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Coral Reef Community Changes in Karimunjawa National Park, Indonesia: Assessing the Efficacy of Management in the Face of Local and Global Stressors

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Abstract: Karimunjawa National Park is one of Indonesia's oldest established marine parks. Coral reefs across the park are being impacted by fishing, tourism and declining water quality (local stressors), as well as climate change (global pressures). In this study, we apply a multivariate statistical model to detailed benthic ecological datasets collected across Karimunjawa's coral reefs, to explore drivers of community change at the park level. Eighteen sites were surveyed in 2014 and 2018, before and after the 2016 global mass coral bleaching event. Analyses revealed that average coral cover declined slightly from $29.2 \pm 0.12\%$ (Standard Deviation, SD) to $26.3 \pm 0.10\%$ SD, with bleaching driving declines in most corals. Management zone was unrelated to coral decline, but shifts from massive morphologies toward more complex foliose and branching corals were apparent across all zones, reflecting a park-wide reduction in damaging fishing practises. A doubling of sponges and associated declines in massive corals could not be related to bleaching, suggesting another driver, likely declining water quality associated with tourism and mariculture. Further investigation of this potentially emerging threat is needed. Monitoring and management of water quality across Karimunjawa may be critical to improving resilience of reef communities to future coral bleaching.

Keywords: benthic community ecology; Coral Triangle; climate change; management; sponges; monitoring; multivariate responses; joint modelling

1. Introduction

Tropical coral communities are degrading globally and at a rapid pace, undermining the functioning of the coral reef ecosystems that they underpin, and the people that depend on healthy reefs for food and jobs [1]. Indonesia, custodians to 17% of the world's coral reefs [2], has the highest human dependence on reefs out of any country [3,4]. Reef degradation is a particularly urgent problem since reefs here support 28% of the world's reef fishers (1.65 million people); protect the home of 12.1 million people, and generate more tourism revenue (US\$2 billion annually) than any other country. Today, just 5% of Indonesia's reefs remain in excellent condition, 25% in good condition, 37% in moderate condition and 32% are badly degraded [5].

Coral declines are driven by multitudinous threats. Poor water quality, disease, coastal development, invasive species and overfishing and destructive fishing practices are among those that can impact reefs locally, but in the past 30 years climate change—particularly ocean warming—has become the primary driver of coral losses both in Indonesia [6] and globally [7,8]. Between 2014 and 2017, an underwater heatwave triggered the third global mass coral bleaching event, with severe and widespread consequences for reefs around the planet [9]. Globally, protecting reefs from climate change requires societal shifts away practises that emit greenhouse gases [10,11], but locally, reef managers have opportunities to alleviate local stressors by limiting harmful activities or establishing protected areas. Improving reef health may buy time, or improve resilience to climate stressors [12,13] (but also see [14]). Assessing efficacy of these types of local management action in the face of multiple local and global stressors requires regular monitoring of reef condition, as well as an understanding of reef communities responses to different drivers of decline. Without being able to disentangle the effects of different stressors, management actions cannot adequately be reviewed and adjusted to improve outcomes. Yet the taxonomic complexity of coral reef communities, different responses to multiple drivers of decline, and the different scales of monitoring and management, present a challenge to achieving this understanding.

1.1. Karimunjawa National Park

Karimunjawa National Park represents one of the world's oldest marine parks [15,16]. Located 120 km north of Semarang in central Java, Indonesia, the park spans an archipelago of 27 coral reef-fringed islands [17] (Figure 1). The park currently incorporates 1101 km² of marine habitat, 13 km² of tropical lowland forest and 3 km² of mangrove forest, and remains one of the largest marine protected areas in Indonesia today [13,18]. This includes 132 km² of coral reefs, including fringing reefs which extend 100 m to 1000 m off rocky slopes of the larger islands of Kemunjan and Kariminjawa, platform reefs such as Menjangan Besar and Menjangan Kecil developed on sand-topped banks, and coral cays [19]. Reefs in the park generally have wide gently sloping reef flats, with steeply sloping (30°) upper fore reef zones where coral abundance is highest, and often a steeper lower fore reef that drops beyond 10 m [20]. These reefs are part of the Coral Triangle, a biogeographic area known to be the global hotspot of marine diversity, and the park hosts a rich diversity of species. Ninety-nine species of coral have been recorded from 51 genera, including protected *Antiphatas* spp. black coral species and 242 species of fish [21]. As well as Karimunjawa's reefs being of biological significance, the park is of vital importance to the region, supporting a local population of 9000 people, including a local fishery and a growing tourism industry [22].

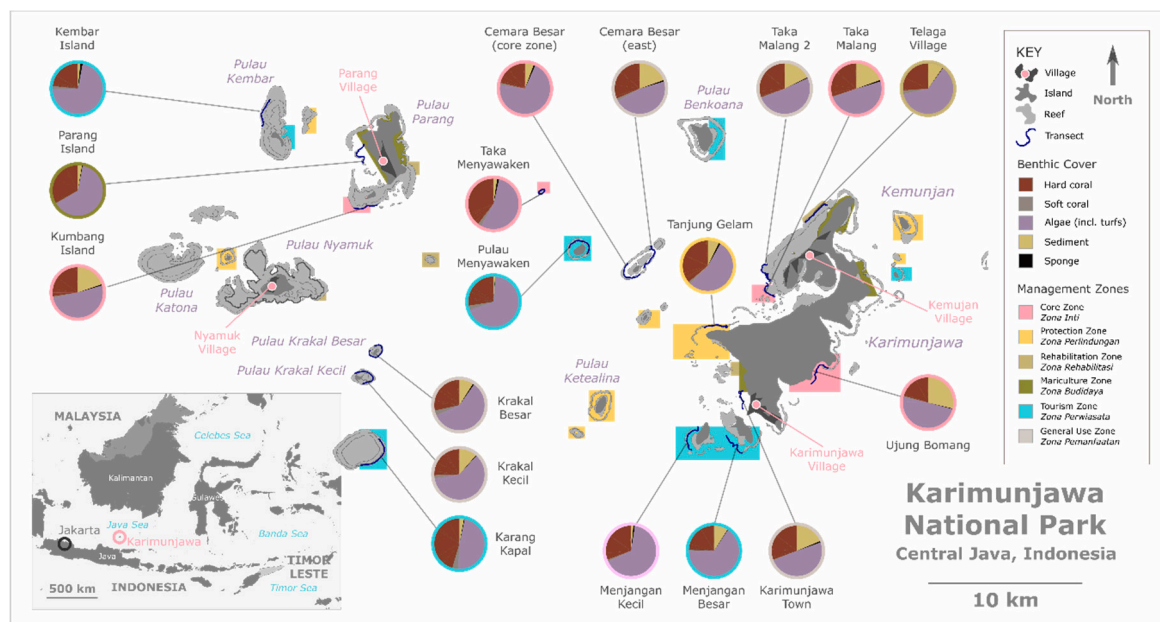


Figure 1. Map of Karimunjawa National Park extent showing islands (dark grey); coral reefs (pale grey); the four major population centres of Karimunjawa Village, Kemunjan Village, Parang Village and Nyamuck Village (pink dots); marine management zones (coloured areas; non-coloured area represent General Use areas); location of the 18 shallow reef surveys (dark blue transect lines), and mean benthic community composition recorded at each site in 2014 (pie charts, border indicates management zone). Sites did not vary significantly in terms of community composition. All sites were dominated by *Algae* (mainly turfs). *Hard coral* cover (mean $29.6 \pm 0.06\%$) ranged from 20.7% at Ujung Bomang to 45.4% at Karang Kapal.

1.2. Threats and Management

Karimunjawa National Park recently ranked in the top third of threatened marine parks in Indonesia, with its reefs scoring highly due to local pressures (a “high vulnerability” anthropogenic threat score, ranking 39/167), in addition to a high likelihood of being exposed to climate change related heat stress compared other areas across the Coral Triangle (“medium vulnerability” climate pressure score ranking 49/167) [16]. These combined local and climate threats are also what make the area a top conservation priority: management action to protect reefs, as well as benefitting fish spawning aggregations and sea turtles, is important to improve resilience to predicted climate stress [13].

Karimunjawa National Park is often used as a case study for collaborative management [18]. Multiple organisations, including the governmental *Karimunjawa National Park Authority* (*Balai Taman Nasional Karimunjawa*), local (e.g., *Taka*, *UCCU underwater coastal clean up group*, *Yayasan 27 Pulo*, *HPI*, *Segoro* and *LSM Karimun*) and international non-governmental organisations (e.g., *Wildlife Conservation Society* (WCS)), and research organisation *University Diponegoro* (UNDIP) recently worked with community members towards a park rezoning plan, and community members are actively involved in ongoing surveillance, monitoring and management implementation [18].

Since its establishment in 1985, management of Karimunjawa National Park has evolved in response to changing threats and feedback from scientific monitoring, as well as changing local and national government policy, and input from the community of 9000 people that live and work in the archipelago [18,23]. Management reviews have led to the park being rezoned twice. The first four zones, established in 1989 based on fishing pressure, were upgraded with the consultation of local stakeholders to an eight zone system in 2005, leading to improved compliance [18,24]. The current six zones were established in 2012 in response to monitoring data (Table 1) [25]. Local threats are also evolving, as tourism and mariculture gradually replace reliance on fishing.

Table 1. Regulations governing activities in Karimunjawa National Park, across the six marine zones (adapted from Campbell et al. 2013 [18]). ‘Traditional Use’ is use by local residents for rituals and for artisanal subsistence fishing (with restrictions on fishing gear and bans on destructive fishing).

	Core Zone	Protection Zone	Tourism Zone	Mariculture Zone	Rehabilitation Zone	General Use Zone
Area (km ²)	4.5	26	27.3	13.1	0.7	1003
Fishing	×	×	P	×	✓	✓
Research	p	p	P	p	p	p
Education	p	p	P	✓	✓	✓
Boat transit	×	✓	✓	✓	✓	✓
Anchoring	×	✓	✓	✓	✓	✓
Tourism	×	×	✓	✓	✓	✓
Restoration	×	×	✓	✓	✓	✓
Traditional use	p	p	P	✓	✓	✓

× = activity forbidden, ✓ = activity permitted, p = permits required, * = except in emergency situation.

Since the 2012 rezoning, the park is divided into six management zones: three designated no-take areas (Zona Inti, or *Core Zones*), seven limited-access *Protected Zones*, seven *Tourism Zones*, three *Rehabilitation Zones* (designed to allow recovery of degraded reefs) and four *Mariculture Zones* (set aside for seaweed farming and fish culture) (Table 1, Figure 1). The remaining park areas are designated as *Traditional Fisheries Utilization area* (Zona Permanfaatan, or *General Use Zone*) where fishing activity remains unregulated.

