Ecological Applications, 30(6), 2020, e02122

Representation and complementarity of the long-term coral monitoring on the Great Barrier Reef

C. Mellin,[1,2,3,8] E. E. Peterson,[4,5,6] M. Puotinen,[7] and B. Schaffelke[2]

[1]*Institute for Marine and Antarctic Studies, University of Tasmania, 15-21 Nubeena Cres, Taroona, Tasmania 7053 Australia*
[2]*Australian Institute of Marine Science, PMB No. 3, Townsville MC, Townsville, Queensland 4810 Australia*
[3]*The Environment Institute and School of Biological Sciences, University of Adelaide, Adelaide, South Australia 5005 Australia*
[4]*Institute for Future Environments, Queensland University of Technology, 2 George St, Brisbane, Queensland 4000 Australia*
[5]*Australian Research Council Centre of Excellence for Mathematical and Statistical Frontiers (ACEMS), 2 George St, Brisbane, Queensland 4000 Australia*
[6]*School of Mathematical Sciences, Queensland University of Technology, 2 George St, Brisbane, Queensland 4000 Australia*
[7]*Australian Institute of Marine Science, Indian Ocean Marine Research Centre, University of Western Australia, Crawley, Western Australia 6009 Australia*

Citation: Mellin, C., E. E. Peterson, M. Puotinen, and B. Schaffelke. 2020. Representation and complementarity of the long-term coral monitoring on the Great Barrier Reef. Ecological Applications 30(6): e02122. 10.1002/eap.2122

Abstract. Effective environmental management hinges on efficient and targeted monitoring, which in turn should adapt to increasing disturbance regimes that now characterize most ecosystems. Habitats and biodiversity of Australia's Great Barrier Reef (GBR), the world's largest coral reef ecosystem, are in declining condition, prompting a review of the effectiveness of existing coral monitoring programs. Applying a regional model of coral cover (i.e., the most widely used proxy for coral reef condition globally) within major benthic communities, we assess the representation and complementarity of existing long-term coral reef monitoring programs on the GBR. We show that existing monitoring has captured up to 45% of the environmental diversity on the GBR, while some geographic areas (including major hotspots of cyclone activity over the last 30 yr) have remained unmonitored. Further, we identified complementary groups of reefs characterized by similar benthic community composition and similar coral cover trajectories since 1996. The mosaic of their distribution across the GBR reflects spatial variation in the cumulative impact of multiple acute disturbances, as well as spatial gradients in coral recovery potential. Representation and complementarity, in combination with other performance assessment criteria, can inform the cost-effective design and stratification of future surveys. Based on these results, we formulate recommendations to assist with the design of future long-term coral reef monitoring programs.

Key words: adaptive management; decision-making; disturbance; ecosystem dynamics; indicators; sampling; survey design.

Introduction

Marine ecosystems worldwide are being increasingly impacted by global change, including ocean warming and acidification, invasive species, pollution, and overexploitation of marine resources. Such stressors can play out across the entire hierarchy of organizational levels, from the molecule (i.e., gene expression) to individuals and populations (through climate-mediated changes in phenology and physiology) and, ultimately, changes in community composition that reflect those in species distributions and abundances (Garcia Molinos et al. 2015, Poloczanska et al. 2016). Ecological monitoring plays a key role in this context, not only by identifying major stressors and quantifying their impacts on marine ecosystems, but also by improving our understanding of why some ecosystem components are better able to withstand and recover from disturbance than others, with important lessons to be learnt for ecosystem management (Obura et al. 2019).

Targeted monitoring is essential to inform decision-making and, in turn, underpins adaptive and cost-effective management (Lindenmayer et al. 2011, Kang et al. 2016). Indeed, the accelerating loss of biodiversity challenges the prioritization of conservation and management efforts, which are typically constrained by available resources and need to accommodate the economic activities that societies rely on for food or livelihoods. Consequently, environmental managers constantly face decisions and trade-offs associated with, for example, conservation strategies (i.e., shall we protect the weak or the strong; Game et al. 2008) and ecological triage (i.e., shall we direct conservation resources toward the most

Manuscript received 26 August 2019; revised 22 January 2020; accepted 6 February 2020. Corresponding Editor: Ilsa B. Kuffner.
[8]E-mail: camille.mellin@adelaide.edu.au

endangered species, and will that simultaneously benefit other species; Bottrill et al. 2008, Wilson et al. 2011). These decisions and the associated risks and trade-offs are best informed by ecological monitoring, reporting, and subsequent evaluation of management effectiveness, with important feedbacks between these steps to ensure adaptability (Day 2008, Richards and Day 2018). However, monitoring programs are notoriously expensive and time-consuming, meaning that survey efforts need to be allocated cost effectively (McDonald-Madden et al. 2010). For example, monitoring ecological surrogates (also known as indicators), such as generic rather than species diversity (Richards 2013), can provide a cost-effective way to document biodiversity status and trends for other unmonitored taxa (Mellin et al. 2011, Hunter et al. 2016). Consequently, the integration of targeted monitoring into conservation practice hinges on a robust design based on (1) a priori hypotheses and associated conceptual models of system responses to management (Nichols and Williams 2006) and (2) clearly defined objectives and measurable indicators (Day 2008, Kang et al. 2016). As knowledge, questions and monitoring technologies evolve, monitoring should ideally adapt with new and better designs and/or additional indicators (Kang et al. 2016), while maintaining as much as possible the integrity of long-term data records (Nichols and Williams 2006). Using these design criteria, most environmental monitoring would include a range of indictors specific to the objectives. However, the growing need for integration of information across geographic and national boundaries also requires continued monitoring of agreed, commonly monitored "essential" variables (Miloslavich et al. 2018, Obura et al. 2019).

The Great Barrier Reef (GBR) stretches over 2,300 km along the northeast coast of Australia, making it the world's largest coral reef ecosystem. In 1981, it was listed as a UNESCO World Heritage Site for its unique natural properties and environmental and scientific importance. In 2004, the GBR Marine Park was rezoned to a multiple-use network accommodating all human activities, while increasing the proportion of "no-take" zones from <5% to >33% (Day 2008). The Australian Institute of Marine Science's Long Term Monitoring Program (LTMP) has monitored status and trends in the abundance and distribution of reef biota across the GBR using standardized methods for more than three decades. This provides the longest continuous record of reef communities over such a large geographic area in the world. Coral reefs go through cycles of disturbance and recovery, however over the last three decades, coral cover on many GBR reefs has been declining (Great Barrier Reef Marine Park Authority 2019) due to the cumulative impact of multiple disturbances including tropical cyclones, outbreaks of the crown-of-thorns starfish (*Acanthaster* cf. *solaris*) and more recently, severe and recurring coral bleaching events (Hughes et al. 2017). In response to concerns about significant losses of coral cover and the declining condition of many of the GBR habitats and species, the Commonwealth of Australia implemented the Reef 2050 Long-Term Sustainability Plan (Australian Government Department of Agriculture, Water and the Environment, n.d.) to address key local and regional pressures and maintain the resilience of the Reef in the face of a changing climate. Central to the Reef 2050 Plan is the development of a Reef Integrated Monitoring and Reporting Program (RIMReP; Great Barrier Reef Marine Park Authority and Queensland Government 2015). Its key objectives are to inform the Reef 2050 Plan's adaptive management approach by (1) evaluating whether actions are on track to achieve targets, (2) enabling early detection of trends and changes in the Reef's environment, and (3) informing the assessment of key threats and future risks to enable timely management decisions.

Assessing the robustness of environmental monitoring programs typically relies on criteria such as the precision and accuracy of population parameters being measured (Tyre et al. 2003) or power (i.e., the ability to detect changes and distinguish them from natural variability; Field et al. 2005, Van Wynsberge et al. 2017). These depend on the indicator being monitored, as well as the level of temporal replication and spatial stratification of survey effort. Furthermore, an effective monitoring program needs to be representative of the system on which it reports (Stevens and Olsen 2004). For the GBR, this means capturing a range of processes that can play out over 100–1,000 km (spatial representation), and shape the condition of a myriad of species groups, each of which is influenced by many environmental variables (Mellin et al. 2010*a*, 2019*a*). Environmental variation and acute disturbances driving biological and ecological change in the system may also act over time scales ranging from weeks (e.g., tropical cyclones, flood events), months (e.g., coral bleaching events), to many years (e.g., ocean warming, invasive species). Thus, a representative monitoring design would be one that sufficiently captures the spatiotemporal dynamics of key system variables and environmental variation to support management decisions related to monitoring objectives.

