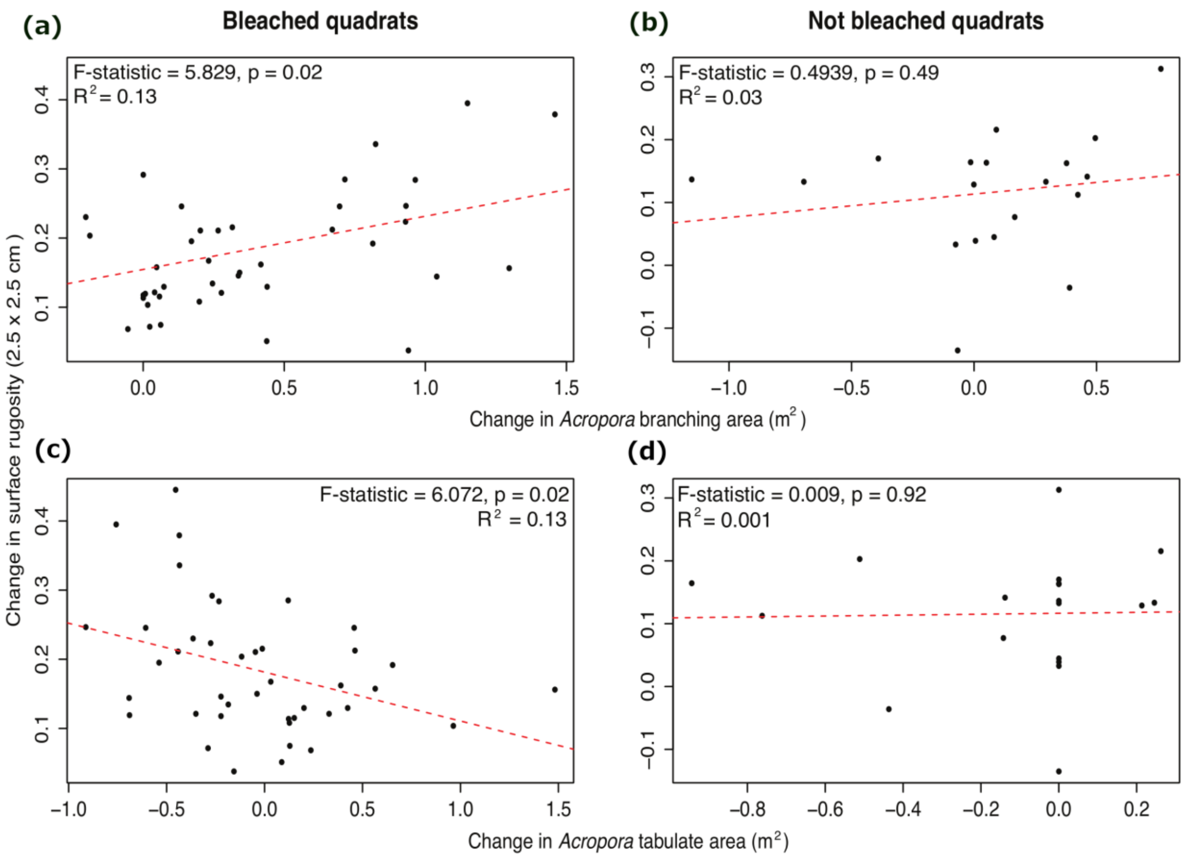
Table 3 Linear model summary table for change in $SR_{2.5}$ and SR_{25} as a function of bleaching, the initial benthic composition and the change in benthic composition of the five dominant taxa (Table 1). Values are model coefficients and in parentheses standard errors and p-values. RDF= residual degrees of freedom, Adj. R^2 = adjusted R squared.

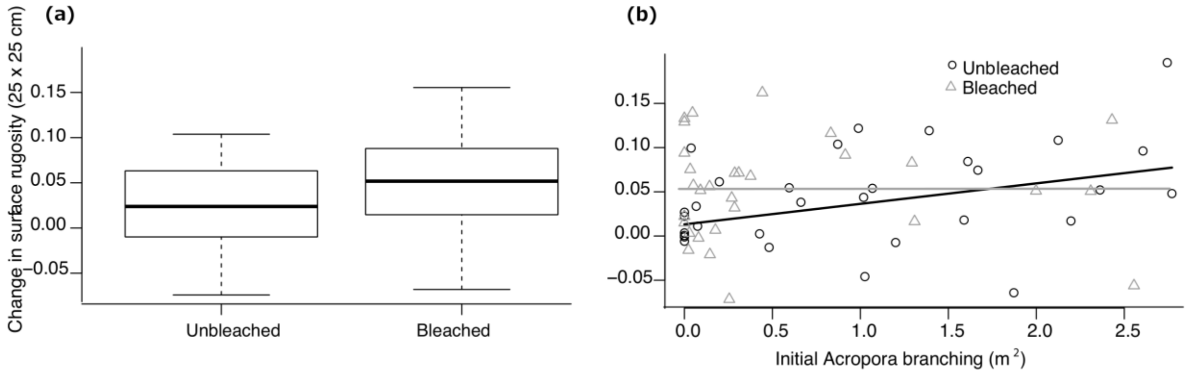
Model term	*Change in surface rugosity from 2010 to 2013*	
	Link size 2.5 x 2.5 cm	*Link size 25 x 25 cm*
Fixed effects	RDF = 58, Adj. R^2= 0.26	RDF = 56, Adj. R^2 = 0.05
Intercept	0.1426 (0.018, $p < 0.001$)	0.0236 (0.013, $p = 0.079$)
Bleaching (bleached)	0.0783 (0.027, $p = 0.005$)	0.0295 (0.015, $p = 0.051$)
2010 Branching *Acropora*	0.0333 (0.013, $p = 0.016$)	0.0129 (0.008, $p = 0.127$)
Δ Branching *Acropora*	0.0531 (0.026, $p = 0.045$)	ns
Δ Tabulate *Acropora*	-0.0503 (0.026, $p = 0.055$)	ns