1.2.1. Local Pressures: Fishing, Aquaculture and Tourism

Fishing

Fishing pressure on Karimunjawa’s reefs has traditionally been intense [15,23]. Seventy-percent of the community are involved in artisanal fishing [24], but the relative proximity of the island group to Java Island, home to more than 60% of the population of Indonesia, also poses a challenge for reef managers [21]. The archipelago continues to be the most important artisanal fishing area in Java Sea region [26] for peri-reefal pelagic fish (70% of the local catch) and reef fish (30%) [21,22]. While the population of Karimunjawa has been stable for over a decade [22], fishing pressure has changed across the park over time [23]. Harmful fishing practices, including cyanide fishing, the use of explosives and poisons, use of rocks for anchors by the fishing community [27] and *muro-ami* were once widespread and practised indiscriminately (except in *Core Zones* [18]). These practises are now less common since protective laws came into effect after much of the reef was damaged [25]. *Muro-ami* was outlawed since June 2011 in Karimunjawa, and more widely across Indonesia in 2015 [28], although some illegal fishing was still occurring in the northwest sector of the park at the time of the study. Reductions in harmful fishing activities have led to an increase in fish biomass, including herbivorous fish (important in maintaining reef health) across the park [23].

Aquaculture

Karimunjawa’s islands have no permanent rivers, human population growth and coastal development are low [29], and the islands are far enough away from the Central Javan mainland to be beyond the influence of run-off. As a result, local reef systems have been traditionally relatively unaffected by pollution [21,30]. However, aquaculture is seeing faster growth than capture fisheries in Indonesia [31], and in Karimunjawa seaweed, grouper and scallop mariculture have increased in recent years [32]. In 2009 seaweed mariculture production totalled 1151 kg, and the 2012 rezoning resulted in a 42% increase in designated *Mariculture Zone* areas in the park [18]. If not adequately managed, increases in mariculture can have consequences for water quality [18,32].

Tourism

Tourism has been actively promoted in Karimunjawa as a strategy to stimulate economic diversification and broaden employment opportunities [29], despite a lack of infrastructure and concerns about impacts on reefs [18]. A ferry from Semarang to Karimunjawa, established in 2003 to support domestic and regional tourism [33], has led to swells in visitor numbers during the tourism season. As a result, the park has experienced an exponential increase in tourism, from 450 visitors in 1998, to >9900 in 2008 to >118,000 in 2016 [34]. Tourism has been accompanied by increased demand for seafood products and shifts in occupations to tour operators, souvenir vendors and boat rentals. Tourism impacts on Karimunjawa's reefs include damage from people walking on the reef, coastal development, an increase in the volume of garbage, and declines in water quality.

1.2.2. Global Pressures: Climate Change

Karimunjawa's seawater is predicted to warm faster than other areas regionally, meaning its reefs are more likely to experience coral bleaching compared to other reefs in the Coral Triangle [13,16,35]. All three global coral bleaching events impacted corals in the park: the 1997–1998 global coral bleaching led to coral mortality rates of 50–60%, and mass bleaching was also reported in 2010. Mean monthly ocean temperatures in Karimunjawa range from 28.3 °C in August to 29.8 °C in April (based on long term average from 2007 to 2020 [20,36]). Between 2015 and 2016 sustained warmer-than-usual conditions were reported in the park with temperatures rising from October 2015 through April 2016 where they peaked around 30.5 °C [37]. Eighty-eight percent of corals surveyed across 19 sites at the time responded negatively to elevated sea temperatures: 49% of corals surveyed during the event showed some paling, 27% were fully bleached and 12% had died [37].

1.3. *The Challenge: Using Monitoring Data to Understand the Effects of Local vs. Global Stressors on Complex Coral Reef Communities*

Disentangling the effects of local and global stressors on reef communities by analysing benthic monitoring data can be challenging. Lack of adequate sampling data and appropriate analytic approaches undermine our ability to determine whether observed shifts in the benthic composition are statistically significant, ecologically meaningful, and whether they are driven by local pressures or wider scale environmental changes.

Firstly, ecological monitoring data are not always sufficient in coverage or detail to confidently draw conclusions [38]. Reefs host complex benthic communities of diverse algae and invertebrate taxa, and in-water assessments relying on SCUBA can be time-consuming and require expertise for identification. This often results in trade-offs in sampling effort, where inferences about reef condition are drawn from limited sampling points representing large areas (e.g., line intercept methods), or from sampling large areas but in a limited level of detail (e.g., manta tows) [39].

Secondly, ecological monitoring data are not always straightforward to interpret. The abundance of reef-building hard corals as a proportion of benthic cover, or “coral cover”, when viewed from above in planar perspective, is widely adopted as a proxy for reef condition. Coral cover is a metric that captures the component of the community responsible for habitat creation, reef framework construction, sand generation and many of the other ecosystem services that make coral reefs so valuable, and importantly can be compared between studies and across space and time. Corals however, comprise taxonomically diverse communities, growing in three dimensions, which interact in a myriad of ways, both with each other and with other components of the benthos (e.g., algae), as well as in response to the external environment: meaning the metric, and the taxonomic level at which its applied, can mask important information [40]. Establishing the drivers and meaning of observed coral cover changes can be further confounded by multiple drivers of coral loss, which may operate over divergent scales from local (point source pollution) to global (climate-driven bleaching). Moreover, these scales often differ to the scales at which monitoring (transect scale) and management (reef/region scale) occur [41]. Appropriate

approaches to understanding multivariate ecological abundance data are needed, to analyse abundance data collected simultaneously across many taxonomic groups [42].

In this paper, we address both these challenges, (1) by using emerging technologies to gather large amounts of fine scale benthic cover data across Karimunjawa's coral reefs, and (2) by employing Bayesian statistical modelling to detect meaningful changes in benthic community composition.

1.4. Aims

The study aimed to (1) identify benthic community changes and (2) attribute these to local and global drivers of stress, in order to assess management efficacy and provide guidance and feedback on coral reef condition. This was achieved firstly by assessing variability in benthic community composition, both (a) *spatially* across the park, looking for variability across different management zones, and (b) *temporally* between 2014 and 2018, to examine changes with time. Secondly, on detection of any meaningful variability, we asked how changes relate to local factors (such as management efficacy, e.g., zonation) and global factors (such as climate change, i.e., the 2016 coral bleaching event).

Underwater camera-scooters allowed significantly larger areas of reef to be assessed compared to standard survey assessments, generating a dataset more appropriate for understanding largescale variability across the park (regional variability) in the context of local and global change [43]. The technology also allowed us to return to the exact same location, to get an accurate representation of change at a very fine level (meter scale), in order to better understand reef-level variability. Deep learning approaches to gathering data allowed us to extract a greater level of taxonomic detail usually available from rapid surveys.

Meanwhile, the analytical approaches employed to explore the dataset allowed us to assess how multiple components of the benthic community were responding and how that related to zonation, bleaching stress and time, and detect subtle effects that would be missed by standard analytical approaches for exploring reef data.

2. Materials and Methods

Karimunjawa was chosen as a study site because of its size, age and importance [18], and to compliment the efforts of the *Indonesian Coral Reef Rehabilitation and Management Program* (COREMAP) in order to deepen the coverage national reef resources [26,44]. Research was conducted in the dry season (May to October), when the prevailing eastward flow of surface current present during the northwest monsoon is in reverse, and salinity is higher (35 PSU compared to 31 PSU during monsoon) [20]. All data presented here, including photo quadrats, are freely available to download at [45].

2.1. Ecological Surveys

Ecological surveys were conducted at 18 reef sites across Karimunjawa National Park between 8th and 18th October 2014, and repeated between 26 May to 5th June 2018, under SIMAKSI Permit numbers B-3181/IPK.2/KS/X/2014 and 2486/FRP/E5/Dit.KI/V/2018, respectively (Figure 1, Table A1). Sites were selected to capture a representative range of reefs across the park different management zones: six *General Use* zones, five *Core Zones* (Zona Inti), five *Tourism Zones* (Zona Pemanfaatan Perwiasata), two *Rehabilitation Zones* (Zona Rehabilitasi), an *Aquaculture Zone* (Zona Budidaya) and a *Protection Zone* (Zona Perlingdungan) [24]. Several sites also coincided with *Balai Taman Nasional Karimunjawa* and *Wildlife Conservation Society* long term monitoring plots across the park, for validation. All surveys were conducted on SCUBA using a custom-built diver operated underwater propulsion vehicle, which had an integrated camera system consisting of three synchronised Canon 5D-MKII cameras [43]. High-resolution (21 mp) images of the benthos were taken every two meters along a 700 m linear transect, following the upper fore reef slope contour at a depth of ~7–9 m. These shallow slopes were targeted as the area of the most living coral growth [20]. Images were geo-referenced using a surface GPS unit tethered to the diver. Depth and altitude of the camera relative to the surface

and the reef benthos were logged at half-second intervals using an altimeter (Echologger AA400, from EofE Ultrasonics Co, Korea) allowing for the selection of imagery within a particular depth and altitude range (7–9 m depth and 0.5–2 m altitude) needed to maintain consistency and address variable environmental conditions.

2.2. Photo Quadrat Processing

Images were analysed using a deep learning framework to extract important biological information about the composition of reef [46,47]. In 2014, 23,135 raw images were initially collected from the area, with a further 19,085 in 2018. Images were flattened, cropped to a standardised 1 m² photo quadrat and colour-corrected prior to automated analysis [43,46]. A subset of 752 randomly sampled images were manually annotated at 100-point locations per image using CoralNet (<http://coralnet.ucsd.edu/>), where the substrate beneath each point was identified and assigned to one of 53 benthic substrate categories (see Appendix A, Table A2 for category labels and descriptions). Categories were derived from existing benthic classifications [48,49], modified to capture broad functional role but also limited by how reliably features could be identified from images by human annotators [47]. These manual annotations were used as training datasets to train a deep learning algorithm for automated image classification. The deep learning framework was then used to automatically analyse each image based on the training dataset of 752 human-annotated images [47].

The deep learning framework employed a number of convoluted filters that examine attributes of texture and colour to identify the parameters that best describe each of the benthic categories, based on the manual annotation dataset. Based on these filters, a weighted neural network architecture is built and optimised through numerous iterations that predict and assign a label to each point in an image in a few microseconds (< 0.2 s/50 points). A standard point sampling protocol of 50 randomly selected points per image was used to estimate coverage on targeted benthic categories. Automated estimations of cover had low errors (between 2% and 6% difference in abundance estimates to a human annotator, well within the range of reported inter-observer variability) and a comparable power in detecting temporal trends (for more details see Gonzalez et al. [47]). Classification using the trained neural networks took about 36 h per 50,000 images (200 × the speed and 1% of the cost of a manual analysis), and was completed for all sites by September 2018. All data are public access and freely available to download [45].