Finally, the concept of complementarity is important because it ensures that additional survey sites selected for monitoring complement those already monitored. While it has mostly been applied to the selection of indicator species (Tulloch et al. 2013) or areas for conservation (Margules and Pressey 2000, Sarkar et al. 2006), it is equally important in marine monitoring programs. For example, the selection of additional survey sites that contribute unrepresented features to an existing survey design ensures that monitoring provides useful information cost-effectively. The alternative, i.e., monitoring survey sites that convey redundant ecological information, might be a desirable feature if replication is required (e.g., for statistical analysis purposes or in the case of surveillance monitoring), but can also represent a waste of resources if left undocumented or uncontrolled for (Nichols and Williams 2006).

This study is part of a larger evaluation of the accuracy, precision, and power of existing long-term coral monitoring programs on the GBR that aims to inform the design of future coral surveys on the GBR. We focus on the complementarity and representation of these programs and address two specific questions: First, how representative have these long-term monitoring programs been of the environmental diversity and disturbance regimes on the GBR? Second, to what extent have these survey data sets provided complementary information on benthic community composition, and coral cover dynamics within major benthic community types during periods of disturbance and recovery? We use these results to provide recommendations for the design of future coral monitoring surveys on the GBR.

Methods

Reef monitoring programs

Our analysis included data from four major long-term, ongoing coral reef monitoring activities in the GBR carried out by a team of expert benthic ecologists from the Australian Institute of Marine Science: the Reef Monitoring (RM), the representative areas program (RAP), the marine monitoring program (MMP), and manta tow survey (MANTA; Fig. 1; Appendix S1: Table S1). In this study, we focused on the analysis of the benthic community data derived from these programs, especially the indicator "percent coral cover," which represents an Essential Ocean Variable (Miloslavich et al. 2018) and is globally the most widely used proxy for coral reef condition.

The RM program is designed to provide information on population trends for key groups of organisms (particularly hard corals and reef fishes) over the length and breadth of the GBR (Sweatman et al. 2008). GBR reef communities were monitored annually between 1993 and 2005, and then biennially thereafter. Benthic cover was monitored at a total of 46 reefs between 1996 and 2015 in six latitudinal sectors (Cooktown-Lizard Island, Cairns, Townsville, Whitsunday, Swain, and Capricorn-Bunker) spanning 150,000 km^2 of the GBR. In each sector (with the exception of the Swain and Capricorn-Bunker sectors), at least two reefs were sampled in each of three shelf positions (i.e., inner, mid, and outer). Transect-based data on benthic assemblages were collected at three sites separated by >50 m within a single habitat on the reef slope (the first stretch of continuous reef on the northeast flank of the reef, excluding vertical drop-offs). Within each site, five permanently marked 50-m transects were deployed parallel to the reef crest, each separated by 10 m along the 6–9 m depth contour.

The RAP program was established in 2006 with the specific objective of examining the effects of the 2004 GBR Marine Park rezoning on reef biodiversity. The pattern of RM surveys was changed in 2006 so that benthic assemblages at the original core monitoring reefs were surveyed every other year (odd years), while in the alternate even years a different series of reefs was surveyed to fulfil the objective of the RAP program. This involved surveying matched pairs of reefs, one of which was rezoned as a no-take area in 2004 while the other remained open to fishing. Six pairs of mid-shelf or outer-shelf reefs with the appropriate zoning history were selected in each of four localities close to population centers: Cairns-Innisfail, Townsville, Mackay, and the Swain Reefs; and four pairs of reefs selected in the Capricorn-Bunker Group. Thus, 56 reefs were surveyed in even years and 46 reefs in odd years from 2006 onward.

The MMP was established in 2005 to quantify temporal and spatial variation in the status of inshore coral reef communities in relation to changes in local water quality (Thompson et al. 2016). Reefs were designated as either 'core' reefs (N = 14) or 'cycle' reefs (N = 18), with a total of 32 reefs surveyed either annually (core) or biennially (cycle) from 2005 through to 2014. Since 2014, all reefs have been surveyed on a biennial basis. Throughout the time series, additional samples have been included to capture the effects of disturbances on reefs that were not scheduled for survey in a given year. In addition, two sites were selected at each survey reef to account for spatial heterogeneity of benthic communities within reefs.

At each survey site of the RM, RAP and MMP programs, the structure and composition of benthic communities was quantified using the photo point intercept (PPI) method (Jonker et al. 2008). Images were taken at 1-m intervals and the percentage cover of benthic categories were estimated for each transect using point sampling based on a random selection of 40 images out of the 50 images available. The benthic organisms under five points arranged in a quincunx pattern in each image were identified to the finest taxonomic resolution possible (N = 200 points per transect) and the data were converted to percent cover. The identified benthos components were then aggregated up to 54 benthic categories that included growth form and taxonomic resolution (species, genus, and family) and were consistently applicable across the time series. In this study, we focused on the 25 categories relevant to hard coral (see table 1 of Mellin et al. 2019*b*) and calculated the total cover of all hard corals averaged at the reef level (i.e., across multiple transects), thereafter referred to as hard coral cover (HC; %). We considered spatiotemporal variation in total hard coral cover within six major benthic communities across the Great Barrier Reef, which were previously identified based on average benthic community composition (Mellin et al. 2019*a*; see *Coral cover model*).

In addition, the entire perimeter of reefs in the RM and RAP programs was surveyed using manta tow (Miller et al. 2009), providing additional estimates of coral cover at the reef scale. The manta tow surveys involved a snorkeler with a "manta board" (hydrofoil) being towed slowly behind a small boat around each survey reef close to the reef crest so that the observer surveyed a 10 m wide swath of the shallow reef slope.

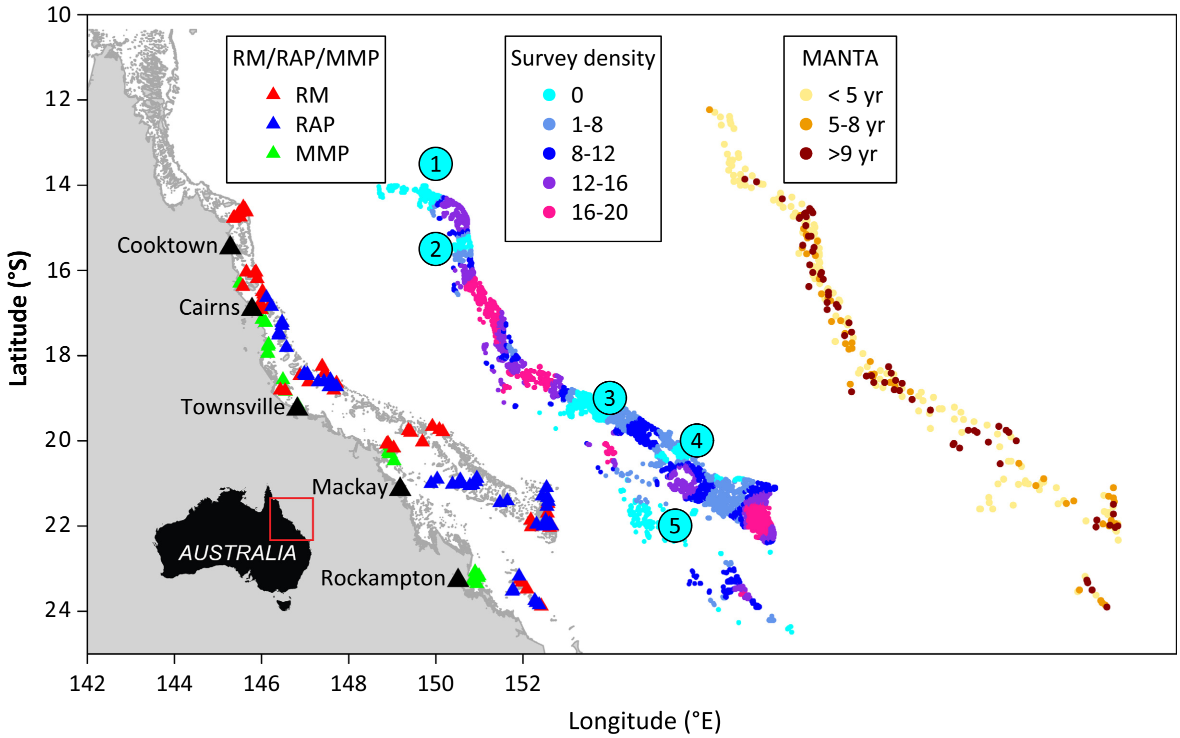

FIG. 1. Spatial distribution of coral reef monitoring sampling effort on Australia's Great Barrier Reef. Left: location of survey sites for the Reef Monitoring (RM), Representative Areas Program (RAP), and Marine Monitoring Program (MMP). Middle: survey density based on the RM, RAP, and MMP monitoring programs. Areas in cyan represent regions with no survey sites within a 50 km radius, with (1) Northern open lagoon and outer barrier reefs north of Cooktown; (2) sheltered mid-shelf reefs between Cooktown and Cairns; (3) strong tidal mid/outer-shelf reefs off Townsville; (4) "hard line" reefs off Mackay; and (5) incipient and high tidal fringing reefs between Mackay and Rockhampton. Right: location of survey sites and number of survey years available for the manta tow surveys.