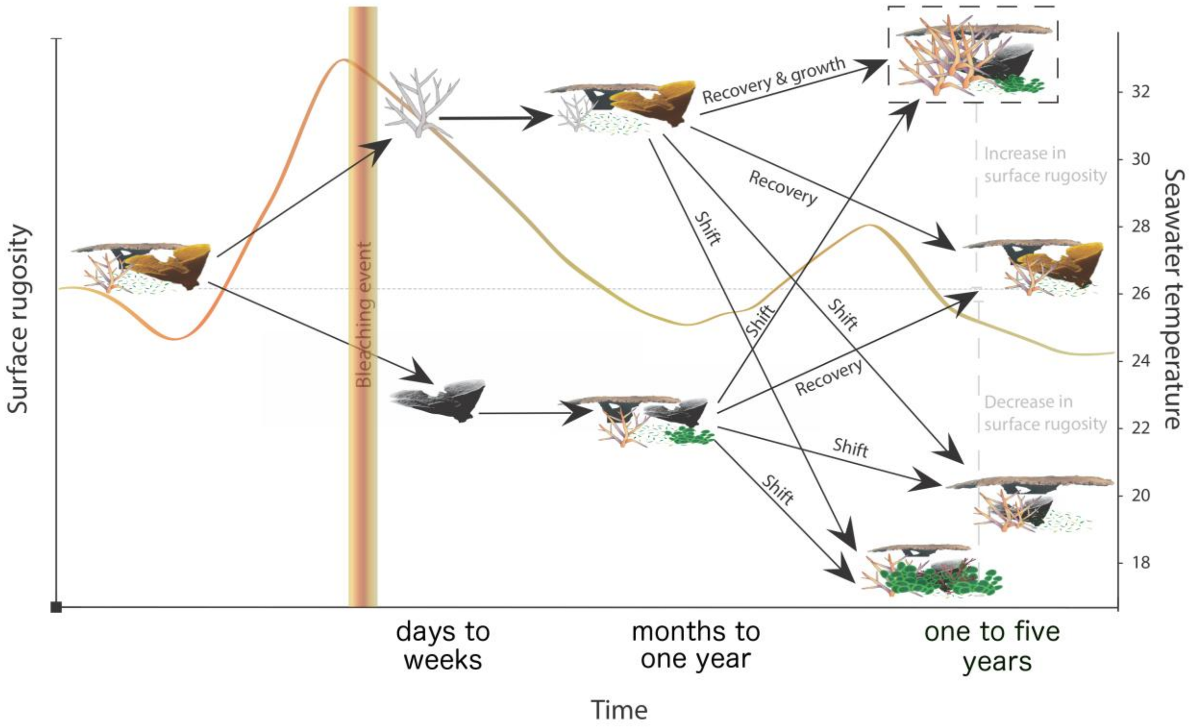

(a)
Indian Ocean
300 km
(b)
Indian Ocean
Australia
(c)
Easter Group
Geebank
Southern (Pelseart) Group
10 km


Imagery Mosaics
Surface Topography
Surface Rugosity
Virtual Quadrat
April 2010
April 2011
April 2013
0
0.3
0.6
0.9 m
Depth (m)
18.4
18.55
18.7
18.85
19m
Rugosity
1.2
1.4
1.6
1.8
>2


Change in percent cover (%) from 2010 to 2013
15
10
5
0
-5
-10
-15
-20
-25
-30
Bleached
Not Bleached
Branching *Acropora spp.*
Tabulate *Acropora spp.*
Montipora spp.
Simple macroalgae
Complex macroalgae


(a)
Bleached quadrats
F-statistic = 5.829, p = 0.02
R² = 0.13
(b)
Not bleached quadrats
F-statistic = 0.4939, p = 0.49
R² = 0.03
Change in *Acropora* branching area (m²)
(c)
F-statistic = 6.072, p = 0.02
R² = 0.13
(d)
F-statistic = 0.009, p = 0.92
R² = 0.001
Change in *Acropora* tabulate area (m²)
Change in surface rugosity (2.5 x 2.5 cm)
0.1
0.2
0.3
0.4
−0.1
0.0
0.1
0.2
0.3
0.0
0.5
1.0
1.5
−1.0
−0.5
0.0
0.5
−1.0
−0.5
0.0
0.5
1.0
1.5
−0.8
−0.6
−0.4
−0.2
0.0
0.2


(a)
Change in surface rugosity (25 x 25 cm)
0.15
0.10
0.05
0.00
−0.05
Unbleached
Bleached
(b)
Unbleached
Bleached
0.15
0.10
0.05
0.00
−0.05
0.0
0.5
1.0
1.5
2.0
2.5
Initial Acropora branching (m^2)


Surface rugosity
Bleaching event
Recovery & growth
Recovery
Shift
Shift
Shift
Recovery
Shift
Shift
Increase in surface rugosity
Decrease in surface rugosity
Seawater temperature
32
30
28
26
24
22
20
18
days to weeks
months to one year
one to five years
Time