2.3. Bleaching Data

Degree Heating Weeks (DHW) were used to estimate heat stress impacts leading to mass coral bleaching across the park, following NOAA Coral Reef Watch (CRW) methods. In this study, DHW was derived from the Coral Bleaching HotSpot product that provides an instantaneous estimate of total heat stress over a 12-week window at a spatial resolution of 5 km [50,51]. Bleaching had been recorded throughout the Karimunjawa National Park in April 2016 [37]. Values of DHW from 1 January 2016 to 31 December 2016 were extracted from the NOAA CRW database and maximum DHW selected [52].

2.4. Statistical Analyses

Data analysis on abundance (percent cover) of benthic groups within the Karimunjawa National Park were performed using the R software (R Core Team 2016), following a methodology developed by Vercelloni et al. [53]. Benthic groups were aggregated into *Hard coral*, *Soft coral*, *Algae*, *Sponge* and *Sediment* by summing different sub-groups to produce group relative abundances (Appendix A, Table A2). *Hard coral* included six broad eco-morphological groups of hermatypic scleractinian corals (Table A2 for full list), as well as the non-scleractinian hydrocoral *Millepora* and blue octocoral *Heliopora* ('NON_HERM' in the public access database); *Soft coral* grouped all Alcyonacea, including the leathery soft corals of the Alcyoniidae family (e.g. *Sarcophyton* and *Lobophytum*); gorgonian sea fans, plumes and whips belonging to the Holaxonia and Scleraxonia sub-orders ('GORG'), and other soft coral groups like *Xeniidae*; *Neptheidae*; *Tubipora*; *Briareum* ('OTH-SF'); *Algae* included all fleshy and encrusting

macroalgae (>1 cm in height) along with cyanobacteria ('MACRO'), crustose coralline species ('CCA') and turf algae growing over rocky reef matrix or rubble (epilithic algal matrix or 'EAM'); *Sponges* include four different types of sponges (barrel forms, branching and rope, encrusting forms and fan-like sponges), and *Sediment* included all loose non-living substrate, such as rubble, sand and sediment.

Quadrats were grouped into 100 m sub-transects, a) in order to exclude any data where transect line deviated, so that the exact same section of reef (to within 5 m, the GPS error range) could be directly compared between years, and b) so that data analysis took place at an appropriate ecological scale [53]. Sub-transects were generated using hierarchical clustering based on Euclidean distance between geo-located quadrats within transects [53]. We retained sub-transects composed of a minimum of three images per surveyed year and repeated in 2014 and 2018. A total of 672 sub-transects matched these two selection criteria, leading to a set of data ranging from 12 to 52 sub-transects across the reef sites.

A multivariate statistical model was developed to estimate changes in benthic groups across the Karimunjawa National Park, using count data extracted from photo-quadrats (equivalent to traditional benthic community coverage "percent cover" metric). Abundance was characterised by count data of the sub-transect i (with $i = 1, \dots, 672$) and benthic group j (with $j = 1, \dots, 4$ corresponding to 1 = hard coral, 2 = soft coral, 3 = algae, 4 = sponge and 5 = sediment) and time t (with $t = 1, 2$), and modelling using a negative binomial distribution. A joint modelling approach was used to estimate the influences of management zoning, (*Zone*), bleaching (*DHW*) and sampling year (*Year*) on the full set of observations of benthic groups [42,54]. The joint modelling approach used latent variables to induce correlation across benthic groups and allows to tease apart the influences of *Zone*, *DHW* and *Year* from missing information in the estimation of co-occurrence patterns. Missing information can be attributed to missing environmental explanatory variables and biotic interactions that were not accounted for. The R package Boral was used to implement the model in a Bayesian framework [54]. The full model equations and diagnostics for model result and validation are presented in Supplementary Materials.

3. Results

Over three hectares of coral reef were photographed and analysed across 32 km of Karimunjawa National Park, before and after the 2016 bleaching event (32,171 m² of detailed benthic data: 16,244 photo quadrats in 2014 and 15,947 in 2018).

3.1. Spatial Variability in Benthic Composition

Hard coral percent cover across the 18 reef sites surveyed appeared uniform at $29.6\% \pm 0.06\%$ (Standard Deviation, SD) in 2014, ranging from 20.7% at Ujung Bomang to 45.4% at Karang Kapal (Figure 1). Coral communities were typically dominated by foliose and massive coral species, which made up ~60% of the coral community at most sites (Appendix A, Figure A1). *Algae* was the dominant benthic group at every site surveyed, accounting for at least half of the benthos in every area ($57.7 \pm 0.09\%$ across the park in 2014; $59.9 \pm 0.09\%$ in 2018, Figures 1 and 2). *Algae* was predominantly comprised of "epilithic algal matrix": rocky substrate covered in turf algae or biofilm ('EAM' category in the database, for full definitions see Table A2), which was responsible for 95–99% of the *Algae* category at every site. Macroalgae ('MACRO', $0.91 \pm 0.10\%$) comprised less than 1% of the benthic cover. The most common macroalga seen was *Padina* spp, and *Halimeda* was also responsible for a large proportion of macroalgae, along with *Caulerpa*, *Dictyota* and cyanobacterial mats. Crustose Coralline Algae ('CCA', $0.13 \pm 0.15\%$), when grouped with Macroalgae made up just over 1% of the *Algae* total cover. The remainder of the cover at most sites was typically loose sandy substrate (*Sediment*), which made up about 10% of the benthos ($10.4 \pm 0.08\%$). Both *Soft coral* and *Sponges* remained low abundance across the Park with less than 3% cover (Figure 2). There were no obvious differences in benthic group abundance across *Zone*, based on percent cover (Figure 2).

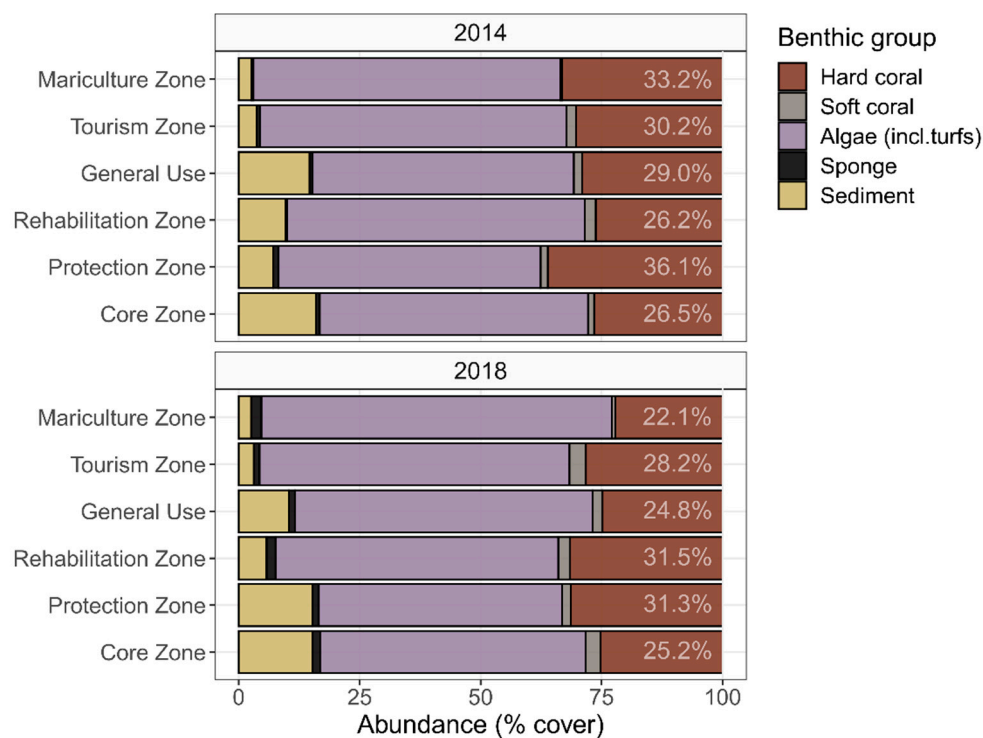


Figure 2. Relative cover of the five benthic categories per management zone (six Zones tested) and sampling year (2014 vs 2018). *Hard coral*, *Soft coral* and *Algae* categories aggregate several benthic communities while *Sediment* and *Sponge* are mainly composed of loose substrates and sponges, respectively (Appendix A, Table A2 for descriptors and access to the dataset). Percent cover values of *Hard coral*, a commonly used reef health metric, are provided on the plot.

Initial inspection of percent cover data suggest little observable difference in benthic community composition between management zones across the park (Figure 1), in either year (Figure 2, see also Figure A1). The statistical model confirmed this (Figure 3a). There was little detectable difference between zones, with *Soft coral*, *Sponge* and *Hard coral* all systematically present in all six management zones. Model uncertainty (width of the 95% credible intervals) was higher for some benthic groups especially for *Soft coral* and *Sponge* and lower for *Algae*, but was considerably higher than for other factors tested (i.e., *Year* and *DHW*: note difference between Figure 3 panel a and b x-axis). Uncertainty usually occurs either where the absolute abundance was low (e.g., in the case of *Sponges*), or where values were similar across different treatments (e.g., *Hard Coral*). This further confirms that management Zones were not particularly good at explaining variability (Figure 3b).