Additional reefs not surveyed by the RM/RAP/MMP were also surveyed by manta tow to extend spatial coverage of coral cover estimates, with a total of 270 reefs surveyed since 1985 (Fig. 1).

For the RM/RAP/MMP, we mapped the distribution of survey sites and quantified their density within a 50 km radius using the "kernel density" function in ArcGIS 10.4 (Silverman 1986). This allowed us to identify unmonitored regions, defined as regions with no survey sites within 50 km, which we compared to the bioregions defined by the Great Barrier Reef Marine Park Authority (GBRMPA; Appendix S1: Fig. S1). The 50 km radius chosen is the same order of magnitude as the best correlate of reef connectivity identified by previous studies (i.e., 70 km; Mellin et al. 2010*b*) yet slightly narrower to provide a better resolution of survey density.

Environmental variables

A set of 31 modeled environmental variables were collated at a national scale at a 0.01° spatial resolution (12,670 reef grid cells across the GBR, spanning a total area of 14,778 km^2) as part of the Commonwealth of Australia's Environment Research Facility (CERF) Marine Biodiversity Hub (Appendix S1: Table S2; Matthews et al. 2019). These environmental variables are fully detailed in Matthews et al. (2019) and include long-term averages of nitrate, oxygen, phosphate, silicate concentrations; temperature and salinity, bathymetry, percentage cover of sediment types, multiple indices of ocean productivity, the shortest distance to the coast and to the edge of the continental shelf (Appendix S1: Table S2).

Among these environmental variables, we identified a subset of 22 ecologically relevant variables based on previously documented responses of hard corals. For example, temperature and salinity were selected as main determinants of coral spatial distribution (especially latitudinal and cross-shelf) and ecophysiological processes such as coral metabolism, calcification, and reproduction (see Table S1 in Mellin et al. 2019*a* for detailed ecological justifications supporting the selection of the 22 environmental variables).

Disturbance data

Spatial layers of disturbance severity during the study period were compiled at a 0.01° spatial resolution for coral bleaching, outbreaks of the coral-eating crown-of-thorns seastar (CoTS; *Acanthaster* cf. *solaris*) and potentially destructive waves generated by tropical cyclones (Matthews et al. 2019, Mellin et al. 2019*a*). We used annual maximum Degree Heating Weeks (1985–2017) derived from satellite sea surface temperature data from the National Oceanic and Atmospheric Administration (NOAA) CoralTemp data set as a proxy for coral bleaching severity and subsequent mortality (Hughes et al. 2017; data *available online*).[9] DHW was calculated using the standard Coral Reef Watch methodology (Liu et al. 2014). The original data had a spatial resolution of 0.05° and were resampled using the nearest neighbor approach to the nominal 0.01° grid. Interpolated maps of CoTS densities were also generated using inverse distance weighting (maximum distance = 1°; minimum observations = 3) from the manta tow data collected by the Australian Institute of Marine Science in every year from 1996 to 2017 (Miller and Müller 1999). The potential for cyclone wave damage was estimated based on 4-km resolution reconstructed sea state as per Puotinen et al. (2016). This model predicts the incidence of physical forcing that severely damages corals (mean top one-third of wave heights >4 m) caused by cyclones for every cyclone between 1996–2016. We then used these spatial layers to associate the binary occurrence of each disturbance with its severity. All environmental and disturbance data used in this study were previously published (Matthews et al. 2019).

Representation of environmental characteristics and past disturbances

To quantify the proportion of the GBR environmental diversity represented by each monitoring program, we used a principal component analysis (PCA; Venables and Ripley 2002) with all 12,670 grid cells as individuals and a selection of environmental covariates as the predictors. To perform this selection, we ran an initial PCA with the subset of ecologically relevant environmental covariates (N = 22) and selected nine variables based on both their collinearity with other covariates (Spearman's $\rho > 0.5$, $P < 0.001$) and their contribution to the prediction of environmental variation. Combined with the ecological justification underlying predictor selection (see *Environmental variables*), this approach thus helped select ecologically relevant predictors that were also the most statistically sound. We then used convex hulls to calculate the proportion of the total environmental variation represented by the existing coral reef monitoring program sites.

We also identified hotspots where each source of disturbance frequently occurred over the period 1985–2017 using the Emerging Hotspot tool in ArcGIS 10.3 software (ESRI, Redlands, California, USA). This tool calculates the percent duration that a given region could be classified as a hotspot (%Hot; i.e., a cluster of grid cells with significantly higher disturbance values than elsewhere) using a space-time implementation of the Getis-Ord Gi* statistic (Getis and Ord 1992). Hotspots were defined as moderate vs. major based on their %Hot value (moderate: 10–40% years; major> 40% years). We subsequently quantified the proportion of hotspots that were encompassed within unmonitored areas (i.e., regions with no long-term survey sites within 50 km).

[9] https://www.nespmarine.edu.au/

Coral cover model and complementarity of coral reef monitoring sites

We used an existing model of coral cover dynamics that accounts for the cumulative effects of multiple disturbances on the GBR (MacNeil et al. 2019) and reconstructs coral cover trajectories at a 0.01° spatial resolution between 1996–2017 (Mellin et al. 2019*a*). This model explicitly accounts for the influence of habitat and environmental conditions on coral growth and recovery rates, benthic community composition and potential maximum coral cover at a given reef. As part of this model, six major benthic community types were identified using multivariate regression trees (De'ath 2002) and mapped across the GBR (Appendix S1: Fig. S2). Coral cover dynamics within each benthic community type were subsequently hindcast at a yearly time step (1996–2017) based on disturbance severity and community-specific coral recovery rates. Model uncertainty was quantified as the coefficient of variation in predicted annual change in coral cover for each grid cell, across a total of 1,000 simulations, where we resampled every parameter from their predicted distribution.

Based on the coral cover trajectories predicted by the model across the GBR from 1996 to 2017, we quantified reef complementarity by defining clusters of reefs with similar coral cover trajectories using a functional clustering for longitudinal data based on k-centers (Chiou and Pai-Ling 2007). We determined the optimal number of clusters based on both the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC), i.e., the number of clusters for which the mean of AIC and BIC was minimal. We then cross-tabulated reef clusters based on coral cover trajectories (this study) and benthic community composition (Mellin et al. 2019*a*) to identify reefs with similar benthic community types and coral cover trajectories.