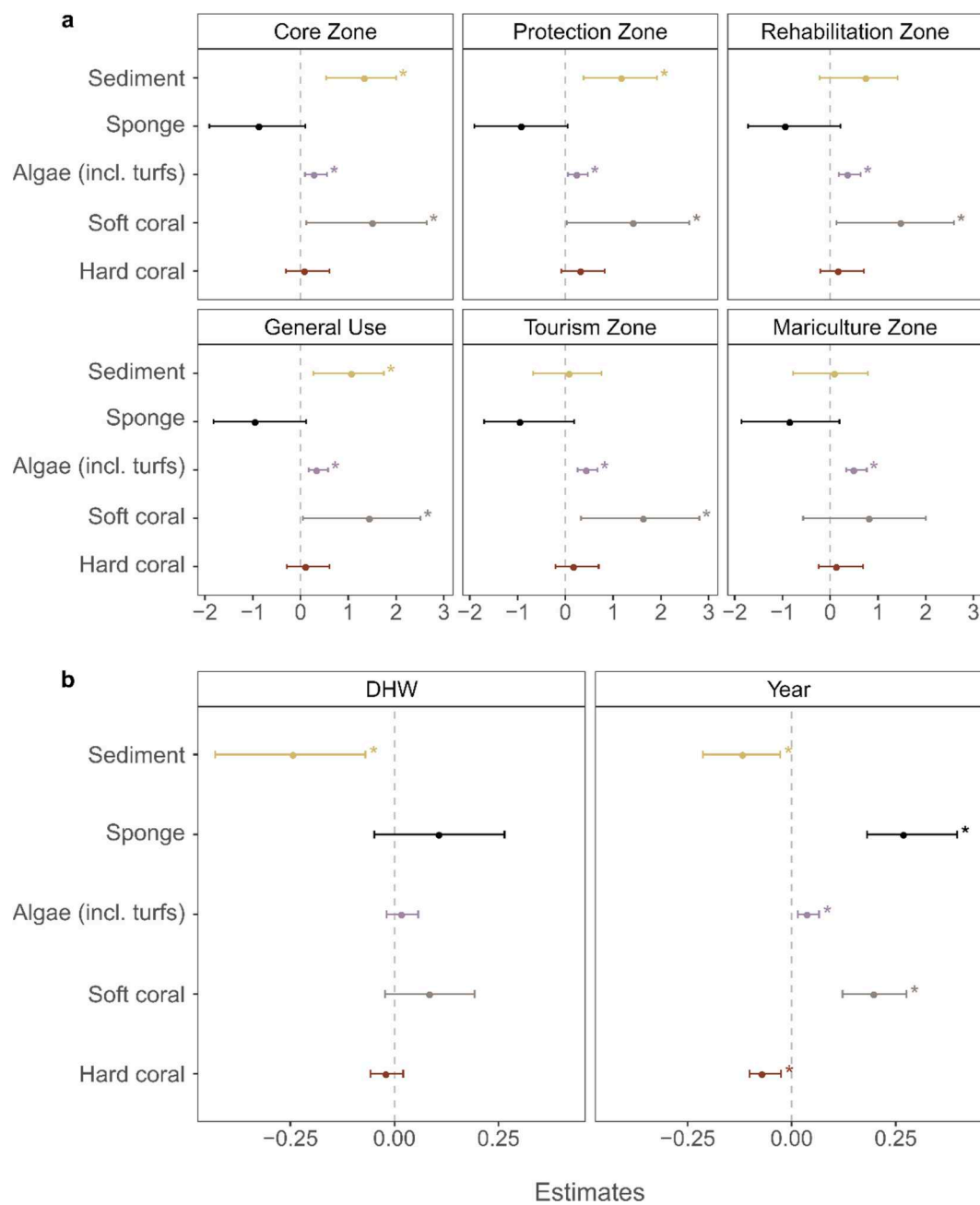


Figure 3. Effect size of local and global pressures on benthic groups. Local pressures are estimated through management zones (**a**) and changes between 2014 and 2018 (Year, **b**), while global pressures include Degree Heating Weeks (DHW). Error bars indicate the 95% credible intervals estimated from the posterior distributions of model parameters. Stars indicate significant effects when 95% credible intervals did not include zero.

3.2. Temporal Variability in Benthic Composition

Hard coral abundance appeared fairly stable across Karimunjawa National Park between 2014 and 2018, with mean percent cover declining slightly from $29.2 \pm 0.12\%$ (SD) in 2014 to $26.3 \pm 0.10\%$ (SD) in 2018 (Figure 2). *Algae* also appeared relatively constant through time ($57.7 \pm 0.14\%$ in 2014, $60.5 \pm 0.14\%$ in 2018). Initial inspection of percent cover of *Sediment* ($10.8 \pm 0.15\%$ to $9.3 \pm 0.12\%$), *Soft Coral* and *Sponge* also suggested these groups appeared stable between the surveys (Figure 2, Table A2).

The joint modelling approach allowed us to explore statistical variability at the park scale, based on fine scale comparisons of 2014 and 2018 data. Model outputs revealed that the observed 2.9% relative decline in *Hard coral* actually represented a significant (i.e., 95% credible intervals did not include zero) shift in benthos by -6.8% (-10.1% ; -2.5% , 95% CI), (Figure 3b, Year). *Sponges* showed the most dramatic change, with an 27.2% increase between 2014 and 2018 (18.1% ; 39.7% , 95% CI). *Soft coral* increased by 20.0% [12.2% ; 27.5% , 95% CI] and *Algae* to a lesser extent by 4.0% [1.4% ; 6.6% , 95% CI]. There were also significant decreases in *Sediment* 11.5% [2.7% ; 21.4% , 95% CI] generally across the park (Figure 3b, Year). In summary despite initial apparent temporal stability, all benthic components measured saw significant park-wide shifts in abundance between 2014 and 2018 (Figure 3b, Year).

3.3. Global Pressures: Effect of Ocean Warming

Thermal stress between 2014 and 2018 was used as a proxy to explore impacts of the global coral bleaching event on Karimunjawa's coral reef benthic communities. Sea surface temperatures recorded in the area between 2014 and 2018 were between 27.05 and 31.10 °C, with average of 29.22 ± 0.71 °C (NOAA). Although the park experienced several warmer than usual periods, only one event occurred where DHW was high enough to trigger mass bleaching. Kembar Island and Telaga Village sites experienced greatest DHW, while the southern half of the park, including Central Karimunjawa Park Islands (Karang Kapal, Krakal Kecil and Krakal Besar) and southern sites on Karimunjawa Island (Menjangan Kecil MDC, Menjangan Besar MDC, Karimunjawa Town and to a lesser extent Ujung Bomang) received lower DHW scores (<2 DHW). Model outputs revealed that DHW alone were unable to explain the minor park-wide declines in *Hard coral*: while the model related DHW to slight *Hard coral* declines (detecting a 1.7% decrease between 2014 and 2018), the associated 95% credible intervals include zero indicating no significant effect [-5.7 ; 2.1%], Figure 3b, DHW). The 2016 bleaching stress could not explain increases in *Sponge*, *Algae* or *Soft Coral* either (Figure 3b, DHW).

Inspection of model outputs at the sub-level revealed that within *Hard Coral* only two of the seven coral sub-groups were not negatively affected by bleaching (Figure 4b, DHW). Branching *Acropora* species ('ACR_BRA' in the database, see Table A2) were the most negatively impacted (-0.73 [-0.86 ; -0.59 , 95% CI]), followed by brain-like massive, submassive and encrusting species ('MSEM', -0.51 [-0.69 ; -0.34 , 95% CI]), and free-living mushroom corals ('FREE', -0.44 [-0.62 ; -0.29 , 95% CI]). Other branching non-Acroporid species ('BRA_nACR', -0.24 [-0.40 ; -0.05 , 95% CI]), and the most abundant group, foliose corals ('FLP', -0.21 [-0.32 ; -0.10 , 95% CI]) were all negatively impacted. *Millepora* ('NON_HERM') and tabulate Acroporid corals ('ACR_TCD') were not significantly affected. DHW were also associated with positive and significant effects on massive corals (MSE, mainly massive *Porites* (0.53 [0.44 ; 0.61 , 95% CI]) and crustose coralline algae (0.30 [0.002 ; 0.53 , 95% CI]), (Figure 3b, DHW).

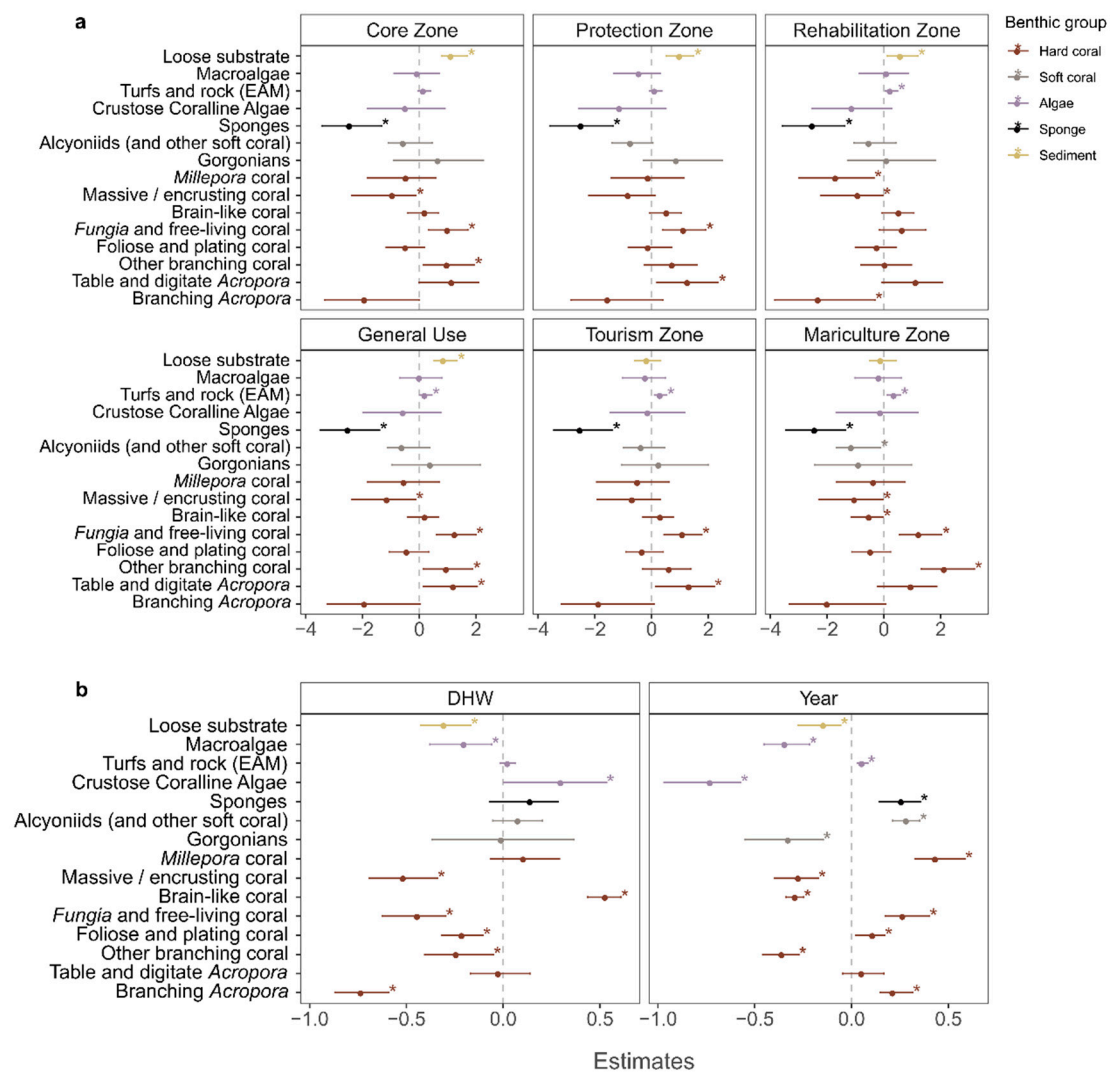


Figure 4. Effect size of local and global pressures on benthic sub-groups (see Appendix A, Table A2 for definitions). Local pressures are estimated through management Zones (a) and changes between 2014 and 2018 (b, Year), while global pressures include Degree Heating Weeks (b, DHW). Error bars indicate the 95% credible intervals estimated from the posterior distributions of model parameters. Stars indicate significant effects when 95% credible intervals did not include zero.

3.4. Local Stressors: Effect of Management Zone

Management zones were used as a proxy to examine the impacts of local pressures on Karimunjawa's coral reefs. The *Rehabilitation* zone was the only zone to see an increase in *Hard coral* cover between 2014 and 2018, with a 20.2% relative increase in coral from $26.2 \pm 0.06\%$ (SD) to $31.5 \pm 0.07\%$ (SD) %. All other zones mirrored the general pattern of slight decline, with *Mariculture* zones seeing the greatest declines -33.3% in *Hard Coral*. The greatest detectable changes occurred for the group of *Sponges* in the *Rehabilitation* and *Mariculture* zones with relative increase of 551.5% and 471.6%, respectively (Figure 2). *Soft coral* and *Sponges* also increased in the *Core Zone* between 2014 and 2018 by 146.3% and 101.4%, respectively. In the *Protection Zone*, the *Sediment* group increased the most, estimated to be 112.6%. The highest relative decreases are for unconsolidated substrates in the *Rehabilitation* and *General Use* zone (40.1% and 34.1%, respectively) and *Hard coral* in the *Mariculture Zone* (33.2%).

Although *Hard coral* appeared to decline slightly across zones and between years, closer examination of sub-benthic groups revealed increases in some coral taxa (Figure 4, Year). Branching

Acroporids ('ACR_BRA') and foliose corals ('FLP') substantially increased in abundance by 21.6% [14.7%; 31.6%, 95% CI] and 11.1% [2.1%; 17.2%, 95% CI], respectively. Free-living mushroom corals ('FREE') and *Millepora* ('NON_HERM') also increased by 26.7% [17.3%; 40.3%, 95% CI] and 43.6% [32.8%; 58.7%, 95% CI]. Meanwhile, massive corals (MSE and MSEM, defined in Table A2) had declined by around 30%, along with branching non-acroporids (−35.7% [−45.9%; −27.2%, 95% CI]). All sub-groups of corals had significantly altered in abundance (with the exception of tabulate *Acropora* ACR_TCD, which had increased but not significantly): these large increases in branching and foliose and declines in massive species masked changes in total percent cover of *Hard coral* (Figure 4, Year).

3.5. Community Co-Occurrence Patterns

Significant interactions were estimated within the two distinct parts of the multivariate model (Figure 5): both the explanatory part of the model including the effects of *Zone*, *DHW* and *Year* (Figure 5, left panel), and the latent variables that could not be explained by the predictors (Figure 5, right panel). Co-occurrence patterns identified included strong negative interactions between *Hard coral* and *Sponges*, and *Algae-Sediment* estimated at −0.51 and −0.92, respectively. A negative co-occurrence was also found for *Hard coral-Sediment* estimated at −0.44. These *Sediment* interactions were also captured and strengthened in the co-occurrence patterns associated to the missing information part of the model (Figure 5, right panel). Additional negative interactions are estimated including *Sediment-Soft coral* (−0.42). *Algae* were also negatively associated with *Soft coral* and *Hard coral* in the latent model (−0.43 and −0.42, respectively). *Soft coral* and *Hard coral* were strongly positively associated (0.99).

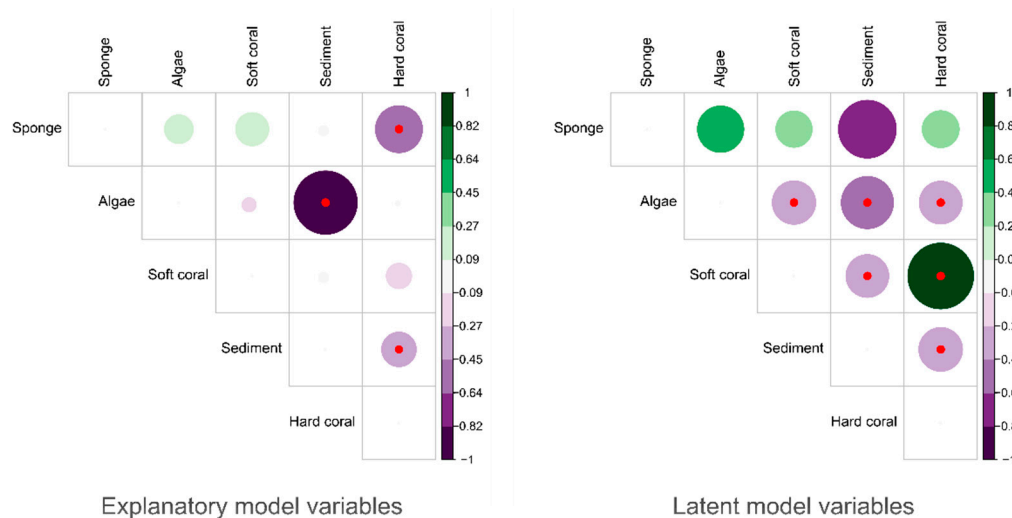


Figure 5. Co-occurrence patterns associated to the explanatory model variables (management *Zone*, *DHW* and *Year*, left panel) and to the unknown information part of the model (latent variables, right panel). Colours and sizes of circles indicate the directions (positive or negative) and strength of interactions, respectively. The red dots highlight significant co-occurrences (whose 95% credible intervals did not contain zero).

4. Discussion

A combination of camera-scooter survey technology and automated image classification enabled collection of larger amounts of consistent fine-detail benthic cover data across Karimunjawa's coral reefs than previously possible, while Bayesian statistical approaches allowed the large multivariate dataset generated to be explored in detail at the regional scale. Results highlighted changes in benthic community composition across the park between 2014 and 2018, including a slight decline in *Hard coral* that masked much larger shifts in coral community from massive to more complex and fragile foliose and branching corals, and a significant increase in sponges and soft corals, all of which occurred across the park. At first glance, most of these patterns appeared to be ubiquitous and unrelated to

management zone, but negative correlation identified between *Sponge* and *Hard coral* suggest that *Zones* (the explanatory variable) with more sponges had much fewer corals, and vice-versa (Figure 5). Total *Hard coral* cover remained relatively high, and the 3% loss observed did not appear to be related to the 2016 bleaching event (Figure 3b, DHW), although minor but detectable effects were observed on most coral groups tested, but particularly branching *Acropora* (Figure 4b, DHW).

4.1. Spatial Variability: Status of Karimunjawa's Coral Reef Benthic Composition across the Park

Surveys indicated that Karimunjawa's benthic reef communities were compositionally similar across the Park (in both years), with little variability in the relative ratios of *Hard coral* (around ~30%) to *Algae* (~60%) and *Sediment* (~10%) and remaining *Sponge* and *Soft coral* (Figure 2). This level of coral cover is generally high compared to reported regional means of <25% cover [6]. Apparent homogeneity across reefs may be due to underlying biogeography: the park covers a relatively small area, and early ecological surveys of the park suggested reef communities were less variable than in other places across South East Asia [21].

Coral communities were dominated by massive *Porites* ('MSE', typically $44.0 \pm 15.1\%$ (SD) of the *Hard coral* abundance), and foliose and plate coral types (FLP typically $27.4 \pm 10.1\%$) (Appendix A, Figure A1), with most coral types not varying spatially within or between zones (Figure 4a). Interestingly, the model detected that branching Acroporids ('ACR_BRA', including branching and bottle brush *Acropora* spp.), typically a more minor part of the community in 2014 (5.2% of coral abundance), were more widespread and consistently pervasive, while the dominant massive *Porites* ('MSEM') showed more spatial variability—or more patchily distributed (Figure 4a).

Different survey methodologies may explain why our finding of ~27% *Hard coral* cover in 2014 was lower than observations of ~38–60% reported in 2009 [55] and 62% (range 34–97%) reported in 2015 [56]. Traditional 50 m survey line intercepts often target locations dominated by corals, while the 750 m+ transects conducted as part of this study would have transited more diverse habitats, including sand filled gullies and rubble patches avoided by standard 50 m transects [57]. This also explains negative correlations identified between *Algae-Sediment*, and *Hard coral-Sediment* that were related to zone (Figure 5): some transects transited more areas of sand, where *Algae* and *Hard coral* which need hard substrate to attach to, cannot grow. Despite reported differences in the absolute values for percent cover *Hard coral*, our 2014 data agreed with the trends and conclusions of both reports. The 2015 Balai Tamen dataset was consistent in showing that *Protection Zones* had slightly higher *Hard coral* cover (70%) compared to *Core Zone* (62%) and *General Use* (50%) zone, although this difference in our data did not appear to be maintained through to 2018 as *Protection Zones* eventually lost coral cover (Figure 2, Figure A1). Meanwhile, the 2009 dataset also agreed with general maintenance of *Hard coral* across all zones and *Algae* cover co-varying with *Hard coral* reported from 2005–2009 [55]. Our percent coral cover values were in line with broader regional assessments [6].

Testing Spatial Variability: Effect of Management Zone

There was no significant spatial difference in benthic community composition between management zones, and no major difference between *General Use* zones and other, more regulated zones (Figures 4a and 5a): a finding that echoes the work of several other studies that set out to examine efficacy of zoning in Karimunjawa. For example, benthic assemblages monitored between 2005 and 2009 [55] and again in 2006 and 2013 [23], did not show any relation to management zone. Previously, this finding has been attributed to a lack of local compliance with zoning, meaning no strong difference in pressures between zones [55,58]. Studies that examined fish biomass similarly found little effect of zoning between 2004 and 2007 (herbivorous fish continued to decline, although *Core Zones* had a positive effect on general biomass, and *Protection Zones* were shown to be less effective) [25] and again in 2006–2013 (herbivorous fish increased in all zones) [23]. Some studies suggested a slight positive impact of the *Core Zones* [24,59], which are longer established and have better compliance, but much of these conclusions were around fish diversity and biomass. *Core Zone* did not appear to influence

benthic community composition in this study. The only indication that zone was having a significant effect spatially was the negative correlation between *Hard coral-Sponge* detected in the known part of the multivariate model. This finding suggests that management *Zone* may somehow be influencing benthic community composition by driving *Hard corals* down where *Sponges* are increasing (or vice versa). Additional surveys would be needed to confirm this signal.