Results

Representation of environmental characteristics

The principal component analysis showed that the environmental characteristics selected for the analysis (i.e., temperature, salinity, chlorophyll *a* concentration, water depth, and sediment cover at the coral monitoring sites) represented 61.7% of GBR environmental variation based on the first two PCA axes (Fig. 2). This subset of variables reflected environmental effects on coral

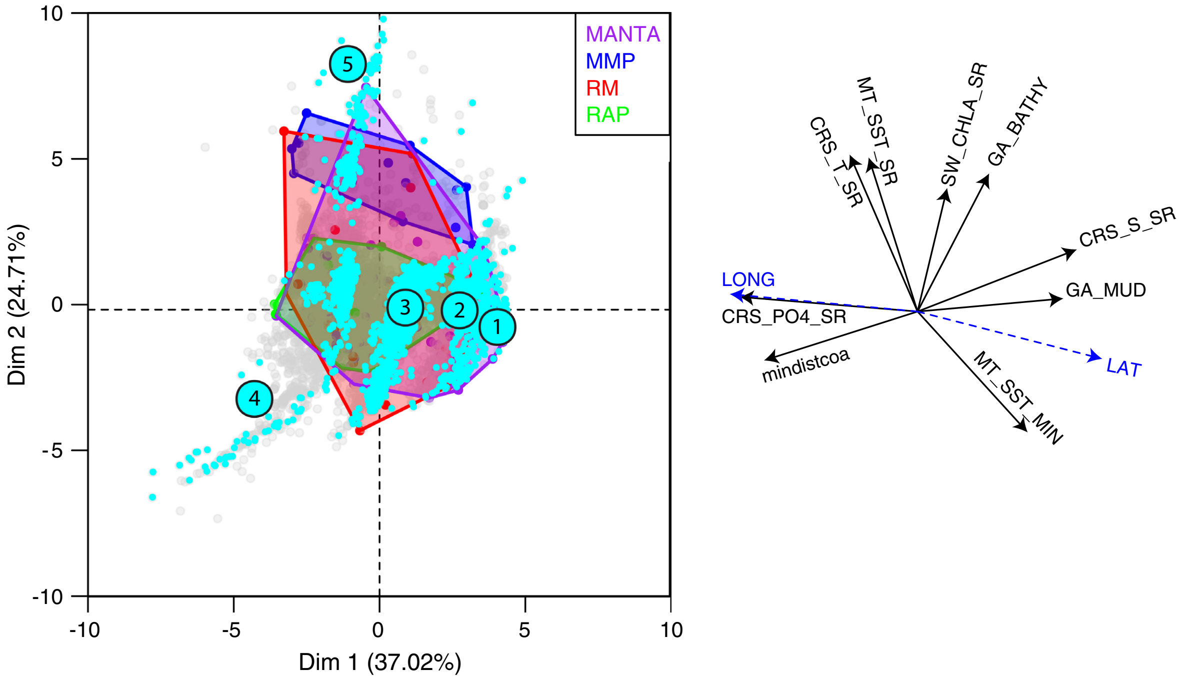

FIG. 2. Representation of environmental characteristics by long-term coral monitoring programs based on a principal component analysis of selected environment variables. Left: individual factorial plan, where convex hulls delineate environmental envelopes of reefs surveyed by mantatow (MANTA), the marine monitoring program (MMP), the reef monitoring (RM), and representative areas program (RAP). Areas in cyan represent regions with no survey sites within a 50 km radius (see location in Fig. 1), with (1) Northern open lagoon and outer barrier reefs north of Cooktown; (2) sheltered mid-shelf reefs between Cooktown and Cairns; (3) strong tidal mid/outer-shelf reefs off Townsville; (4) southern outer-shelf reefs off Mackay; and (5) incipient and high tidal fringing reefs between Mackay and Rockhampton. Right: variable factorial plan, with mindistcoast, minimum distance to the coast; CRS_PO4_SR, seasonal range in phosphate concentration; CRS_T_SR, seasonal range in seabed temperature; MT_SST_SR, seasonal range in sea surface temperature; SW_CHLA_SR, seasonal range in chlorophyll *a* concentration; GA_BATHY, average bathymetry; CRS_S_SR, seasonal range in salinity; GA_MUD, percent mud; MT_SST_MIN, minimum annual mean sea surface temperature. Longitude (LONG) and latitude (LAT) are illustrative variables.

ecophysiology (e.g., temperature, salinity and nutrients can influence coral growth, calcification or metabolic rates) or substrate availability for coral colonization and growth (cover of different sediment types, bathymetry; Mellin et al. 2019*a*).

Several geographic regions were characterized by specific and distinct environmental conditions. For example, the ordination plan clearly discriminated the northernmost reefs (characterized by high minimum sea surface temperature; region 1 on Fig. 2; Appendix S1: Fig. S3) from southern inshore reefs (characterized by high seasonal variation in sea surface temperature and salinity; region 5 on Fig. 2; Appendix S1: Fig. S3) and offshore reefs (associated with large distances to the coast; region 4 on Fig. 2).

Existing monitoring sites of the RM, RAP and MMP programs represented 40.1% of the environmental conditions on the GBR, based on the first two PCA axes (convex hulls on Fig. 2). Manta tow surveys encompassed 34.2% of all environmental diversity on the GBR, resulting in a total of 45.1% of environmental diversity represented by all four monitoring programs combined. The remaining 54.9% (gray dots on Fig. 2 that are not encompassed by any ellipses) represent reefs with environmental characteristics that are distinct from those at the survey sites, but with survey sites in their vicinity (i.e., within 50 km).

Areas with no coral reef monitoring sites within 50 km (cyan dots in Fig. 2) overlapped with at least one convex hull, indicating that their environmental conditions are likely to be similar to those encountered at the survey reefs. However, a large proportion of the reefs located at the outer-shelf barrier in the southern GBR offshore from Mackay (region 4 on Figs. 1 and 2), and incipient and high tidal fringing reefs between Mackay and Rockhampton (region 5 on Figs. 1 and 2) were characterized by distinct environmental characteristics (i.e., falling outside convex hulls). These reefs are currently not monitored by any programs, thus representing a gap in the environmental representation of the current coral monitoring.

Representation of disturbance hotspots

The disturbance hotspot analysis indicated that the northernmost section of the GBR, as well as southernmost and inner-shelf reefs were in the past major hotspots of temperature stress events leading to major coral bleaching between 1985 and 2017, based on the DHW data (Fig. 3). Conversely, the central and southern sections of the GBR were major hotspots of CoTS outbreaks, based on CoTS densities estimated by manta tow. The central section of the GBR was a hotspot of tropical cyclone activity during this period. The sector encompassing reefs between Cairns and Townsville recorded the highest combined severity of disturbance exposure over the study period (Fig. 3).

The spatial comparison of areas with no existing coral reef monitoring sites within 50 km (cyan outlines on Fig. 3) to disturbance hotspots revealed that 88.3% of identified major hotspots (%Hot > 40%) of cyclone activity in the central GBR are presently unmonitored by the RM/RAP/MMP programs (Appendix S1: Fig. S4). This area has to some extent been surveyed using the manta tow technique, which revealed relatively high CoTS densities on average across the same region (Fig. 3). When all disturbance hotspots were combined, unmonitored areas corresponded to moderate disturbance on average (i.e., hotspots in 10–40% of all years; Appendix S1: Fig. S4).

Complementarity

The results of the functional PCA suggested an optimal number of 15 clusters of reefs with similar coral cover trajectories, based on the minimum mean of AIC and BIC (Appendix S1: Fig. S5). The spatial pattern in reef clustering reflected both the mosaic of disturbance impacts across the GBR, and spatial variation in benthic community types and post-disturbance recovery rate of coral cover (Fig. 4; Appendix S1: Table S3). Cluster 6 included the largest number of reefs (N = 261), representing a total reef area of 3,200 km^2 (25% of the GBR). This cluster was characterized by a moderate decline in coral cover (−16.6% on average; Fig. 4; Appendix S1: Table S3). The largest decline in coral cover (−29.6%) was observed for cluster 8, representing 8% of the total reef area, which overlapped major cyclone hotspots. Only three trajectory clusters showed a positive trend in average coral cover. Clusters 3 (+0.69% coral cover; 0.05% of the GBR) and 15 (+1.02% coral cover; 0.005% of the GBR) showed a slight positive trend, but this should be interpreted with caution due to the large amount of variability in the coral trajectories found within these clusters. Cluster 11 also showed a positive trend (+8.02% coral cover, 0.015% of the GBR) and notably included reefs that were the least exposed to tropical cyclones and CoTS outbreaks.

The cross-tabulation of trajectory clusters and benthic community types (Appendix S1: Fig. S2) revealed that most survey reefs with fast-growing, outer-shelf communities characterized by soft corals were part of cluster 3 (moderate to high initial coral cover followed by strong,

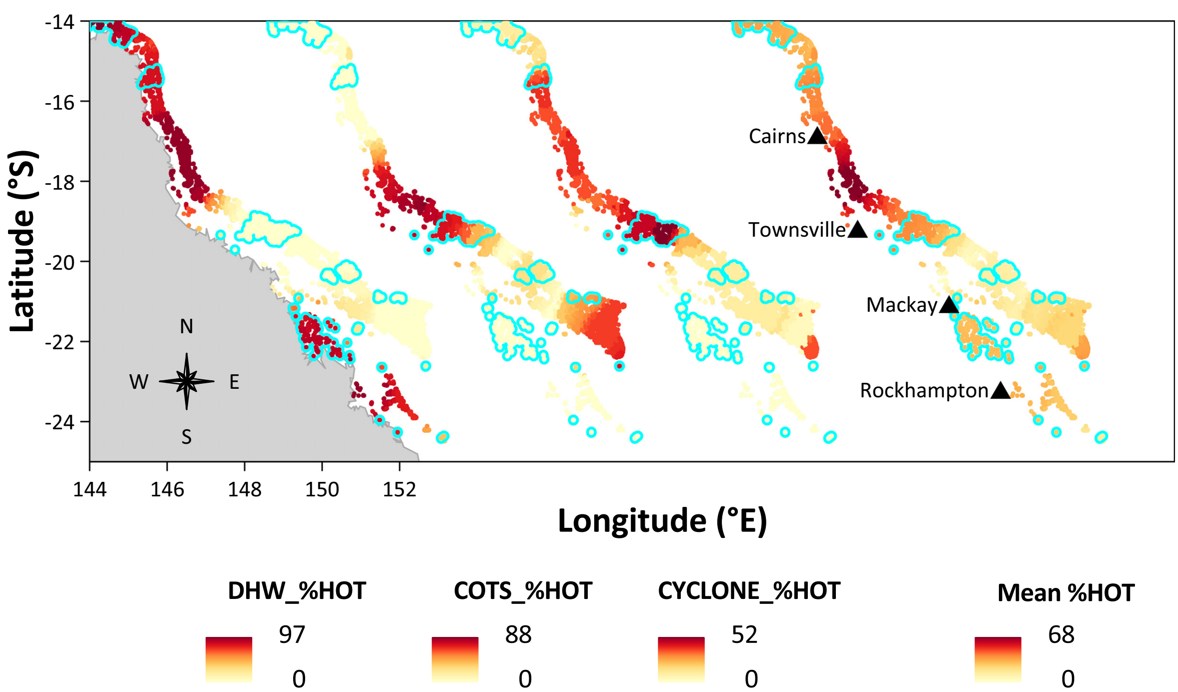

FIG. 3. Disturbance hotspots on the Great Barrier Reef between 1995 and 2016 for coral bleaching (based on degree heating weeks [DHW]), outbreaks of the crown-of-thorns seastar (COTS), tropical cyclones, and all three disturbances combined (Mean % HOT). For each source of disturbance, the color scale represents the percent of the time series a pixel was considered a hotspot. Areas in cyan represent regions with no long-term survey sites within a 50 km radius (see location in Fig. 1).

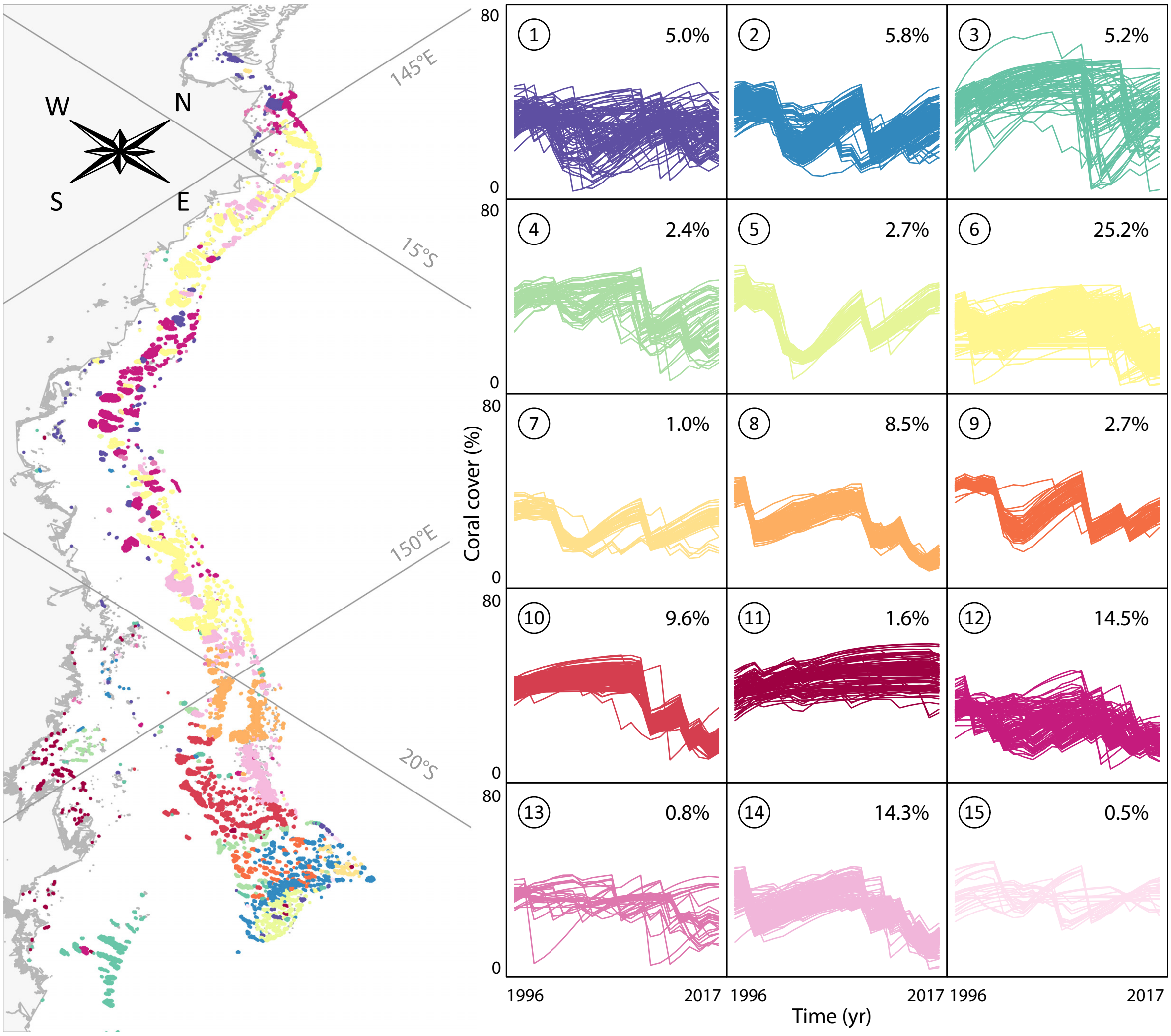

FIG. 4. Reef clustering based on coral cover trajectories predicted by the model between 1996 and 2017. Left: spatial distribution of all clusters ($N = 15$). Right: coral cover trajectories predicted for reefs within each cluster. Percentages show the proportion of total reef area represented by each cluster. Cluster characteristics are given in Appendix S1: Table S3.

late decline; Fig. 5A; Appendix S1: Fig. S6). This category encompasses, for example, Slate and Hyde reefs that were successively exposed to large CoTS outbreaks followed by tropical cyclones, from which they partially recovered by the end of the study period. Another example of similar coral cover trajectories and benthic community composition is that of mid-shelf survey reefs such as Horseshoe or Gannett Cay Reefs (trajectory cluster 1) that experienced early decline due to repeated CoTS outbreaks, followed by a period of general recovery (Fig. 5B). Last, some inner-shelf benthic communities characterized by *Porites* and a relatively slow coral growth rate (such as Linnet or Martin Reef) were grouped in the same trajectory cluster (14), based on an initial ~ 15 yr of stable coral cover in the absence of disturbance, followed by a sequence of CoTS outbreaks and tropical cyclones from 2012 that resulted in a steep decline in coral cover (Fig. 5C). All reefs with fast-growing coral communities characterized by *Acropora* tabulate (in the Capricorn Bunkers section, on the outer-shelf southeast of Rockhampton) were part of cluster 3. Cross-tabulations of all trajectory and benthic clusters, for both survey reefs and all GBR reefs, are given in Appendix S1: Fig. S6.