4.2. Temporal Variation: Trends in Karimunjawa's Coral Reef Benthic Composition between 2014 and 2018

Karimunjawa's *Hard coral* and *Algae* abundances were fairly stable between 2014 and 2018, with *Hard coral* cover declining slightly but significantly across the park (2014: $29.6 \pm 0.06\%$, 2018: $26.7 \pm 0.04\%$ (SD)). *Rehabilitation zone* was the only zone that saw 20.3% relative increase, rather than a drop, in *Hard coral* (Figure 2). This zone had the lowest mean coral cover in 2014 ($26.2 \pm 0.06\%$ SD) of any zone, and the highest mean cover of any zone by 2018 ($31.5 \pm 0.07\%$ SD), suggesting that management may have been having a desired effect in these areas that were targeted for protection because of historic damage. *Mariculture zones* saw the greatest *Hard coral* relative losses of 33.3%, followed by *General Use Zones* 14.5% relative decrease in *Hard coral* (Figure 2). Other studies have also reported stable [23] or slightly negative [24,37] trends in coral cover in Karimunjawa (although various studies have also shown slight increases in coral cover across the park since cessation of unsustainable fishing practices [55]).

Further examination of benthic sub-groups revealed that apparent small but significant declines in *Hard coral* were masking much larger shifts in benthic community assemblage between 2014 and 2018 (Figure A2). *Acropora* corals (both branching *Acropora* ACR_BRA, increased by 21.6%, and tabulate and plate *Acropora* ACR_TCD species up 5.5%) and foliose corals (FLP) also increased by 11%, with the model detecting a significant shift in abundance between 2014 and 2018 in ACR_BRA and FLP (Figure 4: Year). For example, branching *Acropora* typically made up $5.2 \pm 0.37\%$ of the community in 2014, and $8.4 \pm 0.65\%$ in 2018, and plate *Acropora* was 13% of the community in 2018 (previously 2%). At the same time, massive corals (MSE and MSEM) saw significant declines in abundance (Figure 4: Year). In 2018, massive and encrusting species typically made up 20% of the coral cover, compared to 40% in 2014. This strong shift in community composition from massive to more complex foliose, branching and tabulate is in agreement with reported increases in percent cover of complex corals (branching, digitate, tabulate and foliose corals) regardless of management regime [23,55].

Return of more fragile corals may be a response to cessation of destructive fishing, particularly the use of *muro-ami* nets that peaked 2003–2005 and a move towards handlines, *bubu* and spears instead [55]. *Muro-ami* practices would be damaging to corals, particularly fragile branching species, and had largely ceased by November 2011: unlike compliance with zones, gear restrictions were adhered to across Karimunjawa [55]. Other indicators of reef health, such as herbivorous fish abundance were also found to have responded positively to fishing controls [23], and may have played a role. A lag in recruitment and growth would have meant smallish *Acropora* and other branching species would perhaps be 6–8 years old by the time of the 2018 survey, and linear expansion of colony branches could drive greater percent cover values detected.

Another observation was a large and significant increase in fast growing non-scleractinian hard corals—specifically *Millepora*—between years: this occurred particularly in the north-west sector of the park (85.3% relative increases across the park, but particularly at Kembar, Parang and Kumbang Islands, Figure A1), sites where illegal fishing was still occurring in 2014 and blast fishing damage was still observable in 2014 surveys. The increase in these fast weedy growing species might indicate successional recovery of these damaged sites.

Only one group of complex corals—the branching non-Acroporid corals (BRA_nACR)—conversely saw a decline during the study (−35.7% decline). This was also the only non-massive coral sub-group that saw a decline (Figure 4: Year). Massive (MSEM) and branching (BRA_nACR) coral declines were also mirrored in the analysis of the effect of DHW (Figure 4: DHW). This finding is a likely result of

reported susceptibility of many of the members of these subgroups (e.g., *Pocillopora*, branching *Porites* and *Stylophora*) to bleaching, and the high mortality reported at the time in these species [37].

4.3. Impact of Global Climate Change

Karimunjawa's coral reefs are at higher risk of ocean warming due to their location, and were affected by bleaching in 1998, 2000, 2010 and 2016 [7]. This, along with other factors, has led to Karimunjawa being identified as a priority area for conservation [13]. Satellite data suggested that thermal anomalies were greater in the northern part of the park compared to the southern, although the range of recorded maximum DHW values in 2016 was relatively narrow (1.46–2.73). Examining benthic community composition in the context of spatial trends in DHW during the 2016 heatwave, revealed *Hard coral* cover was not significantly impacted by the 2016 bleaching (Figure 3: DHW). However, inspection of coral sub-groups revealed all corals, with the exception of *Millepora* (NON_HERM) and bleaching-resistant massive *Porites* (MSE) were negatively impacted by DHW (Figure 4: DHW). Branching *Acropora* corals were the worst affected (Figure 4: DHW). This finding is in good agreement with surveys conducted in the park during April 2016, which found just 12% of surveyed corals were not visibly affected by bleaching, and reported *Acropora* to be the worst impacted species (99% observed corals bleached, 26% mortality). *Pocillopora* (10% mortality), *Isopora* (5.5%), *Montipora* (5.4%) and *Stylophora* (3.7%) also appeared sensitive to bleaching. Fewer than 30% of *Gardinerosis* and *Pachyseris* colonies bleached [37]. These bleaching observations are in good agreement with the changes in benthic cover seen our data two years on, which similarly detected branching *Acropora* (ACR_BRA) as the most impacted sub-group, but most coral groups being affected to some extent.

Forty long term monitoring sites are also maintained by *Balai Taman Nasional* park rangers and the *Wildlife Conservation Society*, who reported declines in coral cover between 2013 and 2016 that they attributed to 2015/2016 bleaching event, as well as impacts of tourism [37]. However, most of the changes detected in this study could *not* be explained by DHW: neither increased in *Soft coral*, *Sponge* or *Algae*, or declines in *Hard coral* could be adequately explained by DHW (Figure 3: DHW). Furthermore, long-term monitoring sites reported as bleaching badly at the time, (e.g., Menjangan Besar, Taka Malang and Pulau Menyawakan [37]) did not appear to lose significant coral cover in the long term (Menjangan Besar +14% increase in *Hard coral*, from 24.5 to 27.9%; Taka Malang −12% decrease; Pulau Menyawakan +25% increase; see Appendix A, Table A1). Sites that lost around a fifth of their coral cover in this study included Parang Island (−33.3%, a heavily impacted mariculture zone), Taka Menyawakan (−24.2%, that experienced a ship grounding), Karang Kapal (−20.0%) which had the lowest DHW values, Krakal Kecil (−19.7%) and Karimunjawa Town (−18.5%), a heavily populated site vulnerable to land-based runoff.

4.4. Impact of Local Stressors

Interestingly, patterns of community change detected in our study were different compared to patterns of change driven by warming (Figure 4: Year vs. DHW), suggesting that although bleaching impacted communities, the 2016 bleaching event was not the main driver of benthic community change in Karimunjawa (seen in Figure 3: Year). For example, MSE (massive and encrusting *Hard coral*, mainly *Porites*) continued to decline across the park, but was the only coral group not negatively impacted by the bleaching. Conversely, *Acropora* were sensitive to bleaching and were damaged where heat stress was higher, but in spite of bleaching impacts, across the park the main trend was a doubling in abundance. Co-occurrence patterns identified other negative interactions, between *Sponge* and *Hard coral* abundance attributed to the explanatory variables.

4.4.1. Changes in Fishing Pressure

Community involvement and participation has been a focus of the park management since the early 2000s with the knowledge that this can improve outcomes [18]. The lack of detectable impact on coral communities across the park between zones does not necessarily reflect a failure of management,

since park-wide regulation changes to stop destructive *muro-ami* is driving positive and widespread recovery of branching coral species across Karimunjawa. Branching corals can increase reef structural complexity—a feature associated with resilience and other benefits including improved habitat to support animals [60] and better coastal protection [61].

Other studies report this same management action resulted in a doubling of herbivore biomass between 2006 and 2013 [23], again irrespective of zone and in spite of scarids remaining an important target fish [33]. Herbivory is another indicator of reef resilience: changes in herbivore biomass are known to improve coral recruitment, and are also linked to declines in macroalgal abundance. Macroalgae were a benthic sub-group that also showed detectable declines in abundance during the survey period (Figure 4: Year), perhaps reflecting a secondary positive impact of managing fisheries on Karimunjawa's reef health.

4.4.2. Declining Water Quality?

Sponge was the group that saw the biggest consistent increase across Karimunjawa, almost doubling (1.8×) across the park (Figure 2). There are established links between water quality, reef health and sponge abundance in Indonesia [30], and benthic community changes that could not be explained by DHW, namely increases in sponge abundance and declines in massive corals, must be attributable to a driver not included in the model, possibly declining water quality. While mid-1990s studies on water quality in Karimunjawa report good water quality (e.g., low chlorophyll a, suspended particulate matter (SPM) and resuspension values) [30], growth of tourism and mariculture locally may be changing this. Recent water quality testing revealed a poor water quality across Karimunjawa, with seawater concentrations of nitrate (0.04–0.06 mg L⁻¹) and phosphate (0.01–0.03 mg L⁻¹) that exceeded levels permitted by the Indonesian Environment Ministry (0.008 and 0.015 mg L⁻¹, respectively) reported at all sites tested [32]. In our study, three sites saw more than a quadrupling of *Sponge* abundance. Telaga Village, a *Rehabilitation Zone* still used for seaweed cultivation, and close to a settlement (Kemujan Village, home to 31% of Karimunjawa's population), experienced a 7-fold increase in sponges and also the largest associated decrease in coral. Parang Island, an intensively used *Mariculture Zone* and also home to Parang Village with a population of 920 people (10% of the population), experienced the second biggest change in *Sponge* abundance: a fivefold increase from 0.37% to 2.13%. Menjangan Besar, a *Tourism Zone* close to Karimunjawa Town, home to over half of Karimunjawa's population (4900 people) experienced a quadrupling of sponges, and has grouper cultivation. However, all zones and most sites saw significant shifts in *Sponge* abundance, and only remote Krakal Besar, *Core Zone* Taka Menyawaken and Menjangan Kecil (all away from human habitation and mariculture) sponge increases were not statistically significant. Further consultation with the *Balai Taman Nasional* confirmed that patterns of major sponge increases were consistent with increasing mariculture and development activity in the park. However, not all sponge increases could be easily explained: Krakal Kecil and Ujung Bomang both saw tripling of sponges: Krakal Kecil, a private resort has some limited development (three eco-cottages) on its tiny (300 m) island, but Ujung Bomang was far from residential areas. The pervasiveness of these sponge increases across all sites are in agreement with the findings of the water quality study, that was unable to establish a definitive link between proximity to aquaculture and elevated nitrate and phosphate levels, instead finding declines in water quality at all sites [32].