DISCUSSION

On Australia's Great Barrier Reef, increasingly frequent and severe disturbances affecting coral reef communities have raised the need for an efficient, integrated reef monitoring to inform adaptive management. The Australian Institute of Marine Science's Long Term Monitoring Program (Sweatman 2008) represents the longest continuous record of coral reef condition and

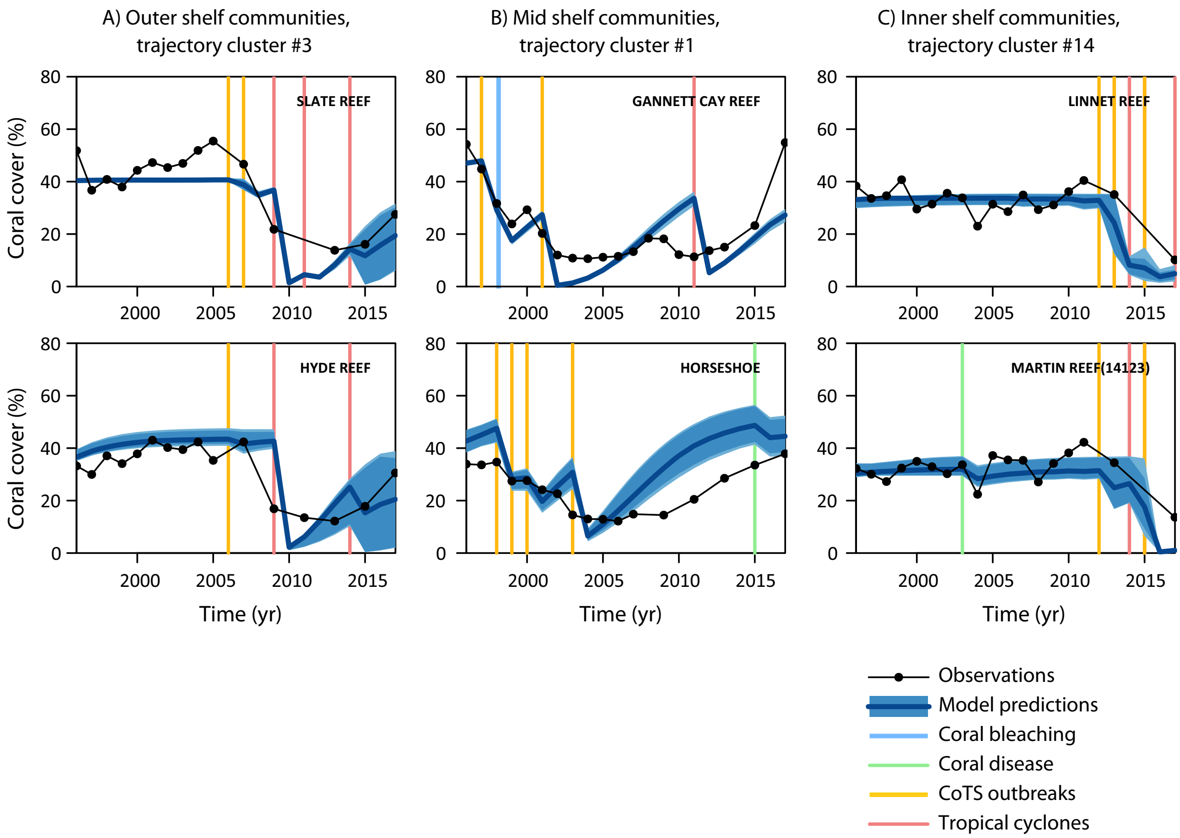

FIG. 5. Example of predicted and observed coral cover trajectories for reefs within the same benthic community (Appendix S1: Fig. S2) and the same trajectory cluster (Fig. 4). The blue envelope shows the 95% prediction interval across a total of 1,000 model simulations, and the thick blue line the median.

trends over the last three decades and, in this context, offers a unique opportunity to learn from the past and inform the design of future coral reef monitoring. By applying a regional model of ecological responses to important drivers (environmental characteristics and gradients, acute disturbance history), our approach has derived useful information to assist with the design of future monitoring. We expect this approach to be transferable to other ecosystems where the availability of long-term data would allow similar model development. Here we focused on two key aspects of ecological survey design, namely representation and complementarity. Indeed, to make inferences and test hypotheses at a regional scale requires a representative sample of the range of environmental conditions and disturbance impacts encountered at that scale (Austin and Heyligers 1989, Margules and Austin 1991). Furthermore, the balanced stratification of survey design across distinct biological communities and the variety of their responses to disturbance is essential to efficiently allocate survey effort. Our results document the extent to which previous long-term monitoring programs have met both criteria, from which we develop recommendations to assist the design of future surveys.

Based on environmental variables modeled and predicted from remotely sensed data across the breadth of the GBR, we showed that the RM, RAP, and MMP programs combined (N = 123 reefs) represent 40.1% of the environmental variation encompassed across a total of 1,531 reefs within our study region, and up to 45.1% when the manta tow surveys were included. Most areas with no survey reefs within 50 km had similar environmental conditions to those encountered at the survey reefs, suggesting that, based on the strong species–environment relationships previously documented (Mellin et al. 2010*a*, Sutcliffe et al. 2014), the benthic communities inhabiting such unmonitored areas are likely to be represented by those monitored elsewhere. However, some of those unmonitored areas were characterized by statistically distinct environmental characteristics, indicating that they are unlikely to be represented by current monitoring programs. These areas are typically difficult to access or survey due to rough oceanographic conditions (e.g., southern outer-shelf reefs off Mackay) or very turbid waters (e.g., high tidal fringing reefs between Mackay and Rockhampton). Nevertheless, some insights into the status and trends of benthic communities in such areas could be obtained using alternative sampling techniques and new technologies such as imagery derived from autonomous underwater vehicles (Bridge et al. 2011), at least where poor visibility does not preclude their use. In the absence of additional data, future studies making regional-scale inferences should use caution and acknowledge that conclusions do not necessarily apply in these poorly understood areas.

As expected, our disturbance hotspot analysis revealed very different spatial footprints of the three most important acute disturbances affecting coral reefs, namely coral bleaching, CoTS outbreaks and tropical cyclone waves between 1985 and 2017. Based on the average spatial patterns of all disturbances, the past disturbance regimes have been relatively well captured by the previous coral monitoring over the past three decades. However, when focusing on the spatial footprint of tropical cyclones alone, our analysis revealed that 88% of all grid cells within the cyclone hotspot (i.e., frequently exposed to cyclone waves; central GBR) fell within an area that has remained unmonitored (numbered 3 on Fig. 1). This is an important result, as the impact of tropical cyclones has been identified as the most important cause of coral cover decline over the course of the long-term monitoring program (De'ath et al. 2012, MacNeil et al. 2019, Mellin et al. 2019a). This suggests that some of the regional decline of coral cover that was previously documented could have been underestimated. However, the uncertainty around the actual cyclone impact in this area is high, because cyclone impact at the sub-reef scale is typically patchy. In addition, cyclone impact is not an inevitable result of exposure to destructive waves generated by cyclones, which we used as a surrogate for cyclone severity in our study, because reef structural vulnerability is highly variable (Puotinen et al. 2016) and strongly depends on benthic community type (Mellin et al. 2019*b*). We recommend that future surveys should strive to monitor more reefs within this area (numbered 3 on Fig. 1), at least on a surveillance or rotational basis (Richards and Day 2018). Although it is unlikely that the spatial footprint of tropical cyclones observed over the last 30 yr will be the same in the future, the temporal pattern of cyclones in this area has been more regular than elsewhere on the GBR since 1906, irrespective of the time period considered (Wolff et al. 2016).

Complementing the previous identification of six major benthic communities across the GBR (Mellin et al. 2019*a*), here we identified 15 clusters of reefs with similar coral cover trajectories predicted by the coral cover model over the study period (1996–2017). The spatial pattern of their distribution reflects not only the mosaic of disturbance impacts across the GBR over this time period, but also the spatial variation in coral recovery potential that varies strongly across the continental shelf (MacNeil et al. 2019). While benthic clusters likely represent bioregions across the GBR based on the composition of hard coral communities (Mellin et al. 2019*a*), coral cover trajectory clusters predict groups of reefs that are at a similar stage of the decline-recovery trajectory. Bearing in mind the inherent uncertainty of the model (Mellin et al. 2019*a*), we suggest that a combination of both clustering methods could be used as prior knowledge to stratify the statistical design of future surveys, instead of the combination of latitudinal sectors and cross-shelf levels that have been used so far. Indeed, survey reefs belonging to a same benthic community and a same trajectory cluster yielded very similar dynamics due to similar disturbance history and recovery potential (Fig. 5). The similarity in the relative abundance of different hard coral taxa suggests that such reefs could also be comparable in terms of the differential susceptibility of coral taxa to a particular type of disturbance (Johns et al. 2014, Mellin et al. 2019*b*). This suggests that, based on our predictive model and field observations over the past 22 yr, such reefs are likely to convey similar ecological information and could thus be considered as pseudo replicates. Future surveys that aim to maximize complementarity among a limited number of reefs could use our methodology to inform statistical and spatially balanced survey designs (Stevens and Olsen 2004) that are as representative as possible of the variety of benthic communities and theirs responses to disturbance.

Our study represents the first effort to understand the extent to which coral monitoring programs have captured 22 yr of disturbance history and their effects on coral communities, as well as spatial gradients of environmental characteristics across the whole Great Barrier Reef. For this, we focused on total hard coral cover (%) as the key indicator of coral reef condition. This indicator represents an "essential ocean variable" and is recommended for global use in coral reef monitoring (Miloslavich et al. 2018). However, coral cover as an indicator has acknowledged limitations. For example, coral cover needs to be repeatedly monitored at the same site to provide useful information about coral "growth" trajectories (Hughes et al. 2010). Coral cover also lacks the taxonomic resolution to monitor changes in reef biodiversity, distinguish a healthy reef recovering toward a coral-dominated state from one being on a downward trajectory to dominance by macroalgae, or reflect different taxon-specific sensitivities to disturbances (Hughes et al. 2018, Mellin et al. 2019*b*). As this is well recognized (Richards 2013, Richards and Day 2018), few coral reef monitoring programs use total hard coral cover as the sole indicator but rather as a convenient reporting variable that, importantly, allows for integration across individual programs. The existing GBR long-term coral monitoring program are based on the collection of species- or genus-level data for benthic communities (not just hard corals) and also include important resilience indicators, for example the abundance of juvenile corals, to allow for more sophisticated analyses and reporting of reef condition and trends. Analysis of these more detailed data was not the purpose of the present study, but should definitely be considered in future research on coral reef responses to disturbance, and on how ecological monitoring can best capture such responses.

While our study focused on the representation and complementarity of existing coral monitoring programs, other criteria should be considered in the design of future surveys. Such criteria include the precision and accuracy of the indicators measured, where both observer error and the spatial design of the survey (e.g., location of sites and transects within them) affect the ability of a monitoring program to detect change and report on coral condition. For example, a companion study showed that variation of up to 40% among observers (which can be reduced by observer training) resulted in low capacity to accurately estimate coral cover (Mellin et al. 2020). Furthermore, spatial heterogeneity in coral distribution across the sampled reef area reduces the precision of coral cover estimates if using random sampling (such as in other coral monitoring designs not considered here; e.g., Beeden et al. 2014). This can be partly compensated for with additional replicates, but not to the precision that can be obtained with the use of fixed sites (such as in the four monitoring programs considered here; Mellin et al. 2020). Another important criterion is the power of the survey design, or its capacity to detect a temporal trend and disentangle it from natural variation in population dynamics (Zar 1984). A parallel study demonstrated that the RM, RAP, and MMP programs had a reasonable power (>0.8) to detect a 1% per annum change in coral cover recovery over a 5-yr period (Thompson and Menendez, 2020). This level of change was reliant, however, on annual samples from four to five reefs in each latitudinal and cross-shelf sector of the GBR, a level of replication higher than the current three reefs sampled biennially by the RM, RAP, and MMP. Where sufficient samples are lacking, the use of citizen science data in conjunction with long-term surveys has been shown to reduce uncertainty around model-based coral cover estimates (Mellin et al. 2020) and to improve our understanding of regional variation in the response of corals (and associated organisms) to disturbance (Stuart-Smith et al. 2018).

As part of any adaptive monitoring design, maintaining the integrity of long-term data records is of utmost importance (Nichols and Williams 2006). However, as pressures, knowledge, questions, and technology evolve, monitoring should adapt with the collection of new variables or different information at different spatiotemporal scales (Richards and Day 2018). For example, a scenario of coupling the long-term monitoring programs considered here with reactive surveys of disturbance impact (Beeden et al. 2015) could provide situational awareness between long-term surveys, and help attribute the observed impacts on coral cover to different pressures. Such reactive surveys would assist evaluation and reporting through near real-time updates of ecological models such as ours, which could be made available via online platforms such as eAtlas (Lawrey 2013) and support adaptive management by rapidly identifying the most impacted reefs to alleviate further impacts and facilitate coral recovery. Based on the existing zoning of the marine park, such adaptive management responses could for instance include (1) assisting coral recovery through temporary restrictions of access and/or activities, (2) implementing targeted CoTS control operations, (3) increasing habitat protection through, e.g., additional permanent moorings to reduce anchor damage, (4) increasing compliance through greater enforcement operations, and (5) increasing public awareness through education and communication.

Overall, our results help identify an optimized subset of the long-term monitoring sites based on their representation of spatial patterns of environmental characteristics and complementarity of reefs with similar disturbance histories, community types and, hence, recovery trajectories. This may allow the allocation of additional resources to sampling currently unmonitored hotspots of disturbance or to reactive surveys in response to disturbances as they occur. Ultimately, an improved monitoring design should provide a better understanding of the driver–state relationships likely to influence coral reef health, and the processes and feedbacks that confer resistance and resilience to disturbance, to inform more efficient and targeted management of the Reef.

Acknowledgments

We thank members of the AIMS long-term coral reef monitoring teams that have contributed to collection of the data; and K. Anthony, A. Thompson, P. Menendez, and two anonymous reviewers for helpful comments. C. Mellin was funded by an ARC grant (DE140100701), and by the Great Barrier Reef Marine Park Authority as part of the RIMReP design phase. The authors have no conflict of interest to declare.

Literature Cited

Austin, M. P., and P. C. Heyligers. 1989. Vegetation survey design for conservation: Gradsect sampling of forests in North-eastern New South Wales. Biological Conservation 50:13–32.

Australian Government Department of Agriculture, Water and the Environment. n.d. The Reef 2050 Plan. http://www.environment.gov.au/marine/gbr/long-term-sustainability-plan

Beeden, R., et al. 2015. Impacts and recovery from severe tropical cyclone yasi on the great barrier reef. PLoS ONE 10: e0121272.

Beeden, R. J., M. A. Turner, J. Dryden, F. Merida, K. Goudkamp, C. Malone, P. A. Marshall, A. Birtles, and J. A. Maynard. 2014. Rapid survey protocol that provides dynamic information on reef condition to managers of the Great Barrier Reef. Environmental Monitoring and Assessment 186:8527–8540.

Bottrill, M. C., et al. 2008. Is conservation triage just smart decision making? Trends in Ecology & Evolution 23:649–654.

Bridge, T. C. L., et al. 2011. Variability in mesophotic coral reef communities along the Great Barrier Reef, Australia. Marine Ecology Progress Series 428:63–75.

Chiou, J.-M., and L. Pai-Ling. 2007. Functional clustering and identifying substructures of longitudinal data. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 69:679–699.

Day, J.. 2008. The need and practice of monitoring, evaluating and adapting marine planning and management—lessons from the Great Barrier Reef. Marine Policy 32:823–831.

De'ath, G.. 2002. Multivariate regression trees: a new technique for modeling species–environment relationships. Ecology 83:1105–1117.

De'ath, G., et al. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences USA 109:17995–17999.

Field, S. A., A. J. Tyre, and H. P. Possingham. 2005. Optimizing allocation of monitoring effort under economic and observational constraints. Journal of Wildlife Management 69:473–482.

Game, E. T., E. McDonald-Madden, M. L. Puotinen, and H. P. Possingham. 2008. Should we protect the strong or the weak? Risk, resilience, and the selection of marine protected areas. Conservation Biology 22:1619–1629.

Garcia Molinos, J., B. S Halpern, D. S. Schoeman, C. J Brown, W. Kiessling, P. J. Moore, J. M. Pandolfi, E. S. Poloczanska, A. J. Richardson, and M. T. Burrows. 2015. Climate velocity and the future global redistribution of marine biodiversity. Nature Climate Change 6:83–88.

Getis, A., and J. K. Ord. 1992. The analysis of spatial association by use of distance statistics. Geographical Analysis 24:189–206.

Great Barrier Reef Marine Park Authority & Queensland Government. 2015. Reef 2050 Integrated Monitoring and Reporting Program Strategy. Great Barrier Reef Marine Park Authority, Townsville, Queensland, Australia.