The encrusting sponge *Terpios hoshinota*, invasive to Western Pacific, has seen recent outbreaks in Indonesian coral reefs since it first appeared in 2012, and was seen during our 2018 surveys [62]. *Terpios* is associated with poor water quality and thrives in polluted and stressed reefs. It can rapidly overgrow corals [63] and has been responsible for significant coral mortality in other areas [64]. Appearance of *Terpios* may have contributed to increases in *Sponge* abundance, and strongly associated declines in *Hard coral*.

Coral disease, also associated with water quality, was recently found in 24% of corals surveyed around Karimunjawa Island, with significantly more disease at sites closer to mariculture and human habitation [32]. Disease (or competition) may be the mechanism behind the negative co-occurrence

patterns between *Sponge* and *Hard coral* across the park. This relationship that was found to be stronger than the co-occurrence between *Hard coral* and *Algae* (Figure 4), and may help explain declines in massive *Porites* (MSE) which we found to be less affected by the 2016 bleaching (Figure 4: DHW) but are reported to be particularly vulnerable to disease in this region [65].

Finally, water quality can affect other aspects of reef biology, for example driving more rapid linear extension in *Acropora* branches [30]. It may be that declining water quality in Karimunjawa may also have contributed to apparent increase in branching *Acropora*. It has long been suggested that pollution in the Coral Triangle is a major driving force on community composition (more significant than underlying biogeography [21]), and exposure to this new threat is likely to see drive rapid changes in benthic community.

Although the absolute percent cover of *Sponge* is low, detection of this subtle but ubiquitous increase in sponge abundance across all management zones in Karimunjawa (Figure 3a) represented the most significant community shift seen across in the park between 2014 and 2018 (Figure 3b). Analyses employed to explore this complex multivariate dataset allowed us to detect these potentially important shifts that traditional inspection of percent cover values may have missed, providing managers with an early indication of a potential emerging threat to the reefs locally. In future, investment in tracking water quality across the park, and an emphasis on monitoring of sponges—and not just coral and algae—may prove valuable in tracking reef health and improving management outcomes in Karimunjawa National Park.

5. Conclusions

Reef communities are complex, and detailed community composition data collected by monitoring programs can be difficult to decipher, particularly when collected across large geographic areas facing multiple local and global stressors. Technology is allowing us to collect more detailed data across ever larger areas, but without appropriate analytical techniques, meaningful changes may be missed and improved capabilities around data collection may not translate into effective real world actions [66].

In this study, models developed specifically to analyse fine-scale multivariate ecological datasets across broad geographies detected small but significant increases in sponges across Karimunjawa National Park, which may be an early indicator of declining water quality across the park. Analyses also revealed community shifts in coral assemblage, from massive towards more complex foliose and branching communities, likely reflecting recovery of more fragile coral species as a result of restrictions to fishing gear, and losses of massive corals to disease. Finally, the model detected a signature of the 2016 coral bleaching at the sub-group level, which significantly affected branching species where thermal stress was high, although was not strong enough to drive any significant declines in coral across the park. Our dataset shows that subtle differences can be missed if simplistic comparisons of coral cover are used to draw conclusions about benthic community variability across space and time.

Karimunjawa's coral reefs are important from a socio-economic standpoint, as well as a biological one, forming the core livelihood for many of the population of 9000 islanders. In the past, management has proved responsive to new threats and data. Local management actions taken, specifically the banning of harmful *muro-ami* fishing, has likely led to stabilisation of coral community and recovery of three dimensional complexity right across the park—and particularly in *Rehabilitation Zones*—a very positive outcome reflective of collaborative community management. As pollution and water quality become an ever more serious threat to reef health in Indonesia [1], Karimunjawa's managers need to be aware of emerging new threats—in the form of tourism and mariculture—that appear to already be influencing benthic communities across the park. Both tourism and mariculture need to be managed carefully to maintain water quality, in order to give Karimunjawa's coral reefs the best possible chance of resisting and recovering from continued ocean warming.

Supplementary Materials: The following are available online at <http://www.mdpi.com/2077-1312/8/10/760/s1>.

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Appendix A

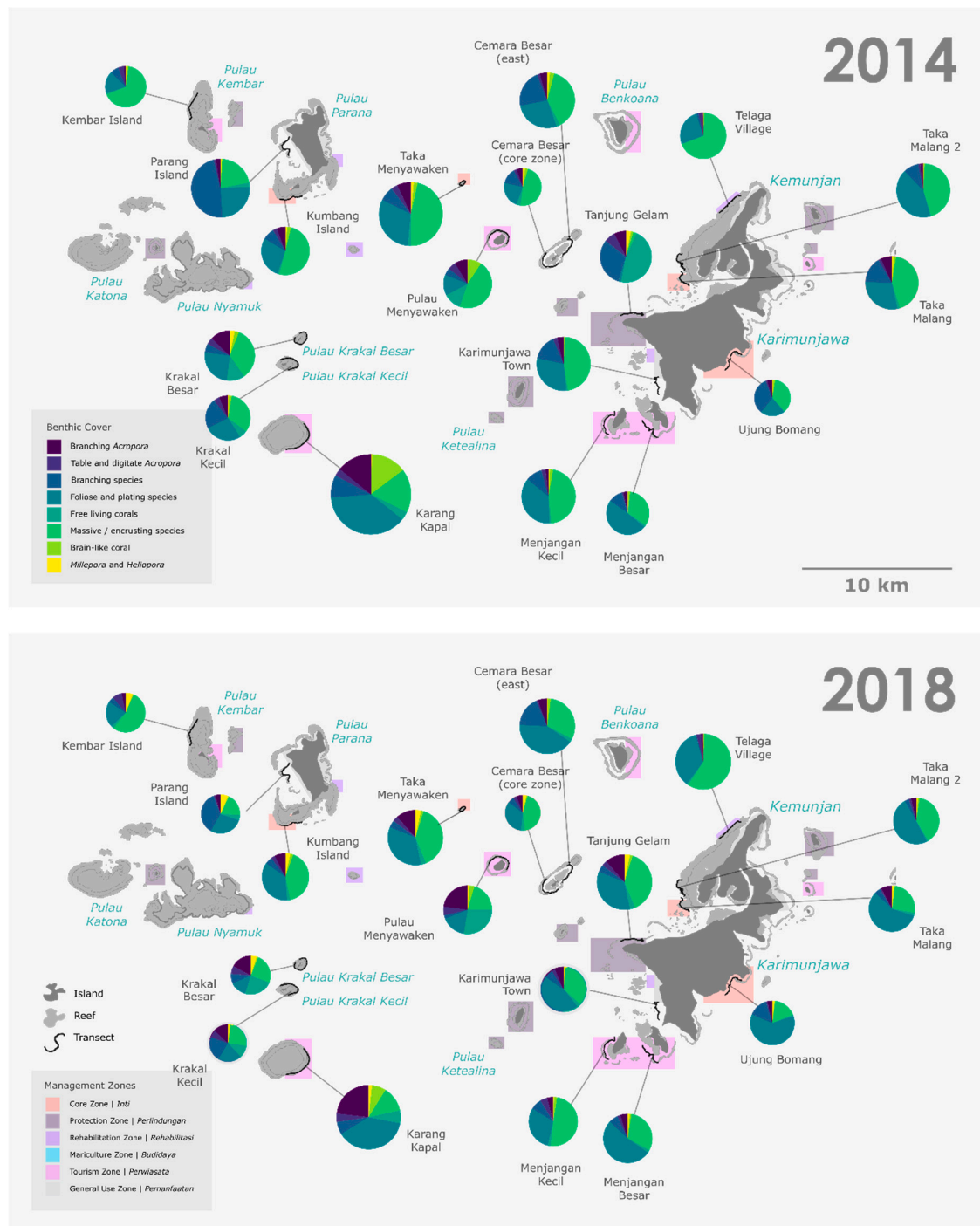


Figure A1. Percent cover of coral type by site, in 2014 (top panel) and 2018 (bottom panel). Pie size reflects total *Hard coral* abundance (range 20.7 to 45.4%), and pie segments represent different coral subgroups (subgroups listed in Table A2). Foliose and plate-like corals dominated most sites, with branching *Acropora* replacing massive and encrusting species by 2018.