Great Barrier Reef Marine Park Authority. 2019. Great Barrier Reef Outlook Report 2019. GBRMPA, Townsville, Queensland, Australia.

Hughes, T. P., et al. 2017. Global warming and recurrent mass bleaching of corals. Nature 543:373–377.

Hughes, T. P., et al. 2018. Global warming transforms coral reef assemblages. Nature 556:492–496.

Hughes, T. P., N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, and R. S. Steneck. 2010. Rising to the challenge of sustaining coral reef resilience. Trends in Ecology & Evolution 25:633–642.

Hunter, M., et al. 2016. Two roles for ecological surrogacy: Indicator surrogates and management surrogates. Ecological Indicators 63:121–125.

Johns, K., K. Osborne, and M. Logan. 2014. Contrasting rates of coral recovery and reassembly in coral communities on the Great Barrier Reef. Coral Reefs 33:553–563.

Jonker, M., K. Johns, and K. Osborne. 2008. Surveys of benthic reef communities using digital photography and counts of juvenile corals. Long-term monitoring of the Great Barrier Reef standard operational procedure number 10. Australian Institute of Marine Science, Townsville, Queensland, Australia.

Kang, S. Y., J. M. McGree, C. C. Drovandi, M. J. Caley, and K. L. Mengersen. 2016. Bayesian adaptive design: improving the effectiveness of monitoring of the Great Barrier Reef. Ecological Applications 26:2637–2648.

Lawrey, E. (2013) Bright Earth eAtlas Basemap v1.0. AIMS, GBRMPA, JCU, DSITIA, GA, UCSD, NASA, OSM, ESRI). eAtlas (Creative Commons Attribution 3.0 Australia). https://eatlas.org.au/

Lindenmayer, D. B., G. E. Likens, A. Haywood, and L. Miezis. 2011. Adaptive monitoring in the real world: proof of concept. Trends in Ecology & Evolution 26:641–646.

Liu, G., et al. 2014. Reef-scale thermal stress monitoring of coral ecosystems: New 5-km global products from NOAA Coral Reef Watch. Remote Sensing 6:11579.

MacNeil, M. A., C. Mellin, S. Matthews, N. H. Wolff, T. R. McClanahan, M. Devlin, C. Drovandi, K. Mengersen, and N. A. J. Graham. 2019. Water quality mediates resilience on the Great Barrier Reef. Nature Ecology and Evolution 3:620–627.

Margules, C., and M. Austin 1991. Nature conservation: cost effective biological surveys and data analysis. CSIRO Publishing, Melbourne, Victoria, Australia.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405:243–253.

Matthews, S., C. Mellin, A. MacNeil, S. F. Heron, W. Skirving, M. Puotinen, M. J. Devlin, and M. Pratchett. 2019. High-resolution characterization of the abiotic environment and disturbances regimes on the Great Barrier Reef; 1985–2017. Ecology 100:e02574.

McDonald-Madden, E., P. W. J. Baxter, R. A. Fuller, T. G. Martin, E. T. Game, J. Montambault, and H. P. Possingham. 2010. Monitoring does not always count. Trends in Ecology & Evolution 25:547–550.

Mellin, C., et al. 2019*a*. Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. Global Change Biology 25:2431–2445.

Mellin, C., K. Anthony, E. Peterson, and C. Ewels, M. Puotinen. 2020. Supplementary report to the final report of the coral reef expert group: S4. Model to inform the design of a Reef Integrated Monitoring and Reporting Program. Great Barrier Reef Marine Park Authority, Townsville, Queensland, Australia.

Mellin, C., C. J. A. Bradshaw, M. G. Meekan, and M. J. Caley. 2010*a*. Environmental and spatial predictors of species richness and abundance in coral reef fishes. Global Ecology and Biogeography 19:212–222.

Mellin, C., C. Huchery, M. J. Caley, M. G. Meekan, and C. J. A. Bradshaw. 2010*b*. Reef size and isolation determine the temporal stability of coral reef fish populations. Ecology 91:3138–3145.

Mellin, C., S. Delean, J. Caley, G. Edgar, M. Meekan, R. Pitcher, R. Przeslawski, A. Williams, and C. Bradshaw. 2011. Effectiveness of biological surrogates for predicting patterns of marine biodiversity: a global meta-analysis. PLoS ONE 6:1–11.

Mellin, C., A. Thompson, M. J. Jonker, and M. J. Emslie. 2019*b*. Cross-shelf variation in coral community response to disturbance on the Great Barrier Reef. Diversity 11:38.

Miller, I., and R. Müller. 1999. Validity and reproducibility of benthic cover estimates made during broadscale surveys of coral reefs by manta tow. Coral Reefs 18:353–356.

Miller, I., M. Jonker, and G. Coleman. 2009. Crown-of-thorns starfish and coral surveys using the manta tow and SCUBA search techniques. Australian Institute of Marine Science, Townsville, Queensland, Australia.

Miloslavich, P., et al. 2018. Essential ocean variables for global sustained observations of biodiversity and ecosystem changes. Global Change Biology 24:2416–2433.

Nichols, J. D., and B. K. Williams. 2006. Monitoring for conservation. Trends in Ecology & Evolution 21:668–673.

Obura, D., et al. 2019. Coral reef monitoring, reef assessment technologies, and ecosystem-based management. Frontiers in Marine Science 6:580.

Poloczanska, E. S., et al. 2016. Responses of marine organisms to climate change across oceans. Frontiers in Marine Science, 3:1–21.

Puotinen, M., et al. 2016. A robust operational model for predicting where tropical cyclone waves damage coral reefs. Scientific Reports 6:26009.

Richards, Z. T. 2013. A comparison of proxy performance in coral biodiversity monitoring. Coral Reefs 32:287–292.

Richards, Z. T., and J. C. Day. 2018. Biodiversity of the Great Barrier Reef—how adequately is it protected? PeerJ 6:e4747.

Sarkar, S., et al. 2006. Biodiversity conservation planning tools: Present status and challenges for the future. Annual Review of Environment and Resources 31:123–159.
Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, UK.
Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.
Stuart-Smith, R. D., et al. 2018. Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. Nature 560:92–96.
Sutcliffe, P., et al. 2014. Regional-scale patterns and predictors of species richness and abundance across twelve major tropical inter-reef taxa. Ecography 37:162–171.
Sweatman, H. 2008. No-take reserves protect coral reefs from predatory starfish. Current Biology 18:R598–R599.
Sweatman, H., et al. 2008. Long-term monitoring of the Great Barrier Reef. Status Report no8. Australian Institute of Marine Science, Townsville, Queensland, Australia.
Thompson, A., et al. 2016. Marine Monitoring Program: Annual Report for Inshore Coral Reef Monitoring. Report for the Great Barrier Reef Marine Park Authority. Australian Institute of Marine Science, Townsville, Queensland, Australia.
Thompson, A., and P. Menendez. 2020. Supplementary report to the final report of the coral reef expert group: S5. Statistical power of existing AIMS Long-Term Reef Monitoring Programs. Great Barrier Reef Marine Park Authority, Townsville, Queensland, Australia.
Tulloch, A. I. T., I. Chadès, and H. P. Possingham. 2013. Accounting for complementarity to maximize monitoring power for species management. Conservation Biology 27:988–999.
Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in ecological surveys: estimating false-negative error rates. Ecological Applications 13:1790–1801.
Van Wynsberge, S., A. Gilbert, N. Guillemot, T. Heintz, and L. Tremblay-Boyer. 2017. Power analysis as a tool to identify statistically informative indicators for monitoring coral reef disturbances. Environmental Monitoring and Assessment 189:311.
Venables, W. N., and B. D. Ripley 2002. Modern applied statistics with S. Fourth edition. Springer, New York, New York, USA.
Wilson, H. B., L. N. Joseph, A. L. Moore, and H. P. Possingham. 2011. When should we save the most endangered species? Ecology Letters 14:886–890.
Wolff, N. H., A. Wong, R. Vitolo, K. Stolberg, K. R. N. Anthony, and P. J. Mumby. 2016. Temporal clustering of tropical cyclones on the Great Barrier Reef and its ecological importance. Coral Reefs 35:613–623.
Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, London, UK.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2122/full

Data Availability Statement

Data are available on the Dryad Digital Repository: https://doi.org/10.5061/dryad.9ghx3ffdk