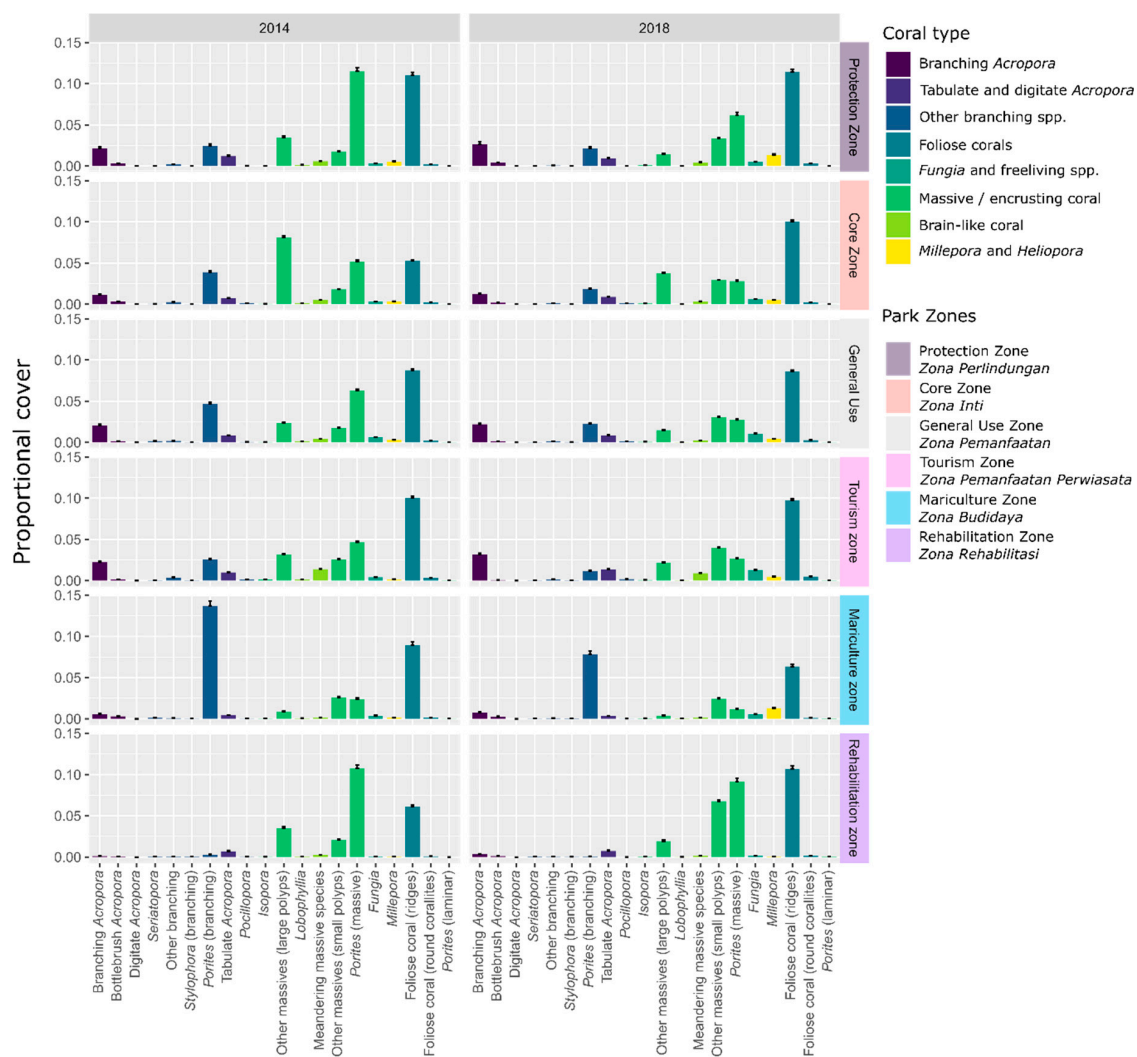


Table A1. Location (lat, long) of each of the 18 survey sites in Karimunjawa National Park, along with percent cover of each of the major benthic groups (Table A2) averaged across all photo quadrats in 2014 and 2018.

Site Information				2014						2018					
Site	Zone	Transect Start	Transect End	Quadrats	Hard Coral	Soft Coral	Algae	Sponge	Sediment	Quadrats	Hard Coral	Soft Coral	Algae	Sponge	Sediment
Tanjung Gelam	Protection Zone	−5.83641, 110.4099	−5.83579, 110.4199	872	0.36	0.01	0.54	0.01	0.07	1022	0.31	0.02	0.50	0.01	0.15
Taka Malang	Core Zone	−5.82016, 110.4453	−5.81611, 110.4408	848	0.30	0.01	0.49	0.01	0.19	808	0.26	0.02	0.48	0.02	0.23
Taka Malang 2	General Use	−5.81281, 110.4429	−5.80416, 110.4411	887	0.30	0.00	0.51	0.01	0.18	1057	0.26	0.02	0.63	0.01	0.07
Cemara Besar East	General Use	−5.80417, 110.379	−5.79646, 110.3811	908	0.31	0.02	0.47	0.01	0.20	987	0.31	0.02	0.50	0.01	0.16
Cemara Besar MDC Site	Core Zone	−5.80364, 110.3699	−5.81044, 110.3745	1006	0.21	0.01	0.71	0.01	0.06	921	0.20	0.03	0.68	0.03	0.06
Taka Menyawakan	Core Zone	−5.7657, 110.327	−5.76774, 110.3256	861	0.40	0.02	0.55	0.01	0.02	848	0.30	0.08	0.59	0.01	0.02
Menjangan Kecil MDC	Tourism Zone	−5.88842, 110.4063	−5.89342, 110.4005	929	0.31	0.01	0.66	0.01	0.01	1040	0.28	0.03	0.67	0.01	0.01
Menjangan Besar MDC	Tourism Zone	−5.89317, 110.4212	−5.90024, 110.427	1055	0.24	0.01	0.66	0.00	0.09	748	0.28	0.04	0.60	0.01	0.07
Karimunjawa Town	General Use	−5.87799, 110.429	−5.86981, 110.4283	916	0.31	0.01	0.49	0.01	0.19	866	0.25	0.02	0.53	0.01	0.19
Kumbang Island	Core Zone	−5.77328, 110.2406	−5.77505, 110.2287	892	0.27	0.01	0.51	0.01	0.20	668	0.27	0.02	0.55	0.01	0.16
Kembar Island	Tourism Zone	−5.73295, 110.1812	−5.72017, 110.1849	1097	0.23	0.02	0.72	0.01	0.02	768	0.22	0.04	0.70	0.02	0.01
Parang Island	Mariculture Zone	−5.75195, 110.2333	−5.74226, 110.2337	914	0.33	0.00	0.63	0.00	0.03	966	0.22	0.01	0.72	0.02	0.03
Ujung Bomang	Core Zone	−5.85618, 110.4712	−5.86506, 110.4651	902	0.21	0.01	0.49	0.00	0.29	1012	0.25	0.02	0.45	0.01	0.27
Telaga Village	Rehabilitation Zone	−5.78234, 110.4616	−5.77334, 110.4722	1027	0.26	0.02	0.62	0.00	0.10	752	0.32	0.02	0.58	0.02	0.06
Pulau Menyawakan	Tourism Zone	−5.79194, 110.3451	−5.79273, 110.348	186	0.27	0.03	0.69	0.00	0.01	807	0.28	0.03	0.66	0.01	0.02
Karang Kapal	Tourism Zone	−5.89661, 110.2433	−5.90763, 110.2321	986	0.45	0.04	0.48	0.00	0.03	708	0.36	0.02	0.58	0.01	0.02
Krakal Kecil	General Use	−5.86028, 110.229	−5.86547, 110.2335	927	0.26	0.02	0.61	0.00	0.11	920	0.21	0.01	0.70	0.01	0.06
Krakal Besar	General Use	−5.84614, 110.2393	−5.84823, 110.237	1011	0.28	0.03	0.58	0.01	0.09	1049	0.23	0.03	0.66	0.02	0.07
Mean					0.30	0.02	0.58	0.01	0.10		0.27	0.03	0.60	0.01	0.09
StDev					0.06	0.01	0.08	0.00	0.08		0.04	0.02	0.09	0.01	0.08

Table A2. Descriptors for the Benthic Groups (5) and sub-groups (15) used in the analysis, along with Table 53 benthic categories to which benthos was initially classified from photo quadrats (full dataset downloadable from Gonzalez et al. 2019 [45]). ‘Benthic Group’ and ‘Benthic sub-group’ identifiers in blue are the keys matching labels in the downloadable dataset. Other categories detected in the full dataset (e.g., Crown of Thorn seastars, crinoids, zoanthids, sea cucumbers, hydroids, tunicates and bryozoans) were removed from the dataset prior to analysis.

Benthic Group	Benthic Sub-Group	Short Descriptor	Full Descriptor Including Pooled Sub-Groups Available in the Full Downloadable Dataset
Hard coral	ACR_BRA	Branching Acropora	Branching coral species from the Family Acroporidae, including bottlebrush (BRA_BOT_Ac) and branching (BRA_ARB_Ac) morphologies
Hard coral	ACR_TCD	Table and digitate Acropora	Other morphologies from the Family Acroporidae, including corymbose, tabular, plate (BRA_TAB_Ac) and digitate (BRA_DIG_Ac) morphologies.
Hard coral	BRA_nACR	Other branching coral	Non-Acroporid branching species. This category pools Pocillopora (BRA_VER_Po), Stylophora (BRA_RND_St), Anacropora and Echinopora (BRA_OTH), branching Porites (BRA_SMO_Po) and fine branching species such as Seriatopora (BRA_FIN_Se)
Hard coral	MSE	Massive to encrusting coral	Massive, submassive and encrusting (“MASE”) coral species with rounded corallites, including those with small to almost invisible corallites, such as Pavona, Psammocora, Coscinaraea, Gardinerosia (MASE_SML_O) or larger rounded corallites such as Diploastrea; Dipsastraea; Favites; Astrea; Galaxea; Goniopora; Astreopora (MASE_LRG_O), Isopora (MASE_LRG_I) and Porites with submassive/massive morphologies (MASE_SMO_P)
Hard coral	MSEM	Brain-like coral	Brain corals: massive, submassive and encrusting (“MASE”) coral species with corallites forming meandering ridges or valleys, such as Platygyra, Leptoria and Goniastrea (MASE_MEA_O) and Lobophyllia (MASE_MEA_L)
Hard coral	FREE	Free-living coral	Free living species, typically Fungia (NON_FREE)
Hard coral	FLP	Foliose coral	Hard corals with foliose morphologies, including those with visible relief structures (TFP_RND_A1) and those with visible rounded corallites (TFP_RND_A2)
Hard coral	NON_HERM	Non-scleractinian coral	Non-scleractinian hermatypic corals, mainly the hydrocoral Millepora (NON_MIL) and blue coral Helipora (NON_HEL)
Soft Coral *	GORG	Gorgonians	Gorgonian corals including families of sea fan, plumes and whips belonging to the sub-orders Holaxonia and Scleraxonia (GORG)
Soft Coral *	OTH-SF	Alycionids and other soft coral	Leathery soft corals from the Family Alcyoniidae, such as Lobophytum and Sarcophyton (SINV_SFC_A) and other non-Alcyoniid species, e.g., Xenidiidae; Nephtidae; Tubipora; Briareum (SINV_SFC_E).
Sponge	SPONG	Sponges	Sponges, including branching and rope forms (SINV_SPO_E), fan-shaped sponges (SINV_SPO_F), massive to encrusting forms (SINV_SPOM) and hollow cups, barrels and tubs (SINV_SPO_V).
Algae	MACRO	Macroalgae	Macroalgae, includes all algae > 1 cm in height, including globular algae such as caulerpa (MACR_GLOB), filamentous forms (MACR_Fil_A), sheeting forms like Ulva (MACR_Fol_S), leathery macrophytes (MACR_LTH_O), foliose forms (either branched, MACR_Fol_B, feathery MACR_Fol_P, fan shaped MACR_Fol_F or other MACR_Fol_O), calcifying algae Halimeda (MACR_Cal_H) and other calcifying species (MACR_Cal_O), and Padina (MACR_Cal_P). This group also includes cyanobacteria found smothering dead coral (CYANO_DHC), rubble (CAL_CCA_RB) and rock (CAL_CCA_Sub) as well as any other algae not fitting into these categories (ALGAE_OTH).
Algae	EAM	Epilithic algal matrix	Turfs and biofilms covering dead hard coral (EAM_DHC), rubble (EAM_RB), rock or other substrate (EAM_Sub).
Algae	CCA	Crustose coralline algae	Crustose coralline algae, including forms encrusting dead hard coral (CAL_CCA_DC) found on substrate (CAL_CCA_RB) and rubble (CAL_CCA_RB).
Sediment	NON_COLONIZABLE	Loose substrate	Loose non-living substrate, including rubble (LSUB_RUB), sand (LSUB_SAND) and sediment (LSUB_SEDI).

* including Gorgonians.

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